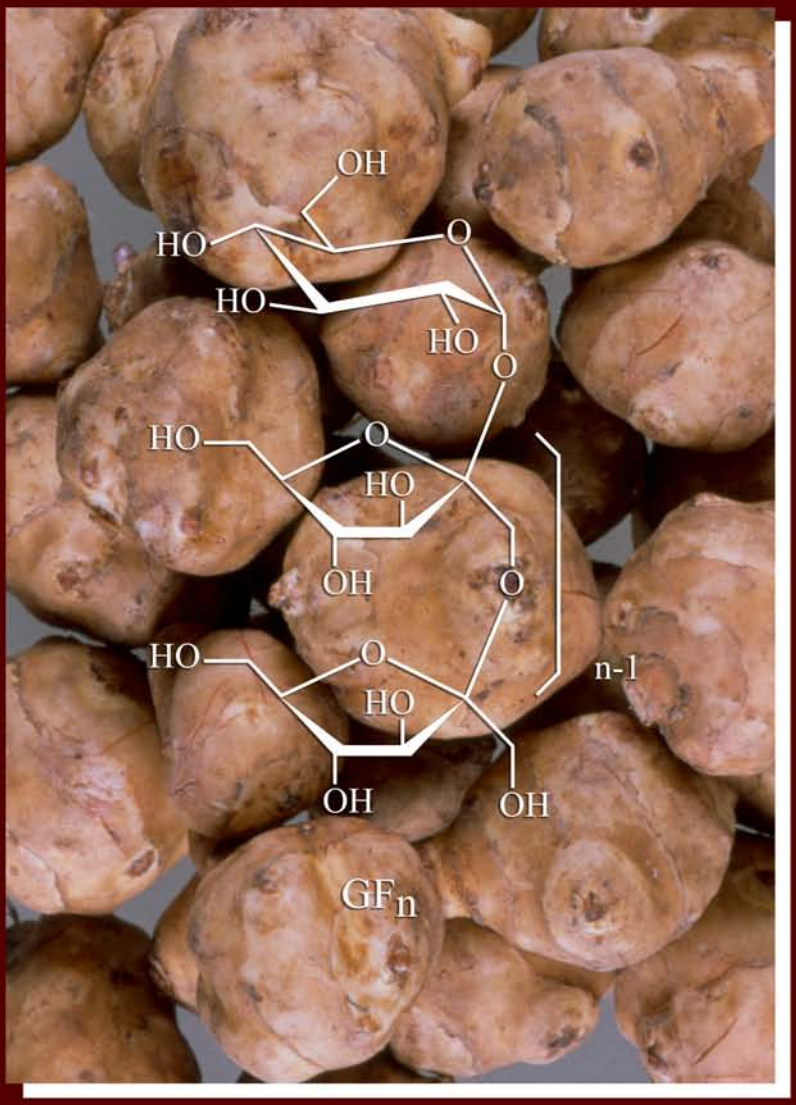
Biology and Chemistry of Jerusalem Artichoke

Helianthus tuberosus L.



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Dedication

In memory of Margaret Nottingham and Raymond and Charlotte Kays, enthusiastic gardeners and lovers of plants.

Contents

Preface

Helianthus tuberosus is in its own right a fascinating species from the standpoint of plant biology. Superimposed on this is an unusually colorful history, common names (Jerusalem artichoke and topinambour) that have virtually nothing to do with the plant, and unique biological and chemical properties that distinguish it from other crops. The plant has been and continues to be far more appreciated in Europe than in the United States, where it originated. Indicative of its popularity is the fact that there have been approximately 35 monographs and books published on the crop since the first in 1789, predominantly in French, German, and Russian, with the last major book being in Hungarian by I'So in 1955. While modest compared to the major field crops, there is a wealth of scientific publications on the Jerusalem artichoke that has increased progressively from approximately 400 titles in 1932 to 1300 in 1957 to over several thousand today.

Our objective with this book was to summarize our current understanding of the basic biology and chemistry of this unique crop. We have cited a diverse and representative cross section of publications, with the intent of providing those interested in delving further into this underexploited resource ready access to the literature and patents. Regrettably, due to limited resources for translations, we have not cited as many Eastern European contributions as we would have liked, some of which are by scientists who were pioneers in Jerusalem artichoke research. It has been over 50 years since the last major textbook on the species, and it is our hope that the information provided will spur additional interest and further development.

The authors acknowledge a number of individuals who have been instrumental in developing the information for this work, in particular Betty Schroeder, who collected and organized reprints of the literature in addition to coordinating a number of research projects over the years. We also acknowledge Drs. Gerard Soja and Chris Stevens for reviewing sections of the text and Tatyana Gavrilenko, Yuriy Posudin, Zana Somda, and Marie-Michele Pratt for assisting with translations. We also acknowledge Will Bonsall and Drs. L. Frese, B. Honermeier, and F.A. Kiehn for providing germplasm for research purposes. For information on genetic resources held in collections worldwide, we are extremely grateful to Drs. Laura Marek (U.S.), Hervé Serieys (France), Helmut Knuepffer and Andreas Börner (Germany), Gitte Kjeldsen Bjørn (Denmark), Jovanka Atlagic (Serbia and Montenegro), and Dallas Kessler (Canada).

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Stephen F. Nottingham is a research entomologist and science writer based in the U.K. His interests include vegetable crop production, plant protection, insect behavior, chemical ecology, and plant genetic modification. At Cambridge University, England, his Ph.D. thesis was on the host plant-finding behavior of phytophagous Diptera. Subsequent research has been conducted within the aphid biology group at Imperial College, London, on aphid behavior and its modification by volatile chemicals, and at the University of Georgia on sweet potato weevil. Dr. Nottingham has published around 25 research papers and several books, including *Eat Your Genes: How Genetically Modified Food Is Entering Our Diet* and the Internet-accessible *Beetroot*. In addition to books, he also writes reports and articles on agriculture and the environment for the European Service Network and other organizations.

1 Introduction: An Underutilized Resource

The Jerusalem artichoke or topinambour (*Helianthus tuberosus* L.) is not only a fascinating species, but also one with an exceptionally colorful history. Over the past 300 years, interest in the crop has vacillated widely. During times of crop failure and food shortage (e.g., potato famine, during and after World War II) or high petroleum prices, a new round of interest in the crop's potential often occurs, all too frequently with only a limited understanding of the extensive body of literature already available. More recently, renewed interest has been spurred by its potential as a feedstock for the synthesis of a diverse cross section of new products, an awareness of its significant health benefits when included in human and animal diets, and the possibility of utilizing it for the production of biofuels.

Jerusalem artichoke, which originated in the north central part of the U.S., is a perennial that is grown as an annual. It is a temperate zone crop with an approximate production range between 40 and 55° N latitude and presumably a similar range in the southern hemisphere. Even within this relatively narrow range, cultivar and production requirements differ markedly as one progresses from north to south. Length of the growing season is critical; generally the longer the season, the greater the yield. It does not, however, do well in the tropics, especially in the humid lowlands, even though the growing season is substantially longer than in temperate regions. Unlike some subterranean crops (e.g., sweetpotato), the tubers mature, and the timing of maturity can be critical depending upon the intended use. As a species, Jerusalem artichoke is highly competitive, quickly shading the soil surface and creating a zone of captured resources, thereby repressing the growth of most other species. The plant's prolific growth is reflected in its efficient calorie production (Table 1.1), which compares well with most major crops.

Unlike most crops that store carbon as starch, a polymer of glucose, in the Jerusalem artichoke carbon is stored as inulin, a fructose polymer. The implications of this have a pronounced influence on the value and utility of the crop. An extremely important attribute derived from inulin is its nutritional contributions, even though the caloric value in humans is low. The evidence for the role of inulin in decreasing blood cholesterol and in enhancing other positive health benefits has been firmly established.

The Jerusalem artichoke is adapted to both high and low technology and inputs. Increased inputs (e.g., fertilization, irrigation) increase yield but not always net income. Conversely, while not having to apply fertilizer to Jerusalem artichoke following the previous crop may appear to be cost effective, it often simply represents a false economy, as the crop mines the soil of nutrients that must subsequently be replaced before the next crop is planted. Other positive attributes of the crop include the fact that it is vegetatively propagated, allowing growers to produce their own "seed tubers," which, unlike hybrids, remain true to form. As a consequence, the purchase of new propagation material each year is not required. Finally, the crop currently has few serious insect or disease pests when grown within its normal geographical zone.

As a crop plant, the Jerusalem artichoke has languished behind most traditional crop species. Its production worldwide is not considered sufficient to be monitored by the Food and Agriculture Organization (FAO) in its annual production statistics of agricultural crops. Lack of production in the past is in part due to the fact that uses for the crop could be readily fulfilled by other species. As indicated, however, periodic surges in production have been common. For example, during, and for a period after, the Second World War production of Jerusalem artichoke increased in Europe,

TABLE 1.1
Average Yield in Fresh Weight and Calories for Jerusalem Artichoke and the 10 Leading Crops

Crop	Yield ($kg \cdot ha^{-1}$)[a]	Calories ($kcal \cdot kg^{-1}$)[b]	Calories ($kcal \cdot m^{-2}$)
Corn (maize)	4,472	3,490	1,561
Jerusalem artichoke	17,843[c]	760[d]	1,356
Sweetpotato	13,493	1,000	1,349
Rice	3,837	3,410	1,308
Potato	16,448	710	1,168
Cassava	10,763	990	1,066
Soybean	2,261	3,920	886
Wheat	2,665	3,330	887
Barley	2,472	3,270	808
Sorghum	2,261	3,420	773
Grape	8,098	390	316

[a] Source: FAO, *FAO Yearbook Production*, Vol. 57, 2003, Statistics Series 177, Rome, 2004.
[b] Source: Leung, W.W. et al., *Food Composition Table for Use in East Asia. I. Proximate Composition Mineral and Vitamin Contents of East Asian Foods*, FAO, Rome, 1972.
[c] Based on one third of the mean for yields reported in Table 10.10.
[d] Source: Haytowitz, D.B. and Matthews, R.H., *USDA Agriculture Handbook 8-11: Composition of Foods — Vegetables and Vegetable Products*, USDA, Washington, DC, 1984.

especially in France and Germany, due to a scarcity of potatoes (Hennig, 2000; Martin, 1963). In France, 99,176 hectares of Jerusalem artichoke were grown in 1905, 131,000 in 1925, and 164,000 in 1956; this declined to 147,000 hectares in 1960 and to only 2,200 hectares by 1987 (Le Cochec, 1988; Shoemaker, 1927).

In the U.S., production of Jerusalem artichoke increased during the 1930s, as the crop was promoted as a feedstock for bioethanol. However, markets for this commodity were not sufficiently in place at that time and production declined, with the result that growers remained wary of Jerusalem artichoke for years to come (Amato, 1993). Today, little is grown in the U.S. In U.S. Department of Agriculture (USDA) production statistics, Jerusalem artichoke is grouped with alfalfa sprouts, cardoons, celeriac, jicama, salsify, radicchio, and tomatillos. Small amounts have been grown in recent years, but in 2003 domestic production of this crop grouping was effectively zero, with 450,000 cwt imported (USDA, 2006).

The degree of genetic manipulation of the crop is far from adequate. Existing Jerusalem artichoke cultivars fall somewhere between wild types and conventional field crops (e.g., rice, corn, soybean) in their level of genetic development. This is due to two primary reasons: (1) Investment in breeding has been virtually nonexistent compared to the major field crops, and when breeding programs are present, they are generally operative for only very short periods. (2) The reproductive biology of the crop is much more complex than that for most seed-bearing species. This latter factor greatly increases the difficulty of developing highly productive clones. Existing cultivars remain to a significant extent dominated by genes essential in the wild, some of which are detrimental in a field crop. For example, the initial storage of carbon in the stems is followed by the onset of flowering and senescence and finally recycling the carbon into the reproductive organs

(tubers). All of these developmental stages are strongly modulated by photoperiod, which makes not only understanding what wild traits need to be circumvented but also doing so a significant undertaking. When the photoperiodic control over flowering is broken, tuberization remains strongly modulated by short days.

Developing Jerusalem artichoke into a highly productive crop is therefore a formidable challenge. Inulin is the crop's primary attribute, but its potential is also overshadowed by advances in molecular biology. The genes required for inulin synthesis have been introduced into existing crops (e.g., sugar beet) for which the entire agricultural package (breeding production harvest processing) is currently operative.

There is a large and growing body of literature on Jerusalem artichoke, which this present volume summarizes. Fermeren (1932) listed 400 published titles concerning Jerusalem artichoke, while Pätzold (1957) referenced around 1300 publications (Rudorf, 1958). Today, many thousands of publications relate to Jerusalem artichoke, in part because of its role as a model species in the study of plant physiology and biochemistry, in areas such as photoperiodism, cytochrome P450 enzymes, mitochondrial oxidation, carbohydrate fermentation, and micropropagation. Therefore, the species has a scientific value above and beyond its importance as a minor crop. The following paragraphs briefly critique the general information contained in the subsequent chapters.

Jersualem artichoke is native to North America, and Native Americans were the first to cultivate it — many years before the arrival of European explorers. The plant's two most frequently used common names, 'Jerusalem artichoke' and 'topinambour,' arose shortly after the crop's introduction into Europe in 1607; both are botanically inappropriate. *H. tuberosus* neither is related to the artichoke (*Cynara scolymus* L.) nor has any connection with the town of Jerusalem; the latter derives from the Topinamboux, a South American tribe whose members first visited France in 1613 (Salaman, 1940). Sunchoke has been proposed as a more appropriate common name, but it has not been widely adopted. The nomenclature, origin, and history of *H. tuberosus* are the subject of Chapter 2.

The genus *Helianthus* (sunflowers), in the family Asteraceae, has around 50 species. The most important species in commercial terms is the cultivated sunflower (*Helianthus annuus* L.), grown mainly for its oilseed. In contrast, *H. tuberosus* is distinguished by its large tubers, which have been selected for their food value. No other species of *Helianthus* is cultivated to a significant extent, although several have value as ornamentals. The classification, identification, and distribution of the genus *Helianthus* are dealt with in Chapter 3. A number of hybrids naturally form between *Helianthus* species, including *H. tuberosus*, within overlapping North American ranges, while further hybrids have been produced as part of plant breeding programs.

Both above- and belowground parts of Jerusalem artichoke are utilizable for various applications, for instance, the tops for biomass and animal feed and the tubers as a feedstock for food and nonfood chemical production. All plant parts can potentially be improved to enhance their commercial value. A great deal of morphological variation has been noted in Jerusalem artichoke, despite it being a crop that has undergone relatively little systematic selection, suggesting that genetic improvement is possible. Tubers, for instance, vary in color, shape, size, and surface topography. Plant anatomy and morphological differences between clones and cultivars are described in Chapter 4.

Inulin is the storage carbohydrate of Jerusalem artichoke, whereas starch is the storage carbohydrate in the majority of plants. Only a small number of plants accumulate inulin in amounts sufficient for cost-effective extraction, with chicory (*Cichorium intybus* L.) and Jerusalem artichoke being the most important inulin-storing species. A survey of the occurrence of inulin in plants is presented in Chapter 5, together with an overview of the plant's chemical composition. Inulin is primarily stored in the tubers, but temporary storage also occurs in the stems prior to tuber filling. Inulin gives the plant its distinctive properties and its particular value for industry. Plant-derived inulin can be processed and modified to serve as a feedstock for numerous industrial applications, as outlined in this chapter.

The demand for inulin is growing, particularly within the food industry. Mammalian digestive enzymes do not target inulin, and it passes undigested to the large intestine, where bifidobacteria and other beneficial bacteria selectively ferment it. Inulin is added as a prebiotic ingredient to an ever-increasing range of food products, because it helps in the maintenance of a healthy intestinal microflora. Inulin-containing foods are marketed for their weight-loss benefits, and as a low-calorie sweetener, bulking agent, and fat replacement. Inulin can play an important role in combating the obesity epidemic. Diabetic foods also contain inulin, as its ingestion affects blood sugars to a lesser extent than other carbohydrates. As a dietary fiber, inulin promotes improved bowel function, while a number of additional health claims have been made for inulin-type fructans, relating to improvements in mineral absorption in the intestines, improvements in blood lipid composition, the suppression of disease, and the stimulation of the immune system. Moreover, inulin is increasingly added to animal feed, particularly to compensate for the banning of antibiotic dietary supplements. The value of inulin in human and animal diets is explored in Chapter 6.

Declining fossil fuel reserves and the need to alleviate the worst consequences of global climate change have stimulated unprecedented interest in alternative fuels and energy sources, including biofuels. Jerusalem artichoke produces large amounts of biomass, is fast growing, needs relatively few inputs in terms of pesticides, fertilizer, and water, and can be grown on marginal land. It is therefore a potentially useful crop for the production of biofuel, and in particular bioethanol (Chapter 7). New strains of inulinase-producing yeast facilitate the conversion of Jerusalem artichoke biomass into ethanol within a single bioreactor. Jerusalem artichoke tops (fresh or ensiled) also have potential for the production of biogas (methane).

Cross-pollinating has been the traditional way of breeding Jerusalem artichoke, to generate clones having considerable genetic diversity for subsequent selection. The aim of plant breeders has been primarily to enhance tuber production and inulin content. New techniques like genetic modification can readily be applied to Jerusalem artichoke, as transgenic lines of the closely related cultivated sunflower have already been produced. Raw material for plant breeding programs is obtainable from several important germplasm collections in North America and Europe. A survey of genetic resources for this crop is presented in Chapter 8, along with a discussion of selection criteria and breeding techniques. The chapter concludes with an extensive alphabetical directory of Jerusalem artichoke clones and cultivars.

Jerusalem artichoke is usually propagated vegetatively, from tubers or tuber pieces (Chapter 9). Reproduction by seed, although of no consequence in commercial production, is a means of dispersal for wild populations and is vital when crossing in plant breeding programs. Propagation is also possible from rhizomes, slips, and cuttings. Jerusalem artichoke is amenable to propagation by tissue culture, being a model species used in pioneering micropropagation studies. Pollination is predominantly via bees in the field, but can be achieved by hand in greenhouses.

Developmental biology, resource allocation, and yield of Jerusalem artichoke form the basis of Chapter 10. Resource allocation in cultivated Jerusalem artichoke differs from that of wild populations, with cultivated clones allocating fewer resources to seeds (sexual reproduction) and more to the tubers (asexual reproduction). The developmental biology of the species is relatively complex when contrasted with most seed-propagated field crops, and as a consequence, understanding the biological and environmental factors modulating growth and development is essential for maximizing productivity. Growth and development are strongly modulated by photoperiod, and while day-neutral cultivars for flowering have been selected, tuberization appears to remain under short-day influence. Photoperiodic control influences what cultivars can be successfully grown in various geographical locations and various aspects of their production. The development of different plant parts is described, with respect to environmental factors, and resource partitioning within plants is discussed with respect to yield. A range of environmental and production factors are noted that can affect yield.

Jerusalem artichoke has relatively few pest and disease problems in the field. The main production losses, which are usually modest, arise due to bacterial and fungal pathogens late in the

season and during storage. Recorded pest and disease organisms known to affect Jerusalem artichoke are described in Chapter 11, along with insects that may play a role in pollination.

A range of agronomic practices increase yield, including choice of planting date, weed control, fertilization, irrigation, and efficient planting and harvesting procedures (Chapter 12). Weeds are rarely a problem in Jerusalem artichoke, because the crop outcompetes most other plant species, although herbicides may be beneficial during crop establishment. Jerusalem artichoke can be a troublesome weed in rotations, and herbicides may be needed to eradicate volunteer plants in following crops. Fertilizers can increase productivity, although excessive nitrogen fertilization may boost top growth to the detriment of tuber yields. Irrigation increases yield in hot, arid regions, although the crop is relatively drought and salt tolerant.

Jerusalem artichoke tubers can be left *in situ* and harvested as needed, or lifted and stored in common stores (e.g., cellars and pits) or under refrigeration. Cold storage is effective, although refrigeration adds to production costs. Tubers can be stored up to 12 months under optimal conditions. However, carbohydrate composition alters significantly during storage, with the depolymerizing of inulin having implications for various industrial applications. Storage options are discussed in Chapter 13.

There is increasing demand for inulin and bioethanol, two products that can be derived from Jerusalem artichoke. Inulin is mainly derived from chicory, which is increasingly grown as an alternative to sugar beet due to a decreasing demand for sucrose. Bioethanol is mainly produced from sugar cane or corn (maize). Jerusalem artichoke must therefore demonstrate economic advantages over these alternative crops. Potential advantages include profitable by-products and cheaper inputs. Jerusalem artichoke has relatively low input requirements and can be cultivated on marginal land, making it a promising additional feedstock for inulin, biomass, and biofuels. Corn, in contrast, has relatively high inputs, and bioethanol production from corn diverts land and grain from food production. Production costs for Jerusalem artichoke vary with region, land price, processing plant size, and other factors. The economics of producing and marketing Jerusalem artichoke are the subject of the final chapter.

Jerusalem artichoke therefore has potential as a multipurpose crop, with the value of its by-products a key to its future commercial exploitation. A listing of patents that relate to Jerusalem artichoke (Appendix), particularly utilizing plant-derived inulin, illustrates an increasing interest in the crop.

The future of the Jerusalem artichoke is far from clear, however, when plotting its course from this point in time; the attributes of the species, especially those that cannot be readily and more efficiently met by existing crops, need to be closely assessed. Jerusalem artichoke has long been known to be highly efficient and competitive. Perhaps rather than removing or repressing the genes that make the species so effective in the wild, the crop could be developed for low inputs and culture in marginal soils, on land that will not displace existing crops. For instance, rather than selecting for the absence of stem storage and early tuberization, the crop could be grown as a perennial, as in the wild, for harvesting just the aerial portion of the plant, before extensive recycling of carbon from the stems into the tubers. In the interim, the Jerusalem artichoke remains an underexploited natural resource awaiting the input of resources and expertise needed for the utilization of its unique attributes.

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2 Nomenclature, Origin, and History

2.1 NOMENCLATURE FOR *Helianthus tuberosus* L.

A diverse assortment of Latin and common names have been ascribed to *Helianthus tuberosus* since its introduction into Europe, making its history and outward dispersal from the New World difficult to trace. Linné assigned the current Latin binomial (*H. tuberosus* L.) for the species in 1753. Today his system of classification is universally accepted, though it was not uniformly welcomed at that time. This sentiment is evident in the following comment by Brookes, published in 1763:

> I hope therefore Students will excuſe me for not having adopted either the ſyſtems of *Tournefort*, or *Linnæus*, in contradiction to nature and experience; my deſign being not to asuſe the ſpeculative, but to direct the induſtrious. Their attempts to reduce the names of plants into a ſyſtem, has rendered the ſtudy more difficult and more ſubject to error, than it would have been if the Student had only uſed his ſight for the diſtinguiſhing of plants, and his memory for regiſtring them.

It is therefore not surprising that there have been a wide assortment of names ascribed to the species, reflecting varying levels of accuracy or appropriateness (Table 2.1). Or as Redcliffe Salaman (1940) aptly states, *H. tuberosus* and *Helianthus annuus* during "their 300 years sojourn in Europe have acquired a bewildering number of aliases." In fact, the two most widely used common names, Jerusalem artichoke and topinambou, are neither accurate nor appropriate. Salaman (1940) presents a detailed account of their possible derivation.

Starting with Jerusalem artichoke, analysis of the literature underscores the fact that the species is not an artichoke, nor does it have anything to do with Jerusalem. The *artichoke* portion of the common name appears to have been added in that the cooked tubers are somewhat reminiscent of the taste and texture of the fleshy receptacle of the globe artichoke (*Cynara scolymus* L.). Samuel de Champlain, the first European to describe the plant in the New World (Massachusetts in 1605), compared its flavor to that of the artichoke in a description of his visit to the homes of the natives with Seigneur De Monts, the leader of the expedition (Bourne, 1906). They passed through fields of Indian corn and "saw an abundance of Brazilian Beans, many edible Squashes of various sizes, Tobacco and roots which they cultivate, the latter having the taste of Artichokes" (Champlain, 1613). The name *artichoke* is believed to have been derived from the Arabic *Al-kharshūf*, meaning rough skinned. By transition through Spanish-Arabic (*Al-kharshōfa*) and old Spanish (*Alcarchofa*), the name was passed to old Italy as *Alcarcioffo*, or in modern Italian, *Articiocco*, which led to *artichoke* in English, which was first used in the English language in 1531 (Simpson and Weiner, 1989).

The use of *Jerusalem* as part of the common name for *H. tuberosus* has two plausible origins. The first is that it is a corruption of the Italian name *girasole articiocco*, or sunflower artichoke, a theory put forward by J.E. Smith in 1807. Difficulty in pronouncing *girasole* by the English led to Jerusalem's etymological derivation. This interpretation, however, is predicated upon the existence of girasole in the 17th century, a fact challenged by Gibbs (1918) and Salaman (1940). The sunflower (*H. annuus*) arrived in Europe during the mid-16th century; for instance, Leonhard Fuchs named and illustrated it between 1544 and 1555 (Meyer et al., 1999). Meanwhile, the girasol appears to

TABLE 2.1
Names used for *H. tuberosus* L. Since the 1600s

Name	Reference
Aardpeer	Becker-Dillingen, 1928; Driever et al., 1948
Adenes Canadenses	Lauremberg, 1632
American artichoke	Sprague et al., 1935
Artichaut de Canada	Géardi, 1854
Artichaut de Jérusalem	Lecoq, 1862; Becker-Dillingen, 1928; Pinckert, 1961
Artichaut de Terre	Lecoq, 1862
Artichaut du Canada	Lecoq, 1862; Becker-Dillingen, 1928
Artichaut of terre	Géardi, 1854
Artichaut Souterrain	Baillarge, 1942
Artichoke	
Artichoke apples of Ter-Neusen	Dodoens et al., 1618
Artichoke d'Inde	Anon., 1658
Artichoke of Jerusalem	A variation of Jerusalem artichoke
Artichokes of Jerusalem	Küppers, 1956
Artichoke under the ground	Translation of Dodoens's Articiochen onder d'aerde
Artichokes van Ter Neusen	Dodoens, 1618
Articiochen onder d'aerde	Dodoens, 1618
Artischockappeln	Lauremberg, 1632
Artischockappeln van Ter Neusen	Lauremberg, 1632
Artischocken unter Erden	Lauremberg, 1632
Artischokenappel van Ter Neuzen	Küppers, 1956
Artischoki sub terrâ	Vallot, 1665
Aster Peruanos tuberosus	Colonna, 1616
Aster Peruanus	Willughby and Ray, 1686
Aster Peruanus tuberosus	Colonna, 1616
Batata carvalha	Becker-Dillingen, 1928
Batatas Canadensis	Beverly, 1722
Batatas Candense	Küppers, 1956
Batatas von Canada	Dodoens, 1618
Battatas de Canada	Parkinson, 1629
Bulwa	Becker-Dillingen, 1928
Canada	Baillarge, 1942
Canada et Artischoki sub terrâ	Bauhin, 1671
Canada potato	
Canadas	Baillarge, 1942
Canadiennes	Sagard-Theodat, 1836
Cartoffel	Rhagor, 1639
Chiquebi	Hegi, 1906/1931
Choke	Shoemaker, 1927
Chrysanthemon latifolium	Bauhin, 1671
Chrysanthemum Canadense	Dodoens, 1618; Moretus, 1644
Chrysanthemum Canadense arumosum	Schuyl, 1672
Chrysanthemum Canadense tuberosum edule	Dodoens, 1618
Chrysanthemum è Canada	Bauhin, 1671
Chrysanthemum latifolium brasilianum	Linnaeus, 1737; Bauhin, 1671
Chrysanthemum perenne majus solis integris, *americanum tuberosum*	Morison, 1680; Linnaeus, 1737

TABLE 2.1 (CONTINUED)
Names used for *H. tuberosus* L. Since the 1600s

Name	Reference
Cičoka	Becker-Dillingen, 1928
Cnosselen	Lauremberg, 1632
Compire	Lecoq, 1862; Baillarge, 1942
Corona solis parvo flore, *tuberosa*	Boerhaave, 1720; Linnaeus, 1737
Cotufa	Becker-Dillingen, 1928; Escalante, 1946
Csicsóka	I'So, 1955
Earth-puff	Angyalffy, 1824; Hegi, 1906/1931
Erd-apfel	Flemish
Erdapfel	Anon., 1731; Rodiczky, 1883; Becker-Dillingen, 1928
Erdartischocke	German
Erdartischoke	Anon., 1731; Angyalffy, 1824; Scheerer, 1947
Erdbirne	Angyalffy, 1824; Rodiczky, 1883; Löbe, 1850
Erdmandl	Küppers, 1949
Erdschocke	Küppers, 1949
Ewigkeitskartoffel	Küppers, 1949; Prehl, 1953
Flos Solis Canadensis	Dodoens et al., 1618
Flos Solis Farnenanious	Salmon, 1710
Flos Solis Farnesianus	Colonna, 1616
Flos Solis glandulosus	Vallot, 1665
Flos Solis Pyramidalis	Gerarde, 1597
Flos Solis tuberosa radice	Linnaeus, 1737
Flos Solis tuberosus	Aldinus, 1625
Frenches Battatas	Parkinson, 1640
Girasole	Hegi, 1906/1931
Girasole del Canada	Becker-Dillingen, 1928; Krafft, 1897
Griasole [Girasole?] de Canada	Targioni-Tozzetti, 1809
Grond-peer	Baillarge, 1942
Ground berry	Prain, 1923
Ground pear	Soviet News, 1947
Grundbirne	Scheerer, 1947
Gyrasol do Brasil tuberoso	Becker-Dillingen, 1928
Hartichokes	Anon., 1649
Helenii tuberosum	
Helenium canadense	Ammann, 1676
Helianthemum indicum tuberosum	Brookes, 1763; Bauhin, 1671
Helianthemum tuberosum	Brookes, 1763
Helianthi	Thellung, 1913
Helianthum tuberosum esculentum	Diderot, 1765
Helianthus radice tuberosa	Linnaeus, 1737
Helianthus tomentosus	Michaux, 1801
Helianthus tuberosus	Linnaeus, 1753
Helianthus tuberosus var. *subcanescens*	Gray, 1869
Heliotropium Indicum tuberosum	Küppers, 1956
Heliotropum Indicum tuberosum	Salmon, 1710
Herba solis tuberosa	Moretus, 1644
Herba solis tuberosa radice	Dodoens, 1618
Hierusalem artichoke	Parkinson, 1640
Honderthoofden	Lauremberg, 1632

TABLE 2.1 (CONTINUED)
Names used for *H. tuberosus* L. Since the 1600s

Name	Reference
Hundred-heads	Dodoens, 1618
Hxiben	Gibault, 1912; Baillarge, 1942; Küppers, 1952b
Jerusalem artichoke	Common English name for the species
Jerusalemartischoke	Germershausen, 1796
Jirasol tuberoso	Becker-Dillingen, 1928
Jordaeble	Becker-Dillingen, 1928
Jordäple	Becker-Dillingen, 1928
Jordärtskocka	Becker-Dillingen, 1928
Jordskokken	Becker-Dillingen, 1928
Judenbirne	Rodiczky, 1883
Judenerdapfel	Rodiczky, 1883
Judenkartoffel	Scheerer, 1947
Kaischuc penauk	Trumbull and Gray, 1877
Kaishcucpenauk	Küppers, 1956
Knauste	Lauremberg, 1632
Knobs	Dodoens, 1618
Knollensonnenblume	Scheerer, 1947
Knollenspargel	Küppers, 1949
Knollige Sonnenblume	Angyalffy, 1824; Linnaeus, 1797
Knollige Sonnenrosen	Schwerz, 1843
Knousten	Lauremberg, 1632
Laska répa	Becker-Dillingen, 1928
Orasqueinta	Sagard-Theodat, 1836
Papežica	Becker-Dillingen, 1928
Papinabò	A corruption of *topinambur* or *topinambour*
Pariser Edelerdartischoke	Wettstein, 1938
Pataca (Argentinean)	Becker-Dillingen, 1928
Patache (Sicilian)	Becker-Dillingen, 1928
Patata	Catalina, 1949
Patata americana	Küppers, 1956; Targioni-Tozzetti, 1809
Patata del Canada	Targioni-Tozzetti, 1809
Patata di Canada	Hegi, 1906/1931
Pero di terra	Becker-Dillingen, 1928
Peruanum Solis florem ex Indiis tuberosum habuimus	Hernandez, 1648
Peruanus Solis flos ex Indiis tuberosus	Hernandez, 1651
Pferdekartoffel	Becker-Dillingen, 1928; Scheerer, 1947
Poire de terre	Géardi, 1854
Poire de Terre	Lecoq, 1862; Baillarge, 1942
Pomme de terre	Initially used in France but subsequently was substituted for *Solanum tuberosum*
Pommes de Canada	Sagard-Theodat, 1836; Baillarge, 1942
Potato of Canada	Parkinson, 1629
Potato plant	
Rehkartoffel	Küppers, 1949
Roßbirne	Scheerer, 1947
Roßgrundbirne	Hegi, 1906/1931
Roßkartoffel	Rodiczky, 1883
Root-artichoke	
Russische Bodenbirne	Hegi, 1906/1931

TABLE 2.1 (CONTINUED)
Names used for *H. tuberosus* L. Since the 1600s

Name	Reference
Salsifis	Caspari, 1948
Schnapskartoffel	Prehl, 1953
Semljannaja gruscha	Fermeren, 1932; Becker-Dillingen, 1928
Sol altissimus radice tuberosa esculenta	Linnaeus, 1737
Soleil vivace	Lecoq, 1862; Baillarge, 1942
Soleil vivace	Géardi, 1854
Solis Flore tuberosus	Aldinus, 1625
Solis flos Farnesianus	Colonna, 1616
Solis herba Canadensis	Dodoens, 1618
Sonnenrose	Nefflen, 1848
Sow bread	Angyalffy, 1824
Stangenerdapfel	Rodiczky, 1883; Pinckert, 1861
Süßkartoffel	Küppers, 1949
Sun-root	Robinson, 1920
Sunchoke	Name given to a *H. annuus* H *H. tuberosus* hybrid
Sunflower artichoke	
Sunroot	Shoemaker, 1927
Tapinabò	A corruption of *topinambur* or *topinambour*
Tartouffe	Géardi, 1854
Tartoufle	Baillarge, 1942
Tartüffeln	Prehl, 1953
Tartuffi bianchi	Küppers, 1956
Tartuffo di Canna	Hegi, 1906/1931
Tartufo bianco	Anon., 1741
Tartufo di Canna	Targioni-Tozzetti, 1809
Tartufoli	Becker-Dillingen, 1928
Taupinambours	Schlechtendal, 1858
Taupine	Baillarge, 1942
Terre à touffe	Géardi, 1854
Tertifle	Géardi, 1854
Tertifle	Lecoq, 1862
Tiramirambo	Ravault, 1952
Topinabò	A corruption of *topinambur* or *topinambour*
Topinamba	Becker-Dillingen, 1928
Topinambou	Petersons, 1954
Topinambour	Driever et al., 1948; Targioni-Tozzetti, 1809; Becker-Dillingen, 1928; Lecoq, 1862
Topinambous	Anon., 1658
Topinambur	Becker-Dillingen, 1928
Topinambur	Griesbeck, 1943; Schwerz, 1843
Topinambura	Fermeren, 1932
Topinambury	Becker-Dillingen, 1928
Topine	Schmitz-Winnenthal, 1951; Anon., 1952
Tropenkartoffel	Küppers, 1952a
Trtur	Becker-Dillingen, 1928
Truffles du Canada	Baillarge, 1942
Tuberous rooted sunflower	Becker-Dillingen, 1928
Tubers	Dodoens, 1618
Tüffeln	Prehl, 1953

TABLE 2.1 (CONTINUED)
Names used for *H. tuberosus* L. Since the 1600s

Name	Reference
Tupinabò	A corruption of *topinambur* or *topinambour*
Underschocken	Lauremberg, 1632
Unter Erdschen	Lauremberg, 1632
Unterartischoke	Scheerer, 1947; Hegi, 1906/1931
Weißwurzel	Scheerer, 1947; Hegi, 1906/1931; Küppers, 1949
Wildkartoffel	Prehl, 1953
Zidovski neb ruski brambory	Becker-Dillingen, 1928
Zuckerkartoffel	Prehl, 1953

Source: Compiled using Pätzold, C., Die Topinambur als Landwirtschaftliche Kulturpflanze, Institut für Pflanzenbau und Saatguterzegung der Forschungsanstalt für Landwirtschaft, Braunschweig-Völkenrode, Germany, 1957 and additional material.

have been used in reference to it toward the turn of the century. For example, in 1598 Phillip Sidney used "Girasol" (Sidney, 1598).

> With gazing eyes he looks, short sighs unsettled feet
> He stood, but turned as Girasol to sun
> His fancies slite did her in halfe way meet
> His soul did fly as she was seen to run.

alluding to the heliotropic response of what one would construe was the sunflower; i.e., the flower heads turn with the movement of the sun from east to west during the day, returning to their original position during the night (Lang and Begg, 1979; Schaffner, 1900). It is apparent, at least, that the term *girasol* was in use, predating the spread of *H. tuberosus* on the continent.

Salaman (1940) argues, based upon Italian dictionaries between 1598 and 1688, that *girasole*, while present, is not used for *H. annuus*. Not until 1729 in *Vocabolario degli Academici della Crusca* is *girasole* used to refer specifically to the sunflower, though as early as 1611 in John Florio's *Queen Anna's New World of Words*, it is used for a plant that turns with the sun. Whether its use is in reference to *H. annuus* or one of several other heliotropic species is not clear, but definitely cannot be ruled out. Salaman concludes that "there appears to be no evidence, whether sought among specialist botanical sources or from the common language of the day, that the word Girasole was used during the period under discussion in Italy or elsewhere either for our Sunflower, *H. annuus*, or for the Jerusalem Artichoke, *H. tuberosus*."

The alternative proposal for the origin of *Jerusalem* in the common name for *H. tuberosus* is that it is a corruption of a location where the crop was grown in the early 1600s. Petrus Hondius, a pastor in the Netherlands, grew and distributed the tubers from Ter Neusen, resulting in the crop being considered a product of Ter Neusen. The 1618 edition of Dodoens's *Cruydt-Boeck* mentions Artischokappeln van Ter Neusen, as did Lauremberg's *Apparatus Planterius Primus* in 1632. David Prain, by way of Salaman (1940), proposed that the crop was imported to England as Artichokes van Ter Neusen, which readily became corrupted to Artichokes of Jerusalem and subsequently to Jerusalem artichokes.

The second common name, which has no apparent relationship to the species, is topinambur. *Topinambur* (or variations thereof) is currently used in Bulgarian, Czech, Dutch, English, Estonian, French, German, Italian, Lettish, Lithuanian, Polish, Portuguese, Romanian, Russian, Slovak, Spanish, and Ukrainian (Table 2.2). The story of how *H. tuberosus* came to be called topinambur is equally intriguing. Between 1609 and 1617, *H. tuberosus* was introduced into France, where it

TABLE 2.2
Current Common Names for *Helianthus tuberosus* L. in Various Languages

Name	Language
Aardpeer	Dutch
Aardaartisjok	Dutch
Aguaturma	Spanish
Alcachofa de Jerusalém	Spanish
Artichaut de Jérusalem	French
Articokks	Maltese
Beyaz yer elmasl	Turkish
Brahmokha	Bengali
Bulwa	Polish
Carciofo di Gerusalemme	Italian
Carciofo di terra	Italian
Castaña de tierra	Spanish
Cotufa	Spanish (Philippines)
Csicsóka	Hungarian
Elianto tuberoso	Italian
Erd-apfel	Flemish
Erdartischocke	German
Erdbirne	German
Girassol batateiro	Portuguese
Girassol tuberoso	Portuguese
Grusha zemljanaja	Russian
Gui zi jiang	Chinese-Wú
Hathipich	Punjabi
Hatichuk	Hindi
Jerusalem artichoke	Assamese
Jerusalem artichoke	English
Jerusalem artisjok	Afrikaans
Jordärtskocka	Swedish
Jordskocka	Swedish
Jordskok	Danish
Jordskokk	Norwegian
Ju yu	Chinese-Mandarin
Kartofel loshadnnyi	Russian
Kikumo [kiku imo]	Japanese
Knolartisjok	Afrikaans
Knollensonnenblume	German
Knollsolsikke	Norwegian
Kollokasi	Greek
Krkŭska	Macedonian
Lashka repa	Slovene
Maa-artisokka	Finnish
Maapirn	Estonian
March-ysgall	Welsh
Mollë	Albanian
Mugul-artishokk	Estonian
Mugulpäevalill	Estonian
Mukula-artisokka	Finnish
Näiteks maapirn	Estonian

TABLE 2.2 (CONTINUED)
Current Common Names for *Helianthus tuberosus* L. in Various Languages

Name	Language
Nyamara	Catalan
Padsolnechnik klubnenosnyi	Russian
Pataca	Spanish
Preeria-auringonkukka	Finnish
Qui zi jiang	Chinese-Cantonese
Slanechnik clubneneosny	Bylerussian
Słonecznik bulwiasty	Polish
Sunchoke	English
Tavuk gökü	Turkish
Tertufa	Arabic
Topìambur	Ukrainian
Topinambas	Lithuanian
Topinambo	Portuguese
Topinambo	Spanish
Topinamboer	Dutch
Topinambour	French
Topinambur	Bulgarian
Topinambur	Czech
Topinambur	English
Topinambur	Estonian
Topinambur	Germany
Topinambur	Italian
Topinambur	Polish
Topinambur	Romanian
Topinambur	Serbo-Croatian
Topinambur	Slovene
Topinambur elianto	Italian
Topinambur hlíznatý	Czech
Topinambūrs	Lettish
Topinembur	Slovak
Ttung dahn ji	Korean
Ttung ttan ji	Korean
Tupinambo	Spanish
Woodland sunflower	English
Yang jiang	Chinese-Cantonese
Yang jinag	Chinese-Wú
Yerelmasi	Turkish
Zi bei tian kui	Chinese-Cantonese

Source: Adapted from Kays, S.J. and Silva Dias, J.C., *Cultivated Vegetables of the World: Latin Binomial, Common Name in 15 Languages, Edible Part, and Method of Preparation*, Exon Press, Athens, GA, 1996, with additional names. With permission.

acquired the name *topinambour*. The name appears to have been derived from the mistaken impression in the early 1600s that the crop was native to and introduced from South America (e.g., Linnaeus in the *Species Plantarum* (1753) described its origin as Brazilian, though in his earlier *Hortus Cliffortianus* (1737) denoted Canada). The Seigneur of Razilly, Claude Delaunay's expedition, visited Brazil in the early years of the 17th century and returned to Paris in 1613 with six natives from the Isle de S. Luiz de Maranhão. They were members of a tribe of the warlike race of Guaranís, known as the Topinambous. The natives, whose appearance in Paris created considerable excitement among the general populace, were presented to Queen Mary de' Medici on April 15, 1613. The idea of their presence creating what is now termed a media event is supported by letters from Francois de Malherbe (1862) to the naturalist Nicholas de Pieresc on April 15 and June 23, 1613.

> To-day [April 15] the Seigneur of Razilly, who in the last few days has returned from the Isle of Maragnan, has shown the Queen six Topinambours whom he has brought from that country. In going through Rouen he dressed them in French style, for according to the custom of their country they go quite naked except for some black rags with which they cover their private parts. The women wear nothing. They dance a kind of swing without holding hands or moving from the place. Their fiddles were a gourd like those which the pilgrims use for drinking, and inside they have some kind of nail or pin.…

> The Topinamboux will be baptised tomorrow [June 24]: if there is a chance of seeing it without being crushed, I shall do so; if not, I shall get those who were there to report to me. Already a couple of wives have been found for them; I understand they are only waiting for their baptism, to celebrate the marriage and ally France to the Island of Maranan.

It is evident that Razilly's exotic natives were a great attraction and the center of attention in Paris in early 1613, the timing of which coincided with the marketing of the latest root crop. Streethawkers, trying to sell the strange and rather uncouth-looking newly introduced tubers of *H. tuberosus*, adopted the term *topinambou* to draw attention to their exotic offering (Salaman, 1940). The word *topinambou* subsequently came to mean something gross and absurd.

The explanations for the origin of *topinambou* as a common name and *artichoke* as part of the common name appear readily acceptable, though the origin of the use of *Jerusalem* is of greater question. While two plausible explanations for the origin of *Jerusalem* in the common name are presented, we are left without a definitive choice. The most commonly quoted derivation to this day (i.e., from *girasole*) now appears to be questionable. Regardless, it is of considerable interest that the common names for the species could have deviated so far from the original Indian names for the plants, such as *kaischuc penauk*, which Salaman (1940) notes as the native name used in Virginia, derived from one of the Algononquian languages (Austin, personal communication), and translated by Trumbull and Gray (1877) as "sun roots." The addition and retention of *Jerusalem* in the common name is illogical at best. Or as Gould so aptly states in *The Flamingo's Smile* (1985), "The propagation of error, by endless transfer from textbook to textbook, is a troubling and amusing story in its own right — a source of inherited defect almost more stubborn than inborn errors of genetics."

What should the common name for the crop be? Alternative names that have been proposed range from sun-root (though technically the edible portion is not a root) proposed by Trumbull and Gray in 1877 to sunchoke. In 1918 the *Gardener's Chronicle* offered a prize for a new, more appropriate English name for the Jerusalem artichoke (Gibbs, 1918); however, from the continued use of *Jerusalem artichoke*, it is evident that the winning name was not considered an acceptable improvement.

2.2 ORIGIN

There was initially confusion concerning where the Jerusalem artichoke originated. Linnaeus, in *Species Plantarum* (1753), indicated a Brazilian origin, though in his earlier *Hortus Cliffortianus* (1737), he listed *H. tuberosus* as from Canada. Paxton also indicated the species as first introduced into England in 1617 from Brazil (Hereman, 1868). The impression of a South American origin may in fact have contributed to the acceptance of the common name *topinambou* adopted from the name of the natives (Topinambous) from the Isle de S. Luiz de Maranhão on the coast of Brazil. The correct center of origin, or at least more nearly correct, keeping in mind that during the 16th and 17th centuries "Canada" represented a much broader area than in modern times, seems to have been relatively widely accepted by European botanists toward the end of the 17th century as evidenced by the names ascribed to the species in the herbals of the day; e.g., "Adenes *Canadenses*" in Peter Lauremberg's *Apparatus Plantarius Primus* (1632); "*Canada*" and "*Artischoki sub terrâ*" by Antoine Vallot in *Hortus Regis Paris* (1665); "Chrysanthemum *Canadense Arumosum*" in F. Schuyl's *Catalogus Plantarum Horti* (1672); and "Helenium Canadense" in Paul Ammann's *Character Plantarum Naturalis* (1676). Alphonse DeCandolle in his *Géographie Botanique* (1855) likewise indicated that the South American origin was in error. Regardless, numerous incorrect listings continued to appear even into the 20th century. For example, Martyn in the 1807 edition of *Miller's Gardener's and Botanist's Dictionary* states that "they are unquestionably the produce of a hot climate, being natives of Brazil," Robinson (1871) "a native of Brazil," and Gray (Torrey and Gray, 1843) "an introduced species, said to have been derived originally from Brazil."

Upon growing a sample of *Helianthus doronicoides* Lam. received from Dr. Short in Kentucky in 1855, the American botanist Asa Gray found that the original long, slender tubers became shorter and thicker after 2 or 3 years of cultivation. He concluded that *H. doronicoides* was the parent of *H. tuberosus* in his *Manual of Botany of the Northern United States* (Gray and Sullivant, 1856). In *Lessons in Botany* (1869) and in subsequent editions of the manual until 1883, he reversed his decision and concluded that the wild species was not *H. doronicoides*.

While a North American center of origin is well accepted based upon the distribution of *H. tuberosus*, it is not certain that the actual center of origin was today's Canada. Gray in 1883 said that the aborigines who cultivated it must have obtained it from the valleys of the Ohio and Mississippi and their tributaries, where it abounds. The natural distribution of *H. tuberosus* unfortunately does not provide an adequate clue in that the species has been distributed widely through human activity and escapes often become naturalized. Therefore, it is doubtful that the highest density of the species in North America reflects the actual center of origin. The natural distribution of possible progenitor species whose union resulted in *H. tuberosus*, assuming neither are extinct nor have been cultivated and thereby distributed by people, would perhaps be more useful (Figure 2.1). Thus, areas of overlap in the natural distributions could point toward a probable area in which the species originated. This scenario requires the distribution of the parent species to not have shifted markedly from the time in which *H. tuberosus* originated. The question then becomes: from which species did *H. tuberosus* most likely originate?

Helianthus tuberosus is a polyploid with 102 chromosomes. Polyploids are thought to originate through the hybridization between two different species, giving rise to a progeny in which chromosome doubling occurs. For example, hybridization between a species with 34 and one with 68 chromosomes would produce a triploid (51 chromosomes), and with chromosome doubling would yield 102 chromosomes. To test the potential for gene flow between *Helianthus* species, crosses have been made among a cross section of species and a number of hybrids produced (Rogers et al., 1982). Heiser (1978) proposed that the 68-chromosome parent "almost certainly" has to be one of three species (*H. decapetalus* L., *H. hirsutus* Raf., or *H. strumosus* L.), which are all found within the central and eastern U.S. Of these, *H. hirsutus* has the greatest morphological resemblance to *H. tuberosus*. For the 34-chromosome species, *H. giganteus* L., *H. grosseserratus* Martens, or less likely *H. annuus* L. could represent the second parent, again assuming that neither of the

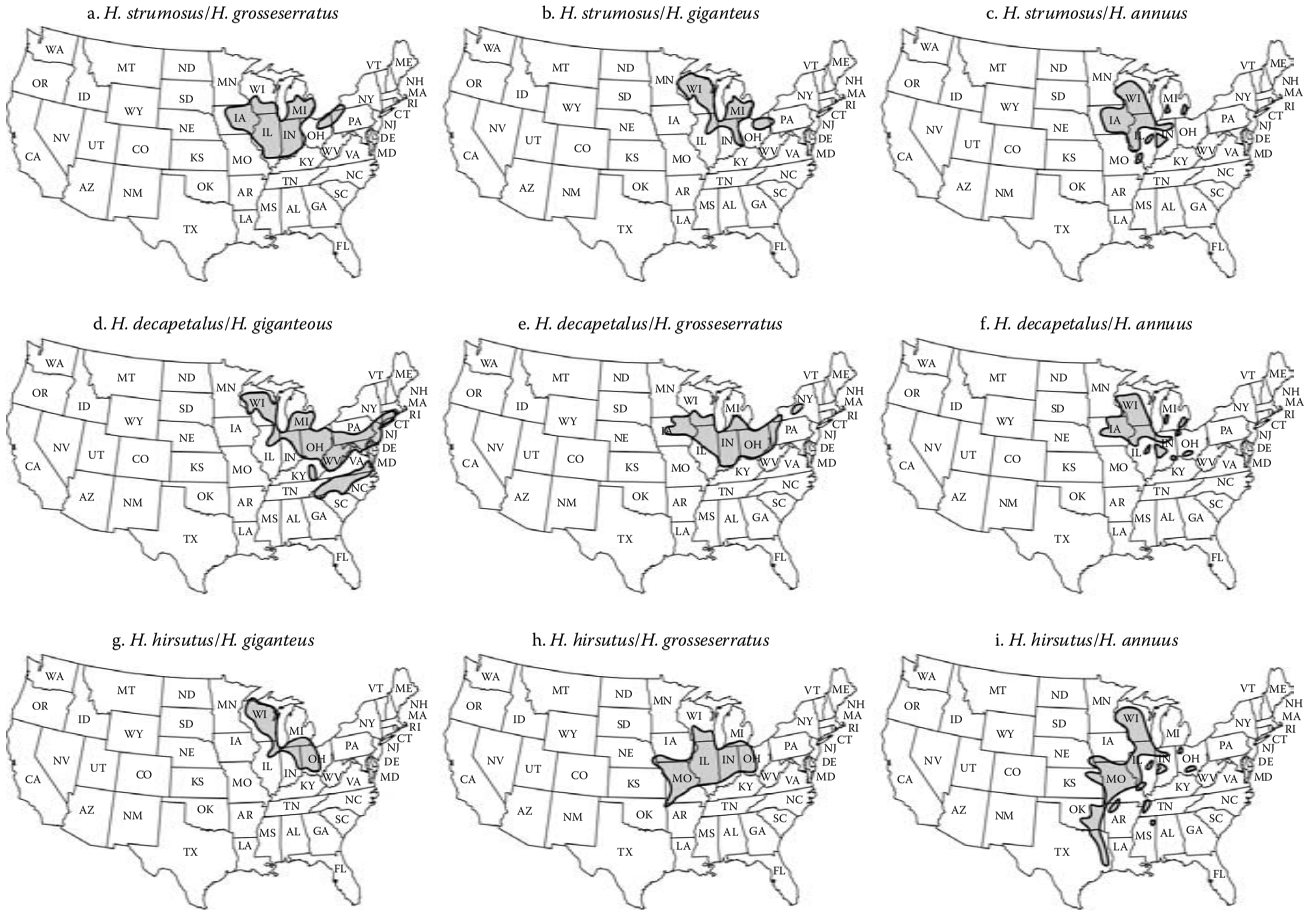

FIGURE 2.1 Overlap of the native distributions of potential 34- and 17-chromosome parent species for *H. tuberosus*: (a) *H. strumosus/H. grosseserratus*, (b) *H. strumosus/H. giganteus*, (c) *H. strumosus/H. annuus*, (d) *H. decapetalus/H. giganteus*, (e) *H. decapetalus/H. grosseserratus*, (f) *H. decapetalus/H. annuus*, (g) *H. hirsutus/H. giganteus*, (h) *H. hirsutus/H. grosseserratus*, (i) *H. hirsutus/H. annuus*. (Distribution data from Rogers, C.E. et al., *Sunflower Species of the United States*, National Sunflower Association, Fargo, ND, 1982.)

parents is now extinct. Artificial crosses between the 34- and 68-chromosome species, however, have produced progeny for only *H. giganteus* × *H. decapetalus* (Heiser and Smith, 1960) and *H. annuus* × *H. decapetalus*, *H. hirsutus*, and *H. strumosus* (Heiser and Smith, 1960; Heiser et al., 1969). The absence of hybrids between *H. hirsutus* and either *H. giganteus* or *H. grosseserratus* does not totally preclude its possible occurrence. Anisimova (1982), using immunochemical methods, suggested that one of the genomes of *H. tuberosus* was that of *H. annuus*, probably the subsp. *petiolaris*. If not extinct, the ancestors will undoubtedly be determined via genetic analysis such as that used (restriction length polymorphism) to establish the origin of the cultivated peanut (Kochert et al., 1996).

2.3 HISTORY

The history of *H. tuberosus* has been described in a number of articles (Decaisne, 1880; Gibault, 1912; Gray and Trumbull, 1883; Hooker, 1897; Lacaita, 1919; Salaman, 1940; Schlechtendal, 1858; Trumbull and Gray, 1877), and the following is therefore a summary. Jerusalem artichoke is thought to be one of the oldest cultivated crops in North America. Although archaeological records are lacking, several Native American groups probably grew the plant centuries before European settlers arrived on the continent. The earliest mention of the crop by a European was by Champlain, who described its cultivation by North American Indians in 1605 (Champlain, 1613).

Tubers of *H. tuberosus* were most probably brought back to France by either Champlain arriving on October 1, 1607 (or possibly the 1608 voyage, which returned October 13, 1609) or Marc Lescarbot in the autumn of 1607. While Lescarbot did not reach New France (in present-day Canada) until approximately 12 months after Champlain observed the crop in cultivation, he presented the first published account in 1609. While it is not possible to definitively establish which of the two introduced the crop into France, or at least did so first, Lescarbot is perhaps a more likely candidate in that he was in charge of the gardens at Port Royal, where the Jerusalem artichoke was apparently grown (Lescarbot, 1609). However, in the first two editions of this book (*Histoire de la Nouvelle France*) he does not indicate bringing the "roots" back to Europe, though in the 1617 edition he claims to have done so. This omission in the early editions may have been due to the fact that initially the species was of minor importance. However, its increasing popularity during the subsequent decade may have spurred Lescarbot to provide a more detailed account.

In the 1617 edition of *Histoire de la Nouvelle France*, Lescarbot indicates that the crop had already acquired the name *topinambaux* or *topinambours*, by which they were generally referred to in France. He states that "they were in everybody's garden in Paris whilst still a rarity at Rome, and an absolute novelty in England" (Lacaita, 1919). If Lescarbot brought the tubers to Port Royal in the autumn of 1607, this would have given sufficient time (10 years) for them to have become common, leading to their subsequent introduction into England in 1617 (Hereman, 1868) and John Parkinson's description of the crop in 1629. Based upon this scenario, Lacaita (1919) believed "there can be little doubt that the roots were imported into France on the occasion of the return of Lescarbot's party of 1607." Early illustrations (Figure 2.2) support the idea that the crop was relatively well known in the early 1600s.

Fabio Colonna (1616) was the first botanist to describe the plant, which no doubt contributed to the incorrect impression that the tubers were distributed throughout Europe from the Farnese Gardens in Rome. The more probable route of introduction into England was by way of Holland, where Petrus Hondius was the first to grow the crop. *H. tuberosus* was not cited in the earliest Dutch literature of the 1600s (e.g., Pelletier and Schilders, 1610) until the 1618 edition of Dodoen's *Cruydt-Boeck*. In an appendix to this edition he lists exotic plants where the crop is mentioned as *Batatas van Canada* and *Articiochen onder d'aerde*. Hondius apparently planted the tubers on February 28, 1613. "This plant was first brought to this country from the French Indies that are called Canada, although it does not multiply its roots there so much as here, nevertheless here it does not bloom, except when the summers are hot and there is a long drought." Hence, they were

(a) (b) (c)

FIGURE 2.2 Early-17th-century botanical drawings of *H. tuberosus* by (a) Colonna (1616), (b) Lauremberg (1632), and (c) Parkinson (1640).

cultivated in the Low Countries prior to being mentioned by Colonna as present in the Farnese Gardens.

Helianthus tuberosus was not described in the English literature in the late 1500s or early 1600s, e.g., Gerarde's *Herball* of 1597. The earliest mention in England was by TobiasVenner in 1622, where he indicates "Artichoks of *Jerusalem* is a roote usually eaten with butter, vinegar, and pepper, by itselfe, or together with other meats." Goodyer in 1617 "received two small roots thereof from Mr. Franquevill of London, no bigger than hen eggs, the one I planted, and the other I gave to a friend: myne brought me a pecke of roots, wherewith I stored Hampshire" (Gerard et al., 1633). One of the earliest illustrations of the species (Figure 2.2) was in Parkinson's *Theater of Plants* (1640).

Thus, the path of early introduction was from North America to France in 1607, and then, based on first statements in the literature, to Holland in 1613, Italy in 1614, England in 1617 (either via the Netherlands or directly from France), Germany in 1626, Denmark in 1642, Poland in 1652, Sweden in 1658, and Portugal in 1661 (Wein, 1963). From this initial distribution, *H. tuberosus* has traveled to all corners of the world, though finding greater interest in temperate regions in which it is adapted. For example, the Jerusalem artichoke reached Russia in the 18th century under Peter the Great (1672–1725) (Vavilov, 1992). Subsequent movement of the crop has in many cases been bidirectional, fluctuating with each oscillation in interest in the species and its path essentially impossible to document accurately.

While the storage organ of the Jerusalem artichoke is anatomically a tuber (i.e., an underground structure consisting of a solid thickened portion or outgrowth of a stem or rhizome, of a more or less rounded form, and bearing eyes or buds from which new plants arise (Simpson and Weiner, 1989)), in the early literature it is referred to as a root. This is because the term *tuber*, derived from the Latin *tuber*, was not in the English language until 1668, when it was first used by Wilkins in his "Essay towards a Real Character, and Philosophical Language" (Wilkins, 1668).

Surprisingly, botanists and gardeners of the 17th and 18th centuries had a fairly good understanding of the crop. For example, Brookes gives the following description of the Jerusalem artichoke (listed as *Helianthemum tuberosum* or *Helianthemum indicum tuberosum*) in 1763:

> One ſtalk or more riſes from each root, which is green, ſtreaked, rough, hairy, and attains the length of twelve feet or upwards, full of a white ſpungy pith. The leaves are many, placed in no order, and from the bottom to the top, and are greeniſh, rough, broad, and acuminated like thoſe of the common ſunflower, but not ſo much wrinkled nor ſo broad. The ſtalks ſoon after their riſe are branched, and the leaves decreaſe in ſize from the bottom to the top. The flowers grow on the top of the ſtalks, and

are of the ſize of marygolds, and radiated. The diſk conſiſts of many yellow floretts, with a crown compoſed of twelve or thirteen ſtreaked pointed gold coloured ſemi-floretts, placed on embryoes in a ſcaly villous cup. The embryoes turn into ſmall ſeeds, and the ſtalk emits ſeveral ſlender creeping roots, that ſpread themfelves on all ſides, between which there are many tuberoſe roots, ſometimes adhering to the chief foot, and ſometimes connected to long fibres a foot diſtant from them. One root will produce thirty, forty, fifty, or more potatoes. Theſe are reddiſh or whitiſh without, and conſiſt of a whitiſh ſubſtance, or fleſh, with a ſweetiſh taſte, and are often bigger than a man's fiſt. They continue in the ground all the winter, and the next year they ſpring again. This plant has been greatly propagated in *England* for this forty or fifty years paſt; for though it was brought from *America* in 1623 it was not much cultivated before, becauſe they were then thought only fit for poor people; but now they are in general eſteem. It always uſed to be ranked among the kinds of ſolanum, and by *Linnæus* it is placed under thoſe of the *Lycoperſicon*, or *the Love Apple*. It is propagated here by the roots, which if large are into pieces, preſerving a bud or eye in each; but the beſt method is to plant the fineſt roots entire, allowing them a pretty large ſpace of ground between the rows, as alſo each root, and then thoſe that are produced will be large the following autumn. A light ſandy loam is beſt, if not too dry or moiſt, and it ſhould be will ploughed two or three times, and the deeper the better. They are of little uſe for any thing but food, and ſome pretend they are very windy, while others inſiſt upon the contary; however they are very nouriſhing, abate the acrimony of the blood and juices, and are conſequently good in diſorders of the breaſt. There are ſome people in *France* that eat them raw with ſalt and pepper.

For a time after its spread around Europe (Bagot, 1847), the tubers of *H. tuberosus* were a significant source of dietary carbohydrate. However, its importance declined after the introduction of the potato (*Solanum tuberosum* L.). It has had surges in cultivation, for example, after WWII in France and Germany, when potatoes were scarce. The extent of its popularity is indicated by the number of books and monographs (~35) published (predominantly in French, German, and Russian) on the crop since 1789 (Table 2.3). Today, Jerusalem artichoke has the potential to once again become an important crop, on the basis of a wide range of nonfood and food applications.

TABLE 2.3
Chronological List of Books and Monographs on Jerusalem Artichoke

Date	Reference
1789	Parmentier
1790	Parmentier
1806	Bagot
1845	Morren
1860	Mollon
1861	Pinckert
1867	Delbetz
1878	Dieck
1881	Vannier
1898	Charavel
1901	Hourier et al.
1921	Brétignière
1932	Fermeren
1934	Lebedev and Petrenko
1942	Baillarge
1943	Griesbeck
1955	I'So
1957	Eikhe
1957	Pätzold
1963	Martin
1968	Institut Biologii
1974	Bauer
1974	Kakhana et al.
1974	Votoupal
1980	Langhans
1986	Leible
1989	Wurl
1990	Grothus
1990	Kochnev et al.
1991	Diedrich
1993	Amato
1995	Merkatz
1997	Cepl et al.
2000	Hennig
2000	Rykhlivs'kyi
2002	Marcenaro

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3 Classification, Identification, and Distribution

The sunflower genus, *Helianthus*, comprises around 50 species native to the Americas and found growing within the U.S. Their distribution varies from restricted to widespread. Two species are important as agricultural crops, the Jerusalem artichoke (*Helianthus tuberosus* L.) and the sunflower (*Helianthus annuus* L.). The Jerusalem artichoke is cultivated as a vegetable, fodder crop, and a source of inulin for food and industrial purposes, while the sunflower is grown as an oilseed crop. Both species are also noteworthy in that, of the diverse cross section of crops that make up the backbone of agriculture in North America, they are the only crops that were domesticated in prehistoric times in what is now the U.S. (Heiser, 1978). In addition, several other species and hybrids are either currently or beginning to be used for ornamental purposes, including *H. annuus*, *H. argophyllus* T.&G., *H. debilis* Nutt., *H. decapetalus* L., *H.* × *laetiflorus* Pers., *H. maximiliani* Schard., *H.* × *multiflorus* L., and *H. salicifolius* A. Dietr. The cut flowers of Jerusalem artichoke have also been used in this way, as evidenced by Claude Monet's painting of 1880, *Jerusalem Artichoke Flowers*, currently in the National Gallery of Art, Washington, D.C. (NGA, 2006).

3.1 CLASSIFICATION

Jerusalem artichoke is classified in the genus *Helianthus* L., in the family Asteraceae (Aster or Daisy family), in the order Asterales (Table 3.1). Asteraceae is the modern family name, introduced to supersede Compositae under Article 18 of the International Code of Botanical Nomenclature, 1972. Compositae is used in the pre-1972 literature as the family name for Jerusalem artichoke, and it is still acceptable to use it as the family name (in the same way Cruciferae, Gramineae, and Leguminoseae, for instance, are used for the Brassicaceae, Poaceae, and Fabaceae, respectively).

TABLE 3.1
Taxonomic Classification for *H. tuberosus* L.

Kingdom	Plantae
Subkingdom	Tracheobionta
Superdivision	Spermatophyta
Division	Magnoliophyta
Class	Magnoliopsida
Subclass	Asteridae
Order	Asterales
Family	Asteraceae
Genus	*Helianthus* L.
Species	*Helianthus tuberosus* L.

Source: Adapted from USDA, Plant Names, http://plants.usda.gov/, 2006.

TABLE 3.2
Taxonomic Classification within the Genus *Helianthus* L.

Section	Series	Species	Common Name[a]
Helianthus	—	*H. annuus* L.	Common sunflower
		H. anomalus Blake	Western sunflower
		H. argophyllus T.&G.	Silverleaf sunflower
		H. bolanderi A. Gray	Serpentine sunflower
		H. debilis Nutt.	Cucumberleaf sunflower
		H. deserticola Heiser	—
		H. exilis A. Gray	—
		H. neglectus Heiser	Neglected sunflower
		H. niveus (Benth.) Brandegee	Showy sunflower
		H. paradoxus Heiser	Paradox sunflower
		H. petiolaris Nutt.	Prairie sunflower
		H. praecox Engelm. & A. Gray	Texas sunflower
Agrestes	—	*H. agrestis* Pollard	Southeastern sunflower
Ciliares	*Ciliares*	*H. arizonensis* R. Jackson	Arizona sunflower
		H. ciliaris DC.	Texas blueweed
		H. laciniatus A. Gray	—
	Pumili	*H. cusickii* A. Gray	Cusick's sunflower
		H. gracilentus A. Gray	Slender sunflower
		H. pumilus Nutt.	—
Atrorubens	*Corona-solis*	*H. californicus* DC.	Californian sunflower
		H. decapetalus L.	Thinleaf sunflower
		H. divaricatus L.	Woodland sunflower
		H. eggertii Small	Eggert's sunflower
		H. giganteus L.	Giant sunflower
		H. grosseserratus Martens	Sawtooth sunflower
		H. hirsutus Raf.	Hairy sunflower
		H. maximiliani Schrader	Maximilian's sunflower
		H. mollis Lam.	Ashy sunflower
		H. nuttallii T.&G.	Nutall's sunflower
		H. resinosus Small	Resindot sunflower
		H. salicifolius Dietr.	Willowleaf sunflower
		H. schweinitzii T.&G.	Schweinitz's sunflower
		H. strumosus L.	Paleleaf woodland sunflower
		H. tuberosus L.	Jerusalem artichoke
	Microcephali	*H. glaucophyllus* Smith	Whiteleaf sunflower
		H. laevigatus T.&G.	Smooth sunflower
		H. microcephalus T.&G.	Small sunflower
		H. smithii Heiser	Smith's sunflower
	Atrorubentes	*H. atrorubens* L.	Purpledisk sunflower
		H. occidentalis Riddell	Fewleaf sunflower
		H. pauciflorus Nutt.	Stiff sunflower
		H. silphioides Nutt.	Rosinweed sunflower
	Angustifolii	*H. angustifolius* L.	Swamp sunflower
		H. carnosus Small	Lakeside sunflower
		H. floridanus A. Gray ex Chapman	Florida sunflower
		H. heterophyllus Nutt.	Variableleaf sunflower
		H. longifolius Pursh	Longleaf sunflower

TABLE 3.2 (CONTINUED)
Taxonomic Classification within the Genus *Helianthus* L.

Section	Series	Species	Common Name[a]
		H. radula (Pursh) T.&G.	Rayless sunflower
		H. simulans E.E. Wats.	Muck sunflower

[a] Local names in native area: USDA, Plant Names, http://plants.usda.gov/, 2006.

Source: After Schilling, E. and Heiser, C., *Taxon*, 30, 393–403, 1981.

The family for Jerusalem artichoke is therefore frequently written as Asteraceae (Compositae). The modern names were introduced as a way of standardizing taxonomic terms (e.g., all family names now end in *aceae* for ease of recognition), and to realign certain groupings so that each family has a nomenclatural-type specimen. The family Asteraceae contains 476 genera in total. The genus *Helianthus* has sometimes been placed in the subtribe Helianthinae of the family Asteraceae (e.g., Robinson, 1981).

The genus *Helianthus* (sunflowers) has been taxonomically separated into as few as 10 to as many as 200 species. This variation is primarily due to whether hybrids and subspecies are counted, but is also due to the ongoing description or reclassification of new species, subspecies, and hybrids. Schilling and Heiser (1981) listed 49 species (Table 3.2), Heiser (1995) around 70 species, and the USDA (2006) 62 species (including hybrids). Several species have recognized subspecies (e.g., *H. petiolaris* Nutt., *H. praecox* Engelm. & A. Gray). The Asteraceae genera *Heliopsis* and *Silphium* also have a few species that are commonly called sunflowers (e.g., the false sunflower, *Heliopsis helianthroides* Sweet.), although they are not true sunflowers.

The *Helianthus* genus is separated into four sections, which are subdivided into a number of series based upon genetic and morphological characteristics (Table 3.2; Schilling and Heiser, 1981). The four sections of *Helianthus* are:

I. Ciliares
II. Atrorubens
III. Agrestes
IV. Helianthus

The sectional name Atrorubens has replaced Divaricati of Schilling and Heiser (1981) due to priority (Anashchenko, 1974). Species in the sections Agrestes and Helianthus are annuals. The section Helianthus includes *H. annuus* and around 10 other species, which are confined largely to the western part of the U.S. and are diploid (2n = 34) (Heiser, 1995). The Jerusalem artichoke and around 30 other members of the section Atrorubens are perennials. They are geographically concentrated in the eastern and central part of the U.S. and include diploid, tetraploid, and hexaploid species. Jerusalem artichoke is a hexaploid species (2n = 102).

Helianthus species form hybrids. A number of hybrids found growing in the U.S. are listed in Table 3.3. Many more have been created as part of plant breeding programs aimed at incorporating traits from wild *Helianthus* species into cultivated sunflowers (see Chapter 8).

3.2 IDENTIFICATION

The main distinguishing feature of Jerusalem artichoke and other members of the section Atrorubens is the formation of relatively large rhizomes or tubers.

TABLE 3.3
***Helianthus* L. Hybrids Growing Wild in the U.S.**

Hybrid Name (pro. sp.)	Parent Species
H. × *ambiguus* (Gray) Britt. Pers.	*H. divaricatus* × *H. giganteus*
H. × *brevifolius* E.E. Wats.	*H. grosseserratus* × *H. mollis*
H. × *cinerus* Torr. & Gray	*H. mollis* × *H. occidentalis*
H. × *divariserratus* R.W. Long	*H. divaricatus* × *H. grosseserratus*
H. × *doronicoides* Lam.	*H. giganteus* × *H. mollis*
H. × *glaucus* Small	*H. divaricatus* × *H. microcephalus*
H. × *intermedius* R.W. Long	*H. grosseserratus* × *H. maximiliani*
H. × *kellermanii* Britt.	*H. grosseserratus* × *H. salicifolius*
H. × *laetiflorus* Pers.	*H. pauciflorus* × *H. tuberosus*
H. × *luxurians* E.E. Wats.	*H. giganteus* × *H. grosseserratus*
H. × *multiflorus* L.	*H. annuus* × *H. decapetalus*
H. × *orgyaloides* Cockerell	*H. maximiliani* × *H. salicifolius*
H. × *verticillatus* E.E. Wats.	*H. angustifolius* × *H. grosseserratus*

Source: Adapted from USDA, Plant Names, http://plants.usda.gov/, 2006.

The following is a key to sections of *Helianthus* (after Schilling and Heiser, 1981):

1. Perennial (except *H. porteri* (A. Gray) Heiser); disk corollas and style branches usually yellow, where disk corollas red or purple; leaves usually all opposite.....2
1. Not with above combination of characters.....3
2. Plants from taproots of long creeping roots; plants less than 1 m tall; basal rosette of leaves lacking or poorly developed; western U.S. and Mexico.....I. Ciliares
2. Plants from rhizomes, tubers, or crown buds (except *H. porteri*); plants greater than 1 m tall, or if less, having a basal rosette of leaves; mostly eastern and central U.S.....II. Atrorubens
3. Annuals; disk corollas red, style branches yellow, stems glabrous and glaucous.....III. Agrestes
3. Annuals; disk corollas and style branches usually red or purple; leaves mostly alternate.....IV. Helianthus

Jerusalem artichoke is quite variable in morphology (see Chapter 4), but can be separated fairly easily from other species of *Helianthus* with the exception *of H. strumosus* L., a closely related species that also forms tubers. Of the two species, *H. tuberosus* typically has a more dense pubescence, more alternate leaves, greater leaf serration, broader and more decurrent leaves, a greater pubescence on the under surface of the leaves, darker bracts, and longer ray petals than *H. strumosus* (Rogers et al., 1982). *H. strumosus* (paleleaf woodland sunflower) occurs throughout the eastern U.S. (USDA, 2006). *H. tuberosus* is found throughout the U.S., and wild populations are found especially in the open in moist soil along streams, ditches, and roadsides.

The advent of molecular genetic techniques such as amplified fragment length polymorphism (AFLP) analysis, where the degree of difference in the DNA between individual lines or species can be compared, has allowed the establishing of a much more precise assessment of genetic relatedness.

3.3 DISTRIBUTION

Species in the genus *Helianthus* are native to North America, but have very different distributions, varying from restricted (e.g., *H. argophyllus* and *H. ludens*) to widespread (e.g., *H. annuus* and *H. tuberosus*). In the U.S., some species are restricted to one or two states, such as *H.carnosus* in Florida, *H. praecox* in Texas, *H. gracilentus* and *H. californicus* in California, *H. arizonensis* in Arizona and New Mexico, and *H. schweinitzii* in North and South Carolina. Others, including *H. annuus*, *H. tuberosus*, and *H. maximiliani*, are found in most states of the U.S. A number of *Helianthus* species are regarded as threatened or endangered within certain states of the U.S.: *H. angustifolius*, *H. carnosus*, *H. eggertii*, *H. giganteus*, *H. glaucophyllus*, *H. laevigatus*, *H. microcephalus*, *H. mollis*, *H. niveus*, *H. occidentalis*, *H. paradoxus*, *H. Schweinitzii*, *H. silphioides*, and *H. strumosus* (USDA, 2006). Wild forms of *H. tuberosus*, on the other hand, are common and potentially invasive, especially in the eastern half of the U.S., being regarded as weeds in some situations. Escapes from cultivation (or plantings as food for wildlife) are also a common weed problem in Central and Eastern Europe, where it is often considered to be an invasive species (Balogh, 2001; Konvalinková, 2003; Řehořek, 1997).

Jerusalem artichoke has predominantly been cultivated in North America and Northern Europe as a minor crop. The recent literature, however, includes reports of cultivation in China, Korea, Egypt, Australia, and New Zealand (e.g., Judd, 2003; Lee et al., 1985; Ragab et al., 2003).

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4 Plant Morphology and Anatomy

The general morphology of a Jerusalem artichoke plant can have a critical impact on its productivity. The rapid canopy development and its general architecture are critical attributes in the competitive success of the species in natural settings. The morphology of the plant is genetically regulated, and there are distinct differences among clones. In addition, within a clone there is tremendous plasticity in the final structure. Two genetically identical plants grown under differing conditions develop morphologically into very different plants. In addition, the plant's structure is not fixed but is constantly changing during the season. New organs are produced while others senesce and are shed from the plant.

Several studies have characterized the range in morphological variation among a relatively broad cross section of germplasm grown under uniform conditions. For example, Pas'ko (1973) published an extensive study on the variation in morphological features among Russian (72), French (9), German (4), Czechoslovakian (2), Hungarian (1), and Iranian (1) clones (examples in Table 4.1). This chapter describes the general morphology of the plant and, when possible, differences among clones. Selected anatomical features are also critiqued.

TABLE 4.1
Variation in Jerusalem Artichoke Morphological Traits among Clones

Clone	Plant Height (cm)	Number of Branches	Leaf Length/ Diameter	Flower Size (cm)		Tuber Length/ Width	Tuber Weight (g)	Number of Tubers/ Plant	Rhizome Length (cm)
				Diameter with Petals	Diameter without Petals				
Blanc précoce	187	30	1.5	8.5	1.3	2.2	49.3	43	16.9
Nahodka	345	21	1.4	9.4	1.4	2.2	44.3	65	14.4
Batat Bhjibmopeha	316	17	1.7	8.4	1.3	2.2	47.0	36	16.0
Kharkov	286	16	1.5	7.3	1.3	1.5	111.7	24	11.2
Majkopskij 33-650	294	14	1.3	8.3	1.3	1.7	58.3	26	10.6
Веπвih Уроханнвih	303	16	1.5	8.1	1.3	2.3	54.3	52	25.0
Фноπетоввih Рehhскhh	313	14	1.3	10.8	1.5	2.0	78.7	32	16.3
Венгерскhh	284	20	1.6	11.2	1.7	2.5	39.3	37	35.0
Tamboy	352	19	1.3	10.9	1.4	2.0	20.0	73	97.2
Topho-Аπтahсkhh	297	23	1.3	11.4	1.3	3.6	10.0	75	75.0
Hybrid 120	274	9	1.1	14.5	3.8	3.5	40.3	50	14.0
Topinsol VIR	367	40	1.5	9.9	2.5	2.5	66.3	29	22.6

Source: Translated and adapted from Pas'ko, N.M., *Trudy po Prikladnoy Botanike Genetike i Selektsii*, 50, 91–101, 1973.

4.1 MORPHOLOGY

4.1.1 Stems and Branches

4.1.1.1 Stem/Plant Height

Jerusalem artichoke stems can grow to 3 m or more in height, though most clones are shorter. Dwarf clones have been selected (Zubr and Pedersen, 1993). The stems are stout and heavily trichomed when young. Initially the stems are quite succulent but become woody over time. Branches vary in number and position on the main stems. The stems arise directly from the "seed tuber," with branches forming at nodes on the stem. Basal branches may form underground and at the soil surface appear to be stems; hence, estimates of stem number per plant are variable.

Stem height varies widely among clones. Under uniform production conditions the height of the plants can be separated into three general categories: (1) high (>3 m), (2) intermediate (2 to 3 m), and (3) low (<2 m) (Pas'ko, 1973). Most clones are in the 1.5- to 2-m range, though a few reach >3 m. Typical ranges in height among clones are 102 to 186 cm (Swanton, 1986), 119 to 164 cm (Hay and Offer, 1992), and 115 to 275 cm (Kiehn and Chubey, 1993). Plant population and cultural conditions can have a pronounced effect on the eventual height of a plant. Under moist conditions in locations protected from the wind, plant heights of 4 m can be attained, though such plants generally lodge and have substantially reduced tuber yields.

4.1.1.2 Stem Gravitropic Response

Most cultivars are erect, though a small number are initially prostrate. The prostrate clones begin to grow in an erect manner after a certain number of nodes (i.e., generally the second, third, or fourth node, depending upon the clone) (Pas'ko, 1973).

4.1.1.3 Stem Number

Pas'ko (1973) categorized clones into three classes based upon the number of stems arising from the seed tuber: (1) >3 (strong), (2) 2 to 3 stems (intermediate), and (3) a single stem (weak). Multiple stems facilitate a rapid increase in leaf area index early in the development of the plant. The number of stems also varies with agronomic practices and seed tuber size. Some clones are highly variable in the number of stems produced, while others are less so.

4.1.1.4 Stem Diameter

The diameter of the stems at the base also varies among clones and with production conditions. The initial diameter increases as the plant grows with mature stems, generally 1.6 to 2.4 cm in diameter.

4.1.1.5 Stem Branching

Branching along the stems varies with clone and plant population density. The greatest variation is in the number of branches (e.g., 30 to 53 (Swanton, 1986)) and their position on the stems. As with leaves, branches may be shed during the growing season. Generally these are less robust, lower and middle branches that are in a poor light reception position in the canopy. Four positional variations for branching were identified: (1) branches all along the stem, (2) only on the lower stem, (3) only on the upper stem, and (4) on the upper and lower stems. Late-maturing clones tended to have a different branching pattern than early-maturing clones (Pas'ko, 1973).

The number of branches varies with plant density, and multiple stems alter the number of branches per stem (Tsvetoukhine, 1960). Most branches are found on the bottom third of the plant, though axillary flowering branches are formed toward the top of the plant before the onset of

flowering. Initial branches tend to be positioned opposite of each other on the stem, but subsequently branches become alternate and the number of nodes with branches decreases. Each node can have three buds, which can develop into a branch or leaves (Tsvetoukhine, 1960). Early-flowering clones are more prone to having flowers toward the base of the stems.

4.1.1.6 Stem Color

Stem pigmentation varies among clones. Many clones have green stems, though violet pigmentation is common with the location and pattern varying (i.e., uniform vs. localized) (Pas'ko, 1973). In some instances, small clear (nonpigmented) stripes or streaks are found on the shoots that go for short distances (Tsvetoukhine, 1960). Violet pigmentation, when present, is often more pronounced in the newer, apical portions of the stem. In some instances, the pigment is located at the base of the trichomes. Stem and tuber color were not correlated (Pas'ko, 1973; Tsvetoukhine, 1960).

4.1.2 Leaves

The leaves are cauline, initially opposite but switching to alternate at varying distances from the base. Occasionally a stem will have three leaves per node while other stems are traditional. Leaves are simple, lanceolate to lance-ovate, 10 to 20 cm long by 5 to 10 cm wide, acuminate, serrate, scabrous above and pubescent below, base rounded to widely cuneate to attenuate, petioles 1 to 6 cm long (Pas'ko, 1973) and winged at the base. The venation is palmate with three distinct main veins emerging near the base, and the leaf margins are coarsely toothed. The leaves along the central portion of the main stems (i.e., nodes 17 to 24) are thought to be of particular importance in the final tuber yield (Ustimenko et al., 1976).

4.1.2.1 Leaf Shape

The leaves are lanceolate to lance-ovate and vary among clones and with position on the plant (Figure 4.1A). Primary leaves vary in length from 10 to 20 cm and width from 5 to 10 cm. The opposite side of a leaf blade (left vs. right) is not always a mirror image of the other. Considerable variation can occur. Leaves on flowering branches tend to be smaller and narrower than those on regular branches and the main stem.

4.1.2.2 Shape at the Leaf Tip

The tip of the leaf blade is acuminate, tapering gradually to a point, with the degree of sharpness varying among clones (Pas'ko, 1973) (Figure 4.1A).

4.1.2.3 Shape at the Leaf Base

The leaf base is rounded to widely cuneate (wedge shaped) to attenuate (elongated and tapering). The base shape tends to be more variable on an individual plant than that of the tip (Figure 4.1A).

4.1.2.4 Serration of Margins

The leaves have teeth pointing toward the apex that vary in height, frequency, pattern, and uniformity (Figure 4.2). The height of the serration may be regular or irregular (Pas'ko, 1973), and the spacing between teeth varies widely; in some clones the distance is substantial. Some clones have relatively smooth margins. The margins often vary significantly with position on the leaf and with the leaf's position on the plant (Figure 4.1B). Tsvetoukhine (1960) listed three primary forms: (1) lanceolate, (2) coniforme, and (3) strongly serrated.

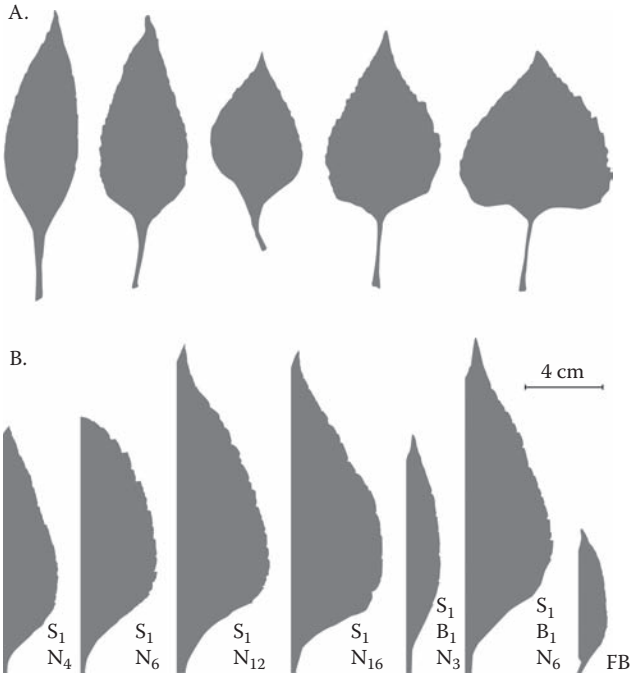

FIGURE 4.1 (A) Leaves are generally lanceolate to lance-ovate in shape but differ considerably among clones. (Redrawn from Tsvetoukhine, V., *Ann. Amelior. Plant.*, 10, 275–308, 1960; Kays, unpublished data.) (B) In addition, there is generally considerable variation within an individual plant, as illustrated by changes in shape moving up the main stem (nodes 4 to 16), on lateral branches and on a flowering stem.

4.1.2.5 Leaf Size

Leaf size varies with position on the plant (Figure 4.1B), clone, and agronomic practices (Pas'ko, 1973). Leaves are smaller at the base of the plant, largest midway up the stem, and then decline in size toward the apex. Leaf size on lateral branches depends upon the branches' position relative to light inception. Leaves on flowering branches are typically considerably smaller than on the stems and lateral branches.

4.1.2.6 Leaf Number

The number of leaves per plant varies widely among clones grown under uniform conditions (e.g., 372 to 953 (Swanton, 1986), 525 (McLaurin et al., 1999)). Production conditions such as soil fertility, moisture availability, and plant population density have a pronounced impact on leaf number as well as the age of the plant. In general, leaf number increases fairly progressively until around flowering, and then declines thereafter (McLaurin et al., 1999). Plants shed leaves during the season, the number of which varies among clones (e.g., 2.5 to 491 per plant; 0.3 to 72.2 g) (Table 10.1), plant population density, and other factors. The greatest losses are toward the base of the plant, where, due to the increasing size of the canopy, they are in a less favorable light reception position.

4.1.2.7 Leaf Angle

Tsvetoukhine (1960) separates leaves into horizontal and angled, the angle of which can be best assessed on small leaves near the tip of the stem. The angle varies among clones and to some extent with position on the plant.

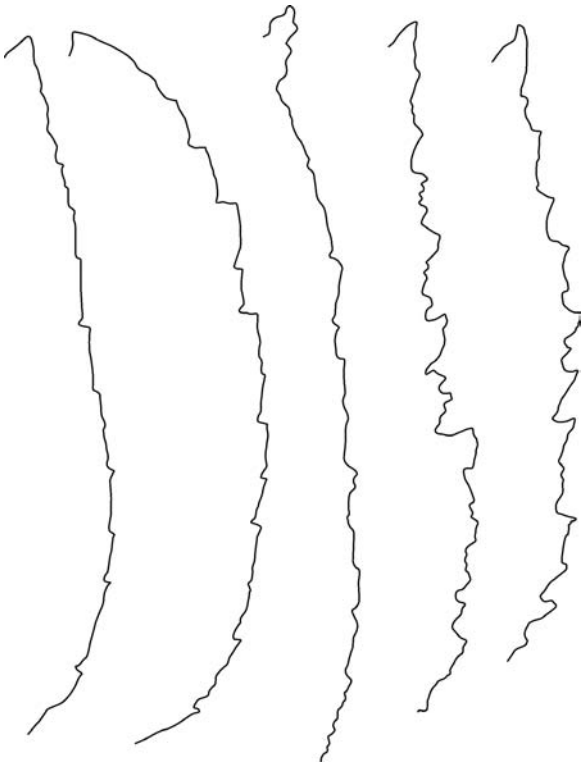

FIGURE 4.2 The margins of the leaves vary widely among clones, with most being serrate, serrate-dentate, or serrulate. Individual teeth point toward the apex and vary substantially in height, frequency, shape, and consistency. (Redrawn from Tsvetoukhine, V., *Ann. Amelior. Plant.*, 10, 275–308, 1960; Kays, unpublished data.)

4.1.2.8 Leaf Coloration

Coloration varies among clones, ranging from light to dark green to grayish. Some clones have a reddish tint in the fall, but this coloration does not occur every year, so climactic conditions, especially temperature in the fall, are thought to be critical (Tsvetoukhine, 1960). The color also varies between the abaxial and adaxial surfaces of the leaf, with the abaxial generally lighter in color.

4.1.2.9 Bract at the Base of the Leaf

The bract at the base of the petiole may be strong or weak (Pas'ko, 1973).

4.1.2.10 Phyllotaxy

Initial leaves are opposite with two (rarely three) per node. The opposite orientation changes to alternate at a node level that varies among clones. The shift from opposite to alternate does not occur at a uniform position within an individual plant, such that some stems or branches may be alternate while others are opposite. Eventually the phyllotaxy shifts from 1/2 to 3/8.

4.1.3 Inflorescence

Flower heads occur alone or in groups at the ends of the stem and axillary branches. Each inflorescence is comprised of many small, yellow, tubular disk flowers in the center, surrounded by 10 to 20 sterile, yellow ray flowers, the ligules of which are often thought of as the petals (Figure 4.3).

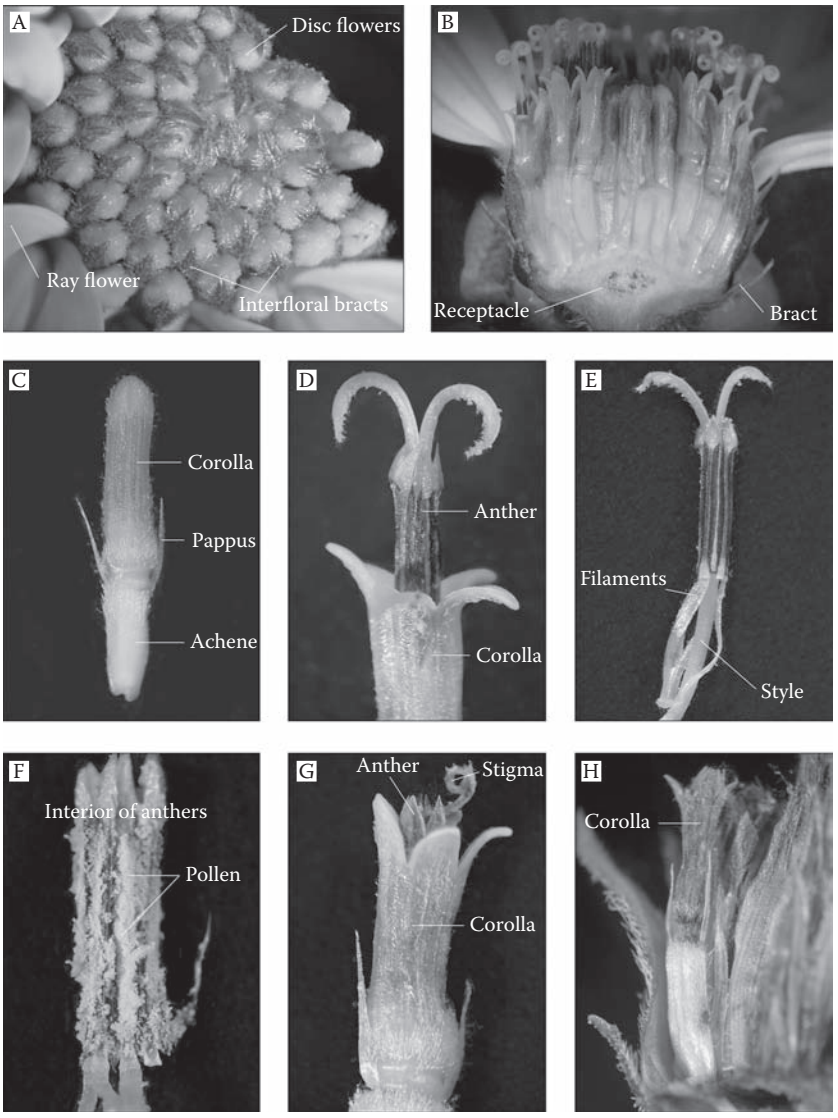

FIGURE 4.3 Anatomy of a Jerusalem artichoke flower. The inflorescence is comprised of a number of individual ray and disk flowers. (A) Ray flowers are sterile and form the outer whorl of bright-yellow ligules. Each of the interior disk flowers is initially covered by an interfloral bract. (B) The inflorescence in cross section shows the receptacle, bracts surrounding the base and disk flowers at varying stages of development. (C) An individual disk flower with an unopened corolla, a pappus on each side, and the immature achene at the base. (D) As the corolla opens, the anthers elongate, and subsequently the stigma and style elongate and emerge from within the anthers. (E) With the corolla removed, the base of the anthers and the subtending filaments can be seen along with the style. (F) The interior of the anthers is filled with pollen, through which the stigma passes; however, since the flowers are self-incompatible, they must be pollinated by another clone for successful fertilization. (G) The stigma and anther subsequently senesce and are often colonized by fungal hyphae. (H) Eventually the corolla desiccates followed by the unfertilized ovary. (Photographs courtesy of Betty Schroeder.)

4.1.3.1 Size of the Inflorescence

The size of the inflorescence (flower head) varies among clones. When the ray flower ligules were included, the range in diameter was from 7.3 to 11.4 cm. The ligules are typically 2 to 3.5 cm long (range, 0.8 to 3.5). The actual head size (without ligules) was slightly larger on lateral flowering branches, i.e., 7.5 cm in diameter vs. 6.5 cm for those on the main stems.

The range in the diameter of the disk flowers in the inflorescence was 1.3 to 1.8 cm (Swanton, 1986). The inflorescences can be separated into size categories (e.g., large, medium, and small) (Pas'ko, 1973).

4.1.3.2 Number of Inflorescences

The number of inflorescences per plant was separated into three classes — small (1 to 15), medium (16 to 49), and large (50 to 155) — which varied between early and late clones and with the number of branches (Pas'ko, 1973). Swanton (1986) found a range of 6 to 78 inflorescences per plant among clones from different ecological niches; the range in dry weight was also substantial (i.e., 2 to 17 g per plant). The number of flowers also varies with production year and growing conditions (Tsvetoukhine, 1960).

4.1.3.3 Number of Disk Flowers per Inflorescence

The number of disk flowers varies among clones and with position on the plant. In a representative clone, there was an average of 58.8 disk flowers per inflorescence, with the inflorescences ranging from 4 to 8.5 cm in diameter. The diameter was slightly larger on flowering branches than on the main stem.

4.1.3.4 Number of Ray Flowers per Inflorescence

The number of ray flowers varies substantially among clones and individual inflorescences on a plant. In a representative clone, there was an average of 11.5 ray flowers per inflorescence; however, this ranged from 9 to 14 flowers.

4.1.3.5 Ligule Shape

The shape of the individual ligules (often considered to be the petals) varies, with some being wide at the base and others narrow (oblong), the length being 2.6 to 4 times the width. There may be defects in the flower heads such as in the shape, size, presence of doubles, and various deformities. One clone ('Hybrid 120') often had flowers that were fused, forming double or triple flowers (Pas'ko, 1973).

4.1.3.6 Ligule Density

The ligules may be physically separated from each other (low density, i.e., not touching), somewhat overlapping (medium density, as in the cultivar 'Vilmorin'), or very dense (the base of the ligule overlaps the adjacent ligule) (Pas'ko, 1973).

4.1.4 Fruit

The fruit is an achene and generally few are formed (Russell, 1979; Swanton, 1986; Westley, 1993; Wyse and Wilfahrt, 1982). Seeds are × 5 mm long × 2 mm wide, flattened wedge shaped (obovate to linear-obovate), and smooth. Their external color is mottled black, gray, tan, or brown and may have black spots (Alex and Switzer, 1976; Konvalinková, 2003; USDA, 2006).

Wild clones typically have significantly more seed (e.g., 3 to 50 seeds per flower head; Wyse and Wilfahrt, 1982; Westley, 1993) than cultivars (0.08 to 0.66 seed). Individual seeds can vary widely in weight (0.8 to 10.8 mg), though the variation in mean weight among clones is relatively small (i.e., 3.5 to 4.8 mg, mean of 4.5 mg) (Swanton, 1986).

4.1.5 Rhizomes

Extending outward and slightly downward from the subterranean stem are thin cord-like rhizomes (underground stems) that grow as long as 1.5 m (Figure 4.4). The rhizomes are generally white and form tubers at their tips. They routinely undergo branching with secondary and tertiary rhizomes being formed (Dambroth et al., 1992). Branching results in the number of tubers greatly exceeding the number of rhizomes emerging from the underground portion of the stem. When rhizome formation is inhibited, yield can be drastically reduced. For example, plants grown in a very tight clay soil that the rhizomes could not penetrate formed tubers along the base of the aboveground portion of the stem. Considerable physical variation in rhizomes (diameter and length) is found among clones, especially between wild and cultivated clones (Swanton, 1986). Wild clones had more and longer rhizomes, more buds per rhizome, and higher total rhizome dry weight than cultivated clones in keeping with their role as asexual propagules.

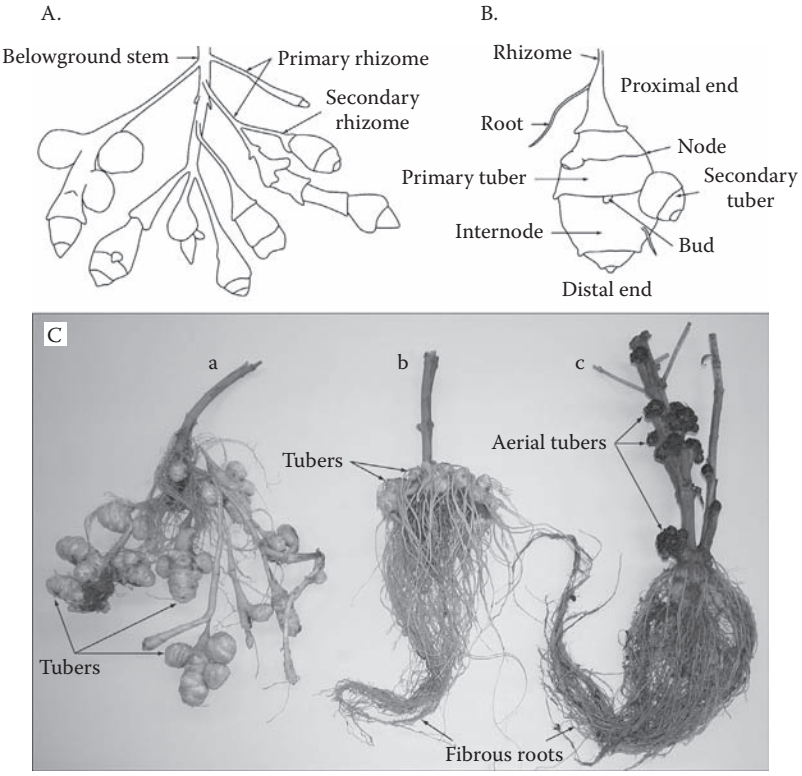

FIGURE 4.4 (A) General morphology of the belowground stem, rhizomes, and tubers of a small Jerusalem artichoke plant. (B) External morphology of a tuber. (C) Belowground morphology of plants grown in compacted clay + perlite mediums: (a) 1:1, (b) 3:1, and (c) 100% clay. As the mechanical impedance of the media increased (a → c), the tubers shifted to the base of the belowground stem (b). With very high mechanical impedance (c), tubers did not form underground but did so on the lower portion of the aboveground stems, illustrating the importance of rhizome penetration and development in tuberization. (Kays, unpublished data.)

4.1.5.1 Length

The length of rhizomes varies substantially among clones, but also due to soil strength and production conditions. Cultivated clones tend to have substantially fewer, shorter rhizomes with a lower number of buds and total dry weight than wild clones (Swanton, 1986). Rhizome lengths (based upon the mean of the six longest rhizomes per plant, measured from the base of the plant to the tuber) can be separated into four classes: short (5 to 15 cm), medium (16 to 25 cm), long (26 to 40 cm), and very long (>40 cm) (Pas'ko, 1973). Using Pas'ko's classification, the cultivated clones in Swanton's study (1986) would be classified as short and the wild clones as very long.

4.1.5.2 Diameter

The rhizome diameter vacillates with position; the widest areas are around the nodes. In a cultivated clone grown under conditions of low mechanical impedance, the diameter ranged from 2 to 6 mm. Rhizome diameter varies with clone and stage of development.

4.1.5.3 Number

The number of rhizomes per plant varies widely among clones. Pas'ko (1973) separated clones into four classes: (1) compact (26 rhizomes per plant), (2) semispreading (30 per plant), (3) spreading (37 per plant), and (4) very spreading (69 per plant). Both the number and length of rhizomes increase together (Pas'ko, 1973). In Swanton's study (1986), the cultivated clones would be considered compact and the wild clones very spreading.

4.1.6 Tubers

The tubers are modified stems and represent the primary reproductive propagules of the plant. Like stems, they have nodes, though in cultivated clones they are compressed and exhibit substantial secondary thickening. Branching is a common but undesirable trait. Branching is genetically and culturally modulated, neither of which is well understood. The tubers exhibit a strong apical dominance that controls the number of shoots that emerge. The degree of dominance varies among clones; those in which apical dominance is weaker or those that are branched generally produce multiple shoots.

4.1.6.1 External Color

The epidermis ranges in coloration from uniform to variable, e.g., stripes, concentrated at the nodes, varying from the tuber to the rhizome (Tsvetoukhine, 1960; Pas'ko, 1973). Colors may be white, red, violet, light brown, or red-brown (Pas'ko, 1973). Tsvetoukhine (1960) found the uniformity of the external anthocyanins could be classified as (1) uniform, (2) intermediate, (3) patchy, or (4) pigmented only at the nodes. Clones without external anthocyanins were either white or bronze. The white tubers become brownish when exposed to light after harvest. Prior to harvest when exposed to light they become green due to the synthesis of chlorophyll, which for fresh market is considered aesthetically unpleasing. The pigmentation also varies within an individual plant, with the size of the parent plant, and when in the season it is assessed (Tsvetoukhine, 1960).

4.1.6.2 Internal Color

The internal color may also be uniform or variable. Generally it is white or light brown, though some clones display pink to red coloration, seldom uniformly distributed. In some instances the coloration is localized around the eyes (Pas'ko, 1973).

4.1.6.3 Shape

Tuber shape is highly variable, ranging from round to long slender to irregular, knobby clusters (Alex and Switzer, 1976). The length-to-diameter ratio varies among clones, age of the tuber, and cultivation conditions. For example, Swanton (1986) found that cultivated clones had a mean diameter of 8.7 cm and length of 11.5 cm, while wild clones were 1.4 cm in diameter and 16.8 cm long. Tuber shape also varies on the plant; for example, the first tubers are often elongated and on long rhizomes, while the last formed tend to be rounder and on short rhizomes (Barloy, 1984). Young tubers tend to be more uniform in shape than older tubers in that as the eyes grow, forming branches, the shape alters substantially (Pas'ko, 1973). The shape can also vary with growing conditions. Pas'ko (1973) classified tubers into four shape categories: (1) pear shaped, (2) short pear shaped (1.5 to 1.7 times longer than wide), (3) oblong (2.2 to 2.5 times longer than wide), and (4) spindle shaped (3 or more times longer than wide). Wild types tend to be spindle shaped, while pear shaped is most common among cultivated clones. The first three categories approximately correspond to those of Tsvetoukhine (1960), i.e., (1) pear shaped, (2) potato shaped, and (3) spindle shaped (fusiform).

4.1.6.4 Tuber Size

Pas'ko (1973) separated tubers into three general size categories: (1) large (>50 g per tuber), (2) medium (20 to 50 g), and (3) small (<20 g). Tuber size and number tend to be inversely related. In addition to varying among clones, tuber size also varies within a plant and with production conditions.

4.1.6.5 Number of Internodes

Spindle-type tubers tend to have fewer nodes than other types (Pas'ko, 1973).

4.1.6.6 Surface Topography

Most clones have tubers with an irregular surface. Spindle-shaped tubers generally have the smoothest surface (Pas'ko, 1973). An irregular surface is undesirable in that it makes preparation for cooking more difficult.

4.1.6.7 Depth of Eyes

This trait ranges from deep to shallow (Pas'ko, 1973).

4.1.7 Subterranean Stem

The underground portion of the stem represents the site for rhizome development and, in many instances, the formation of lateral branches. The length of this portion of the stem depends on the planting depth of the seed tubers; shallow planting is undesirable. Swanton (1986) found that the dry weight of the underground stem was substantially higher in cultivated clones (35.3 g) than in wild clones (16.2 g).

4.1.8 Roots

The Jerusalem artichoke has a fibrous root system. The dry weight in cultivated clones in a study by Swanton (1986) was greater (15 g per plant) than in wild clones (12.7 g per plant) and differed among clones within each classification (range, 6.1 to 19.5 g). In a single cultivar, McLaurin et al. (1999) found the root weight to increase progressively until around 24 weeks after planting, reaching

TABLE 4.2
Stomatal Size[a]

Location	Area (μm^2)	Length		Width	
		Mean (μm)	Range (μm)	Mean (μm)	Range (μm)
Adaxial	1.1/10	26	21.2–30.6	15.8	12.1–17.5
Abaxial	4.5/10	22.8	14.6–29.7	17.8	14.9–21.1

[a] Measurements were made on closed stomata.

over 25 g per plant and then declining thereafter. Root weights in existing studies represent only approximations of the total root mass in that collection is exceedingly difficult.

4.2 ANATOMY

4.2.1 Stomata Size and Density

The stomata represent the primary sites for gas exchange. Data for one clone (Table 4.2) indicate that the size of stomata are essentially the same between the adaxial (343 μm^2) and abaxial (323 μm^2) surfaces; however, their shape varies, with lower stomata being rounder (1.3:1 length-to-width ratio) than those of the upper surface, which are more oval (1.6:1). The data represent only one clone and may not be indicative of the variation over the entire leaf surface of the plant.

4.2.2 Trichomes

Trichomes are specialized structures on aboveground surfaces of the plant that originate and project from epidermal cells. There is a diverse cross section of trichome types in the plant kingdom that may be composed of one or more cells, branched or unbranched, and found in a diverse range of shapes. Different types of trichomes are commonly found on the same plant, and their size, shape, and density often vary with location. The molecular genetics of trichome formation are just beginning to be elucidated in *Arabidopsis thaliana*; two loci have been identified: *TRANSPARENT TESTA GLABRA 1* (*TTG1*) and *GLABROUS 1* (*GL1*). *GL1*, a gene encoding for a myb-class transcription factor, is required for trichome development (Payne et al., 1999). Whether trichome formation in *H. tuberosus* is controlled similarly has yet to be determined.

The Jerusalem artichoke and other members of the sunflower family display a profusion of trichomes that often give the plant a very abrasive surface texture (Seiler, 1981). Trichomes are thought to function in part as a component of the herbivore defense system of the plant. In sunflower, introgression of biotic resistance traits is thought to have been important in adaptation (Whitney et al., 2006). The Jerusalem artichoke has at least four types of trichomes that differ in location, size, and density (Figure 4.5).

4.2.2.1 Stems

The surface of young stems is covered with very long acuminate trichomes comprised of six or seven cells. Unlike leaf trichomes, their growth is more or less directly outward from the stem, often reaching 2.6 mm in length or more. The number of trichomes per unit surface area is substantial (Figure 4.5E) and varies among clones, though none were devoid of trichomes. The tip of the stem, especially the upper 30 cm, has more trichomes than the base (Tsvetoukhine, 1960). As the stem increases in radial diameter, the density decreases, and with time, many trichomes are lost due to breakage or other means.

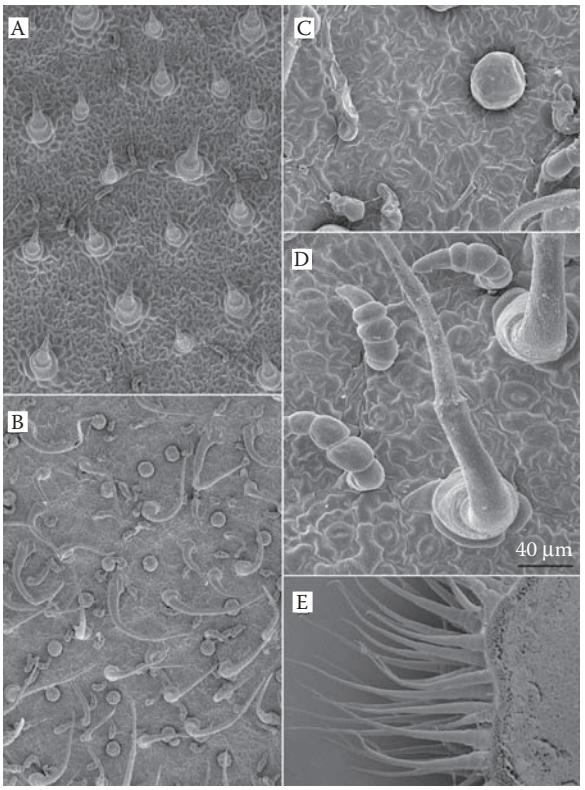

FIGURE 4.5 Leaf and stem trichomes: (A) adaxial surface, falcate and moniliform trichomes pointing toward the leaf apex; (B) abaxial surface displaying falcate, moniliform, and glandular trichomes, the orientation of which is more random; (C) glandular trichome found only on the abaxial surface; (D) falcate and moniliform trichomes; and (E) acuminate trichomes on an immature stem.

4.2.2.2 Leaves

The leaf blade and petiole have abundant trichomes. Three forms are found on the blade: curved multicellular falcate, multicellular moniliform, and single-celled glandular trichomes (Figure 4.5). The size, structure, and density of the three types vary between the adaxial and abaxial surfaces. On the upper leaf surface (adaxial) the falcate trichomes are comprised of 3 cells, the combined length of which is ~208 µm, at a density of 12 per mm^2 (Table 4.3). Moniliform trichomes are shorter (i.e., ~92 µm in length), comprised of 4 to 6 cells at a density of 15 per mm^2. The adaxial surface was devoid of glandular trichomes. Interestingly, the orientation of the trichomes differs between the adaxial and abaxial surfaces. On the adaxial surface they point toward the apex of the leaf blade, whereas on the abaxial surface the orientation is more random.

The adaxial surface has falcate, moniliform, and glandular trichomes that are of greater length and at much greater density than the adaxial surface (Table 4.3). The average length of the falcate trichomes is 366 µm; however, the length varies substantially (i.e., 202 to 576 µm). The differential in length of these trichomes between the two surfaces is not due to the number of cells per trichome, but rather the length of the cells. Abaxial moniliform trichomes are likewise longer (112 µm) than their counterparts on the adaxial surface and, while longer, are comprised of fewer cells (e.g., two to five). In both instances, the trichrome density is more than double the adaxial surface. The abaxial surface also has a relatively large number of single-celled glandular trichomes (e.g., 14 per mm^2), which are absent on the adaxial surface.

TABLE 4.3
Leaf and Stem Trichomes[a]

Plant Part	Location	Trichome Type[b]	Length (μm)	Length (range)	Number of Cells/Trichome	Density (number/mm^2)
Leaf	Adaxial	Falcate	208	136–377	3	12
		Moniliform	92	72–124	4–6	15
		Glandular	—	—	—	—
	Abaxial	Falcate	366	202–576	3	30
		Moniliform	112	73–165	2–5	41
		Glandular	58	54–61	1	14
Stem	Immature	Acuminate	2227	1516–2720	6–7	—

[a] Kays, unpublished data.
[b] Descriptive terminology after Payne, 1978.

4.2.2.3 Flowers

Small trichomes are found on various flower parts, for example, the base of the corolla, the upper portion of the immature achene, the stigma, pappus, and bracts (Figure 4.3).

4.2.3 Flowers

Disk flowers are found in concentric circles surrounded by sterile ray flowers with their bright yellow ligules (Figure 4.3). An individual disk flower prior to anthesis is illustrated in Figure 4.3C. The corolla is four or five lobed, there are four or five stamens, anthers are fused into a cylinder around the style, filaments are attached to the corolla near the base, and there is one pistil, an ovary inferior, one seed, and a single chamber. Two pappus are found at the base of the corolla, below which is the immature achene, most of which aborts without cross-pollination; the mortality rate is exceptionally high even with crossing.

The corollas of the disk flowers elongate, starting with those in the outermost whorl. The tip of the corolla opens (Figure 4.3D), typically into five segments, and the anther elongates upward through the opening. Subsequently, the stigma and style emerge from the center of the anthers with the stigma curling downward and inward. The degree of elongation of the style varies among individual flowers within an inflorescence and flowers of different clones. The filaments and the base of the style remain enclosed within the corolla (corolla removed in Figure 4.3E). The interior of the anthers is laden with pollen (Figure 4.3F), much of which remains enclosed, eventually dying. A small amount is deposited on the stigma and style as they elongate through the interior of the anthers. Eventually the stigma and style wither (Figure 4.3G), followed by the anthers. Fungal hyphae are often seen on the withering flower parts. Eventually the corolla desiccates (Figure 4.3H), followed by the unfertilized achene.

4.2.4 Calcium Oxalate Crystals in Floral Organs

Calcium oxalate crystals are found in a diverse range of species (215 families; Franceschi and Horner, 1980) and in a cross section of plant parts (e.g., leaves, stems, roots, seeds, floral organs). Their precise role is not certain, though a number of functions have been proposed (e.g., protection against herbivory, binding oxalate, calcium regulation). The crystals are categorized into classes based upon shape (raphides, druse, styloid, prism, and crystal sand; Ilarslan et al., 1997). Prismatic and styloid crystals were found in the igulate and tabulate corollas of Jerusalem artichokes (Meric

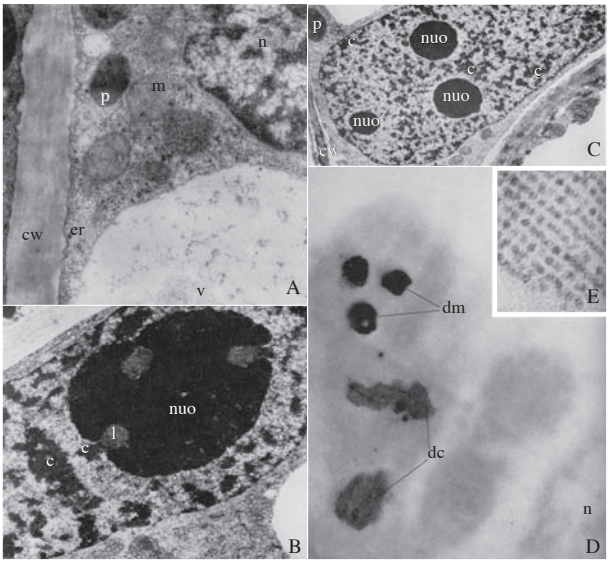

FIGURE 4.6 Tuber storage parenchyma ultrastructure: (A) cell wall region to which the cytoplasm is compressed (× 15,000) (From Ishikawa, M. and Yoshida, S., *Plant Cell Physiol.*, 26,1331–1344, 1985); (B) nucleus showing condensed chromatin (c) and what is thought to be nucleolar-organizing regions in the nucleolus that appear to move from the exterior to the interior with "ageing" (× 22,000) (Jordan, E.G. and Chapman, J.M., *J. Exp. Bot.,* 22, 627–634, 1971); (C) nucleus displaying dense chromatin and three nucleoli (× 10,000) (Jordan, E.G. and Chapman, J.M., *J. Exp. Bot.,* 22, 627–634, 1971); (D) a plastid containing membrane bound structures (× 63,000) (From Tulett, A.J., et al., *Ann. Bot.*, 33, 217–226, 1969); and (E) a plastid crystal (× 540,000) (From Tulett, A.J., et al., *Ann. Bot.*, 33, 217–226, 1969).

and Dane, 2004). Styloid crystals were found in endothecial layer and tapetum cells of the anthers and in the style. Druse crystals were found in the stigma trichomes. The ovary was devoid of crystals; no raphides were found in the floral parts studied.

4.2.5 Tuber Storage Parenchyma Ultrastructure

Jerusalem artichoke tubers have been used in a number of cytological studies in that they provide morphologically and physiologically homogeneous parenchyma cells in the G_1 phase of the cell cycle (Adamson, 1962). This allows studying many of the initial events of the first cell cycle after dormancy break (Yeoman, 1974), such as the synthesis and content of polyamines, cell division, and the formation of polysomes (Bagni et al., 1972; Fowke and Setterfield, 1968; Fraser, 1975; Serafini-Fracassini et al., 1980; Sparkhul and Setterfield, 1977).

The dormant parenchyma cells contain plastids (Gerola and Dassù, 1960; Tulett et al., 1969), mitochondria, dictyosomes (Kaeser, 1988), a nucleus, and nucleoli (Williams and Jordon, 1980). The cells have high levels of arginine, glutamine, and asparagines, very low metabolism of DNA and RNA, low amounts of polysomes, and low levels of polyamines (Favali et al, 1984). They are highly vacuolated, causing the nuclei and other organelles to be adjacent to the cell walls. The vacuoles are the storage site for fructans, and vesicles are formed in the cytoplasm, facilitating fructan synthesis from sucrose entering the cell (Kaeser, 1983). There is a close association of the plastids with mitochondria and the nucleus (Figure 4.6A) (Ishikawa and Yoshida, 1985). The nuclei display regions of condensed chromatin and contain several nucleoli (Figure 4.6C) (Jordan and Chapman, 1971). The plastids vary in structure and are found both scattered in the peripheral

cytoplasm and in compact clusters often near the nucleus (Figure 4.6B) (Tulett et al., 1969). Within the plastids are membrane-bound structures containing electron-dense material in the form of particles scattered in the matrix, crystals (Figure 4.6D&E), and dense masses.

There are distinct changes in the nucleus and nucleoli with the onset of cell division, such as a redistribution of chromatin, an increase in size of the nucleoli, along with changes in DNA and RNA metabolism within the cell (Favali et al., 1984; Fowke and Setterfield, 1968; Jordan and Chapman, 1971; Kovoor and Melet, 1972; Minocha, 1979; Mitchell, 1967; Serafini-Fracassini and Alessandri, 1983; Torrigiani and Serafini-Fracassini, 1980; Williams and Jordan, 1980; Yasuda et al., 1974). The sharp increase in nuclear volume occurs during the first mitotic division; however, the frequency of nuclear pores remains constant (Williams and Jordan, 1980). With activation of the cells, there is an increase in the number of Golgi vesicles, endoplasmic reticulum-dilated vesicles, and polysomes, and increased synthesis of DNA in the plastids and mitochondria (Favali et al., 1984).

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5 Chemical Composition and Inulin Chemistry

Plants sequester carbon in specialized reproductive organs (e.g., storage roots, tubers, and seeds) as a source of energy and as carbon skeletons for the onset of growth the following season. Starch, a polymer of glucose, is the most prevalent form of stored carbon. It is composed of a mixture of straight-chain (amylose) and branched (amylopectin) molecules, the ratio of which is genetically controlled. Amylose contains 200 to 1,000 glucose subunits linked via α-(1-4) glucosidic bonds, while amylopectin is substantially larger, 2,000 to 200,000 subunits with similar bonds; however, every 20 to 25 glucose molecules there is a branch formed through an α-(1-6) bond (Kays and Paull, 2004). Inulin, in contrast, is a mixture of fructose polymers used as a means of carbon storage in a number of species, though as the primary storage form of carbon in only a few species, including Jerusalem artichoke.

5.1 CHEMICAL COMPOSITION

5.1.1 Tuber Composition

The tubers of Jerusalem artichoke typically comprise about 80% water, 15% carbohydrate, and 1 to 2% protein. Data on the composition of Jerusalem artichoke are relatively sparse in comparison to other vegetables, however, and significant variation has been recorded for certain parameters. Differences in cultivar, time of harvest, production conditions, postharvest treatment, and preparation methods most likely account for this variation (Table 5.1).

Jerusalem artichoke tubers contain little or no starch, virtually no fat, and have a relatively low calorific value. Of the small amount of fat present, trace amounts of monounsaturated and polyunsaturated fatty acids have been reported, but no saturated fatty acids (Whitney and Rolfes, 1999). The polyunsaturated fatty acids linoleic (18:2 cis, cis n-6) and α-linoleic acid (18:3 n-3) have been recorded as present at 24 mg and 36 mg·100 g^{-1} of raw tuber, respectively (Fineli, 2004). The tubers are a good source of dietary fiber, because of the presence of inulin.

The principal storage carbohydrate of Jerusalem artichoke is inulin, and therefore carbon in the tubers (93.26 mg·g^{-1}; Somda et al., 1999) is predominantly in the form of inulin. The inulin content of tubers ranges from 7 to 30% of fresh weight (around 50% of dry weight); an inulin content of between 8 and 21% of fresh weight is considered typical (Van Loo et al., 1995). The carbohydrate content of two accessions was between 13.8 and 20.7% of the total weight of fresh tubers at harvest in a Canadian study, with fructose levels falling and glucose levels rising at later harvest dates (Stauffer et al., 1981). For 11 cultivars, inulin with a degree of polymerization (dp) over 4 ranged from 55.8 to 77.3% (average, 65.8%) of total tuber carbohydrate, with trisaccharides (dp 3) ranging from 9.7 to 16.5% (average, 13.2%) and disaccharides (dp 2) from 8.2 to 18.3% (average, 13.8%). 'Reka' was the cultivar with the most inulin over (dp 4), while 'D19' had the least (Zubr and Pedersen, 1993). The inulin in Jerusalem artichoke tubers ranges up to above (dp 40) (Bornet, 2001).

The protein in Jerusalem artichoke tubers comprises around 1.6 to 2.4 g·100 g^{-1} of fresh weight (Table 5.1). Protein and nitrogen levels remain relatively constant in the tubers during development (Kosaric et al., 1984). Tuber protein contains all the essential amino acids in favorable proportions. It is rich in lysine and methionine, in comparison to proteins of other root and tuber crops, and is

TABLE 5.1
Composition of Jerusalem Artichoke Tubers (per 100 g Fresh Weight)

	A	B	C	D	E	F	G	H
Preparation	Raw	Raw	Raw	Raw	Boiled	Raw	Raw	Raw
Water (%)	—	82.1	80.1	78	80.2	—	79	78.9
Energy (kcal)	38	65	70	76	41	—	—	—
Protein (g)	0.5	2.1	2.1	2.0	1.6	—	2.4	—
Total carbohydrate (g)	15.9[a]	14.1[a]	16.7[a]	17.3	10.6	—	15	15.8
Dietary fiber (g)	4.0	2.6	0.6	1.3	3.5[b]	—	—	—
Total sugars (g)	1.0	—	—	—	1.6	—	—	—
Sucrose (g)	0.6	—	—	—	—	—	—	—
Lactose (g)	0	—	—	—	—	—	—	—
Total starch (g)	7.2	—	—	—	Trace	—	—	—
Total fat (g)	0.2	0.6	0.1	<1	0.1	—	—	—
Total fatty acids (g)	<0.1	0.48	—	<1	—	—	—	—
Saturated fatty acids (g)	<0.1	0.17	—	0	—	—	—	—
Monounsaturated fatty acids (g)	<0.1	0.01	—	<1	—	—	—	—
Polyunsaturated fatty acids (g)	<0.1	0.3	—	<1	—	—	—	—
Cholesterol (mg)	0.3	0	—	0	—	—	—	—
Total sterols (mg)	5.2	—	—	—	—	—	—	—
Ash (g)	—	1.2	1.2	—	—	—	—	—
Nitrogen (g)	—	—	—	—	0.25	0.38	—	—
Calcium (mg)	25	28	37	14	30	—	29.4	—
Iron (mg)	3.4	0.6	—	3.4	0.4	1.5	2.1	3.7
Magnesium (mg)	16	16	—	17	—	17	14.4	—
Potassium (mg)	560	561	—	429	420	603	657	478
Sodium (mg)	3	3	—	4	3	1.8	—	—
Phosphorus (mg)	78	72	63	—	—	73	—	78
Copper (mg)	—	0.12	—	—	—	0.10	0.12	—
Boron (mg)	—	—	—	—	—	0.24	0.21	—
Manganese (mg)	—	—	—	—	nd	0.30	0.28	—
Sulfur (mg)	—	—	—	—	22	27	—	—
Chlorine (mg)	—	—	—	—	nd	—	—	—
Zinc (mg)	0	0.10	—	12.0	—	0.32	0.40	—
Aluminum (mg)	—	—	—	—	—	4.0	—	—
Barium (mg)	—	—	—	—	—	0.33	—	—
Silicon (mg)	—	—	—	—	—	4.4	—	—
Nickel (μg)	—	15.0	—	—	—	nd	16.0	—
Iodine (μg)	0	0.10	—	—	nd	—	—	—
Chromium (μg)	—	6.4	—	—	—	nd	84.0	—
Selenium (μg)	0.2	0.1	—	—	nd	—	0.25	—
Lead (μg)	—	—	—	—	—	—	6.3	—
Cadmium μ(g)	—	—	—	—	—	—	1.1	—
Vitamin A (retinol) (μg)	0.6	1.0	—	1.0	—	—	—	—
Carotenoids (μg)	28.9	9.0	—	—	20.0	—	—	—
Vitamin B_1 (thiamin) (mg)	0.2	0.07	—	0.2	0.1	—	—	0.2
Vitamin B_2 (riboflavin) (mg)	0.05	0.06	—	0.06	Trace	—	—	0.16
Niacin (mg)	0.5	1.3	—	1.3	—	—	—	1.3
Vitamin B_6 (mg)	—	0.09	—	—	—	—	—	—
Pantothenic acid (mg)	—	0.38	—	—	—	—	—	—
Biotin (μg)	—	0.50	—	—	—	—	—	—
Folates (μg)	13.0	22.0	—	13.3	—	—	—	—

TABLE 5.1 (CONTINUED)
Composition of Jerusalem Artichoke Tubers (per 100 g Fresh Weight)

	A	B	C	D	E	F	G	H
Vitamin B_{12} (cobalamin) (µg)	0	—	—	—	—	—	—	—
Vitamin C (mg)	5.0	6.0	—	4.0	2.0	—	—	4.0
Vitamin D (µg)	0	—	—	—	—	—	—	—
Vitamin E (mg)	<0.1	0.15	—	—	0.2	—	—	—
Vitamin K (µg)	1.44	—	—	—	—	—	—	—
Tryptophan (mg)	—	0.23	—	—	—	—	—	—

Note: nd = not detected (i.e., below detection level).

[a] Total carbohydrate calculated by difference (minus protein, fat, water, and ash).

[b] Nonstarch polysaccharides only.

Source: (A) Fineli Food Composition Database, National Public Health Institute of Finland, http://www.fineli.fi/, 2004; (B) Danish Food Composition Database, Danish Institute for Food and Veterinary Research, http://www.foodcomp.dk/, 2005; (C) FAO, *Food Composition Tables for the Near East*, FAO Food and Nutrition Paper P-85, http://www.fao.org/, 1982 (data for edible portion); (D) Whitney, E.N. and Rolfes, S.R., *Understanding Nutrition*, 8th ed., West/Wadsworth, Belmont, CA, 1999 (data for edible portion; calculated from original value, 150 g); (E) Holland, B. et al., *5th Supplement to McCance and Widdowson's The Composition of Foods*, Royal Society of Chemistry, Cambridge, U.K., 1991 (data reproduced in Vaughan, J.G. and Geissler, C.A., *The New Oxford Book of Food Plants*, Oxford University Press, Oxford, 1997, p. 222) (data for an edible portion; tuber flesh only); (F) Somda, Z.C. et al., *J. Plant Nutr.*, 22, 1315–1334, 1999 (data calculated from original values, mg·g^{-1}); (G) Stolzenburg, K., *Topinambur*, LAP Forchheim, Germany, 2003, http://www.landwirtschaft-bw.info; (H) Kaŕa, J., Strašil, Z., Hutla, P., and Ustak, S., *Energetiché Rostliny Technologie Pro Pěstování a Využití*, Výzkumný Ústav Zemědělské Techniky, Praha, Czech Republic, 2005.

considered of high quality for food and feed applications (Cieślik, 1998a; Rakhimov et al., 2003; Stauffer et al., 1981). For tubers having a mean total crude protein of 5.9% of tuber dry matter, the predominant constituent amino acids (g·100 g crude protein) were asparatic acid (14.6), glutamic acid (14.0), arginine (11.1), lysine (5.2), threonine (3.4), phenylalanine (3.9), cysteine (1.0), and methionine (1.0) (Stolzenburg, 2004). The corresponding data for all amino acids, expressed as a percentage of total tuber dry weight, are included in Table 5.2. For an inulin-extracted tuber pulp, with a protein content of 16.2%, amino acid content (g·100 g sample N) was given as lysine (49), histidine (13), arginine (32), asparatic acid (60), threonine (33), serine (30), glutamic acid (71), proline (22), glycine (32), alanine (35), methionine (12), isoleucine (31), leucine (46), tyrosine (22), phenylalanine (28), and valine (38) (Stauffer et al., 1981). Crude protein content was found to vary among cultivars, with a mean 5.9% crude protein recorded for the tubers of 26 cultivars; for example, an experimental clone ('2071-63') had 8% crude protein, while a number of cultivars ('Monteo,' 'Rico,' 'Boynard,' and 'Lola') had around 5% crude protein content (Stolzenburg, 2004). Ash content is around 1.2% of tuber dry weight, although some reports give an ash content as high as 4.7% (Eihe, 1976; Conti, 1953).

Jerusalem artichoke tubers have a high mineral content. The tubers are especially rich in iron (0.4 to 3.7 mg·100 g^{-1}), calcium (14 to 37 mg·100 g^{-1}), and potassium (420 to 657 mg·100 g^{-1}), although they have relatively little sodium (1.8 to 4.0 mg·100 g^{-1}) (Table 5.1). Iron concentrations, for instance, are around three times higher than in potatoes (Cieślik, 1998b). Relatively high levels of selenium have also been noted, up to 50 µg·100 g^{-1} (Antanaitis et al., 2004; Bärwald, 1999), although reported levels are usually lower (Table 5.1). High concentrations of lead and other heavy metals (e.g., cadmium) are sometimes reported (Cieślik and Barananowski, 1997; Stolzenburg, 2003). Heavy metal concentrations increase as levels in the soil increase, and Jerusalem artichoke

TABLE 5.2
Amino Acid Content of Crude Protein from Jerusalem Artichoke Tubers (expressed as % dry matter)

	% of Dry Matter	
Amino Acid	**A**	**B**
Asparatic acid	0.86	—
Threonine	0.20	0.30
Serine	0.19	—
Glutamic acid	0.83	—
Glycine	0.21	—
Alanine	0.23	—
Cysteine	0.06	—
Valine	0.22	1.33
Methionine	0.06	—
Isoleucine	0.19	—
Leucine	0.27	0.85
Tyrosine	0.12	0.12
Phenylalanine	0.23	—
Histidine	0.17	0.21
Lysine	0.30	0.33
Arginine	0.65	0.46
Proline	0.30	—

Source: Adapted from (A) Stolzenburg, K., *Rohproteingehalt und Aminosäuremuster von Topinambur*, LAP Forchheim, Germany, 2004, http://www.landwirtschaft-bw.info (mean figure from 27 cultivars and clones); (B) Eihe, E.P., *Lativijas PSR Zinatmi Akademijas Vestis*, 344, 77, 1976.

is a promising crop for bioremediation in contaminated soils (Antonkiewicz and Jasiewicz, 2003; Jasiewicz and Antonkiewicz, 2002). Somda et al. (1999) looked at nutritional element allocation from planting to storage in the cultivar 'Sunchoke.' The levels of carbon and phloem-mobile elements dramatically increased in the tubers during the phase of rapid growth. By the time of the final harvest, high levels of potassium, phosphorus, and calcium were found in the mature tubers.

The tubers are a good source of vitamins, especially vitamins in the vitamin B complex, vitamin C (ascorbic acid), and β-carotene (Van Loo et al., 1995). They have relatively high levels of folates or folic acid (13 to 22 $\mu g \cdot 100\ g^{-1}$), while other vitamins in the B complex are present (thiamin, riboflavin, niacin, B6, pantothenic acid, biotin, and cobalamin) (Table 5.1). Vitamin C concentrations (2 to 6 $mg \cdot 100\ g^{-1}$) are lower than in the aboveground plant parts, but are superior to other root and tuber crops, for example, around four times higher than in potatoes (Eihe, 1976). Carotenoids have also been noted at relatively high concentrations (9 to 29 $\mu g \cdot 100\ g^{-1}$), β-carotene being a precursor of vitamin A (0.6 to 1.0 $mg \cdot 100\ g^{-1}$) (Table 5.1). A correlation has been noted between vitamin C and levels of nitrates in the tubers (Cieślik et al., 1999). In fact, considerable variation has been reported for vitamin content in the literature, because vitamin concentrations are highly dependent on development stage, climatic conditions, agronomic practices, and other factors.

In addition to inulin and the tuber chemical components listed in Table 5.1, notable phytochemicals present in the tubers include gentisic acid (antibacterial and antiviral activity), heliangin (plant

growth regulatory activity), and spermine (ubiquitous in plants and involved in protein synthesis) (Harbourne and Baxter, 1999).

The aroma of uncooked tubers appears to be comprised largely of the sesquiterpene β-bisabolene with smaller amounts of long-chain saturated hydrocarbons (MacLeod et al., 1982). During cooking, inulin partially degrades and its chemical composition changes. The inulin undergoes depolymerization at around 150°C (Shu, 1998), forming fructose and short-chain-length polymers. While inulin does not react directly with nitrogen-containing compounds in Maillard reactions, fructose derived from inulin can potentially form a cross section of pyrazines. As in raw tubers, inulin and other fructans account for essentially all the carbohydrates in cooked tubers (Vaughan and Geissler, 1997).

5.1.2 Aerial Plant Parts

Glucose is the first sugar to form in the leaves, with fructose and sucrose occurring soon after. Fructose in the leaves accumulates first in the petioles and veins, and later in the parenchyma (Strepkov, 1960a, 1960b). The glucose content of the leaves varies between 1 and 4% of dry weight, while fructose content rises to about 7% over the summer (Rashchenko, 1959). Carbohydrate is temporarily stored in the form of inulin, but also to a much lesser extent as starch (Ernst, 1991; Schubert and Feuerle, 1997). Storage carbohydrates in the leaves are converted to sugars at night for translocation around the plant.

The crude protein content of the leaves is around four times higher than for the tubers (Schweiger and Stolzenburg, 2003) and three times higher than in the stems (Malmberg and Theander, 1986). Leaf protein is particularly rich in the amino acids lysine and methionine (Stauffer et al., 1981). The nitrogen content of the leaves decreases during growth, for example, from 30% in young leaves to 16% in older leaves, just prior to senescence (Rashchenko, 1959). Similarly, crude protein in the leaves was found to decrease from 181 to 122 $g \cdot kg^{-1}$ from the vegetative to flowering stage of plant development (Seiler, 1988).

Leaves have relatively high levels of β-carotene and vitamin C, higher than for the tubers and other plant parts. A leaf vitamin C content of 151 $mg \cdot kg^{-1}$ dry weight was recorded by Underkofler et al. (1937), about 10 times the level occurring in the stems. In general, stems have 3 to 10 times lower vitamin concentrations than the leaves (Kosaric et al., 1984). Rashchenko (1959) found levels of β-carotene and vitamin C in mature plants of 12 to 15 $mg \cdot kg^{-1}$ and 100 to 160 $mg \cdot kg^{-1}$, respectively. However, the highest concentrations of these vitamins in Jerusalem artichoke have been obtained from the leaves in July, with 371 $mg \cdot kg^{-1}$ for β-carotene and 1,662 $mg \cdot kg^{-1}$ for vitamin C, respectively (Eihe, 1976; Kosaric et al., 1984). The leaves also contain higher levels of uronic acids, lignin, and ash than the stems (Malmberg and Theander, 1986). Levels of ash are around two to three times higher in the aboveground than the belowground plant parts, with the leaves especially abundant in terms of ash (12 to 16%). Data on the composition of the leaves and stems of Jerusalem artichoke are given in Table 5.3.

The aboveground stems or stalks contain inulin, fructooligosaccharides, and sugars (mainly fructose). The stems contain more structural carbohydrates (cellulose and hemicellulose), fructans, and low molecular weight sugars than the leaves (Malmberg and Theander, 1986). Apart from fructose, the sugars found in the leaves and stems are predominantly glucose, along with some sucrose, xylose, galactose, mannose, arabinose, and rhamnose (Malmberg and Theander, 1986). Inulin in the stems increases from the top to the bottom. Inulin with a higher degree of polymerization (dp) is more likely to be found toward the middle of the stem in lignin-containing tissue, while low-dp molecules may be more prevalent toward the base of the stem (Strepkov, 1960a, 1960b). Strepkov (1959) isolated inulins with 4, 6, 8, and 12 subunits (dp) in mature stems in the autumn. Rashchenko (1959) also noted the presence of inulin in flower buds.

In the total aboveground parts, the predominant minerals are potassium, sodium, calcium, magnesium, and phosphorus (Hay and Offer, 1992; Rashchenko, 1959). A recent analysis found

TABLE 5.3
Composition (% Dry Matter) of Leaf (L), Stem (S), and Total Aerial Parts (LS) of Six Jerusalem Artichoke Clones

Clone	'1926'[a]	'1926'[a]	'1927'[a]	'1927'[a]	Topinanca[b]	'1168'[b]
Plant part	L	S	L	S	LS	LS
Protein	26.9[c]	8.8[c]	29.4[c]	11.9[c]	7	9
Sugars	2.4	6.0	0.8	5.0	—	—
Fructose	—	—	—	—	1.8	2.2
Glucose	—	—	—	—	1.2	2.1
Sucrose	—	—	—	—	2.1	1.2
Fructans	—	5.4	—	3.2	4.5	2.0
Cellulose	6.6	14.2	7.3	13.1	20	17
Hemicellulose	4.5[d]	9.3[d]	4.3[d]	9.6[d]	21[e]	21[e]
Lignin (Klason)	17.9	10.8	21.7	14.1	14	12
Uronides	15.8	9.2	13.2	10.9	—	—
Ash	13.4	6.8	14.9	9.4	8	10

[a] Adapted from Malmberg, A. and Theander, O., *Swedish J. Agric. Res.*, 16, 7–12, 1986.
[b] Adapted from Gunnarson, S. et al., *Biomass*, 7, 85–97, 1985.
[c] Crude protein (N × 6.25).
[d] Hemicellulose (neutral part).
[e] Hemicellulose (plus pectin).

calcium levels in the aerial parts to be around eight times higher than in the tubers, with phosphorus and potassium levels around five and four times lower, respectively, and equivalent magnesium levels (Schweiger and Stolzenburg, 2003). The nutrient composition of the aerial parts of Jerusalem artichoke is considered further in the following chapter (see Section 6.2.1).

5.2 OCCURRENCE OF INULIN IN PLANTS

Inulin molecules are much smaller than starch molecules, with the degree of polymerization (i.e., the number of individual monosaccharide subunits) ranging from 2 to only about 70. The average number of fructose subunits varies with species, production conditions, and temporally (De Leenheer, 1996). Molecules with a degree of polymerization below 10 are called fructooligosaccharides (FOSs) or oligofructose. Short-chain fructooligosaccharides have two to four subunits. There are several commercially important short-chain fructooligosaccharides, including Neosugar®, Nutraflora™, Meioligo®, Beneo™, and Actilight® (Roberfroid, 2005).

Inulin is predominantly a mixture of linear β-(1-2)-linked fructose chains with a terminal glycopyranose unit at the reducing end (Figure 5.1). There can be a small percentage of inulin chains that exhibit a very limited degree of branching (De Leenheer and Hoebregs, 1994) via β-(2-6)-linkages (Figure 5.1). The extent of branching varies among and within species (e.g., dahlia has 1 to 2% and chicory 4 to 5%). In addition, a small percentage of inulin molecules do not contain a terminal glycopyranose unit (Fm) (Figure 5.1). These molecules have a terminal fructoside unit found primarily in the pyranose form in aqueous solution (De Leenheer and Hoebregs, 1994).

The term *inulin* first appeared in the literature in 1818 (Thomson, 1818), predating the discovery of fructose by about 30 years. It was ascribed to a substance, first isolated from elecampagne (*Inula helenium* L.) in 1804 (Rose, 1804). Jerusalem artichoke was first recorded as a source of inulin in around 1870. The actual linear structure of the molecule was not elucidated until the 1950s, and the small degree of branching that can occur only in the mid-1990s (De Leenheer and Hoebregs, 1994). As a polymer of fructose, inulin is classified as a fructan of which there are several types

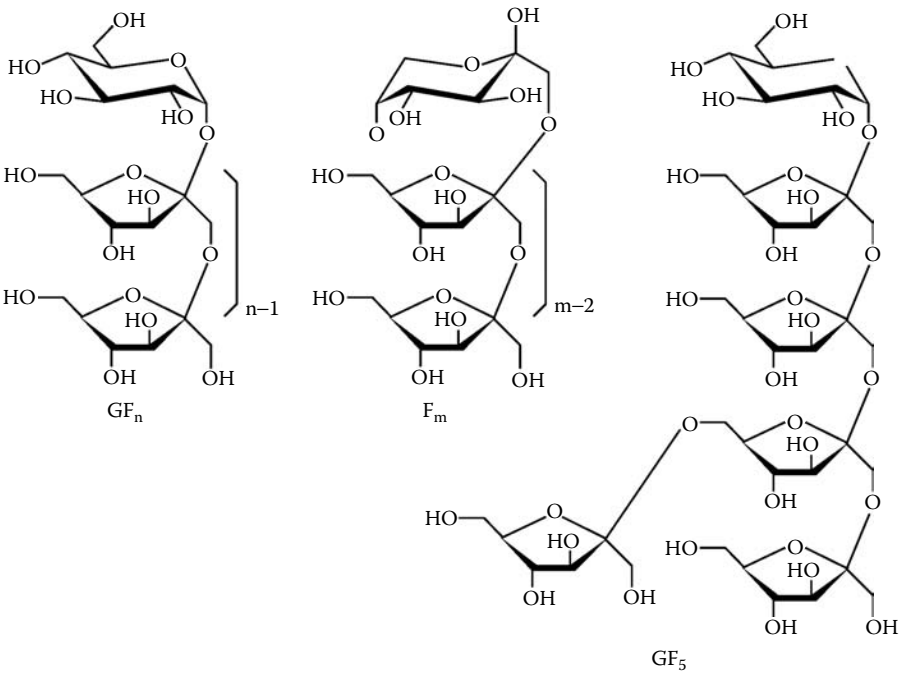


FIGURE 5.1 Structure of inulin containing a terminal glucopyranose unit (GF_n), inulin with a terminal fructoside unit (GF_m), and a branched inulin (GF_5).

(inulins, levans, and branched fructans). Levans are mainly comprised of β-(2-6)-linkages, though they may also be branched. Fructans are found in a cross section of families (Agavaceae, Asteraceae, Boraginaceae, Campanulaceae, Goodeniaceae, Gramineae, Haemodoraceae, Iridaceae, Liliaceae, Menyanthaceae, Monotropaceae, Pyrolaceae, Stylidiaceae) and a wide range of species (Table 5.4) (Incoll and Bonnett, 1993). Many members of the Asteraceae (Compositae) accumulate fructans in underground storage organs, including elecampagne, dandelion (*Taraxacum officinale* Weber), salsify (*Tragopogon porrifolius* L.), and yacon (*Polymnia sonchifolia* Poeppig & Endlicher) (Hendry and Wallace, 1993). However, on a quantitative basis, Jerusalem artichoke and chicory (*Cichorium intybus* L.) are the most important inulin-storing plant species. Fructans are also synthesized by a number of microorganisms (Hendry, 1987; Yun et al., 1999).

During the past two decades, interest in inulin and inulin-containing crops in Europe has increased substantially due to their often unique and diverse range of potential uses. While inulin has been found in a relatively wide range of species, only in Jerusalem artichoke, chicory, and dahlia does it appear to accumulate in sufficient quantity to be considered a primary storage form of carbon. Moreover, only in Jerusalem artichoke and chicory are the dry matter yields·ha^{-1} currently of sufficient magnitude to make them viable agricultural sources for inulin. It is through two seeming quirks of nature (i.e., the formation and concentration of inulin) and the fact that inulin has a number of unique chemical properties that the Jerusalem artichoke has become more than just a colorful North American weed.

In addition to its limited role as a storage form of carbon, inulin is thought to be more widely involved in membrane protection during dehydration of many species (Vereyken et al., 2003). The interaction of inulin with membrane lipids in a model system was found to be chain length dependent. Inulin-type fructans had a more pronounced interaction with the membrane lipids than levan-type fructans.

Both the quantity and quality of inulin in various plant sources are of considerable importance in terms of its utilization. Both Jerusalem artichoke and chicory have inulin contents of >15% on

TABLE 5.4
Food Plants Containing Fructans

Adenophora liliifolia	*Cyperus esculentus*	*Paspalum scrobiculatum*
Allium ampeloprasum	*Cyperus papyrus*	*Pennisetum cinereum*
Allium cepa	*Dendrocalamus asper*	*Pennisetum nigritarum*
Allium chinense	*Digitaria exilis*	*Pennisetum typhoides*
Allium fistulosum	*Digitaria iburua*	*Phyllospadix* spp.
Allium sativum	*Dracaena australis*	*Phyllostachys dulcis*
Allium schoenoprasum	*Echinochloa crus-galli*	*Phyteuma orbiculare*
Allium tuberosum	*Echinochloa frumentacea*	*Polymnia sonchifolia*
Arctium lappa	*Eleocharis dulcis*	*Portulaca oleracea*
Artemisia lactiflora	*Eleusine coracana*	*Saccharum barberi*
Asparagus officinalis	*Eragrostis tef*	*Saccharum edule*
Asparagus racemosus	*Fritillariacamschatcensis*	*Saccharum officinarum*
Asphodelus aestivus	*Fritillaria lanceolata*	*Saccharum sinense*
Avena abyssinica	*Gigantochloa verticillata*	*Scolymus hispanicus*
Avena byzantina	*Gladiolus italicus*	*Scorzonera hispanica*
Avena sativa	*Gyandriris sisyrinchium*	*Secale sativa*
Bambusa beecheyana	*Gynura bicolor*	*Setaria italica*
Brachiaria deflexa	*Helianthus tuberosus*	*Sonchus oleraceus*
Camassia (2 species)	*Hemerocallis fulva*	*Sorghum bicolor*
Campanula rapunculus	*Hordeum vulgare*	*Symphytum officinale*
Chrysanthemum moriflorum	*Inula helenium*	*Taraxacum officinale*
Chrysanthemum spatiosum	*Lactuca indica*	*Tragopogon porrifolius*
Cichorium endivia	*Lactuca sativa*	*Triticum aestivum*
Cichorium intybus	*Menyanthes trifoliate*	*Triticum dicoccum*
Cirsium oleraceum	*Microseris lanceolata*	*Triticum durum*
Claytonia perfoliata	*Muscari comosus*	*Triticum monococcum*
Coix lachryma-jobi	*Oryza glaberrima*	*Yucca filamentosa*
Cordyline terminalis	*Oryza sativa*	*Zea mays*
Cynara cardunculus	*Panicum miliaceum*	*Zizania aquatica*
Cynara scolymus	*Panicum sumatrensis*	*Zizania caduciflora*
Cynoglossum officinale		*Zostera marina*

Source: Adapted from Incoll, L.N. and Bonnett, G.D., in *Inulin and Inulin-Containing Crops*, Fuchs, A., Ed., Elsevier, Amsterdam, 1993, pp. 309–322.

a fresh weight basis and >75% on a dry weight basis. The degree of polymerization of inulin is a critical quality trait that ranges from 2 to about 70, with the mean varying depending upon species, cultivar, production conditions, physiological age, and other factors (De Leenheer, 1996). Onion fructans are very short (<5 dp); the degree of polymerization increases from Jerusalem artichoke to chicory to globe artichoke (Table 5.5).

Degree of polymerization can have a pronounced impact on the potential use of the inulin and fructooligosaccharides. Short-chain fructooligosaccharides (i.e., ≤ GF_5) are of interest because of their health benefits, sweetness (~30% of sucrose), and as a substrate for the synthesis of certain chemicals (e.g., fermentation products). Inulins with higher degrees of polymerization can be used for fat replacement and high-fructose syrups (longer chain lengths decrease the percentage of glucose in the syrup). Likewise, longer chain lengths can be systematically reduced in size by partial hydrolysis using an endo-inulinase, while lengthening is not a commercially viable option.

TABLE 5.5
Distribution of Fructan Polymers in the Edible Portion of Selected Crops

Crop	% Fructan (dm)	Degree of Polymerization (%)			
		≤9	10–20	20–40	>40
Jerusalem artichoke	16–20	52	22	20	6
Chicory	15–20	29	24	45	2
Globe artichoke	2–9	0	0	13	87

Source: Adapted from Bornet, F.R.J., in *Advanced Dietary Fibre Technology*, McCleary, B.V. and Prosky, L., Eds., Blackwell Science, Oxford, 2001, pp. 480–493.

5.3 COMPOSITION, STRUCTURE, AND PROPERTIES OF INULIN AND INULIN OLIGOMERS

5.3.1 Crystal Structure of Inulin Oligomers

Electron diffraction assessments of single crystals from inulin fractions indicate two antiparallel six-fold helices (Andre et al., 1996); a five-fold model has also been proposed (Marchessault et al., 1980). The hemihydrate molecule contains one water molecule for each two fructosyl units, while the monohydrate has one water molecule per fructosyl unit. When intermolecular hydrogen bonds are present, however, there is no evidence of intramolecular hydrogen bonding in the crystals. Crystal structures of 1-kestose (GF_2) (Jeffrey and Park, 1972), nystose (GF_3) (Jeffrey and Huang, 1993), and cycloinulohexaose (cF_6) (Sawada et al., 1990) have been reported.

5.3.2 Structure in an Aqueous Solution

Nuclear magnetic resonance (NMR) spectroscopy has been used to study the structure of inulin in aqueous solutions. In addition, the use of low-angle laser light scattering, dynamic light scattering, and small-angle x-ray scattering following size exclusion chromatography has yielded information on the molecular weight distribution, hydrodynamic radii, and geometry of Jerusalem artichoke inulin (Eigner et al., 1988). Inulin was found to have a rod-like shape with maximum dimensions of 5.1 × 1.6 nm (length × mean diameter). ^{13}C relaxation rate measurements indicate that the fructofuranoside units are not part of the polysaccharide backbone; therefore, the structure is like a polyethylene glycol polymer with furanosides attached (Figure 5.1). This greatly increases the flexibility of the chains, which is reflected by a segmental motion that is two to three times faster than amylose (Tylianakis et al., 1995).

^{13}C NMR assessment of oligomers from GF_3 to GF_6 and inulins with an average degree of polymerization of 17 and 31 indicated that simple helical structures are not the predominant conformation in solution (Liu et al., 1994), but rather inulin consists of randomly ordered saccharide chains. With crystallization, the molecules form helices that are stabilized by intermolecular hydrogen bonds. During gel formation, there is an increasing number of hydrogen bonds, the formation of helix domains, and an increasing crystallinity (Haverkamp, 1996). The helix domains do not contain a core in which linear molecules can be included (Dvonch et al., 1950).

^{13}C NMR spectra of the inulooligosaccharides 1-kestose (GF_2) and nystose (GF_3) have also been assessed (Jarrell et al., 1979), as have the ^{1}H and ^{13}C chemical shifts of 1-kestose (Calub et al., 1990), nystose (Liu et al., 1993; Timmermans et al., 1993a), and 1,1,1-kestopentaose (GF_4)

TABLE 5.6
Physical and Chemical Characteristics of Inulin (Chicory): A High-DP Fraction and Oligofructose

Parameter	Inulin	High-DP Inulin	Oligofructose
Chemical structure	GFn (n = 2–60)[a]	GFn (10–60)	GFn + F (2–7)
Average DP[b]	12	25	4
Dry matter (%)	95	95	95
Inulin/oligofructose content (% of dm)[c]	92	99.5	95
Sugar content (% of dm)	8	0.5	5
pH (10% w/w)	5–7	5–7	5–7
Sulfated ash (% of dm)	<0.2	<0.2	<0.2
Heavy metals (% of dm)	<0.2	<0.2	<0.2
Appearance	White powder	White powder	White powder
Taste	Neutral	Neutral	Moderately sweet
Sweetness vs. sucrose (%)	10	None	35
Solubility @ 25°C ($g \cdot l^{-1}$)	120	25	>750
Viscosity in water (5%) @ 10ºC (mPa.sec)	1·6	2·4	1·0
Functionality in foods	Fat replacement	Fat replacement	Sugar replacement

[a] G = glucosyl subunit; F = fructosyl subunit; n = number of fructosyl subunits.
[b] DP = degree of polymerization.
[c] Dry matter (dm).

Source: Adapted from Franck, A., *Br. J. Nutr.*, 87, S287–S291, 2002.

(Liu et al., 1993; Timmermans et al., 1993b), using two-dimensional homonuclear and heteronuclear NMR spectral methods.

5.3.3 Properties of Inulin

A detailed characterization of the physical and chemical properties of (1) chicory inulin, (2) a high-DP fraction of inulin, and (3) fructooligosaccharides (oligofructose) is presented in Table 5.6. A similar assessment for Jerusalem artichoke inulin is not currently available. Due to the lower average degree of polymerization of Jerusalem artichoke inulin, the properties will differ somewhat from those for chicory. As the percent inulin in water increases (Table 5.7), the viscosity increases, which affects the physical properties of the product in which it is an ingredient.

5.4 ANALYSIS OF INULIN COMPOSITION

Inulin is a highly heterogeneous substance that is comprised of molecules ranging in degree of polymerization up to approximately 70. In addition, some molecules are devoid of the terminal glycopyranose unit and others display a very limited degree of branching (Figure 5.1). Since the properties of inulin differ with its composition, it is desirable to be able to fractionate and quantify individual oligomers. This is especially important with inulin in that the degree of polymerization varies among species, with storage organ maturity, handling conditions, storage time, and other factors. Jerusalem artichoke inulin and other oligosaccharides are routinely analyzed using high-performance anion exchange chromatography with pulsed amperometric detection (HPAE-PAD) (Figure 5.2) (Saengthongpinit and Sajjaanantakul, 2005). The first application of HPAE-PAD to plant-derived carbohydrate polymers with varying degrees of polymerization was by Koizumi et

TABLE 5.7
Concentration Dependency of Inulin Viscosity in Water

Inulin in Water (%)	Viscosity (cp @ 11°C)
2	1.25
4	1.35
6	1.70
8	1.80

Source: Adapted from Baal, H., in *Fourth Seminar on Inulin*, Wageningen, The Netherlands, 1993, pp. 1–66.

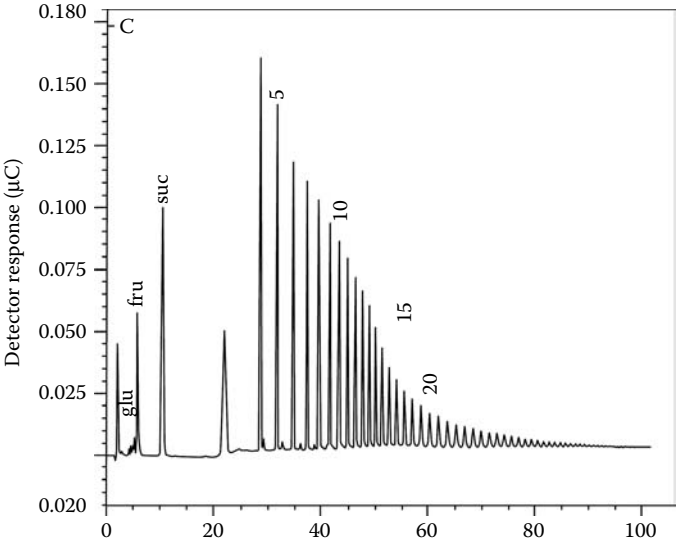


FIGURE 5.2 High-performance anion exchange chromatography with pulsed amperometric detector chromatogram of Jerusalem artichoke inulin separating the sample into discrete dp fractions. (After Saengthongpinit, W. and Sajjaanantakul, T., *Postharvest Biol. Technol.*, 37, 93–100, 2005. With permission.)

al. (1989). During storage inulin continues to be degraded, forming some fructans without a terminal glucose, which can also be separated using HPAE-PAD (Saengthongpinit and Sajjaanantakul, 2005). An alternative HPAE method using gradient elution in combination with a refractive index detector has been developed (Timmermans et al., 1997a, 1997b). The sample can be split with a portion going to a quadrupole mass spectrometer, allowing identification of polyfructans up to a molecular mass of cf. 7000 g·mol^{-1} (Bruggink et al., 2005). HPAE-PAD has been used to determine the fructooligosaccharide content of over 80 fruits, vegetables, and grains (Campbell, 1997).

The concentration of short-chain fructooligosaccharides in foods is of interest in that they comprise part of the total dietary fiber. The standard Asssociation of Official Analytical Chemists (AOAC) method for dietary fiber does not measure short-chain fructooligosaccharides due to their ethanol solubility; however, several alternative methods have been developed (Hoebregs, 1997; McCleary et al., 2000; Ouarné et al., 1997; Simonovska, 2000; Zuleta and Sambucetti, 2001).

5.5 INULIN EXTRACTION, ISOLATION, PURIFICATION, FRACTIONATION, DRYING, AND STORAGE

There have been a number of methods developed for the extraction of inulin from Jerusalem artichoke tubers (Aravina et al., 2001; Barta, 1993; Ji et al., 2002; Vogel, 1993), a composite of which is illustrated in Figure 5.3. The specific method selected will depend on the end product desired, resources available, volume, and other factors.

Jerusalem artichoke tubers arriving from the field or storage are first washed to remove any soil and extraneous matter, and then mechanically cleaned (Barta, 1993). At this point, the tubers can be ground to produce Jerusalem artichoke flour for bread and other products (Leyst-Kushenmeister,

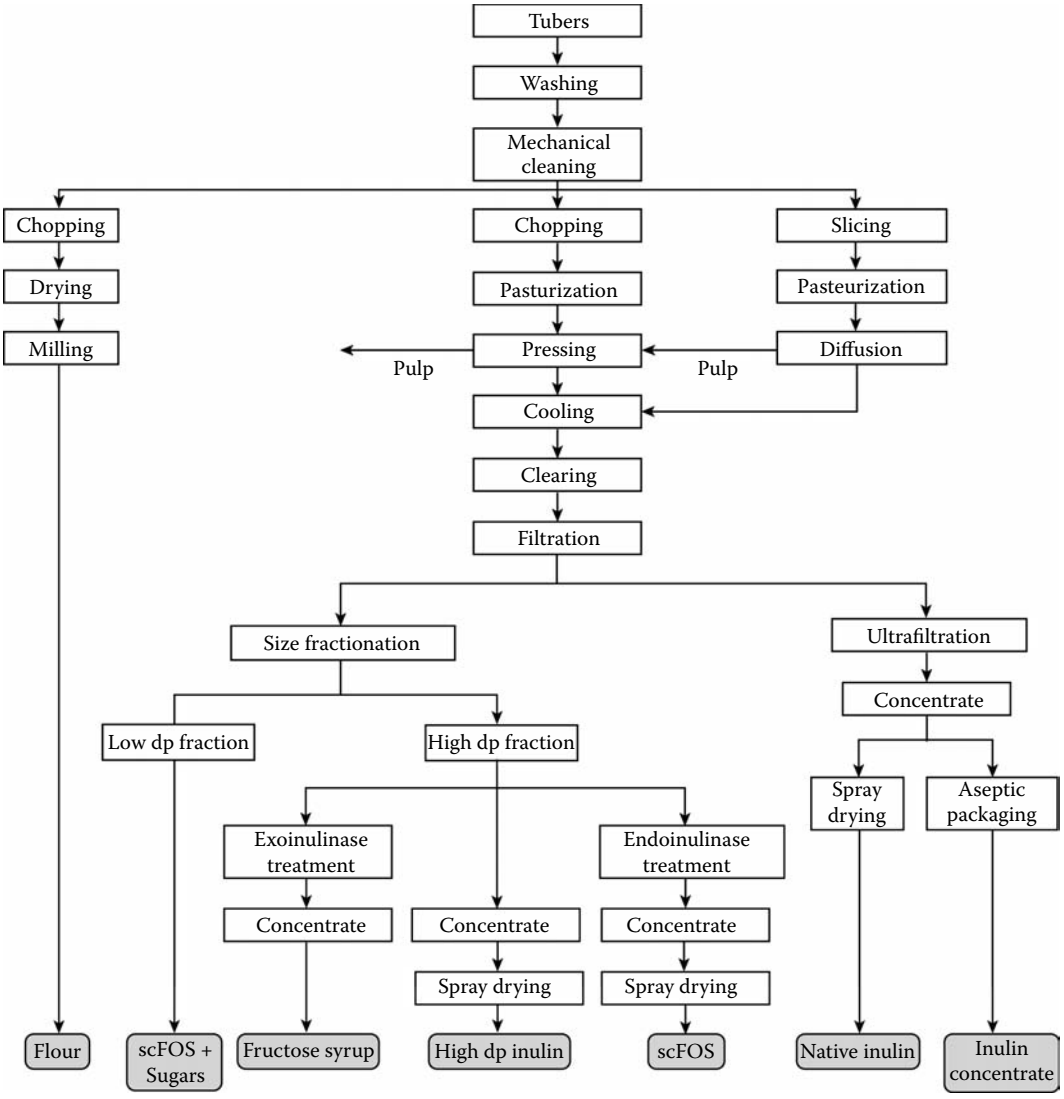


FIGURE 5.3 Flow diagram for the extraction and fractionation of Jerusalem artichoke inulin into various products (a composite of work by Aravina et al., 2001; Barta, 1993; Ji et al., 2002; Vogel, 1993). Abbreviations: dp = degree of polymerization; scFOC = short-chain fructooligosaccharides.

1937) or chipped, dried, and then ground (Figure 5.3). Heating the tubers prior to grinding inactivates polyphenol oxidase and other enzymes, improving the color of the flour (Modler et al., 1993a).

For the production of inulin and related products, the tubers are chopped or sliced and then pasteurized to deactivate enzymes (e.g., inulinase). Slicing is used for aqueous diffusion extraction (Barta, 1993). After extraction, the residual pulp is pressed and the combined extracts (aqueous and pressed) cooled. Aqueous extraction of slices followed by pressing gives a slightly higher yield than pressing of chopped material without water (~80 vs. 75%). Extraction is facilitated by the elevated temperature of the water and product (~80°C), which increases the yield to 95 to 98% (Vukov and Barta, 1987). The extract is primarily composed of inulin; however, it also contains mono- and disaccharides, amino acids, cations, colloids, floating contaminants, and colorants, which require removal. Clarification utilizes calcium hydroxide; the temperature during clarification varies depending upon whether the liquid represents a pressed or extracted juice. Colloids and floating contaminants can be coagulated at pH 10 to 11.5 using calcium hydroxide at 0.2% for extracted material or 0.4% calcium oxide equivalent for pressed juice. The cleared material is then filtered, at which point it may be fractionated to increase the purity of the individual fractions or handled as native inulin (a composite of sugars and inulin of varying degrees of polymerization). Chromatographic fractionation by size exclusion generally yields two fractions: short-chain fructooligosaccharides with mono- and disaccharides, and a high-dp fraction. Fractionation may also be achieved using low temperature (Silver, 2002) or ethanol precipitation of the high molecular weight fraction (Aravina et al., 2001), or using ultra- and nanofiltration (Kamada et al., 2002).

Another option for native inulin is fermentation using microorganisms that utilize only sugars and short-chain fructooligosaccharides that yield ethanol and a residual high molecular weight inulin fraction. This fraction, regardless of the method of separation, can then be either processed as is or treated with endo- or exo-inulinase to produce a high-purity fructose syrup, or with endo-inulinase to give short-chain fructooligosaccharides. Alternatively, instead of fractionation via chromatography or other means, the filtered material can be passed through an ultrafiltration system, concentrated, and either spray-dried to produce dried "native inulin" or aseptically packaged to give an inulin concentrate. Dried inulin should be stored in moisture-proof packages.

5.6 SOURCES OF INULIN

5.6.1 Traditional Plant Sources

Currently the primary commercial plant-derived sources for inulin are Jerusalem artichoke and chicory. The former is grown more so in Eastern Europe and the latter in Northwestern Europe. There is increasing interest in the commercial production of Jerusalem artichoke in China and several other countries. At present, neither crop is grown to any extent in the U.S., although there is some fresh-market production of Jerusalem artichoke.

5.6.2 Transgenic Crops

Instead of establishing breeding programs to further develop the Jerusalem artichoke as a crop, several groups have approached commercialization of an inulin source by creating transgenic plants of other well-established crops (e.g., sugar beet, potato, corn, and soybean). Production, harvest, storage and processing expertise, facilities, and equipment are already available for these crops. However, Jerusalem artichoke does have several major advantages over sugar beet and potato in that it can be grown over much wider ecological conditions and in soils that will not support these other crops.

In transgenic crops a specific fructosyltransferase and promoter can be selected to tailor the degree of polymerization and branching to certain needs. For example, using a *Streptococcus mutans* fructosyltransferase gene in which the C- or N-terminal peptide encoding portions are deleted,

inulin can be produced having a degree of polymerization of >100 and degree of branching of <3% (Engels et al., 2002; Hellwege et al., 2000). The gene from globe artichoke also produces long-chain-length inulin molecules (Heyer et al., 1999). Fructosyltransferase genes from guayule, Jerusalem artichoke (Stoop, 2004), onion (Vijn et al., 1997), and other sources have also been tested. In potato, the promoter of the B33 patatin gene is used to limit expression to the tubers and the signal sequence from the gene to direct the protein to the vacuole (Heyer and Wendenburg, 1997). A gene isolated from Jerusalem artichoke that expresses fructosyltransferase, introduced into sugar beet, caused up to 90% of the sucrose in the transgenic sugar beet roots to be converted into fructans in one experimental study (Sévenier et al., 2002). To date, however, transgenic plants do not represent a commercial source of inulin. In addition, the ecological flexibility of Jerusalem artichoke greatly increases the land area in which it can be grown, making Jerusalem artichoke a desirable inulin source for many locations.

5.6.3 Synthesis Using Microorganisms

An alternative to transgenic plants is expression of either β-fructofuranosidases (EC 3.2.1.26) or β-fructosyltransferases (EC 2.4.1.100) in a microorganism such as *Escherichia coli* for the synthesis of inulin or short-chain fructooligosaccharides from sucrose. In this case, sucrose acts as both the fructose donor and initial acceptor (Fishbein et al., 1988). β-Fructofuranosidases with sufficient transfructosylation activity can produce fructooligosaccharides; for example, the enzyme from *Aspergillus niger* ATCC 20611 has been used successfully for industrial production (Hidaka et al., 1988; Hirayama et al., 1989). The product is separated into two commercial classes: Neosugar G and Neosugar P (Hidaka et al., 2001). Neosugar G contains ~35% glucose and fructose (w/w), 10% sucrose, and 55% fructooligosaccharides. To increase the fructooligosaccharide concentration to ~95%, the monosaccharides are removed from Neosugar G, yielding Neosugar P. The sweetness of each fraction is about 60% (G) and 30% (P) that of sucrose, and both are stable at neutral pH and at temperatures up to 140°C.

Fructosyltransferases from several sources (e.g., *Streptococcus mutans*, *Aspergillus sydowi*) have also been inserted into microorganisms such as *E. coli* for the production of inulin (Engels et al., 2002; Heyer and Wendenburg, 2001). In the initial reaction, two sucrose molecules lead to kestose and glucose. Acting on the kestose (GF_2), the enzyme produces nystose (GF_3), and subsequently on nystose, producing fructosylnystose (GF_4). Alteration of the fructosyltransferase through the deletion of the C- or N-terminal peptide encoding portion of the gene improved production in recombinant *E. coli* (Engels et al., 2002). Inulin could be produced from sucrose with a degree of polymerization of >100 and a degree of branching of <3%. Alternatively, the reaction can be stopped to optimize the formation of short-chain fructooligosaccharides with a ratio of 37% (GF_2): 53% (GF_3): 10% (GF_4) (Fishbein et al., 1988).

5.7 USES FOR NATIVE AND FRACTIONATED INULIN

5.7.1 Native Inulin

5.7.1.1 Bulking Agents

Considerable interest was focused in the 1990s on inulin as a bulking agent in low-calorie foods, due to its limited utilization by humans. A bulking agent increases the weight or volume of a food without altering its functionality or utility. If an artificial sweetener is used to replace the sugar in a cake mix, the differential in sweetness (e.g., 600×) results in potentially a tremendous loss in volume. The addition of an acceptable bulking agent, especially one that confers few calories, restores the necessary bulk and functional properties of the sugar. The primary disadvantage of inulin as a bulking agent is the production of gas (see Section 6.1.8).

5.7.1.2 Bakery and Dairy Products

The addition of inulin or Jerusalem artichoke flour to bread generally confers several positive attributes (e.g., improved softness of the crumb, prolonged preservation, and improved bread volume) (De Man and Weegels, 2005; Miura and Juki, 1995). White and wheat/rye breads can be made with Jerusalem artichoke flour or inulin; as the inulin content increases, the crumb hardness decreases (Filipiak-Florkiewicz, 2003). Typically, the upper limit is around 8% inulin (Meyer, 2003). In wheat/rye breads, Jerusalem artichoke flour gave the highest quality. The amount of inulin hydrolyzed to fructose during the baking process is dependent upon its degree of polymerization, which varies between autumn and spring harvest. The addition of fructooligosaccharides decreases the calorie content and increases the fiber content of the bread, making it a healthier food. Inulin is also used as thickener in ice cream, sandwich spreads, mayonnaise, chocolate products, and pastries (Berghofer et al., 1993a; Frippiat and Smits, 1993).

5.7.1.3 Fructose and Short-Chain Fructans

The characteristic inulin biochemistry of Jerusalem artichoke makes it an excellent source of fructose. Fructose is the sweetest of the natural sugars; its sweetness is around 16% greater than sucrose (Shallenberger, 1993). Fructose syrups are widely used by the food industry. They have a high solubility in water, fewer calories than sucrose, and are less viscous. With these properties, fructose has gained in importance within the food processing industry as a sweetener. It is an ideal sugar for use in reduced-calorie foods, foods for diabetics, and products to combat obesity. A range of fructose-containing products can be obtained from Jerusalem artichoke, including sugar solutions, pure fructose syrup, and crystalline fructose.

Inulin, fructooligosaccharides, fructose, and other useful compounds can all be purified from the juice extracted from Jerusalem artichoke tubers. Fleming and GrootWassink (1979) describe a process for obtaining high-fructose syrup (75% yield) using enzyme hydrolysis. Fermentation using yeasts converts inulins and fructooligosaccharides to fructose, although the larger inulin polymers are difficult to convert (Fontana et al., 1993; Schorr-Galindo et al., 1995). Jerusalem artichoke yields more fructose than sugar beet or maize. The fructose in Jerusalem artichoke derives from inulin, whereas it derives from sucrose in sugar beet and starch in maize. Barta (1993) reported total fructose yields ($t \cdot ha^{-1}$) for Jerusalem artichoke, sugar beet, and maize of 4.5, 2.9, and 2.1, respectively. Jerusalem artichoke cultivars with higher inulin content are preferred for fructose production.

5.7.1.4 Nutraceutical Supplements

A Nutraceutical is any substance that is a food or a part of a food and provides medical or health benefits. Nutraceutical products are also known as functional foods. Inulin-containing foods have long been known to be beneficial for health. Inulin is fermented in the colon, selectively altering the microflora present (Gibson et al., 1995). Bifidobacteria, a genus considered to have health-promoting properties, displaces a number of undesirable microbes. Inulin is a component of many probiotic food supplements (see Section 6.1.3).

Fructooligosaccharides have been used as food supplements in Japan since 1983. A wide range of inulin-containing functional foods are marketed as beneficial for gastrointestinal conditions and for the promotion of mineral absorption (Hidaka et al., 2001). Over 700 products in Europe included inulin as a nutraceutical ingredient by 2000, including yogurts. One of these yogurts became the first functional food to have its health-promoting claims challenged in court. The yogurt, containing *Lactobacillus acidophilus* and inulin, was claimed to have cholesterol-lowering properties. The claim was upheld and the company (Mona, The Netherlands) won the case (Heasman and Mellentin, 2001).

5.7.1.5 Medical Applications

Pure inulin powder is sold for nutritional and medicinal purposes. For nutritional purposes, it is sufficient that any toxic components and pathogenic organisms are removed from the inulin. However, for medical and diagnostic uses, inulin must be extremely pure and have a high degree of polymerization (>20). Inulin from Jerusalem artichoke typically has only half of its inulin above a degree of polymerization of 10, with 12 the most frequently occurring chain length in raw tubers. Therefore, the inulin from Jerusalem artichoke, unless fractionated, is less suited to medicinal applications. A number of methods are available to obtain pure inulin for medical usage, including microwave drying and ultrafiltration (Vukov et al., 1993).

Inulin is used in an important test for renal failure called the inulin clearance method (Gretz et al., 1993; Chiu, 1994). As inulin is neither secreted nor reabsorbed in the kidney, it can be administered by injection to measure glomerular filtration rate. The relative amounts of inulin in the plasma and urine give an indication of renal function.

5.7.2 Inulin Fractionated by Degree of Polymerization

5.7.2.1 Fat Substitutes

The use of low-calorie fat replacers in foods facilitates reductions in the energy density of the diet. However, since fat confers a number of important quality attributes, it is critical that such foods be highly palatable. When all or part of the fat is replaced, the foods must have comparable rheological and sensory-quality attributes to the original high-fat food. Textural properties are particularly important since fat has a pronounced impact on texture, mouthfeel, and hence eating quality. Therefore, in addition to lowering the calorie density, an acceptable fat substitute must have the appropriate functional properties, such as heat stability, emulsification, aeration, lubricity, spreadability, texture, and mouthfeel (Lukacova and Karovicova, 2003; Silva, 1996).

Inulin can be used to replace a significant portion of the fat in certain meats (Archer et al., 2004) and traditional squeezable and spreadable food products. As the fat is reduced, the amount of water increases to the detriment of the product's structure. The water binding capacity and melting and rheological properties of inulin in such products, however, allow reducing the fat content from around 80% to 20–40% (Silva, 1996).

The higher molecular weight fractions of inulin function more like fats than lower-dp fractions. Therefore, when inulin is used as a fat substitute, generally the low molecular weight fraction is removed, leaving a product with an average degree of polymerization of 25 or higher. The higher molecular weight inulin can form a gel that has excellent spreadability (Kasapis, 2000). Unless very high levels of inulin are used (25%), gel-forming proteins and hydrocolloids may need to be added to alter the structural properties of the product.

Low-fat squeezable spreads and soft products (e.g., soft cheese, spreadable margarine) require a ratio of plastic stress to maximum stress of 0.95 to 1.0 (Kasapis, 2000). Typically around 15% of a high-dp fraction (~25 dp) can be used in these products. Interestingly, the physical structure of the material does not develop immediately with formulation but requires 1 to 2 days of storage.

Inulin is soluble in water, though its solubility is strongly modulated by temperature (e.g., ~6% at 10°C and 35% at 90°C) (Silva, 1996). It has a water binding capacity of approximately 2:1 and, when in solution, reduces the freezing point of the water. It is dispersible in water but tends to clump due to its hydroscopic characteristics, a problem that can be partially circumvented by mixing it with sugar or starch. Commercially available inulin has a slightly sweet taste due to the presence of glucose, fructose, and sucrose. The odor is neutral.

The functionality of inulin as a fat replacer is due to its effect on water (Silva, 1996). As the inulin concentration in the solution increases, the viscosity of the solution increases (Table 5.7). Initially at 1 to 10% there is a small but gradual increase in viscosity; between 11 and 30% there is a more pronounced increase, but without gel formation. Above 30% inulin in water, discrete

particles form and a gel develops within 30 to 60 minutes of cooling. With increasing inulin concentration, gel formation occurs more rapidly, and at very high levels (i.e., 40 to 45%), gelling occurs very rapidly. Such gels are very creamy and fat-like, and their strength is a function of the concentration of inulin, though other factors can also influence gel strength. Further increases in inulin result in gels of increasing firmness, and as the level of inulin approaches about 50%, the gels become very firm but retain their fatty feel.

Gel formation inhibits hydrolysis of the inulin (Silva, 1996). At low concentrations (i.e., below gelling), inulin may be hydrolyzed at a pH below 3 and at very high temperature due to the presence of "free water." In gel form, inulin is stable in acidic and high temperature conditions due to the lack of available water.

5.8 MICROBIAL AND ENZYMATIC MODIFICATION OF INULIN

5.8.1 Hydrolysis

5.8.1.1 Complete Hydrolysis: Fructose Syrups

Fructose syrups are widely utilized in the food industry in that they are sweeter than sucrose, thus allowing less sugar to be used to achieve a given level of sweetness (i.e., fructose is 1.2 times sweeter than sucrose on a weight basis (Shallenberger, 1993)). In addition, fructose metabolism in humans is not insulin dependent, and it produces less tooth decay than other sugars (Roch-Norlund et al., 1972). Currently, much of the fructose used by the food industry is produced from corn starch, a glucose polymer, via hydrolysis followed by isomerization. The fructose content is around 42% but can be increased to 95% by chromatographic separation of the residual glucose and further isomerization.

In contrast, as a polymer of fructose, inulin is an excellent candidate for producing a high-fructose syrup. It can be readily hydrolyzed enzymatically or chemically (GrootWassink and Fleming, 1980). Chemical hydrolysis can be achieved, for example, by acidifying to pH 2 to 3 with a strong acid cation exchanger and heating at 70 to 100°C (Yamazaki and Matsumoto, 1986). However, undesirable contaminants are produced and must be removed.

Enzymatic hydrolysis requires a single enzyme, inulinase, which yields a high-purity product (Bärwald and Flother, 1988; Zittan, 1981). The percentage of fructose varies with the degree of polymerization of the inulin, a condition that is influenced by species, cultivar (Chabbert et al., 1985a), time of harvest (Chabbert et al., 1983), and other factors (Modler et al., 1993b). The average degree of polymerization for early harvested Jerusalem artichoke inulin was 10 to 15, while for late harvest it was only 3 to 5. Shorter chain lengths yield syrups with progressively higher glucose and lower fructose contents (e.g., 96% fructose for early harvest vs. 65% for late harvest). Therefore, the production of high-fructose syrups from inulin involves two processes: hydrolysis and, when required, fructose enrichment.

Several classes of enzymes are capable of hydrolyzing the fructosidic linkages of inulin. The endo-inulinases cleave linkages within the chain, yielding fructans with reduced degrees of polymerization (e.g., β-D-fructofuransoidase (EC 3.2.1.26)). Exo-inulinases (2,1-β-D-fructan fructanohydrolase (EC 3.2.1.7)), in contrast, cleave single D-fructose molecules from the terminal end. Exo-inulinases are preferred and can be produced by a host of microorganisms, including fungi, yeast, and bacteria (Khanamukherjee and Sengupta, 1989; Pandey et al., 1999); typically, the enzyme is isolated from the organism for use. Microorganisms used for the production of inulinases include (Pandey et al., 1999):

Fungi:
- *Aspergillus* sp.: *A. aureus*, *A. awamori*, *A. ficuum*, *A. fischeri*, *A. flavus*, *A. nidulans*, *A. niger*, *A. phoenicis*
- *Cladosporium* sp.

Chrysosporium pannorum
Fusarium sp.: *F. oxysporum*
Penicillium sp.: *P. purpurogenum* var. *rubisclerotium*, *P. rugulosum*, *P. trzebinskii*
Streptomyces sp.: *S. rochei*

Bacteria:

Acetobacter sp.
Achromobacter sp.
Arthrobacter sp.
Bacillus sp.: *B. subtilis*
Clostridium sp.: *C. acetobutylicum*, *C. pasteurianum*, *C. thermoautotrophicum*, *C. thermosuccinogenes*
Escherichia coli
Flavobacterium multivorum
Pseudomonas sp.
Staphylococcus sp.

Yeast:

Candida sp.: *C. kefyr*, *C. pseudotropicalis*
Kluyveromyces sp.: *K. fragilis*, *K. lactis*, *K. marxianus*
Pichia sp.

Isolated inulinase is utilized for either batch hydrolysis of inulin or immobilization for flow-through column hydrolysis systems. For example, purified inulinase from *K. fragilis* has been immobilized on 2-aminoethyl cellulose (Kim et al., 1982).

To achieve high-purity fructose syrup, it is necessary to remove either inulin with a lower degree of polymerization before or the glucose after hydrolysis. Removing shorter-chain-length inulin can be achieved by chromatography, enzymatic removal, precipitation of higher molecular weight fractions using ethanol or low temperatures (Chabbert et al., 1985b), or ultrafiltration (Kamada et al., 2002). Enzymatic removal generally utilizes yeast strains whose fermentation of inulin is restricted to lower molecular weight fractions (e.g., *Saccharomyces cerevisiae*, *Saccharomyces diastaticus*) (Schorr-Galindo et al., 1995). The raw inulin is initially fermented, producing ethanol from the low molecular weight fraction. The residual high-dp inulin is then hydrolyzed using an exo-inulinase. Using this technique, both early- and late-harvest Jerusalem artichoke inulin can produce syrup of up to 95 and 90% fructose, respectively.

5.8.1.2 Partial Hydrolysis: Inulin Oligomers

Inulin oligomers are generally considered to be fructooligosaccharides with a degree of polymerization of <9. Within this group are the short-chain fructooligosaccharides with a degree of polymerization of 2 to 4. Inulin oligomers have a number of uses. For example, the short-chain fraction can be used for its nutraceutical prebiotic properties, and also as a sweetener in that it is around 45% the sweetness of sucrose.

Inulooligosaccharides are produced by either synthesis (see Section 5.6.3) or partial hydrolysis of higher molecular weight fractions (e.g., degree of polymerization of 20 to 25). The method of preparation of an oligomer fraction depends upon the range in degree of polymerization desired in the end product and that of the starting material. Jerusalem artichoke inulin has a lower degree of polymerization than chicory, and as harvest is delayed, it becomes progressively lower. Therefore, it is possible using ultrafiltration, chromatography, or other means to separate a lower molecular weight fraction without hydrolysis.

Typically, however, native inulin is fractionated to remove mono- and disaccharides and oligomers in the low-dp range. This can be accomplished using an exo-inulinase followed by separation of the mono- and disaccharides from the higher molecular weight polymers using a cation exchange

TABLE 5.8
Fermentation Products from Jerusalem Artichoke Tubers

Product	Microorganism	Max. Yield (%)	Reference
Ethanol	*Zymomonas mobilis*	100	Fuchs, 1987;
	Debaryomyces polymorphus		Barthomeuf etal., 1991
	Kluyveromyces marxianus var. *bulgaricus*		
	Kluyveromyces marxianus var. *marxianus*	96	
	Saccharomyces cerevisiae		
	Schwanniomyces occidentalis var. *occidentalis*		
	Torulaspora delbrückii		
Acetone-butanol	*Clostridium acetobutylicum*	38	Marchal et al., 1985
	Clostridium pasteurianum	27	
2,3-Butanediol	*Bacillus polymyxa*	43	Fages et al., 1986
Lactic acid	*Lactobacillus* spp.	—	Middlehoven et al., 1993
	Pediococcus pentosaceus	—	
	Streptococcus bovis	—	Shamtsyan et al., 2002
Succinic acid	*Clostridium thermosuccinogenes*	—	Drent and Gottschal, 1991;
			Drent et al., 1991; 1993

Source: Adapted from Fuchs, A., in *Science and Technology of Fructans*, Suzuki, M. and Chatterton, N.J., Eds., CRC Press, Boca Raton, FL, 1993, pp. 319–351.

column (Ca^{2+} form) or other methods (e.g., chromatography, ultrafiltration, crystallization). The longer-chain-length fraction is then hydrolyzed using an endo-inulinase (Vogel, 1996), yielding a mixture with relatively high levels of homooligomeric fructooligosaccharides (1 to 7 degrees of polymerization) with reducing ends and a fraction terminating in glucose. These can be chromatographically separated on a Ca^{2+}-loaded, strongly acidic cation exchange resin with low cross-linkage, yielding a fraction of >90% homooligosaccharides in the 2- to 7-dp range. This fraction can be hydrogenated with Raney nickel and hydrogen under pressure to produce fructosyl-mannitol and fructosyl-sorbitol (Vogel and Pantke, 1996).

5.8.2 Fermentation

Interest in bioconversion of polysaccharides into refined chemicals has vacillated with the market price of traditional sources. Due to its relatively low production cost, Jerusalem artichoke-derived inulin is an attractive feedstock for commercial production of several common reagents (e.g., ethanol, acetone, butanol, 2,3-butanediol, lactic acid, succinic acid) (Barthomeuf et al., 1991; Drent and Gottschal, 1991; Drent et al., 1991, 1993; Fages et al., 1986; Fuchs, 1987; Marchal et al., 1985; Middlehoven et al., 1993). Selection of the appropriate microorganism (Table 5.8) and fermentation conditions is essential for maximizing the yield of a desired component.

5.8.2.1 Ethanol

Jerusalem artichoke tuber mash, pulp and juice, and stem extract, the latter a temporary storage site for inulin prior to tuberization, have been utilized for ethanol production. The process includes saccharification of the inulin via acid or enzymatic hydrolysis, followed by fermentation (Lampe, 1932; Vadas, 1934) or the direct conversion to ethanol utilizing a microorganism that is capable of both hydrolysis and fermentation (Guiraud et al., 1981; Margaritis and Bajpai, 1982a, 1982b, 1982c). Initially acid hydrolysis was applied prior to fermentation with yeasts, such as *Schizosaccharomyces pombe*, or the bacterium *Zymomonas mobilis*, which are not capable of direct conversion; however, undesirable by-products are formed during the acid hydrolysis and the step

increases production costs. As an alternative, both hydrolysis and fermentation steps have been combined by using immobilized *Aspergillus ficuum*-derived inulinase and the yeast organism (Kim and Rhee, 1990); however, the maximum yield was lower than with direct fermentation.

The subsequent isolation of several species of yeast (e.g., *Kluyveromyces marxianus*) that can both hydrolyze inulin and convert the monosaccharide to ethanol has allowed eliminating the separate hydrolysis step. The efficiency of the conversion is a function of a number of process parameters (e.g., temperature, pH, nutrients added, degree of polymerization of the inulin, sugar concentration, method of fermentation). For example, higher molecular weight inulin can be precipitated by the ethanol formed, substantially decreasing the conversion efficiency (Guiraud et al., 1986). Likewise, the tolerance of the yeast strain to ethanol can also affect the conversion efficiency, which can be modulated by aeration or the addition of ergosterol and unsaturated fatty acids to the medium (Janssens et al., 1983).

Fermentation may be via batch or continuous fermentation systems (Bajpai and Bajpai, 1991; Guiraud and Galzy, 1990; Margaritis and Merchant, 1984). Other options include free vs. immobilized cells (Daugulis et al., 1981; Ryu et al., 1982) and the use of cell recycling (Cysewski and Wilke, 1977). For example, immobilized cells increased the alcohol productivity by 10× in contrast to a free cell system (Margaritis and Bajpai, 1982a, 1982b), and continuous fermentation increased ethanol synthesis 3.8× over batch fermentation (Kim and Ryu, 1993). However, the highest ethanol yields (expressed as percent of theoretical) typically are with batch rather than continuous culture systems (Fuchs, 1993), with yields reaching the 98 to 99% range. Cell immobilization allows their reuse, in some instances up to 11 times (e.g., *S. cerevisiae*), with relatively constant yield (~95%) (Barthomeuf et al., 1991). Using *K. marxianus* and typical Jerusalem artichoke dry matter yields·ha^{-1}, it is estimated that 7,500 to 8,500 l of ethanol·ha^{-1} or higher could be obtained (Bajpai and Bajpai, 1989; Guiraud et al., 1982). See Chapter 7 for further information on ethanol production using Jerusalem artichoke.

5.8.2.2 Butanol and Acetone

Several isolates of *Clostridium* species have been assessed in regard to their potential to form butanol and acetone under anaerobic conditions. *C. acetobutylicum* and *C. pasteurianum* are gram-positive anaerobic bacteria that produce butanol, acetone, and ethanol from inulin. The organisms utilize nearly all common plant sugars as substrates; therefore, acidic or enzymatic hydrolysis of inulin to fructose and glucose is an essential first step. Strains containing inulinase (2,1-β-D-fructan fructanohydrolase (EC 3.2.1.7)) activity are capable of hydrolyzing inulin directly. However, the level of activity varies widely, and even strains with relatively high hydrolysis potential benefit from supplemental enzyme. For example, using *C. acetobutylicum* and Jerusalem artichoke inulin, a medium with inulinase added (50 to 500 units·l^{-1}) was held under anaerobic conditions for 24 h at 35°C. Additional inulinase (375 units·l^{-1}) was then added and the fermentation continued for 40 h, yielding 13.5 g·l^{-1} butanol, 6.3 g·l^{-1} acetone, and 0.1 g·l^{-1} ethanol (Blanchet et al., 1985). *C. pasteurianum* var. I-53 gave a slightly higher total solvent yield due primarily to increased ethanol formation (Oiwa et al., 1987). Research continues on the identification of *Clostridium* strains (Montoya et al., 2000, 2001) that give superior butanol:acetone:ethanol ratios and total solvent yields.

5.8.2.3 Other Fermentation Products

Succinic acid has a diverse range of applications in the synthesis of specialty chemicals used in agriculture, foods, medicine, textiles, plating, and waste-gas scrubbing (Winstrom, 1978). Currently, succinic acid is produced via the hydrogenation of maleic anhydride to succinic anhydride and hydration to succinic acid (Winstrom, 1978; Zeikus et al., 1995). The thermophylic anaerobic bacteria *Clostridium thermosuccinogenes* can convert inulin to succinate and acetate as major

products (i.e., 0.36 g succinate·g hexose unit^{-1}) (Sridhar and Eiteman, 1999). Strain DSM 5809 produced the highest succinate using batch fermentation (pH 6.75 at 58°C). Maintaining the redox potential of the solution at ~275 mV gave the highest yield over higher or lower potentials.

2,3-Butanediol has a range of uses (e.g., fuel additive, intermediate in plastics and paints) and can be converted to 1,3-butadiene, methylethylketone, and several other useful chemicals (Fuchs, 1993). The bacterial species *Bacillus polymyxa* can convert Jerusalem artichoke juice to 2,3-butanediol (Fages et al., 1986). Maximum yield (44 g·l^{-1}) is strongly modulated by an oxygen transfer rate requiring a programmed decrease during batch culture.

Lactic acid has a number of applications in the food industry as well as nonfood uses. The bacterium *Pediococcus pentosaceus* has the ability to hydrolyze inulin via an exo-inulinase and convert it to lactic acid (Middlehoven et al., 1993). Likewise, a number of *Lactobacillus* sp. strains and *Streptococcus bovis* can form lactic acid from inulin (Shamtsyan et al., 2002).

5.8.3 Cyclization

5.8.3.1 Cyclic Inulooligosaccharides

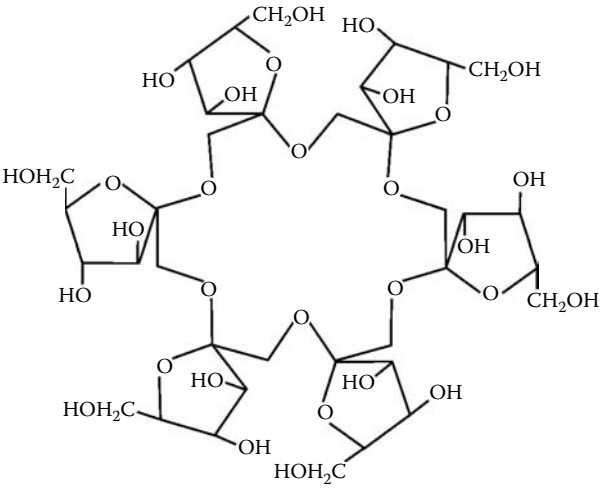
Inulin can be used to produce cyclic inulooligosaccharides in which the fructose chain closes back on itself, eliminating the presence of a reducing end (Figure 5.4). These compounds are thought to be potentially useful for food, drug, cosmetic, surfactant, catalyst, and purification and separation applications. The cyclic compounds contain six, seven, or eight fructose subunits (i.e., cycloinulohexaose (**1**), cycloinuloheptaose, cycloinulooctaose), with the distribution favoring the six-subunit form (i.e., 1.23, 0.44, and 0.09 g, respectively) (Oba et al., 1992). The primary attribute of these compounds is the presence of a hollow cavity in the center, which is surrounded by a relatively hydrophobic surface. This allows certain hydrophobic molecules to enter and form a stable inclusion complex. Cyclic inulooligosaccharides, for example, can be used to form water-soluble complexes with hydrophobic drugs, fragrances, or oil-based flavors (Okamura et al., 1997). They can also potentially be used in deodorizing sprays where they complex with odorants, thereby removing them.

Cycloinulohexaose is synthesized using *Bacillus circulans* (Kuwamura et al., 1989) or a similar microorganism containing a fructanotransferase (e.g., *B. polymyxa*, *B. subtilis*) in a shake-culture medium of inulin, yeast extract, and salts at 30°C for 30 h and then heated to 100°C for deactivation (Oba et al., 1992) or by using the cycloinulooligosaccharide fructanotransferase directly (Nanjo, 2004). Cycloinulohexaose has a characteristic 18-crown-6 skeleton (Figure 5.4) and forms 1:1 complexes with metal ions such as Ba^{2+} (Uchiyama et al., 1993). The permethylated derivative of a cycloinulohexaose has been synthesized and its metal binding association constants in acetone determined ($Li^+ < Na^+ < Cs^+ < K^+ < Ba^{2+}$) (Takai et al., 1994) (See Section 5.9.19). Interestingly, the metal ions are not found in the central cavity but rather in a pocket formed by the upper rim 3-OMe oxygens and the crown ether oxygens.

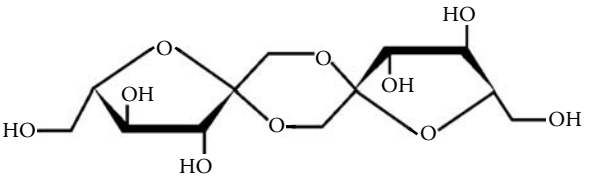
Other uses of cyclic inulooligosaccharides include the removal of harsh tastes from alcohol and spirits (Katsuragi and Nishimura, 1992) and the trapping of metal ions such as Ba^{2+}, K^+, Rb^+, Cs^+, Ag^+, and Pb^{2+} (Uchama, 1993).

5.8.3.2 Fructose Dianhydrides

Fructose dianhydrides (**2**) are dimers of fructose (Figure 5.4) that may be used as low-calorie sweeteners in foods. They also appear to act as prebiotics, causing a selective enhancement of beneficial microorganisms in the large intestines with accompanying health benefits (Gibson and Roberfroid, 1995). They are formed in relatively low amounts during the acid hydrolysis of inulin. Treatment of inulin with anhydrous hydrogen fluoride (Defaye et al., 1985) or citric acid (Christian et al., 2000) greatly increases the yield and gives a cross section of dianhydrides (i.e., 14, predominantly comprised of two fructose moieties) and oligomers derived from them (Manley-



1
Cycloinulohexaose



2
D-Fructose dianhydride I

FIGURE 5.4 Structure of cycloinulohexaose and D-fructose dianhydride, the most common cyclic fructosans derived from inulin.

Harris and Richards, 1996). Difructose anhydride III (α-D-fructofuranose-β-D-fructofuranose-2′,1:2,3′-dianhydride), one of the most common forms, can be produced by incubating inulin with the exo-acting inulin D-fructotransferase (EC 2.4.1.93; inulinase II) (Taniguchi and Uchiyama, 1982) or microorganisms possessing the enzyme. Difructose anhydride III is about one half the sweetness of sucrose and does not appear to be digested (Saito and Tomita, 2000). A cross section of microorganisms are capable of producing difructose anhydrides I, III, and V (i.e., *Arthrobacter* sp. H65-7, *Arthrobacter ureafaciens*, *Arthrobacter globiformis* C11-1, *Arthrobacter ilicis* OKU17B, *Pseudomonas fluorescens* no. 949, and *Bacillus* sp. snu-7 form difructose anhydride III; *A. globiformis* S14-3, *Arthrobacter* sp. MCI-2493, and *Streptomyces* sp. MCI-2524 form difructose anhydride I; and *Aspergillus fumigatus* forms difructose anhydride V). A technique for mass production of difructose anhydride III from inulin using *Arthrobacter* sp. H65-7 has been described (Saito and Tomita, 2000). Low levels of fructose and linear oligosaccharides are subsequently removed using baker's yeast. At low inulin concentrations, the yield is 93%.

Ingestion of difructose dianhydride III improves the population and properties of the microorganisms in the intestines, but apparently differently from other oligosaccharides (Saito and Tomita, 2000). Likewise, it improves calcium absorption in the small intestine via a mechanism that appears to differ from other known stimulants.

5.9 CHEMICAL MODIFICATION OF INULIN

Inulin represents a renewable resource that can be modified to form a cross section of products, many of which have superior attributes to similar products derived from glucose polysaccharides. Modification of inulin expands the amount and type of functional properties available, opening the door to many new uses. Most of these compounds are readily biodegradable. To date, there are over 17,000 citations for inulin in chemistry abstracts. The chemical modification of inulin, pioneered by the work of Dorine Verraest and Herman van Bekkum in the Netherlands, and Takao Uchiyama in Japan, has been reviewed by Fuchs (1987), Verraest (1997), and Stevens et al. (2001). The following critiques a portion of the diverse range of potential chemical modifications of inulin.

5.9.1 Reduction

An inherent problem with reducing sugars (e.g., glucose, fructose, and fructosylfructose) is their tendency to undergo undesirable discoloration and side reactions under alkaline conditions or at high temperature. Inulin also has sufficient residual reducing power to discolor (Kuzee, 1997). Exposure of inulin to a reducing agent or by electrochemical reduction prior to subsequent modification minimizes potential color alterations.

5.9.2 Hydrolysis

In addition to enzymatic hydrolysis (see Section 5.8.1), inulin can be hydrolyzed chemically and subsequently dehydrated to yield hydroxymethylfurfural (van Dam et al., 1986), a key industrial chemical (Gretz et al., 1993; Fuchs, 1987; Kunz, 1993; Makkee et al., 1985; van Dam et al., 1986). Likewise, catalytic hydrogenation of D-fructose yields D-mannitol and D-sorbitol mixtures from which mannitol can be removed via crystallization (Fuchs, 1987).

5.9.2.1 Hydroxymethylfurfural

Hydroxymethylfurfural is a key industrial chemical that has a wide range of applications. It is a good starting material for the synthesis of precursors (e.g., 2,5-furandicarbaldehyde, 2,5-furandicarboxylic acid) of pharmaceuticals, thermoresistant polymers, and complex macrocycles (Fuchs, 1987; Gretz et al., 1993; Kunz, 1993; van Dam et al., 1986). Using aromatic diamines and 2,5-furanic dicarboxylic acid derived from the oxidation of hydroxymethylfurfural or its dichloride, furan-containing polyamides have been prepared (Fuchs, 1987; van Dam et al., 1986). It can be synthesized by heating inulin in an acidic media, where the parent molecule is first hydrolyzed to fructose and then dehydrated to hydroxymethylfurfural. Yields of 80% can potentially be obtained (Kuster and van der Wiel, 1985). Losses due to side reactions such as rehydration to levulinic acid can occur, especially during distillation; however, acetylation of hydroxymethylfurfural to acetoxymethylfurfural reduces losses (Nimz and Casten, 1985).

5.9.2.2 Mannitol

D-Mannitol has a diverse range of industrial applications. It is a nonhydroscopic, low-calorie, noncariogenic sweetener utilized by the food industry as well as a feedstock for the synthesis of other compounds. For example, mannitol can be oxidized at the 3 or 4 position to form two molecules of glyceraldehyde or glyceric acid, which can be used as building blocks for other compounds (Heinen et al., 2001; Makkee et al., 1985; van Bekkum and Verraest, 1996). Mannitol is formed from inulin via hydrolysis followed by catalytic hydrogenation. This yields mannitol and sorbitol from which the mannitol can be readily crystallized (Fuchs, 1987). Currently mannitol is primarily synthesized from starch.

5.9.3 Hydrogenolysis

The reaction of inulin with hydrogen gas in the presence of a catalyst results in cleavage, similar to the role of water in hydrolysis, and the formation of polyols such as glycerol, 1,2-propanediol, and ethylene glycol. Yields of up to 60% glycerol have been achieved (Fuchs, 1987).

5.9.4 Esterification

Esters of polysaccharides such as inulin have a diverse range of applications depending upon the chain length of the carbohydrate portion and the esterified component. Inulin esters (Figure 5.5) can be formed by reaction with acid chlorides or with anhydrides of certain carboxylic acids in which the introduced alkyl chain is typically from C_{12} to C_{22} (**3**) altering the compound's surface tension. The products produced can be varied by altering the length of the alkyl chain or degree of substitution, giving a diverse range of properties. Those with short chain lengths and low degrees of substitution decrease surface tension and may be used as nonionic surfactants, binders in paints, and softeners. With higher degrees of substitution they can be used as plasticizers (Bognolo, 1997). With longer alkyl chains, inulin esters are useful as textile sizing agents, film and fiber thickeners, and polymeric surfactants in detergents or emulsifiers in cosmetics (Ehrhardt et al., 1997; Rogge and Stevens, 2004). Copolymeric surfactants consist of an A and a B chain, the former (e.g., an alkyl chain) being randomly grafted on to the B chain (e.g., inulin or other polysaccharide).

Esterification of succinic anhydride in dimethylformamide with 4-dimethylaminopyridine gives *O*-succinoylated inulin (Vermeersch and Schacht, 1985), which can be used as a drug carrier. Esterification of alkenyl succinic anhydrides having chain lengths of C_8 to C_{20} in dimethylformamide, with or without a catalyst, produces potential deflocculating agents for use in detergents

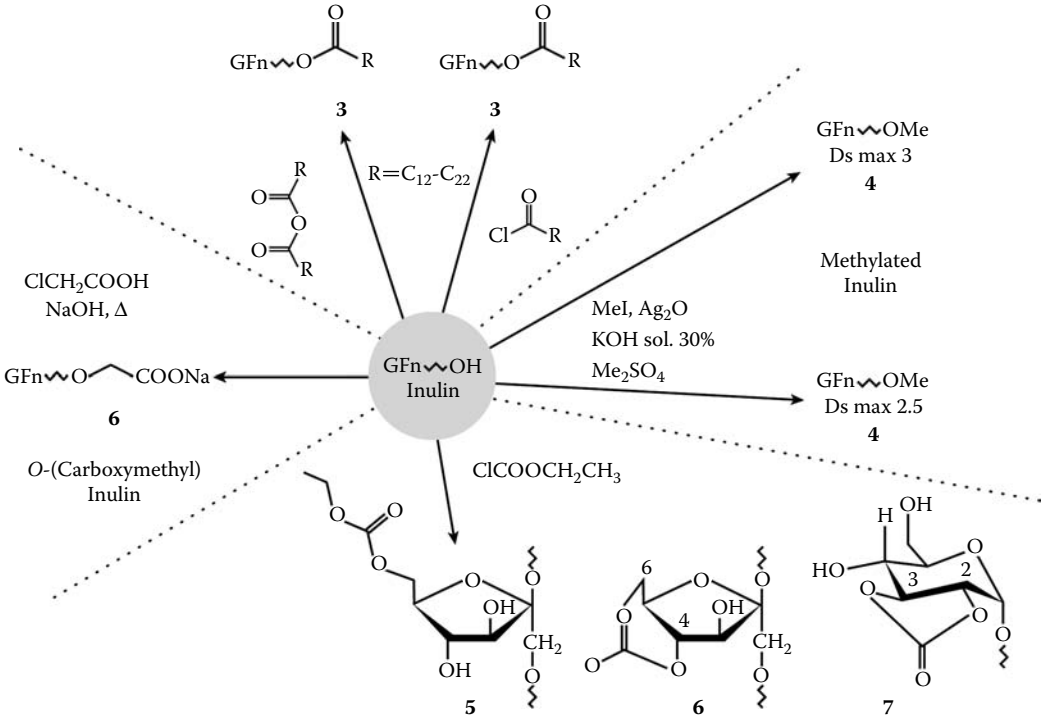


FIGURE 5.5 Synthesis of inulin esters, methylated inulin, inulin carbonates, and *O*-(carboxymethyl) inulin.

(Brouwn et al., 1996). When 50% of the hydroxyl groups are esterified with unbranched fatty acids (C_8 to C_{24}) and the remaining esterified with C_1 to C_7 acid chlorides (e.g., acetyl chloride), the resulting product is useful as a crystallization modifying agent in triglyceride fractionation (van Dam et al., 1999). Inulin can also be esterified using fatty acid methyl esters (Rogge and Stevens, 2004).

5.9.5 Methylated Inulin

Complete methylation of inulin (**4**) can be achieved by reaction with potassium hydroxide solution followed by the addition of dimethyl sulfate (Figure 5.5) (Irvine and Steele, 1920; Irvine and Montgomery, 1933; Irvine et al., 1922). Alternatively, complete methylation can be accomplished using methyl iodide and silver oxide (Karrer and Lang, 1921; Vaughn and Robbins 1975). Trimethyl inulin can be hydrolyzed to form 3,4,5-trimethylfructofuranose (Smeekens et al., 1996).

5.9.6 Inulin Carbonates

Inulin carbonate can be synthesized with ethyl chloroformate in dimethyl sulfoxide with triethylamine as the catalyst (Figure 5.5) (Kennedy and Tun, 1973). This yields a mixture of two products: one with *O*-ethoxycarbonyl groups (**5**) and the second with *trans*-4,6-carbonate (**6**) on the fructofuranose groups of the inulin chain and a *trans*-2,3-cyclic carbonate on the terminal glucose (**7**). Inulin carbonates have utility in the insolubilizaton of biologically active molecules such as enzymes or immunoglobulins.

5.9.7 *O*-(Carboxymethyl)inulin

An assortment of mono-, oligo- and polysaccharides have been carboxymethylated (e.g., cellulose, sucrose) for a diverse range of applications. Carboxymethylation of a polysaccharide involves primary or secondary alcohol groups being esterified with carboxymethyl groups. Inulin can be carboxymethylated in an aqueous alkaline solution by reacting with monochloroacetic acid (Figure 5.5) forming *O*-(carboxymethyl)inulin (**8**) (Verraest et al., 1996a). The degree of substitution is affected by the ratio of inulin to monochloroacetic acid and the reaction temperature. As the degree of substitution increases (i.e., >1.0) and the degree of polymerization increases (i.e., average of 30 or above), its effectiveness in inhibiting the precipitation of calcium carbonate increases. *O*-(Carboxymethyl)inulin displays a very low viscosity in aqueous solutions, and in certain applications, this is a distinct advantage over *O*-(carboxymethyl)cellulose.

Inhibition of the precipitation of calcium carbonate is one potential commercial application for *O*-(carboxymethyl)inulin. The formation of calcium carbonate crystals is a major problem in boilers, heat exchangers, saltwater desalination, gas and oil production, laundry, and other fields. As the water temperature increases, the solubility of calcium carbonates decreases, resulting in crystallization/scale formation/incrustation, decreasing the efficiency of the operation and increasing costs.

Certain compounds can inhibit the growth of calcium carbonate crystals via several avenues (e.g., absorption on the surface of the crystal inhibiting subsequent additions, dispersing the calcium carbonate within the solution, and sequestering the calcium ions (Hudson et al., 1988; Nagarajan, 1985; Verdoes, 1991)). Current inhibitors tend to be nonbiodegradable; hence, more environmentally sound chemicals that inhibit crystallization would be advantageous. The introduction of carboxylate groups on inulin by way of carboxymethylation forms *O*-(carboxymethyl)inulin that acts as an effective inhibitor of calcium carbonate precipitation.

The effectiveness of *O*-(carboxymethyl)inulin in preventing calcium carbonate crystallization is related to the carboxylate content, chain length of the inulin molecule, and concentration of the compound within the solution (Verraest et al., 1996b). A high degree of substitution (i.e., >1) and polymerization of the inulin backbone (i.e., an average degree of polymerization of 30) increases

the degree of inhibition. The lower the viscosity of *O*-(carboxymethyl)inulin relative to *O*-(carboxymethyl)cellulose makes it superior to the latter (Verraest et al., 1996c).

O-(Carboxymethyl)inulin acts as a polyelectrolyte that can be used as a dispersing agent or metal ion carrier. Carboxymethyl cellulose, for instance, is used as an antiredeposition agent in detergents, in the oil, paper, textile, and mining industries, and as a thickener in foods and drug preparations. Hundreds of thousands of tons of the latter are used per year.

O-(Carboxymethyl)inulin also has excellent potential as a detergent builder. Detergents are cleaning substances that aid in the removal of dirt, acting mainly on the oily films that trap dirt particles. In addition to laundry and dishwashing uses, detergents are used in toothpastes, shampoos, dry-cleaning solutions, antiseptics, and other applications. Builders are substances that are added to detergents to enhance their cleaning function. The use of polysaccharides such as inulin for the synthesis of builders is advantageous in that they are nontoxic, represent a renewable resource, and are generally biodegradable. Certain derivatives of inulin improve the function of detergents via several mechanisms (e.g., enhanced stain removal, acting as a sequestering or thickening agent, altering the surface tension). For example, the addition of 2% carboxymethyl inulin increases the stain (tea and wine) removal ability of detergents (Feyt, 2004), while the added fructan polycarboxylic acids act as sequestering agents (Kuzee and Raaijmakers, 2001). Propoxylated and quaternized inulin functions as a thickening agent in dishwashing detergents and shampoos (Rathjens and Nieendick, 2001).

5.9.8 Inulin Ethers

Etherification of inulin with *O*-carboxymethyl groups forms a polycarboxylate (Chien et al., 1979) that can be further modified to facilitate its conjugation with erythrocytes for immunological assays. Even with an excess of monochloroacetate, products with a degree of substitution of only about 0.1 are obtained.

Etherification with epoxides, such as ethylene oxide or propylene oxide, in aqueous medium in the presence of a basic catalyst yields *O*-hydroxyalkyl derivatives (**11**, **12**) (Figure 5.6). The degree of substitution varies with the amount of epoxide ranging from 0.1 to 2. As the chain length of the epoxide increases, the water solubility decreases; however, small amounts of 2-propanol increase the solubility.

To enhance the drug carrier properties of inulin, it has been reacted with epichlorohydrin, the product of which is highly reactive and couples readily with substances containing amino groups (Schacht et al., 1984). The 3-chloro-2-hydroxypropyl derivative (**9**) of inulin is formed in reaction with epichlorohydrin. Likewise, an allyl bromide derivative (**10**) can be prepared using sodium hydroxide as a catalyst (Tomecko and Adams, 1923).

Inulin etherification products have utility in cosmetics or pharmaceuticals as carriers for water-insoluble substances or to stabilize aqueous solutions of compounds with low water solubility. They may also be used as emulsifiers or as an additive in textiles and paper and as softeners of thermoplastic polymers (Kunz and Begli, 1995).

5.9.9 Dialdehyde-Inulin

Dialdehyde-inulin is formed through the oxidation of neighboring hydroxyl groups to aldehyde functions (Figure 5.6). This is accomplished using periodate as the oxidizing agent (Painter and Larsen, 1970). Six-membered hemiacetal rings form by intramolecular reaction between the aldehyde groups of oxidized fructose residues on the inulin chain and the closest hydroxyl groups on neighboring unoxidized fructose residues. An equilibrium is thought to be established between the free aldehyde (**13**) and hemiacetal (**14**) forms. The hemiacetal function, however, reduces the accessibility of the aldehyde function, decreasing the potential for subsequent reactions (Stevens et al., 2001).

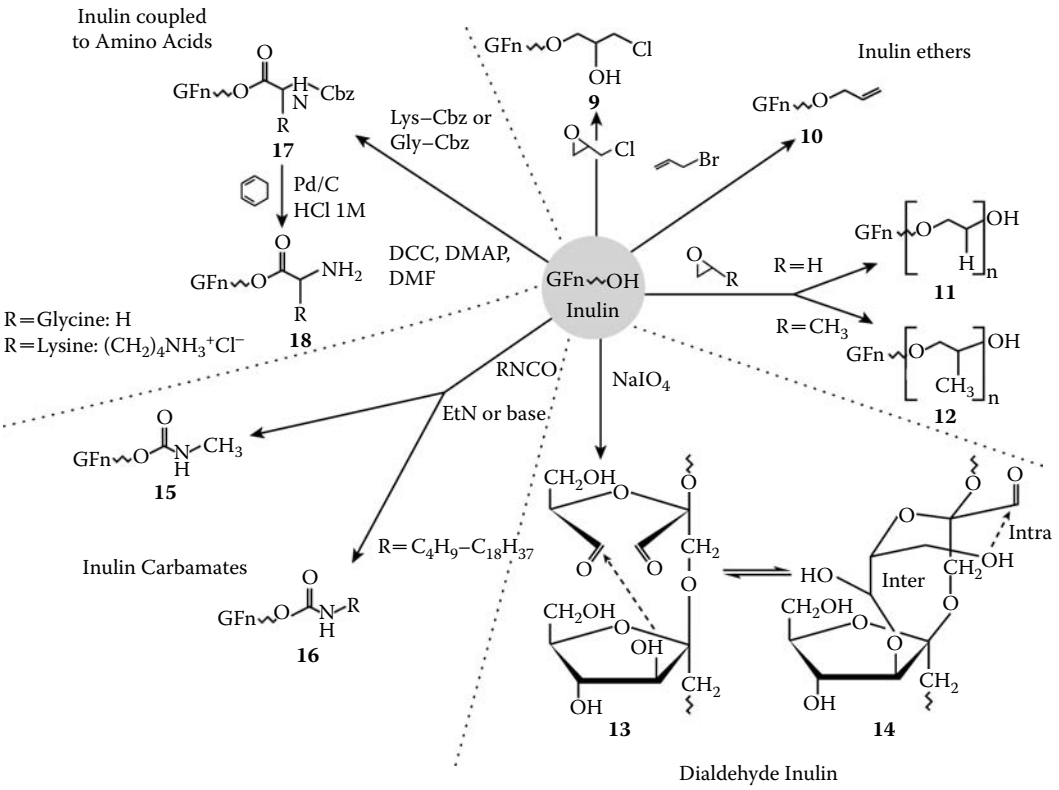


FIGURE 5.6 Synthesis of inulin ethers, dialdehyde-inulin, inulin carbamates, and inulin coupled to amino acids.

5.9.10 Inulin Carbamates

Inulin can be modified to carbamates using methyl isocyanates with a basic catalyst. Inulin carbamates can be used in chromatography applications as packed columns, as coating in capillary columns, or as spun fiber columns (Okamoto and Hatada, 1985). Carbamoylation with a range of alkyl isocyanates results in a variety of inulin carbamates (**15**, **16**) (Figure 5.6) (Stevens et al., 2001) that have industrial applications in suspensions (solid/liquid) and emulsions (liquid/liquid). Inulin carbamates are grafted copolymers with the alkyl groups (C_4H_9 to $C_{18}H_{37}$) randomly distributed on the polyfructose backbone. The alkyl groups represent the B chains, which become strongly absorbed on a hydrophobic surface such as an oil droplet (Tadros et al., 2004). Such inulin-based surfactant emulsions tend to have large droplets that can be reduced using a cosurfactant. Inulin carbamate emulsions are very stable (i.e., >1 year) at temperatures up to 50°C and at high electrolyte concentrations (Tadros et al., 2004). Various inulin carbamates may be suitable as surfactants for household and industrial applications such as detergents, emulsifiers, emulsion stabilizers, foam stabilizers, and wetting agents (Stevens et al., 1999).

5.9.11 Inulin–Amino Acids

Covalent bonding of an amino acid to inulin (Figure 5.6) allows further chemical modification of the polymers for possible medical use, peptide synthesis, or producing chelating agents for metal ions. The terminal primary amino acid could be more reactive toward acylating agents and potentially allow the attaching of a cross section of molecules of interest. Such compounds are attractive since both amino acids and inulin are expected to be nontoxic, biocompatible, and biodegradable

(Won and Chu, 1998). Lysine and glycine have been esterified to inulin using the respective *N*-protected amino acid (*N*,*N*-di-benzylocarbanyl-L-lysine; *N*-benzylocarbonyl-glycine) (**17**) and a two-step process in the presence of a catalyst ((dimethylamino) pyridine) and a condensing agent (dicyclohexyl carbodiimide). The amino groups are then deprotected (**18**) by hydrogenation using cyclohexadiene with palladium and activated carbon as catalyst.

5.9.12 *O*-(Cyanoethyl)inulin

The cyanoethylation of polysaccharides has been studied extensively in starch and cellulose. The hydroxyl groups (typically the C-4) on the molecule react with acrylonitrile in the presence of alkali to form a cyanoethyl ester. *O*-Cyanoethylated cellulose is used in the paper industry to enhance the mechanical strength, heat resistance, and microbiological resistance of the paper. Cyanoethylated starch is used in the textile industry.

The addition of cyanoethyl groups to inulin (Figure 5.7) results in a compound that can be modified to a number of products in that the nitrile groups are reactive and can be readily converted to other functional groups. The advantages of these compounds over those derived from cellulose and starch are a generally lower viscosity and solubility (Verraest et al., 1996b). For example, an amine (i.e., *O*-(aminopropyl)inulin), *O*-(carboxymethyl)inulin, and an amidoxime can be produced. *O*-(Cyanoethyl)inulin (**19**) is formed by reacting inulin (inulin/water/NaOH) with acrylonitrile at 45°C. The degree of substitution varies, and as it increases, the solubility decreases (i.e., a degree of substitution of >1.5 is insoluble) (Verraest et al., 1996c).

5.9.13 *O*-(3-Amino-3-oxopropyl)inulin

To convert a nitrile into an amide by hydration requires strongly acidic or basic catalysts; however, with *O*-(cyanoethyl)inulin (**19**) such conditions cause glycosidic bond cleavage and decyanoethylation to occur (Verraest, 1997). The nitriles of *O*-(cyanoethyl)inulin can be converted to amides by the use of metal ion catalysis (Ghaffar and Parkins, 1995) or by using hydrogen peroxide (Vaughn and Robbins, 1975; Verraest et al., 1995). The latter is a strong nucleophile that hydrolyzes the nitrile group, forming an intermediate percarboxylic imide that decomposes into the amide, *O*-(3-amino-3-oxopropyl)inulin (**20**) (Figure 5.7) (Verraest, 1997). This is accomplished by reacting *O*-(cyanoethyl)inulin with two molar equivalents of hydrogen peroxide at pH 9.5 and 60°C for 1 h (Verraest et al., 1996c). The degree of substitution was 0.66 to 0.68 and the amount of decyanoethylation low (i.e., 5 to 6%). Alternatively *O*-(3-amino-3-oxopropyl)inulin can be synthesized by reacting acrylamide with inulin, giving a degree of substitution of 1. The compound can be used as an emulsifier or surfactant.

5.9.14 *O*-(Carboxyethyl)inulin

Hydrolysis of the amide groups on *O*-(3-amino-3-oxopropyl)inulin (**20**) using aqueous sodium peroxide yields *O*-(carboxyethyl)inulin (**21**) (Figure 5.7). There is some chain length degradation in the hydrolysis when sodium peroxide is used, and the degradation is greater in fractions with higher degrees of substitution. *O*-(Carboxyethyl)inulin can be used to inhibit the precipitation of calcium carbonate, especially when it has a lower degree of substitution (i.e., 0.65).

5.9.15 *O*-(3-Hydroxyimino-3-aminoproply)inulin

O-(3-Hydroxyimino-3-aminoproply)inulin can be synthesized from *O*-(cyanoethyl)inulin (**19**) by reaction with hydroxylamine in a neutral medium (Figure 5.7), giving about 80% conversion (Verraest, 1997). The amidoximes can be found in two forms (**22**, **23**), the *syn*-hydroxyimino being the most stable. Amidoximes are particularly reactive compounds and will effectively chelate transition cations such as Cu^{2+} (**24**).

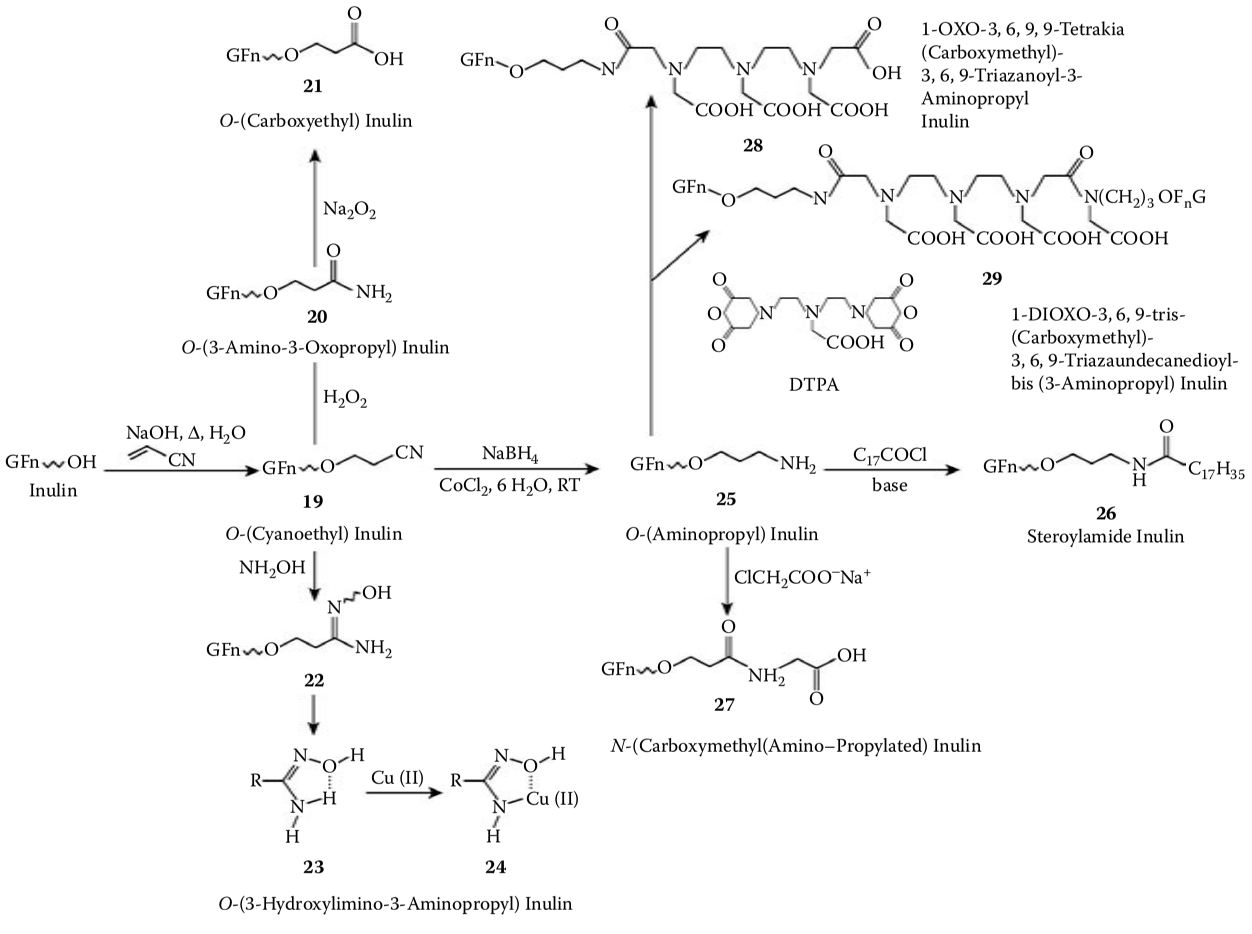


FIGURE 5.7 Synthesis of *O*-(cyanoethyl) inulin, *O*-(3-amino-3-oxopropyl) inulin, *O*-(carboxyethyl) inulin, *O*-(3-hydroxylimio-3-aminopropyl) inulin, *O*-(aminopropyl) inulin, steroyl amide inulin, *N*-carboxymethyl(aminopropylated) inulin, 1-oxo-9-tetrakia(carboxymethyl)-3,6,9-triazanoyl-3-aminopropyl inulin, and 1,11-dioxo-3,6,9-tris-(carboxymethyl)-3,6,9-triazaundecanedioyl-bis(3-aminopropyl) inulin.

5.9.16 *O*-(Aminopropyl)inulin

O-(Cyanoethyl)inulin (**19**) can be reduced to an amine, *O*-(aminopropyl)inulin (**25**), by several methods: (1) using sodium borohydride in the presence of cobalt chloride hexahydrate (Figure 5.7) (Satoh et al., 1969); (2) catalytic hydrogenation (Verraest, 1997); and (3) using a metal (sodium, lithium, or calcium) in liquid ammonia and methanol (Doumaux, 1972; Schroter and Möller, 1957). Only about 10% of the cyanoethyl groups are converted to *O*-aminopropyl groups, and this decreases with increasing chain length and degree of substitution. The yield can be substantially increased through the addition of ammonia to the reaction (Bikales, 1971) or an acid. When using method 3, the addition of methanol as a cosolvent and proton source increases the yield to about 70% (Popovych and Tomkins, 1981).

5.9.17 Stearoyl Amide and *N*-Carboxymethylaminopropylated Inulin

O-(Aminopropyl)inulin (**25**) can be converted to stearoyl amide inulin (**26**) using stearoyl chloride (Figure 5.7). Steroyl amide inulin has utility as a surfactant or emulsifying agent. *O*-(Aminopropyl)inulin can also be converted to *N*-carboxymethylaminopropylated inulin (**27**) by reaction with sodium chloroacetate. It has utility as a sequestering agent for detergents, a crystallization inhibitor of calcium carbonate, and a dispersing agent (Stevens et al., 2001).

5.9.18 Derivatives of *O*-(Aminopropyl)inulin

Reaction of *O*-(aminopropyl)inulin with diethylenetriaminepentaacetic acid (DTPA) (Figure 5.7) yields 1-oxo-3,6,9,9-tetrakia(carboxymethyl)-3,6,9-trisazanonanoyl-3-aminopropyl inulin (**28**) and 1,11-dioxo-3,6,9-tris(carboxymethyl)-3,6,9-triazaundecanedioyl-bis(3-aminopropyl)inulin (**29**); both products are thought to be good contrasting agents when complexed with Gd or Dy (Verraest et al., 1996a) and potentially have a diverse range of applications, from medical diagnostics to basic research. For example, gadolinium (Gd^{3+}) complexed with diethylenetriaminepentacetate (GdDTPA) enhances the contrast of magnetic resonance images. Macromolecule carriers for drugs are used to facilitate organ selectivity and prolong drug lifetime in the vascular system. Conjugates of inulin and GdDTPA are formed by reacting inulin with DTPA bisanhydride in a dry organic solvent (Armitage et al., 1990; Rongved and Klaveness, 1991), and the Gd^{3+} complex formed by adding the hexahydrate of $GdCl_3$. A variation of this (i.e., replacing the central pendant arm by a phosphinic acid functional group) gives a molecule with an average molecular weight of 23,110 and an average number of Gd^{3+} ions per mole of 24 (Lebduskova et al., 2004).

5.9.19 Cycloinulohexaose Derivatives

Cycloinulohexaose can be derivatized to additional structures of interest (Figure 5.8), e.g., fructosylated branched cyclic inulooligosaccharides (Kushibe and Morimoto, 1994), or cross-linked to give a solid electrolyte (Shimofusachi, 1998). When esterified to fatty, benzoic, or other acids, cycloinulohexaose can potentially be used as an oily base, oily gelation agent, or film-forming agent for cosmetics (Shimizu and Suzuki, 1996). Modification of cycloinulohexaose via sulfonylation of the primary hydroxyl with 2-naphthalenesulfonyl chloride yields three possible isomers (**30** to **32**) (Atsumi et al., 1994). Subsequent treatment with thiophenol/Cs_2CO_3 yields the sulfite of each isomer (**33** to **35**). Cycloinulohexaose may also be permethylated, peracetylated, or perbenzoylated (Takai et al., 1994).

5.9.20 Oxidation

By altering the degree of oxidation, a diverse range of potential products can be formed from inulin. For example, selective oxidation yields polycarboxylates, having a number of possible applications.

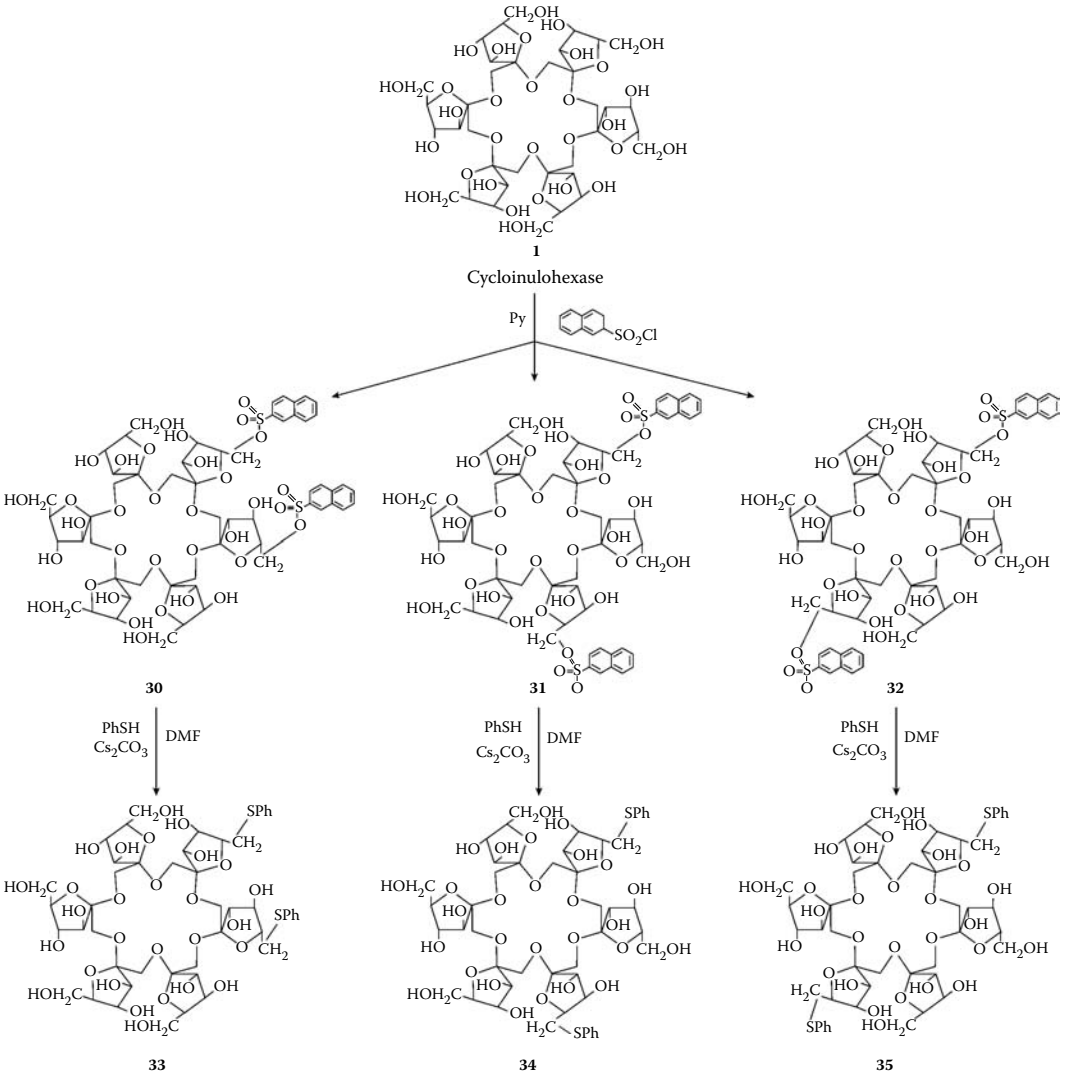


FIGURE 5.8 Synthesis of derivatives of cycloinulohexaose.

Limiting the oxidation to the primary hydroxyl groups on the fructofuranoside subunits yields polyuronates, which are thought to display similar properties to natural polyuronates, such as the industrial gum alginate (Clare, 1993) and pectate (Rolin, 1993). More extensive glycolic oxidation, in contrast, results in ring opening and the formation of polycarboxylates that have potential as calcium binding agents. Such compounds may represent commercial substitutes for existing non-biodegradable synthetic polycarboxylates (polyacrylate type) currently used in detergent formulations (Besemer, 1993; Floor, 1989).

5.9.20.1 Selective Oxidation of the Primary Hydroxyl Group

The direct oxidation of hydroxyls on inulin allows the potential introduction of carbonyl and carboxyl groups, altering the properties of the polysaccharide and opening additional commercial applications (Bragd et al., 2004). The primary hydroxyl in the C-6 position on the fructofuranoside subunits can be selectively oxidized using 2,2,6,6-tetramethyl-1-piperidinyloxy (TEMPO). This forms a stable radical that can be oxidized by hypobromite, or similar reagent, to give a nitrosonium

ion (Bragd et al., 2004; de Nooy et al., 1994, 1995). The preferred reaction pH is 9.5 (de Nooy, 1997); however, at pH 10.5, 6-carboxy-inulin is formed with a good yield (82%) (de Nooy et al., 1995). A variation in this approach utilizes 4-acetamido-2,2,6,6-tetramethyl-piperidine-1-oxyl (4-acNH-TEMPO) and peracetic acid or monoperoxysulfate as the oxidant, the former giving the better conversion efficiency (Bragd et al., 2002).

Platinum (catalyst) and molecular oxygen (oxidant) have been used to selectively oxidize carbohydrates (Abbadi and van Bekkum, 1996; Gallezot and Besson, 1995) such as sucrose (Fritsche-Lang et al., 1985; Kunz and Recker, 1995). Inulin is readily oxidized using O_2 and platinum in the presence of sodium hydroxide (Verraest et al., 1998). Oxidation occurs selectively at the C-6 position with a relatively high yield (79%). Sucrose is also selectively oxidized at the C-6 and C-6′ positions under similar conditions (Edye et al., 1991, 1994). The molecular weight of the inulin influences the reaction rate and degree of oxidation. Nystose (GF_3) had a degree of oxidation of 40%. As the chain length increases, the degree of oxidation declines. Inulin with an average degree of polymerization of 10 had a degree of oxidation of 28%, while at an average degree of polymerization of 30, it decreased to only 20%. In addition, the amount of by-products increases with increasing chain length and degree of oxidation.

5.9.20.2 Glycolic Oxidation

Glycolic oxidation involves ring opening and can be accomplished in several ways. In a two-step oxidation process, sodium periodate is used to convert the glycolic subunits to the dialdehyde form, followed by reaction with sodium chlorite or sodium chlorite and hydrogen peroxide to form dicarboxy-inulin (Besemer and van Bekkum, 1994d). Inulin prepared in this manner, however, has a poor calcium binding capacity (Nieuwenhuizen et al., 1985), possibly due to the formation of relatively stable hemiacetals in the first step (Besemer and van Bekkum, 1994a). If the pH is lowered (i.e., to pH 2.5 to 3.0), a high yield (i.e., 99%) of dicarboxy-inulin is formed with good calcium-sequestering capacity (2.58 $mmol \cdot g^{-1}$) (Besemer et al., 1995). Dialdehyde-inulin may also be coupled with amine-carrying molecules such as drugs via Schiff base formation and subsequent reduction.

Inulin oxidation can also be accomplished in a single step via direct oxidative cleavage of the glycolic units with sodium hypochlorite in the presence of sodium bromide, which increases the yield and reaction rate (Besemer and van Bekkum, 1994a, 1994b, 1994c, 1994d). Dicarboxy-inulin is formed in a high yield (80 to 95%) and has a calcium carbonate binding capacity (2.0 to 2.5 $mmol \cdot g^{-1}$) comparable to that of commercial detergent builders (Besemer, 1991; Besemer and van Bekkum, 1994a).

These products are of particular interest due to their calcium binding capacity (Nieuwenhuizen et al., 1983). Each oxidized fructofuranoside subunit on the inulin molecule provides an oxydiacetate unit that can bind calcium. As a consequence, there is a linear relationship between the degree of oxidation of the molecule and its calcium-sequestering capacity (Besemer and van Bekkum, 1994d). In contrast, α-1,4-glucans require two neighboring glucopyranoside subunits to be oxidized to sequester calcium, making their efficiency much lower than that of dicarboxy-inulin, especially at lower degrees of oxidation (Besemer and van Bekkum, 1994d). As a consequence, even partially oxidized inulin can be used in detergent formulations, where they are expected to exhibit greater biodegradability than when completely oxidized. Biodegradability makes inulin-derived calcium binding agents of greater utility than existing nonbiodegradable synthetic polyacrylate-type polycarboxylates (Besemer and van Bekkum, 1994d).

5.9.21 Alkoxylated Inulin

Inulin alkoxylates are reported to have surface-active, emulgating, and stabilizing properties. They may also be further altered via reaction with other epoxides. Initial synthesis methods utilized

aqueous solutions with sodium hydroxide as the catalyst; however, the yield was generally only around 80% and substantial amounts of glycols were formed (Cooper, 1993; Kunz and Begli, 1995). Alkoxylation in a water-free system (i.e., *N*-methylpyrrolidinone as the solvent) with either ethylene oxide or propylene oxide, and using triethylamine as a basic catalyst, produces alkoxylated inulins without the formation of alkylene glycols (Rogge et al., 2004). Purification of inulin ethoxylates utilizes supercritical CO_2 extraction, the method varying with the chemistry of the derivative. If the theoretical molar substitution is less than 2, liquid–solid extraction is used; if greater than 2, liquid–liquid extraction is required. The compounds have increased water solubility, moderate surface activities, and very high cloud points in electrolyte media. Inulin ethoxylate with a theoretical degree of substitution of 0.5 confers beneficial effects when used as an additive in water-blown polyurethane foams (Rogge et al., 2005).

5.9.22 Inulin Phosphates

Mono- and diphosphates of inulin have been produced by esterifying inulin using mixed acetic–adipic acid anhydride and sodium trimetaphosphate (Berghofer et al., 1993a). Inulin phosphates are thermally reversible gels that display an increased viscosity compared to inulin. They are in a stable gel form at room temperature, with the viscosity remaining fairly constant over a relatively wide temperature range, but melting at about 60°C. Phosphate derivatives can also be formed using phosphorous oxychloride in pyridine (Ludtke, 1929).

5.9.23 Complexing Agents

Inulin can be modified to compounds that display good heavy metal complexing properties similar to ethylene diamine tetra-acetic acid (EDTA) but with better biodegradation properties (Bogaert et al., 1998). Inulin is first oxidized using sodium periodate to the dialdehyde, and then reduced to a polyol using Pt/C and hydrogen. The polyol can then be modified with carbon disulfide to form xanthate or with SO_3-pyridine to obtain an inulin sulfate. Alternatively, the dialdehyde can be aminated with diaminoethane and sodium cyanoborohydride and the product reacted with monochloroacetic acid sodium salt to form carboxymethylamino inulin. Each of these compounds can be used to precipitate heavy metals.

5.9.24 Cationic Modification

Cationic inulin containing a nitrogen group can be formed using several reagents (Kuzee et al., 1998). Other modified inulins (e.g., hydroxyalkylated, carboxymethylated, oxidized) can also be subjected to cationic modification to yield compounds with better solubility, lower viscosity, and better degradation properties than similar compounds derived from other polysaccharides. Such products have potential utility as disinfectants, hair conditioners, molding gels, flocculants, corrosion inhibitors, demulsifiers, textile additives, and adhesives.

5.9.25 Cross-Linked Inulin

Higher molecular weight inulin forms gels under appropriate conditions; however, for certain applications (e.g., drug delivery), it is desirable to increase the gel stability through the formation of covalent cross-links between neighboring molecules (Grinenko et al., 1998). The initial step in cross-linking involves methacrylation of the inulin using glycidyl methacrylate (Vervoort et al., 1997) in the presence of (dimethylamino)pyridine as catalyst. Methacrylation of inulin occurs at carbon C-6 with a degree of substitution ranging from 0.015 to 0.1, representing approximately 0.7 to 0.8% of the theoretical maximum substitution. Free radical polymerization is then instigated using ammonium persulfate or *N*,*N*,*N*′,*N*′-tetramethylenediamine, which converts the double bonds to covalent cross-links. The rigidity and biogradability of the hydrogel is related to its concentration

in the initial solution and degree of substitution (Vervoort et al., 1998c). Such gels allow sequestering drugs that are targeted to the colon, where the gel is degraded, releasing the chemical (Vervoort et al., 1998a, 1998b, 1999).

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6 Value in Human and Animal Diets

Jerusalem artichoke is a plant with distinctive chemical properties. Inulin is stored as a reserve carbohydrate in the tubers, whereas starch is the storage form of carbon in most plants. Together with a low-fat and mineral-rich profile, inulin gives Jerusalem artichoke tubers their unique value in the human diet, in nutritional and medicinal products, and in animal feed.

Both the tubers and the aerial parts of Jerusalem artichoke are fed to animals. This can be in the form of forage, silage, food pellets, or prebiotic feed supplements. The leaves of Jerusalem artichoke, in particular, are protein-rich and nutritionally comparable to better known forage crops.

6.1 IN HUMAN DIETS

Jerusalem artichoke tubers have been utilized as a staple or sustenance crop at various times and in diverse places; other parts of the plant are not part of the human diet. Native Americans were the first to cultivate the crop and consume it in substantial amounts, as it originated in North America. After its introduction in 1607, it became for a time a major source of carbohydrate in the Western European diet, until the potato replaced it in the mid-18th century. It was again cultivated as a staple in Europe immediately after the Second World War, especially in France and Germany, due to a scarcity of potatoes. Today, the consumption of Jerusalem artichokes is much less than it has been in the past in the U.S. and Europe.

The taste of Jerusalem artichoke tubers is usually said to be nutty and a little sweet. The misnomer "artichoke" is after the globe artichoke (*Cynara scolymus* L.), which is said by some to have a similar flavor (Salaman, 1940). Samuel de Champlain, the first Frenchman to describe the tubers, for instance, saw them being consumed by the Eastern Abenaki people of Cape Cod in 1605 and wrote, "the roots which they cultivate, have a taste of artichokes" (Champlain, 1929). Marc Lescarbot, who brought the tubers to Europe in 1607, described them as "most excellent to eat, tasting like chards [cardoons, *Cynara cardunculus* L.], but more pleasant" (Lescarbot, 1914). The common names used today in Scandinavia (Table 2.2) are also derived from this resemblance in taste. For instance, the plant's Danish name, *Jordskok* or *jordskokkens* (plural), which comes from the older Danish name *jordærteskok*, arises because the tubers are in the soil and taste like *artiskokkens* (*C. cardunculus*) (Bjørn, 2007). The flavor of Jerusalem artichoke has also been compared to sweet chestnuts.

Native Americans ate the tubers both raw and cooked. The Cree and Huron Indians named it *askipaw* and *skibwan*, respectively — the translation of *skibwan* being "raw thing." There is evidence that Native Americans also cooked the tubers in a thick soup or pottage (Kosaric et al., 1984). Today, raw tubers are sometimes thinly sliced in salads to impart a crunchy texture and a nutty flavor. Raw slices can also be marinated in vinaigrette or pickled. However, Jerusalem artichoke tubers are usually cooked, especially in soups and other savory dishes. Palestine soup (e.g., puréed Jerusalem artichoke, onions, celery, garlic, chicken stock, herbs, butter, and cream) has long been one of the most popular methods of consuming Jerusalem artichoke in Europe (Grigson, 1978), the name deriving from a pun on *Jerusalem*. The flavor of Jerusalem artichoke in soups, chowders, and stews marries well, for example, with bacon, chestnuts, horseradish, parsley, or rosemary, and the tubers have a culinary affinity with seafood (e.g., scallops). Roasted tuber pieces can also be

ground into a coffee substitute or additive, which has a sweeter flavor than regular coffee by virtue of its inulin content (Turner and Szczawinski, 1978).

As a vegetable, the tubers are mainly roasted or boiled. Aldini (1625) described their culinary merits, and Lauremberg (1632) presented several methods of preparing the tubers. La Varenne (1651) braised them until well cooked, serving them peeled and sliced with onions, butter, nutmeg, and seasoning. Menon in *Cuisinière bourgeoise* (1746) boiled them in water, peeled them, and served them in a white sauce with mustard. Parmentier (1779) described various preparation methods for human and animal consumption. In more recent times, a tremendous number of recipes for Jerusalem artichoke have been published in cookbooks. A cookbook devoted entirely to Jerusalem artichoke was published in the early 1980s by a division of American Energy Farming Systems (AEFS), when farmers grew the crop in abundance as an alternative energy source — many years before the market was ready for it (Laidlaw, 1983; Amato, 1993). Jerusalem artichoke has undergone a minor revival since the 1980s, as a novelty vegetable and a health food. It has been found to be a versatile ingredient. In recipes, for instance, it can be served puréed or mashed; shallow-, deep, or stir-fried; steamed; cooked in salads, casseroles, gratins, or risottos; in soufflés; and in bread, biscuits, and cakes (e.g., Shoemaker, 1927; Grigson, 1978; Schneider, 1986). In France, the tubers were for many years regarded as either animal food or an emergency source of sustenance, but they are now appearing on fashionable restaurant menus, for example, served with *foie gras*, in *velouté avec œuf cassé aux truffes* or *purée au cumin frais*, and in warm salads with citrus or walnuts (Hennig, 2000).

Jerusalem artichokes are often cooked in their skins, especially when baked. If peeled, they should be placed in cold water prior to cooking to reduce discoloration. Discoloration also occurs after cooking, with the exposed flesh turning from cream to dull gray. Discoloration is due to iron, a beneficial mineral that is abundant in the tubers at levels (3 $mg \cdot g^{-1}$; USDA data in McGee, 1992) five times higher than in potatoes. Iron reacts with phenolic compounds, particularly chlorogenic acid, in damaged tissue to form a dark-colored complex. Adding vinegar to water containing peeled tubers helps avoid discoloration by increasing acidity and reducing the amount of chlorogenic acid available to react with the iron. After cooking, cream of tartar or lemon juice reduces discoloration by binding to the iron and reducing the formation of the dark-colored complex (McGee, 1992).

With concern about the rising incidence of obesity and diabetes, increasing the dietary intake of Jerusalem artichoke, and inulin-containing products derived from it, could bring major health benefits. Historically, the average daily intake of inulin from all sources has been estimated to be around 25 to 33 g. However, by the 1990s, consumption was as low as 2 to 12 g per person per day (Roberfroid et al., 1993). The current estimated consumption in the U.S. is around 1 to 4 g per day, while in Europe it is 3 to 11 g per day; wheat and onions mainly account for this inulin consumption (Moshfegh et al., 1999; Roberfroid and Delzenne, 1998; Van Loo et al., 1995).

Inulins and fructooligosaccharides (oligofructose)* are increasingly being added to foods, as described in the previous chapter, in high-intensity sweeteners; as sugar and fat replacements; to improve texture, taste, and mouthfeel (organoleptic qualities); to enhance fiber content; to preserve moisture; and to improve the stability of foams and emulsions (Franck, 2002). These food applications are summarized in Table 6.1. Many applications are aimed at reducing calories in food or promoting a healthy colonic microflora. Jerusalem artichoke is gaining in importance as a source of inulin and fructooligosaccharides in novel food preparation, as evidenced in patent applications (see Appendix). The benefits of consuming inulin and fructooligosaccharides in the diet are discussed in the following sections.

* Oligofructose was introduced as a synonym for fructooligosaccharide in 1989 (Coussement, 1999). It has become the preferred term in popular and marketing literature and is used to an increasing extent in the scientific literature.

TABLE 6.1
Food Applications with Inulin and Fructooligosaccharides (Oligofructose)

Application	Functionality	Inulin (% w/w)	Oligofructose (% w/w)
Dairy products	Sugar and fat replacement; synergy with sweeteners; body and mouthfeel; foam stability; fiber and prebiotic	2–10	2–10
Frozen desserts	Sugar and fat replacement; texture and melting; synergy with sweeteners; fiber and prebiotic	2–10	5–12
Table spreads	Fat replacement; texture and spreadability; emulsion stability; fiber and prebiotic	2–10	—
Baked goods and breads	Fiber and prebiotic; moisture retention; sugar replacement	2–15	2–25
Breakfast cereals	Fiber and prebiotic; crispness and expansion	2–25	2–15
Fillings	Sugar and fat replacement; texture improvement	2–30	2–50
Fruit preparations	Sugar replacement; synergy with sweeteners; body and mouthfeel; fiber and prebiotic	2–10	5–50
Salad dressings	Fat replacement; body and mouthfeel	2–10	—
Meat products	Fat replacement; texture and stability; fiber	2–10	—
Dietetic products and meal replacers	Sugar and fat replacement; synergy with sweeteners; low calorie value; body and mouthfeel; fiber and prebiotic	2–15	2–29
Chocolate	Sugar replacement; fiber; heat resistance	5–30	—
Tablets	Sugar replacement; fiber and prebiotic	5–100	2–10

Source: Adapted from Franck, A., *Br. J. Nutr.*, 87 (Suppl. 2), S287–S291, 2002.

6.1.1 Inulin and Obesity

Obesity represents a major global health crisis. Figures produced by the World Health Organization (WHO) in 2002 revealed that worldwide more than a billion adults were overweight and 300 million were clinically obese. In 2003, the International Association for the Study of Obesity calculated that up to 1.7 billion people in the world were overweight or obese. Organization for Economic Cooperation and Development (OECD) data published in 2002 showed that over 26% of the population of the U.S. was clinically obese, while over 20% of the populations of the U.K. and Australia were obese. Until recently, obesity was thought to be a problem only for rich countries. However, obesity is now prevalent in both developed and developing world nations; undernutrition and overnutrition coexist in many countries (Gardner and Halweil, 2000; Lang and Heasman, 2004).

Overnutrition is the root cause of the obesity epidemic. The consumption of excessive amounts of high-energy fatty and sugary foods leads to the accumulation of body fat. Obesity is defined as an excessively high amount of body fat in relation to lean body mass. The standard for obesity is usually expressed in the form of body mass index: a person's weight divided by the square of his or her height in meters ($kg \cdot m^{-2}$). A body mass index of 25 to 30 is considered overweight, while an index of 30 or above is considered obese. Extreme degrees of obesity are rising at alarming rates. By 2003, over 6% of the U.S. population was morbidly obese, with a body mass index over 40. A body mass index above 25 increases the risk of premature death due to a range of degenerative diseases and health conditions, including cardiovascular disease, hypertension, stroke, osteoporosis, some cancers (endometrial, breast, and colon), and diabetes mellitus (type 2 diabetes) (CDC, 2006; Lang and Heasman, 2004).

The World Health Organization estimates that over 3 million deaths a year can be attributed to overweight and obesity, a figure that is predicted to increase (WHO, 2002). Obesity increased 74% between 1991 and 2001 in the U.S., and steep increases like this are now occurring elsewhere. The rapid rise in obesity has made it one of the greatest risks to human health worldwide. Of particular concern is the obesity rate among children, which increases disease risk throughout their lifetime.

The number of overweight children in the U.S., for instance, tripled between 1980 and 2005 (CDC, 2006), while the number of clinically obese children in secondary schools in the U.K. doubled between 1994 and 2004 (NHS, 2006). The health care costs are already enormous. In 1998, it was estimated that medical expenses arising from overweight and obesity accounted for 9.1% of the total U.S. medical expenditure. The health care costs of overweight and obesity in the U.S. probably exceeded $78.5 billion in 2005 (CDC, 2006; Lang and Heasman, 2004).

The forecasts are alarming, but obesity is largely preventable. Reduced food consumption, dietary change, and more exercise, for instance, could help stem the obesity epidemic. To facilitate dietary change, there is an urgent need for food products that satisfy hunger without contributing to obesity. Jerusalem artichoke is a bulky low-energy food that fits this profile. It has a low energy (calorie) value because enzymes in the digestive system do not degrade inulin and fructooligosaccharides, a prerequisite for absorption by the body. For this reason, inulin and fructooligosaccharides are often referred to as nondigestible oligosaccharides.

The utilization of inulins as a fermentable substrate by microflora in the colon, however, means they are broken down and absorbed to a limited extent. Inulin therefore has a small caloric value. Molis et al. (1996) calculated an energy value of 2.3 $kcal \cdot g^{-1}$ (9.5 $kJ \cdot g^{-1}$) for fructooligosaccharides, while Livesey et al. (2000) proposed a value of 2.0 $kcal \cdot g^{-1}$ (8.4 $kJ \cdot g^{-1}$) for all carbohydrates that undergo microbial fermentation. However, most energy values calculated for inulin and fructooligosaccharides in the literature have been lower than this. A calorific value of 1.5 $kcal \cdot g^{-1}$ (6.3 $kJ \cdot g^{-1}$) was reported by Hosoya et al. (1988) and Ranhotra et al. (1993), for instance, while Roberfroid et al. (1993) gave a range between 1.0 and 1.5 $kcal \cdot g^{-1}$ (4.2 and 6.3 $kJ \cdot g^{-1}$). The differences reported for the caloric value of inulin are effectively insignificant in nutritional terms (Roberfroid, 2005). Although there is at present no universally accepted figure, the energy value for inulin is usually given as 1.5 $kcal \cdot g^{-1}$ (6.3 $kJ \cdot g^{-1}$) on food labels and in nutritional advice (Roberfroid, 1999). Therefore, the caloric value of Jerusalem artichoke is much less than for most other root vegetables. While 100 g of boiled potato, for example, has a caloric value of 76 kcal, the same amount of boiled Jerusalem artichoke tuber has 41 kcal (Vaughan and Geissler, 1997). Jerusalem artichoke is therefore an ideal vegetable to include in a weight-losing diet. As an ingredient (e.g., flour), Jersualem artichoke inulin can replace fat and sugar in low-calorie foods.

6.1.2 Inulin and Diabetes Mellitus

Diabetes mellitus is a disease in which blood sugar is not properly taken up into cells. Thus, the level of glucose in the blood remains high. The uptake of glucose into the body's cells is controlled by the hormone insulin, which is produced by the pancreas. Type 1 diabetes is due to the pancreas failing to produce sufficient insulin. It is often caused by genetic factors. Non-insulin-dependent diabetes, or type 2 diabetes, occurs when the body's cells are unable to respond very efficiently to the insulin produced. It is associated with obesity, overnutrition, excess dietary fat and sugar, and other factors. Type 2 diabetes accounts for around 90% of all diabetes. Both types of diabetes are treated by the injection of insulin, which acts to reduce the blood glucose concentration by facilitating the uptake of glucose by the cells in type 1 diabetes, and by supplementing the body's insulin in type 2 diabetes.

Over 18 million adults in the U.S. have diabetes (CDC, 2006), and over 170 million people worldwide have the condition, while its incidence is rising dramatically. The World Health Organization estimates that there may be 300 million people with diabetes by 2025 (WHO and FAO, 2002). There is a pressing need to develop a range of approaches to tackle type 2 diabetes and also address the root causes of its increased incidence, such as obesity and poor diet. Improvements in diet are therefore an important strategy in combating type 2 diabetes.

Foods containing inulin are beneficial in the diet of people with diabetes mellitus. Inulins and fructooligosaccharides are not absorbed in the intestines (Rumessen et al., 1990), and therefore do not affect insulin levels, because the body does not sense a need to produce insulin. The ingestion

of sucrose or glucose prompts blood sugar and insulin changes, but no corresponding effects are noted when equivalent amounts of inulin or fructooligosaccharides are ingested (Roch-Norlund et al., 1972). Therefore, consuming inulin-rich foods helps to restore normal levels of blood sugar, whereas foods containing starch and sucrose further raise blood sugar levels. Experiments during the 1980s and 1990s confirmed the beneficial role of inulin-rich foods in diabetic diets. Daily intake of fructooligosaccharides has been shown to reduce blood sugar levels in both diabetic and healthy subjects (Luo et al., 1996; Yamashita et al., 1984), for instance, while inulin reduced insulin peaks compared to diets containing other carbohydrates (Rumessen et al., 1990). An intake of around 16 to 23 g of inulin per meal has been recommended in diabetic diets (Van Loo et al., 1995).

There is a long history of inulin-containing plants being used to treat diabetes. The Greek physician Theophrastus used dandelion (*Taraxacum officinale* L.) to treat the condition, a plant also used as an early treatment in Eurasia. In North America, the root of elecampagne (*Inula helenium* L.) has historically been used to lower blood sugar levels (Tungland, 2003). In 1874, it was reported that no sugar appeared in the urine of diabetics who were given a daily inulin dose of 50 to 120 g (Külz, 1874). Jerusalem artichoke tubers are rich in inulin and fructooligosaccharides and are therefore an ideal item to include in diabetic diets. Jerusalem artichoke was fed to diabetic patients in the 1920s with promising results (e.g., Carpenter and Root, 1928). It proved beneficial when substituted for other carbohydrate foods, such as potatoes, over periods ranging from 6 days to several months. The increase in blood sugar after eating Jerusalem artichokes (0.02 to 0.07% in 3 h) was significantly lower than when consuming an equivalent amount of fructose or other carbohydrates (Root and Baker, 1925). However, gastrointestinal side effects in patients limited the extent to which the vegetable was subsequently prescribed.

Today, a moderate quantity of Jerusalem artichoke is recommended in diets aimed at countering diabetes and obesity. Eating Jerusalem artichoke daily, however, could become monotonous. Fortunately, foods incorporating tuber extracts also provide the health benefits of Jerusalem artichoke. Flour from Jerusalem artichoke, for instance, replaces wheat flour in a range of food products aimed at the weight-loss, health food, and diabetic food markets (Roberfroid and Delzenne, 1998). Jerusalem artichoke is also being added to butter, purée, drinks, and other products aimed at diabetics.

The flour made from Jerusalem artichoke tubers is a low-calorie, fat-free source of energy and fiber, which is rich in nutrients, including calcium, potassium, and iron. For the health food market, Jerusalem artichoke flour is often included in products that also contain live bacteria, especially bifidobacteria. The bacteria (probiotic) and food substrate (prebiotic) act to maintain a healthy balance of microflora in the colon (see below).

To make flour, Jerusalem artichoke tubers are macerated, heated, and spray-dried. In the process, inulin is hydrolyzed to short-chain fructooligosaccharides (Yamazaki et al., 1989). Jerusalem artichoke flour is also used to supplement animal feed. In one study, the composition of a typical Jerusalem artichoke flour was 2.1% (of dry weight) nitrogen, 16.2% insoluble fiber, 4.2% ash, and 77.5% soluble carbohydrate. The carbohydrate comprised fructans with degrees of polymerization of 1 to 2 (33.3%), 3 to 4 (46.4%), and over 5 (20.3%) (Farnworth et al., 1993).

Fructans and fructose extracts, which can potentially be obtained from Jerusalem artichoke, have become attractive to industry for a number of food and nonfood applications because of their health benefits (e.g., Fleming and GrootWassink, 1979; Fontana et al., 1993; Fuchs, 1993; Roberfroid, 2005). Short-chain fructooligosaccharides (degree of polymerization of 2 to 5), for example, are increasingly used as low-calorie sweeteners in processed foods, and their utilization is anticipated to expand significantly in the future.

6.1.3 Probiotics, Prebiotics, and Bifidobacteria

A number of health benefits attributed to Jerusalem artichoke tubers in human and animal diets are related to its role as a promoter of probiotic activity in the large intestine. Probiotics have been a dietary element for thousands of years. However, the term *probiotic* only gained its current usage

in the early 1970s, as an organism or substance that has a beneficial effect on the balance of microorganisms in the colon. This definition coincided with work revealing the essential role of intestinal microflora in the digestion of food and in promoting general well-being. Today, a probiotic is generally defined as a live microbial feed supplement that beneficially affects the host animal by improving its intestinal microbial balance (Fuller, 1992).

The large intestine is the most heavily colonized region of the digestive system, with up to 10^{12} bacteria per gram of intestinal content. Around 50 genera are represented, with hundreds of different species and strains occurring. The vast majority of these bacteria are anaerobes, and they range from the beneficial to the pathogenic. The balance of the intestinal microflora greatly influences digestive processes. Beneficial bacteria naturally present in the large intestines include species of *Bifidobacterium* and *Lactobacillus*. Probiotics and substrates that promote their activity help shift the balance toward the optimum for these beneficial bacteria, so they constitute at least one third of the total bacterial population (Gibson and Roberfroid, 1995).

The earliest probiotic was probably fermented milk. From biblical times to the present day, yogurts and other fermented dairy products have been recognized as having health-promoting properties. The importance of bacteria in giving fermented milk products these properties was recognized at the beginning of the 20th century (Metchnikoff, 1907). From the 1950s onward, experiments have elucidated the role that ingested beneficial bacteria (good bacteria) play in maintaining a favorable microflora balance, and thereby countering the impact of pathogenic bacteria (bad bacteria). For instance, lactobacilli were identified as the key probiotic ingredient in fermented milk products.

A number of bacteria and yeasts have probiotic activity. However, in commercial applications, bacteria associated with four genera have predominated: *Bifidobacterium*, *Lactobacillus*, and, to a lesser extent, *Enterococcus* and *Streptococcus*. Collectively, these are called lactic acid bacteria (LAB) in the nutrition literature, although *Bifidobacterium* and the minor commercial genera are not strictly part of the lactic acid group. The following species are utilized in commercial products: *Bifidobacterium breve*, *B. bifidus*, *B. infantis*, *B. lactis*, *B. longum*, *B. thermophilum*, *Lactobacillus acidophilus*, *L. delbrueckii* subsp. *bulgaricus*, *L. helveticus*, *L. casei*, *L. fermentum*, *L. johnsonii*, *L. plantarum*, *L. rhamnosus*, *L. salivarius*, *Enterococcus faecium*, and *Streptococcus salivarius* subsp. *thermophilus* (Lee et al., 1999). A number of claims are made for these products, including improvement of the colon microflora balance, stimulation of the immune system, enhanced resistance to bacterial infection, and general health benefits.

Many factors contribute to the effectiveness of probiotic organisms, including their ability to adhere to the lining of the intestine (Crociani et al., 1995). A crucial factor in the survival and proliferation of both native and introduced beneficial bacteria (i.e., bifidobacteria, lactobacilli) in the lower intestines is the availability of a carbohydrate source that has not been digested by the human digestive system and that can be used as a substrate for growth. A range of nondigestible oligosaccharides have been shown to stimulate the activity of bifidobacteria and lactobacilli in the colon (Fuller, 1997). Nondigestible substances that stimulate the growth or activity of beneficial bacteria in the colon are called prebiotics; they have become an important component in probiotic supplements (Gibson and Roberfroid, 1995; Gibson et al., 2005; Tuohy et al., 2005). Jerusalem artichoke tuber extracts are rich in inulins and fructooligosaccharides, and are therefore a potential source of prebiotics.

Probiotic supplements can take the form of powders, dried tablets, pellets or cubes, and pastes or sprays, depending on their use. They usually contain an active bacterial ingredient (probiotic) plus a carbohydrate source that can be selectively fermented by the bacteria (prebiotic). A combination of an active bacterial ingredient and carbohydrate source is also called a synbiotic (Gibson and McCartley, 1998; Roberfroid et al., 2002a). *Synbiotic* has been slowly accepted as a term, however, and *probiotic* is still commonly used for mixtures of probiotics and prebiotics (Heasman and Mellentin, 2001). A typical synbiotic (probiotic) supplement may therefore contain a culture of bifidobacteria together with inulins or fructooligosaccharides. Inulin prebiotic supplements are

also added to food without a probiotic component to promote the activity of indigenous bifidobacteria. Some probiotic products (e.g., yogurt drinks) have come under critical scrutiny because the probiotic bacteria added, including bifidobacteria, do not survive beyond the stomach to contribute to the colon microflora (e.g., Graham-Rowe, 2006). However, there is no doubt that prebiotic inulin and fructooligosaccharide do reach the colon.

Inulin and fructooligosaccharides are excellent prebiotics because they are not digested or absorbed in the small intestine. The characteristic (1-2)-bonds, which link the fructose units, cannot be degraded by mammalian digestive enzymes (Oku et al., 1984), and therefore reach the colon as intact molecules. Around 85% of ingested inulin survives to the colon, where it acts as a fermentable substrate for the colonic microflora. Inulin and fructooligosaccharides selectively stimulate the growth of bifidobacteria and lactobacilli, an effect not achieved with other types of carbohydrate such as starch or pectin (Gibson et al., 2005; Mitsuoka et al., 1987; Wang and Gibson, 1993). They therefore influence species composition in the colon in favor of beneficial bacteria (Gibson et al., 1995; Gibson and Wang, 1994). A daily intake of around 8 to 10 g of fructooligosaccharides significantly increases bifidobacteria in the large intestine (e.g., Bouhnik et al., 1997; Hidaka et al., 1991; Tuohy et al., 2001). As little as 5 g of inulin a day in the diet can produce an observable bifidogenic effect (Bouhnik et al., 1999; Williams et al., 1994).

By promoting bifidobacteria and other beneficial microorganisms, prebiotics help to suppress harmful microorganisms through competitive inhibition. Thriving populations of beneficial bacteria can outcompete other bacteria for nutritional resources and adhesion sites on epithelial cells lining the intestinal wall. Good adhesion is important to prevent bacteria being removed by host secretions and intestinal flow; the attachment ability of different *Bifidobacterium* species is correlated with their ability to colonize the large intestine (Crociani et al., 1995). Bifidobacteria also release antibacterial agents, as a result of fermenting inulins (Gibson and Wang, 1994). Lactobacilli secrete bacteriocins — peptides with specific antibacterial action (Dodd and Gasson, 1994). Numbers of pathogenic bacteria in fecal samples are often reduced when inulin and fructooligosaccharide supplements are included in the diet (e.g., Gibson and Wang, 1994). Among the potentially harmful bacteria that have been reported to be suppressed are *Clostridium perfingens* and *C. difficile* and pathogenic strains of *Escherichia coli*, *Staphylococcus aureus*, *Campylobacteria jejuni*, *Salmonella enteritidis*, and *Candida albicans* (Araya-Kojima et al., 1995; Buddington et al., 2002; Fooks and Gibson, 2002; Gibson et al., 1995; Gilliland and Speck, 1977; Harmsen et al., 2002; Kleessen et al., 1997; Rao, 2001; Wang and Gibson, 1993; Yamazaki et al., 1982). However, not all dietary trials with inulin and fructooligosaccharide supplements resulted in significantly reduced counts of pathogenic bacteria (Roberfroid, 2005).

Prebiotic and synbiotic supplements containing inulins and fructooligosaccharides can be particularly effective after illness and antibiotic treatments, to help bifidobacteria recolonize the large intestine, as bifidobacteria can be eradicated by certain antibiotics (Colombel et al., 1987). They are also particularly helpful for other at-risk groups, such as the elderly, babies and infants, and people traveling or on holiday abroad, as a preventative measure against illness. In addition to their bifidogenic effect, inulin-type fructan prebiotics have been reported to have a range of other beneficial health effects. These claims are supported by data from studies with animal models and from clinical trials, although it should be noted that large variability often occurs between different studies. The main health claims relate to mineral absorption and bone health, decreased blood lipids and heart disease, stimulation of the immune system and disease prevention, and improved bowel function (Boeckner et al., 2001; Roberfroid, 1995; Tungland, 2003).

6.1.4 Inulin and Bone Health

Prebiotics and synbiotics containing fructooligosaccharides enhance mineral bioavailability by improving the absorption of minerals in the colon, especially calcium, iron, and magnesium (Caers, 2004; Coudray, 2004; Hidaka et al., 2001; Ohta et al., 1994; Roberfroid, 2005). The mechanism

for this is probably enhanced passive and active mineral transport across the intestinal epithelium, mediated by increased levels of butyrate and other short-chain fatty acids and decreased pH (Scholz-Ahrens and Schrezenmeir, 2002). Improvements in calcium and iron absorption may help prevent osteoporosis and anemia, respectively (Ohta et al., 1998; Weaver and Liebman, 2002). Fructooligosaccharide ingestion enabled rats, for instance, to recover from experimentally induced anemia and to increase levels of minerals in their bones (Ohta et al., 1998; Oda et al., 1994).

Osteoporosis is a condition characterized by a decrease in bone mass and density that causes the bones, especially in postmenopausal women, to become fragile and vulnerable to fracture. It is a growing global problem, which can be alleviated by dietary approaches. Calcium is a key factor in bone strength. By optimizing peak bone mass in early adulthood and by minimizing bone loss during the postmenopausal period, the risk, for example, of hip fracture can be significantly reduced. Improved calcium nutrition during development is critical and can reduce hip fracture rates later in life by around 50% (Coxam, 2005).

Prebiotic inulin and fructooligosaccharides added to the daily diet of animals significantly increase calcium absorption in animals (e.g., Coudray et al., 2003; Mineo et al., 2001; Ohta et al., 1994; Rémésy et al., 1993). This can increase mineralization and bone mineral density (Roberfroid et al., 2002b). In humans, a beneficial effect on calcium absorption is found in both adolescents (Griffin et al., 2002, 2003; van den Heuvel et al., 1999) and postmenopausal women (van den Heuvel et al., 2000). In both groups, a mixture of inulins having low and high degrees of polymerization (DP) were the most effective treatment for enhancing mineral absorption (Coudray et al., 2003; Griffin et al., 2002, 2003). Such a mixture (e.g., a 1:1 ratio of fructooligosaccharides (average DP of 4) and long-chain inulin (average of DP 25)) increased the calcium accretion to the skeleton by ~30 mg Ca·day^{-1} (Abrams et al., 2005). Polymorphisms in the vitamin D receptor gene (Fok1), however, appear to strongly modulate calcium absorption and the magnitude of the response to supplementation.

In Japan, where mineral deficiency can be a nutritional problem, the beneficial effects of fructooligosaccharides on calcium absorption have been recognized in the labeling on dietary supplements since 1999 (Hidaka et al., 2001).

6.1.5 Blood Lipids and Heart Disease

Inulins and fructooligosaccharides help maintain the health of the cardiovascular system and may reduce the risk of heart disease. A key factor in this is the maintenance or improvement of blood lipid composition, through decreases in triglycerides (triacylglycerols), and the lowering of cholesterol and homocysteine levels (Hidaka et al., 2001; Luo et al., 1996; Tungland, 2003). Convincing lipid-lowering effects have been demonstrated in animals (e.g., Delzenne et al., 1993; Fiordaliso et al., 1995; Kok et al., 1998; Trautwein et al., 1998). Rats on inulin-rich diets, for example, had lower blood cholesterol and total lipid levels than control animals, while reductions in serum triglycerides were reported for rats on diets containing 5 to 20% fructooligosaccharides (Roberfroid, 1993). However, the situation is less clear-cut for humans, where higher inulin doses (over 30 g·day^{-1}) can produce adverse gastrointestinal symptoms (Williams, 1999). Some human studies have found no effects, while a number of others have shown decreases in triacylglycerol or cholesterol levels for groups taking inulin and fructooligosaccharide supplements (Williams and Jackson, 2002). Roberfroid (2005) reviewed 12 studies, finding 8 to have positive and 4 negative outcomes. Positive outcomes were more likely for subjects with moderate hyperlipidemia (Causey et al., 2000; Davidson et al., 1998; Hidaka et al., 1991; Jackson et al., 1999; Letexier et al., 2003) than for normal lipidemic volunteers (Brighenti et al., 1999; Luo et al., 1996; Pedersen et al., 1997; van Dokkum et al., 1999) or non-insulin-dependent diabetics (Alles et al., 1999; Luo et al., 2000; Yamashita et al., 1984). Inulin-type fructan supplements act to reduce lipogenesis in the liver, and this lowers lipid concentrations in the blood (Letexier et al., 2003).

Inulin and fructooligosaccharides are more effective at lowering serum levels of lipids (triglycerides) than cholesterol, with inulin more effective than short-chain fructooligosaccharides in

both cases (Roberfroid, 2005). The moderate cholesterol-lowering action observed in several studies may arise as a result of the metabolism of inulin and fructooligosaccharides to short-chain fatty acids, which inhibit hepatic cholesterol biosynthesis, although the mechanism involved is not yet fully understood. Prebiotics may also help redistribute cholesterol from the blood plasma to the liver, while beneficial bacteria stimulated by prebiotics may interfere with cholesterol absorption from the colon, or directly assimilate cholesterol (Pereira and Gibson, 2002). High homocysteine levels can damage artery tissue, and interfere with the constriction and dilation of blood vessels and blood clotting processes. By lowering levels of homocysteine and undesirable lipids, inulin and fructooligosaccharide supplements may help to reduce the long-term risks of heart disease. The risk of atherosclerosis (thickening of the arteries), for example, may be reduced through a lowering of triglycerides and fatty acid levels in the blood serum.

6.1.6 The Immune System and Cancer Prevention

Inulin and fructooligosaccharides modulate the response of the immune system to illness, through the stimulation of bifidobacteria and lactobacilli, and the improvement of the general microfloral balance in the colon (Watzl et al., 2005; Yasui et al., 1992). In this role, prebiotics have been shown to promote the production of macrophages, lymphocytes, and antibodies, in particular the local production of immunoglobulin A (IgA)-positive cells in the intestines and cecal mucosa (Bornet, 2001; Hosono et al., 2003; Kadooka et al., 1991; Roberfroid, 2005; Yasui et al., 1992). In addition, thriving bifidobacteria and lactobacilli populations help to strengthen the mucosa–blood barrier in the intestine lining. They do this by outcompeting pathogens for adhesion sites on the intestinal lining, producing short-chain fatty acids that nourish cells in the mucosal layer, lowering intestinal pH to levels unfavorable to pathogens, and releasing bacteriocins against pathogens (Anon., 2006; Wang and Gibson, 1993). Fructooligosaccharides may therefore help to prevent a wide range of illness and disease conditions, including ulcerative colitis, symptoms of inflammatory bowel diseases, and *E. coli* O157 infection (Hidaka et al., 2001; Kanauchi et al., 2003; Oike et al., 1999; Wolf et al., 2003). The ability of inulins to stimulate the immune system has also led to interest in their use as vaccine adjuvants (Cooper, 1995; Silva et al., 2004).

Newborn babies and infants have underdeveloped immune systems. Breast milk contains natural prebiotic oligosaccharides that stimulate bifidobacteria and lactobacilli, which tend to be more prevalent in the gastrointestinal flora of breast-fed babies. Infant formula and cow's milk are deficient in oligosaccharides, a factor holding back the development of an infant's immune system. The addition of fructooligosaccharide prebiotics to infant formula can increase gastrointestinal bifidobacteria and lactobacilli counts (Boehm et al., 2002; Knol et al., 2000; Moro et al., 2002), while daily fructooligosaccharide supplements (e.g., 2 $g \cdot day^{-1}$) can lower the prevalence of sickness (e.g., vomiting, diarrhea) in infants (Saavedra et al., 1999; Vandenplas, 2002; Waligora-Dupriet et al., 2005).

By boosting the immune system, it has been claimed that fructooligosaccharide supplements reduce the risk of colorectal cancer developing (Kowhi et al., 1978, 1982; Pool-Zobel et al., 2002). In mice and rats, for example, fructooligosaccharides reduced colon carcinogens and the occurrence of colon tumors (Pierre et al., 1997), while dietary inulin and fructooligosaccharides suppressed chemically induced tumors (Taper and Roberfroid, 2002) and reduced genotoxic damage to the colonic epithelium in rats (Rowland, 1998). The release of the short-chain fatty acid butyrate, from fermenting inulin and fructooligosaccharides, may play a role in suppressing colon cancer. Butyrate has been shown to have a direct antiproliferation effect on tumor cells *in vitro* (Kruh, 1982), while the release of butyrate has been correlated with a protective effect against colon cancer in experimental studies with rats (Bornet, 2001; McIntyre et al., 1993). Moreover, inulin injections can prolong the survival of melanoma-bearing mice (Cooper and Carter, 1986). However, more proof is needed before dietary fibers such as inulin can be said to definitely prevent colorectal cancer (Baron, 2005; Park et al., 2005).

6.1.7 Bowel Function

Inulins and fructooligosaccharides in the diet promote gastrointestinal health and improve bowel function. They do this primarily by contributing to dietary fiber — a heterogeneous group of plant-derived carbohydrates that are not digested by human enzymes and are not absorbed in the small intestine (Flamm et al., 2001). Dietary fiber plays an important role in nutrient absorption, digestive transit time, and stool composition and quantity, while providing the main nutrient source for colonic microflora (Trepel, 2004). Through its effect on the colonic microflora, dietary fiber has a bulking effect. In general, for every additional 1 g of dietary fiber consumed, stool weight increases by up to 5 g (Roberfroid et al., 2002a).

Fermentation products arising from the metabolism of prebiotics by colonic microflora, such as bifidobacteria and lactobacilli, include vitamins and short-chain fatty acids. These are largely absorbed in the colon and are metabolized to provide energy for the body. Probiotics containing strains of bifidobacteria have been shown to raise levels of water-soluble vitamins (e.g., thiamine, nicotinic acid, folic acid, and vitamin B_{12}) in the large intestine (Deguchi et al., 1985; Lee et al., 1999). Short-chain fatty acids comprise acetates (e.g., acetic acid), propionates (e.g., propionic acid), butyrates (e.g., butyric acid), and lactates (e.g., lactic acid). They exert systematic effects on the metabolism of carbohydrates, fats, and cholesterol, and are vital for normal colonic function (Hidaka et al., 2001). The types of fermentation products arising from digestion depend on the makeup of the intestinal microflora and the amount and structure of the inulin and fructooligosaccharides present. The fermentation and digestion of prebiotics increase the amount of bacterial biomass and raise intestinal levels of carbon dioxide, hydrogen, and methane, in addition to short-chain fatty acids (Andrieux et al., 1993; Roberfroid et al., 2002a).

Fructooligosaccharide supplements (e.g., 3 $g \cdot day^{-1}$) improve bowel function by relieving moderate constipation and increasing stool frequency (Kameoka et al., 1986; Tokunaga et al., 1993; Tominaga et al., 1999; Wolf et al., 2003). Inulin and fructooligosaccharides lower intestinal pH and increase the weight of the stools, while also raising the levels of butyrate and other gaseous fermentation products (Campbell et al., 1997). Stool weight in humans can be increased by about 20% and breath hydrogen by around three-fold (Alles et al., 1997). The production of short-chain fatty acids reduces pH, while the increase in stool weight is mainly attributable to increased microbial biomass in the colon. As the water content is high, stools are softer and easier to expulse — thereby increasing stool frequency (Churbet, 2002).

Gastrointestinal disturbances can lead to several types of diarrhea, such as pseudomembranous colitis (caused by overgrowth of *Clostridium difficile*), rotavirus diarrhea, antibiotic-associated diarrhea, and travelers' diarrhea. Prebiotics and synbiotic supplements containing bifidobacteria with inulin or fructooligosaccharides have the potential to treat these conditions (Gibson et al., 1997). Travelers are prone to gastrointestinal disorders, through exposure to unfamiliar strains of microorganisms in food and drink. A trend toward fewer attacks of diarrhea and a better sense of well-being were reported for a group of travelers taking fructooligosaccharide supplements (10 $g \cdot day^{-1}$) compared to a control group (Cummings et al., 2001). Patients just recovered from the diarrhea symptoms of *C. difficile* infection receiving fructooligosaccharides (12 $g \cdot day^{-1}$) had higher levels of bifidobacteria than controls after 12 days and were less likely to suffer relapses of diarrhea (Lewis et al., 2005).

6.1.8 Digestive Downsides

Jerusalem artichoke has beneficial effects on digestion. It is a good source of dietary fiber, for instance, which helps to bulk food and reduce constipation. However, there can be digestive downsides too.

Human digestive enzymes do not target inulin. Around 89% (and up to 97%) of the inulin and fructooligosaccharides that we consume, on average, remain intact in the small intestine (Andersson

et al., 1999; Molis et al., 1996). As it is not digested, there tends to be a lot of inulin in the large intestine or colon after eating a meal rich in inulin. However, none reaches the stools, and only a small fraction occurs in the urine (Molis et al., 1996). This is because inulin is completely fermented by the general microbial fauna in the large intestine, especially by bifidobacteria and lactobacilli (Nilsson and Björck, 1988; Nilsson et al., 1988). The digestion of inulin and fructooligosaccharide is accompanied by the production of hydrogen, carbon dioxide, and other gaseous products (Stone-Dorshow and Levitt, 1987). This leads to an undesirable side effect of eating Jerusalem artichoke and other inulin-rich foods: flatulence.

The wind-inducing effects of Jerusalem artichoke have been known for many years. Although the tuber spread rapidly throughout France in the 10 years after its introduction in 1607, it was not universally popular due to overindulgence of the unfamiliar vegetable revealing its digestive downsides. Jean-Luc Hennig, in *Le Topinambour et Autres Merveilles*, writes of the variety of nicknames the street sellers and people gave the tubers after their introduction, before the visit of the Topinambous Indians from Brazil in 1613 suggested an exotic moniker that stuck. The names, often derived from the coarse vocabulary of the countryfolk, referred to a perceived indigestibility and invoked lice (*pou-terre*), swine (*soleil de pourceau*), and rotten feet. Philibert Guybert, in *le Médecin Charitable* (1629), described the topinambour as giving wind ("crudités et vents à ceux qui en usent"), giddiness, and headaches. Meanwhile, in England, Tobias Venner, a physician in Bath, warned in 1622 that the vegetable was "somewhat nauseous or fulsome to the stomach, and therefore very hurtful to the melancholic, and them that have weak stomachs." In Johnson's 1633 revision of Gerard's *Herball*, John Goodyer's entry for Jerusalem artichoke concluded: "In my judgement, which way soever they be dressed and eaten, they stir up and cause a filthie loathsome stinking wind within the body, thereby causing the belly to be much pained and tormented, and are a meat more fit for swine than man; yet some say they have usually eaten them, and have found no such windy quality in them."

In addition to flatulence, excessive inulin consumption can cause a range of abdominal symptoms, such as osmotic diarrhea, pain, and bloating (Roberfroid et al., 2002a). There are recognized upper limits to the amount of inulin that it is wise to eat in a day. This takes into account figures for human tolerance to inulin, which is dependent on fructan chain length or degree of polymerization, and the amount consumed (Rumessen and Gudmand-Høyer, 1998). Human tolerance to fructans with a degree of polymerization over 5 is greater than for short-chain fructooligosaccharides with a degree of polymerization less than 5. The literature suggests that up to 70 g of inulin per day can be consumed in various foods without causing undesirable side effects (Coussement, 1999; Kleessen et al., 1997; Tungland, 2003). Studies have shown that daily inulin doses of 5 to 20 g produce beneficial effects, and these relatively small amounts are usually well tolerated by the human digestive system (Rumessen et al., 1990).

The amount of inulin that can be eaten without digestive difficulties can depend on an individual's physiology, with some people relatively tolerant to the side effects and others much more susceptible to digestive disturbance. To a certain extent, it also depends on how much inulin has been eaten in the past. Although there is no evidence of physiological adaptation to inulin over the short term, the microflora population in the colon may evolve enzymes that target inulins in the long term. Therefore, the more Jerusalem artichoke that is eaten over a long period of time, the more likely it is that the digestive system can adapt to it. Where Jerusalem artichoke is utilized as a sustenance crop, for instance, people appear to be able to eat significantly more of it without experiencing problems of flatulence or digestive disturbance. This accounts for a tendency to exaggerate the problems of flatulence arising from Jerusalem artichoke consumption, as it is mainly inexperienced consumers who complain of their "loathsome stinking wind." Nevertheless, Jerusalem artichoke will never become a widely accepted staple like potato, because its popularity will always be tempered by its digestive downsides. It is best consumed for its benefits a little at a time.

Harold McGee (1992) has outlined culinary procedures to tone down the undesirable side effects of Jerusalem artichoke. These procedures either remove some of the inulin from the tubers

prior to consumption or alter its composition. Raw or quickly cooked tubers have a high inulin content and should only be used as a minor component of a meal. Boiling the tubers in copious amounts of water, which is then discarded, reduces inulin and fructooligosaccharide content — the fructans remain in the pan as a fine white precipitate. The effectiveness of boiling is increased if the tubers are sliced to increase the surface area exposed to the water. Fifteen minutes of boiling draws out around 40 to 50% of the indigestible carbohydrate from sliced tubers. Precooking the tubers (e.g., in water or in water and milk) has been a culinary practice for many years and is mentioned, for instance, in the 1633 edition of Gerard's *Herball* and in the 1738 edition of La Varenne's *le Cuisinier François* (McGee, 1992; Schneider, 1986). The most dramatic reductions in inulin content, however, are obtained by slow cooking. Another inulin-rich plant, the camas lily (*Camassia* spp.), was traditionally pit cooked by Native Americans. This involved burying the camas lily bulbs in a pit and covering them with dry wood and stones and, once the fire had established, earth and grass. The food was cooked for between 12 and 36 h. This method was also possibly used for Jerusalem artichoke tubers. McGee adopted a slow-cooking method in a kitchen for Jerusalem artichoke tubers, over a 12-h period. Cooking by this method eventually turns all the inulin to fructose, leaving a very sweet and soft-textured food (McGee, 1992). The inulin and fructooligosaccharide content is also reduced in chilled and stored tubers, due to chemical breakdown (Edelman and Jefford, 1968; Rutherford and Flood, 1971). Cooked tubers that have been stored under cold conditions for a month or two will therefore have less inulin than fresh tubers, although the effect is small compared to differences obtained through different cooking procedures (McGee, 1992).

Apart from flatulence and minor digestive disturbances, inulin has few adverse effects in the human body. However, there has been one report of a severe allergic reaction (four episodes of anaphylaxis) attributed to an accumulated dosage of inulin from multiple sources, including vegetables and processed food (Gay-Crosier et al., 2000). Inulin and fructooligosaccharides are being added to an ever-increasing range of processed foods, where they are classified as food ingredients rather than additives, and are considered safe to eat. There is therefore a very small chance that their increased use in processed foods might make allergic reactions to them more frequent than is currently recognized.

6.2 IN ANIMAL DIETS

6.2.1 Forage

The aboveground parts of Jerusalem artichoke are not consumed as human food, but both the tops and tubers can be utilized as animal feed, either fresh or in silage and feed formulations. Jerusalem artichoke typically yields around 500 to 700 $t \cdot ha^{-1}$ of green material. As a forage crop, it can be grown as a permanent planting since the tops are regenerated each year from tubers left in the ground (Gunnarson et al., 1985). All the aerial parts are included in fodder, although the leaves and stems differ in their nutrient and mineral content (Table 6.2). The leaves contain more protein than the stems, while the stems contain more carbohydrate than the leaves (e.g., Hay and Offer, 1992; Luske, 1934). The leaves are therefore generally considered better in terms of fodder than the stems (Hay and Offer, 1992; Malmberg and Theander, 1986; see also Table 5.3).

The leaves are a good source of protein for animal forage, being particularly rich in the amino acids lysine and methionine compared to other forage (Stauffer et al., 1981). The protein dry matter content of the leaves can be as high as 20% of the total aerial parts, of which 5 to 6% is the essential amino acid lysine (Rawate and Hill, 1985). Crude protein content of between 9.5 and 17.3% was recorded for eight Canadian accessions (Stauffer et al., 1981). The amino acids (percent dry weight basis) for herbage protein have been given as: lysine (5.4%), histidine (1.8%), arginine (5.2%), asparatic acid (9.1%), threonine (4.4%), serine (4.0%), glutamic acid (10.5%), proline (4.1%), glycine (5.1%), alanine (6.3%), methionine (1.4%), isoleucine (4.6%), leucine (8.3%), tyrosine

TABLE 6.2
Composition of Stems and Leaves ($g \cdot kg^{-1}$ DM Unless Stated Otherwise) of Jerusalem Artichoke

	Leaves	Stem
Dry matter (DM)	210	333
Crude protein	128	14
NDF[a]	238	292
ADF[b]	218	261
Lignin	33	65
Calcium	24.8	3.2
Phosphorus	3.4	0.7
Magnesium	6.9	0.6
Potassium	36	7
Sodium ($mg \cdot kg^{-1}$ DM)	70	40
Copper ($mg \cdot kg^{-1}$ DM)	12.9	2.3
Zinc ($mg \cdot kg^{-1}$ DM)	69	44
Iron ($mg \cdot kg^{-1}$ DM)	80	<10
Manganese ($mg \cdot kg^{-1}$ DM)	58	11

[a] Neutral Detergent Fiber
[b] Acid Detergent Fiber

Source: Adapted from Hay, R.K.M. and Offer, N.W., *J. Sci. Food Agric.*, 60, 213–221, 1992.

(2.8%), and phenylalanine (5.0%) (Rawate and Hill, 1985). Lignin is generally higher in the stems than the leaves (e.g., Hay and Offer, 1992), although Malmberg and Theander (1986) found the reverse could occur. Leaves have a higher ash and trace element content than stems, with fiber fractions tending to be higher in the stems (Hay and Offer, 1992). Leaf protein levels decline toward the end of the growing season, and therefore, crude protein levels desirable for fodder may decrease if harvesting is delayed.

Mean forage yields for 10 wild and cultivated Jerusalem artichoke genotypes were 1.99 and 4.24 $Mg \cdot ha^{-1}$ for the vegetative and flowering stages of plant development, respectively. The cultivar 'Sunchoke' had the highest forage yield of 6.3 $Mg \cdot ha^{-1}$, at flowering, which is comparable to yields of some common forage species (Seiler, 1993). Nutritional elements in individual plant parts were established at 2-week intervals in 'Sunchoke' by Somda et al. (1999). Overall, nutrient element levels in vegetative structures declined with the onset of rapid tuber development. This was particularly the case for phloem-mobile elements (e.g., nitrogen, phosphorus, potassium), although less mobile elements (e.g., calcium and manganese) remained in the leaves and stem. During vegetative growth, leaves had the highest nutrient levels, except for iron and sodium.

An analysis of the nitrogen and mineral content of 19 wild and cultivated Jerusalem artichoke genotypes grown in Texas revealed whole-plant crude protein content ranging from 60 to 90 $g \cdot kg^{-1}$, which is considered adequate for the maintenance of ruminant animals (National Academy of Sciences, 1984; Seiler, 1988). A crude protein content of 140 $g \cdot kg^{-1}$ occurred in the leaves of 11 of the genotypes at the vegetative stage. At maturity, the allocation of biomass was 68, 23, and 9% for stems, leaves, and heads, respectively, when grown as a perennial, with whole-plant levels of *in vitro* digestible dry matter (598 $g \cdot kg^{-1}$) being more than acceptable for animal nutrition purposes (Seiler, 1993). Nutritionally adequate amounts of calcium, sodium, magnesium, and potassium were present at all stages of plant maturity, but phosphorus levels were considered inadequate.

Seiler and Campbell (2004) reported genetic variability in the mineral content of Jerusalem artichoke forage and concluded that there was potential for improvement in nitrogen, calcium, and potassium content through hybridization and selection. However, population variance for phosphorus and magnesium was low, suggesting that it would be difficult to raise levels of these minerals through selection. Therefore, Jerusalem artichoke, when mixed, for example, with grasses, provides a satisfactory nutrition level for ruminants, although when fed alone phosphorus supplementation is advisable (Seiler, 1988; Seiler and Campbell, 2004).

Since the mid-1600s, Jerusalem artichoke has been used as forage and feed for livestock, especially in Europe (Kosaric et al., 1984). In the 1920s in France, for example, all of the crop (2,750,000 tons) was fed to cattle, sheep, pigs, and horses, and it was considered important for this purpose in several French regions. All plant parts have often been used as animal feed, for example, having a recognized nutritive value in cattle feed (Leroy, 1942). After harvesting the tops for forage or other uses, tubers can be lifted for animal feed or left in the ground. For instance, pigs can be introduced into fields where tops have been cut, to dig up and consume the tubers *in situ* (Shoemaker, 1927). The tubers are a recognized substitute feed for pigs in times of potato shortage (Dijkstra, 1937; Scharrer and Schreiber, 1950).

Cultivars having high yields of green material are of particular interest when using the crop directly for animal feed (Rawate and Hill, 1985). The cultivar 'Fuseau' has been recommended as a producer of high yields of forage, for example, and it is amenable to multiple cuttings (Shoemaker, 1927). Foliage is best cut when the stems are green and succulent. It can therefore be difficult to obtain good yields of both foliage and tubers from the same crop. Cutting the foliage reduces tuber yields, while the foliage is well past its peak for forage at the time the tubers are typically harvested. However, Rawate and Hill (1985) found that an early cutting of immature foliage, at a time before the tubers begin to develop, had only a minimal impact on tuber yields, whereas later cuttings reduced yields. For three top cuttings at monthly intervals, they recorded total yields for dry matter and protein of 26,956 and 5,392 $kg \cdot ha^{-1}$, respectively.

The optimum time for harvesting Jerusalem artichoke tops, in terms of protein level, was September in Minnesota (Cosgrove et al., 2000). However, tuber yields are relatively low this early in the season. At the optimum time for top harvesting, just prior to flowering, tubers have typically only attained around 20 to 30% of their ultimate yield. If tops and tubers are to be combined in animal feed, then harvest is recommended later in the season, at some loss to foliage dry matter yield, to enable tubers to start filling out (Boswell et al., 1936). After flowering, the percentage of protein in forage declines, while lignin content increases (Stauffer et al., 1981).

In a survey of the feed value of Jerusalem artichoke compared to other forage crops in the U.S., it was concluded that the crop makes a suitable livestock feed, although it has few nutritional advantages over other forage crops (Table 6.3). Total digestible nutrients were higher, and protein concentrations lower, in Jerusalem artichoke tops than in alfalfa (lucerne, purple medic (*Medicago sativa* L.)). Digestible nutrients and protein compared favorably with other crops (e.g., corn or maize silage (*Zea mays* L.) and sugar beet pulp (*Beta vulgaris* L.)). However, the cultivation of Jerusalem artichoke for forage may be advantageous in soils and regions where other forage crops are difficult to grow.

The nutritive value of Jerusalem artichoke foliage as an animal feed was reported in a Hungarian study to be comparable to that of oilseed rape (*Brassica napus* L.) and purple medic, and higher than that of silage sunflower. In this case, the biggest advantage of Jerusalem artichoke grown as a perennial for foliage over 4 or 5 years was the low overall planting costs (Barta and Pátkai, 2000). Davydovic (1960) reported that Jerusalem artichoke had a higher value as a stock feed than fodder beet, carrot, or turnip. In Central Russia, the Jerusalem artichoke–sunflower hybrid 'Novost' gave high green matter yields (80.5 $t \cdot ha^{-1}$ and 23.2 t $DM \cdot ha^{-1}$) in fodder trials. Fertilizer application and higher planting densities produced the highest yields. The cultivar 'Skorospelka,' however, produced the highest levels of aboveground digestible protein (2.03 t $DM \cdot ha^{-1}$) (Kshnikatkina and Varlamov,

TABLE 6.3
Feeding Value and Forage Quality of Jerusalem Artichoke Tops and Tubers Compared to Alfalfa and Corn Silage

Forage	Dry Matter %	Digestible Nutrients %	Digestible Protein %	Crude Fiber %
Jerusalem artichoke tops	27	67	3	18
Jerusalem artichoke tubers	21	78	6	4
Alfalfa, full bloom	91	53	10	35
Corn silage	29	70	5	22

Source: Adapted from Cosgrove, D.R. et al., Jerusalem Artichoke, 2000, http://www.hort.purdue.edu/newcrop/afcm/jerusart.html. Morrison, F.B., *Feeds and Feeding: A Handbook for Students and Stockmen*, 22nd, ed., Morrison Publishing Co., Ithaca, NY, 1959.

2001). The cultivar 'Nahodka' was the best of five cultivars assessed in Kazakhstan in terms of feed value and digestible protein (Martovitskaya and Sveshnikov, 1974).

Jerusalem artichoke tops have good potential as an alternative forage crop in cool, wet areas of Northern Europe (Hay and Offer, 1992). Being perennial, Jerusalem artichoke offers advantages over annual crops whose establishment can be affected each year by adverse spring conditions. Stands of Jerusalem artichoke in Scotland, grown continuously over 3 years, were pest- and disease-free and had no weed problems. Under low-input management conditions they produced yields over 30 t DM·ha^{-1}, comparable with cereals or grassland in the U.K. Fertilizer applications would be needed, however, for successful perennial cultivation under Northern European conditions. Optimal shoot yields occurred shortly after the highest rate of tuber filling in late August, suggesting an optimum forage harvest date in Scotland during late August, which should ensure enough tuber mass in the ground to regenerate the crop in the following season. Digestibility studies showed that shoot tissues had a nutritional value to ruminants similar to that of grass hay, but with a lower protein level. Therefore, if used as the only feed, it requires supplementation with (inexpensive) rumen-degradable protein.

The tubers of Jerusalem artichoke ('Kulista czerwona' cultivar) fed to Polish Merino wethers (castrated rams) were found to have good digestibility and feeding value compared to other root crops in a study conducted in the Czech Republic. In 1 kg of fodder, Jerusalem artichoke provided 3.26 (MJ) ME of energy and 12.5 g of digestible protein. The authors concluded that Jerusalem artichoke tubers were a suitable feed for sheep, although they should be supplemented with feeds of high protein content and also bulk feed in the case of ruminants (Petkov et al., 1997a). In a related study, green fodder from Jerusalem artichoke, gathered prior to tuber harvest, was found to contain 1.72 MJ of energy and 13.6 g of total digestible protein per 1 kg of fodder. In feeding studies with sheep, the high lignin content of the fodder reduced its nutritional value and digestibility compared to other green fodder, and therefore its potential as an animal feed. However, it can be a useful additive in feeding rations for ruminants (Petkov et al., 1997b). Jerusalem artichoke feeds can have physiological effects on animals due to their high inulin content. Tubers fed to horses, for example, resulted in a 4.9-fold increase in hydrogen and methane exhalation compared to horses fed a grass-based diet (Mosseler et al., 2005), while tubers fed to cattle increased methane emissions compared to other feeds (Hindrichsen et al., 2005).

Recent interest in Jerusalem artichoke as forage has focused on the tops alone. Whereas most food and nonfood applications of the crop involve cultivation as an annual, production of tops for forage exploits the crop's potential as a perennial, with tubers left in the ground to regenerate the crop. However, relatively few studies have looked at Jerusalem artichoke as a perennial crop. Tops can be harvested for optimum yields and high levels of protein obtained, including protein that

would not subsequently be translocated to the tubers. The amount of fructans in the aerial parts increases with harvest time, up until flowering. Therefore, a high production of fructans in the green plant parts is possible, even though tuber maturation has started and a decrease in dry matter has begun, due to temporary storage of fructans in the aerial parts (Kosaric et al., 1984; Malmberg and Theander, 1986).

6.2.2 Silage and Feed Pellets

Silage is a method of preserving forage, through the process of fermentation, so that it can be utilized over an extended period. Factors that affect silage production include the stage of crop maturity at harvest and the type of fermentation that occurs in the silo. During fermentation, bacteria breakdown cellulose, hemicellulose, sugars, and storage compounds into simple sugars and acetic, lactic, and butyric acids. Good-quality silage is achieved when lactic acid is the predominant acid produced. Lactic acid fermentation is the most efficient type of fermentation and drops the pH of the silage the fastest; the faster the fermentation, the more nutrients that are retained in the silage (Schroeder, 2004). Silage can be inoculated with lactic acid bacteria, selected to grow rapidly under silo conditions, to start the fermentation process.

Ensilage is a preferred method of conserving the aboveground parts of Jerusalem artichoke for winter feeding, yielding a more palatable feed than dried material, while the tubers can also be ensiled. Silage from Jerusalem artichoke tubers is typically sugar-rich, with high lactic acid and low butyric acid content (Bondi et al., 1941). Ensilage of Jerusalem artichoke tops with molasses yielded well-preserved lactic silage of pH 4.0, with a digestible energy of 11 MJ·kg^{-1} DM. Finely chopped stems (1 to 3 cm cf. 2 to 5 cm) gave the best product in terms of dry matter yield (Hay and Offer, 1992); the composition of this silage is given in Table 6.4. A silage made from the tops comprised 31.9% crude fiber, 42.0%, carbon, 2.5% nitrogen, and 0.13% sulfur, on the basis of total solids (Zubr, 1985). The overall composition in another study was 65 to 68% water, 3.2% protein, 21.2% N-free extract, 0.7% fat, and 2.8% ash (Davydovic, 1960).

TABLE 6.4
Composition (g·kg^{-1} DM Unless Stated Otherwise) of Silage Made from Jerusalem Artichoke Shoots, Chopped to 1 to 3 cm in Length

Component	Content
Dry matter (DM)	273
Crude protein	75
Calcium	13.2
Phosphorus	2.2
Magnesium	2.9
Sodium	0.9
Gross energy (MJ·kg^{-1} DM)	17.0
Ethanol (g·kg^{-1} fresh weight)	1.0
Acetic (g·kg^{-1} fresh weight)	3.0
Propionic (g·kg^{-1} fresh weight)	0.1
Butyric (g·kg^{-1} fresh weight)	<0.1
Lactic (g·kg^{-1} fresh weight)	20.3

Source: Adapted from Hay, R.K.M. and Offer, N.W., *J. Sci. Food Agric.*, 60, 213–221, 1992.

The inulin and fructooligosaccharides in Jerusalem artichoke stems are a good substrate for lactic acid bacteria, but overall the crop does not perform as well as the most frequently utilized silage crops. The minimal amount of sugar sufficient to create lactic acid, maintain pH 4.2 to 3.9, and efficiently produce silage is called the sugar minimum. It is determined by the amount of dry matter, sugar, buffering capacity, and other factors. The lower the sugar minimum, the better a crop is for producing silage. Barley (*Hordeum vulgare* L.), maize, and sugar beet tops have sugar minimums of 1.42, 2.86, and 4.75, respectively. Jerusalem artichoke has a sugar minimum of 8.13, although this was lower than for lucerne, vetch (*Vicia sativa* L.), and some other crops tested (Vidica, 2002).

The total herbage is a good source for the preparation of a high-quality protein isolate. Total aboveground dry matter can be over 25 $t \cdot ha^{-1}$, with crude protein dry matter yields of around 5.0 $t \cdot ha^{-1}$, although yields of purified protein are lower due to losses during preparation (Ercoli et al., 1992; Rawate and Hill, 1985). The protein content of one such isolate varied between 67 and 76%, which compared favorably with traditional protein concentrations such as fish meal and soybean meal. From three cuttings of herbage, yields of concentrated protein isolate were around 800 $kg \cdot ha^{-1}$. The overall amino acid composition compared well with that of major cereal proteins, with levels of lysine that were several times higher than those in maize and wheat proteins and comparable to those of soybean protein. A yield of 48 $kg \cdot ha^{-1}$ lysine was recovered from the protein isolate. The powdered protein concentrate stored well at room temperature, can be compacted into pellet form, and has potential for a variety of applications, including diet enrichment. A by-product of the process, the press cake, may be an acceptable silage-like animal feedstock (Rawate and Hill, 1985).

In an Italian study, Jerusalem artichoke was grown to obtain a protein isolate from the herbage and ethanol from the tubers. Eight cultivars were grown, with a dry matter production of forage of up to 24 $t \cdot ha^{-1}$ in the most productive cultivars ('Topino' and 'Fuseau 60'). The study was conducted over 2 years, although plants derived from tubers left in the ground generally gave lower yields of both above- and belowground biomass, aerial biomass yields being around 15 $t \cdot ha^{-1}$ in the second year. The total protein content obtained from a juice extracted from Jerusalem artichoke leaves was 0.7 $t \cdot ha^{-1}$ in the first year of cultivation and 0.4 $t \cdot ha^{-1}$ in the second year (Ercoli et al., 1992).

Zitmane (1958) prepared an animal feed product from the leaves and hydrolyzed stems of Jerusalem artichoke, with the addition of oat flour and salt. Fodder additives containing Jerusalem artichoke as their main component have been added to enrich fodder mixtures, for their curative-prophylactic properties in the rations of domestic and farm animals (e.g., Zelenkov, 2000).

6.2.3 Probiotic Feed Supplements

Antibiotics are substances obtained from microorganisms (e.g., fungi) that inhibit or destroy the growth of other microorganisms, in particular pathogenic bacteria. Since the 1950s, antibiotics have been utilized extensively in animal feed. They have been used routinely to reduce the incidence of disease, and as growth promoters in animals and poultry. However, the overuse of antibiotics has led to disease-causing intestinal bacteria evolving resistance to them. Furthermore, the use of antibiotics on animals has potential implications for resistance to pathogenic bacteria in humans.

A move away from antibiotics has therefore started. Bans and restrictions on antibiotics in animal feed have been implemented in many countries, while consumer demand for meat produced without the use of growth promoters has risen. However, there is a problem: effective alternatives to antibiotics have been slow in reaching the market. Probiotic food supplements are seen as one solution to this problem (Flickinger et al., 2003).

Probiotic supplements contain viable bacteria (e.g., bifidobacteria and lactobacilli), designed to shift the balance of the microflora in the large intestines to the detriment of harmful bacteria. Probiotics can contain prebiotics as substrates (synbiotics), while prebiotics can be administered alone to promote endogenous populations of bifidogenic or lactic acid bacteria. These represent a

fundamentally different strategy to the use of antibiotics, which work directly against harmful bacteria. Many claims have been made for probiotic supplements in animal feed, including improved growth rates, possibly due to the suppression of subclinical infection, increased feed conversion efficiency, increased milk production in dairy cows, increased egg production in poultry, and general benefits in terms of animal health. However, the evidence has often been variable and inconsistent, although scientific studies have started to verify some of the claims made for probiotics and prebiotic supplements in animal feed (Fuller, 1997). The mechanisms involved are the same as in humans, with prebiotics promoting the activity of beneficial bacteria that outcompete other bacteria for nutritional resources and adhesion sites on the intestinal wall, produce antibacterial substances that impact harmful bacteria, and modify the host's immune response (Lee et al., 1999).

Extracts from Jerusalem artichoke tubers have great potential as additives to animal feed, for their bifidogenic effect. Inulin and fructooligosaccharides, at present mainly extracted from chicory, are added to the diets of domesticated animals, although less is known about their health benefits in animals than in humans (Flickinger et al., 2003). Different animals have different digestive tract morphologies, and so the same fructooligosaccharides in diet supplements may not be ideal in all cases. Depending on species, a supplement may have suboptimal effects or result in digestive problems such as loose stools or excessive flatulence (Flickinger et al., 2003). There is therefore scope to produce tailor-made fructooligosaccharide mixtures for particular animals and animals of different ages.

The addition of inulin and fructooligosaccharides to animal diets brings about changes in the makeup of the intestinal microflora population. This can lead to changes in the metabolism and physiology of livestock, poultry, and companion animals. The addition of Jerusalem artichoke tuber extracts to diets, for instance, could lead to improvements in feed efficiency, improved digestion, and reductions in diarrhea.

6.2.3.1 Pigs

Pigs are excellent models for human intestinal physiology, and therefore many probiotic studies have been done with them. The results can also be applied to the formulation of animal feed supplements. Synbiotic supplements containing fructooligosaccharides have been shown to increase the body weight and food conversion efficiency of piglets (Fukuyasa et al., 1987), although not in all cases (Flickinger et al., 2003). In weanling swine, however, fructooligosaccharides in the diet invariably increase the incidence of bifidobacteria in the large intestine (Flickinger et al, 2003; Houdijk et al., 1997; Howard et al., 1995). Fructooligosaccharides in the diet of growing pigs can decrease fecal mass (Houdijk et al., 1998) and fecal volume (Houdijk et al., 1997, 1999) and reduce the malodor of pig slurry (Flickinger et al., 2003; Kotchan and Baidoo, 1997). In growing pigs, the large intestine is an important site of fermentation, and it has a complex bacterial microflora. The fermentation of short-chain fatty acids derived from fiber can contribute up to 30% of maintenance energy for growing pigs (Flickinger et al., 2003; Varel and Yen, 1997).

A critical period for pig nutrition occurs immediately after weaning, when populations of lactobacilli fall and *E. coli* rise, increasing the risk of digestive disturbance (Mulder et al., 1997). This is the optimum time to give prebiotic and synbiotic supplements. Inulin supplements can reduce the levels of pathogenic bacteria, including *E. coli* and *Clostridium* species, in the colon of pigs (Flickinger et al., 2003; Nemcová et al., 1999), resulting in healthier animals. For instance, a synbiotic containing fructooligosaccharides and lactobacilli increased both lactobacilli and bifidobacteria counts, and decreased clostridia, enterobacteria, and enterococci counts, in the feces (Bomba et al., 2002). In another study of fructooligosaccharide supplements, pigs with induced diarrhea had more lactobacilli and fewer enterobacteria in both the small and large intestines than pigs in a control group (Oli et al., 1998).

Cooked and spray-dried Jerusalem artichoke tuber flour was included in a dietary study with weaner pigs. The flour contained 77.5% soluble carbohydrate (of total dry weight) and was

particularly rich in fructooligosaccharides with a wide range of degrees of polymerization. Pigs were fed a control diet, purified Neosugar (a commercial fructooligosaccharide formulation with a low degree of polymerization), or Jerusalem artichoke flour. No differences in feed intake, body weight gain, or feed efficiency were found between treatments, but pronounced differences in the color and smell of the manure were noted. The manure from the control pigs smelled stronger than the manure from pigs fed Neosugar and Jerusalem artichoke flour. The main benefits of incorporating fructooligosaccharides and Jerusalem artichoke flour in pig diets may therefore be in terms of improved barn environment and general well-being through disease suppression (Farnworth et al., 1993; Flickinger et al., 2003).

6.2.3.2 Ruminants

In cattle and sheep, fermentation of inulin and oligosaccharides can occur in the rumen prior to the large intestine, although most fermentation occurs in the large intestine or colon. Although trials with prebiotics and synbiotics in cattle have produced variable results, they have generally been shown to be beneficial (Huber, 1997; Kaufhold et al., 2000; Wallace and Newbold, 1992). There is a suggestion that the variability observed may be due in part to synbiotic additives becoming less effective over time in an animal, as the general microflora adapts to them (Huber, 1997).

Fructooligosaccharide-containing synbiotics increased bifidobacteria populations in the colon and may protect against pathogenic *E. coli* (Bunce et al., 1995; Flickinger et al., 2003). They have also been shown to reduce digestive disturbances, increase weight gain, and increase milk production in dairy cattle (Huber, 1997). The use of prebiotics and synbiotics in cattle production systems has increased, as an inexpensive replacement for antibiotics in feed.

6.2.3.3 Poultry

Bacterial infection, from *Salmonella* spp., *Campylobacter* spp., and strains of *E. coli*, are the most serious cause of problems in poultry rearing (Mulder et al., 1997). Measures to reduce the use of antibiotics in poultry feed have necessitated a search for alternatives. Synbiotics containing fructooligosaccharides are a promising method of manipulating the microflora in chicken intestines to combat disease and enhance growth. Dietary fructooligosaccharides have been shown to increase levels of beneficial bacteria and reduce the incidence of salmonella in feces and chicken carcasses (e.g., Bailey et al., 1991; Fukata et al., 1999; Waldroup et al., 1993). These studies suggest that low levels of supplementary fructooligosaccharides in the diet can enhance broiler growth and feed efficiency in a manner similar to that of antibiotics (Ammerman et al., 1989; Flickinger et al., 2003).

Flour from Jerusalem artichoke (as described above for weaner pigs) was fed to starter chicks in one study, which also included purified Neosugar and control diets. The birds receiving the diets with the Neosugar or the Jerusalem artichoke flour had increased feed consumption and body weight gain. The use of Jerusalem artichoke flour may therefore produce benefits in terms of production efficiency (Farnworth et al., 1993).

Jerusalem artichoke syrup (0.5% concentration) in water was found to be effective against selected cecal bacteria in a trial with broiler chickens over the first 35 days of life. All the chickens were given access to a standard diet without growth-promoting antibiotics. Birds with access to the syrup had significantly smaller numbers of total aerobic bacteria, including Enterobacteriaceae and *C. perfingens*, and reduced bacterial endotoxin levels compared to the control birds without the syrup. In addition, increased body weights were found in the birds consuming the Jerusalem artichoke syrup. Therefore, a small amount of syrup in broilers' drinking water can have a beneficial effect on growth performance and can suppress potential pathogens in broilers' ceca. It was concluded that Jerusalem artichoke syrup could serve as a substitute for antibiotics or as a prophylactic feed additive (Kleessen et al., 2003).

6.2.3.4 Domestic Animals

The addition of inulin and fructooligosaccharide prebiotics to pet foods represents a lucrative market, which is only just starting to be exploited (Flickinger and Fahey, 2002; Flickinger et al., 2003). Dogs and cats have complex and diverse colonic bacterial populations, which can be influenced by prebiotics. Fructooligosaccharide supplementation, for example, increased the number of bifidobacteria in dog feces in one study, while decreasing concentrations of ammonia and amines (Hussein et al., 1999). Inulin and fructooligosaccharide supplementation could reduce the malodor of cat and dog feces and may help prevent disease, such as colorectal cancer. Gritsienko et al. (2005) proposed a prophylactic feed for dogs containing Jerusalem artichoke green mass, and many pet food preparations containing inulin and fructooligosaccharides may soon be on the market.

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7 Biomass and Biofuel

Industrial societies have come to rely on fossil fuels for their energy needs. However, fossil fuels (i.e., oil, coal, and natural gas) are nonrenewable resources extracted from rapidly depleting reserves, the major factor contributing to the rising levels of atmospheric carbon dioxide responsible for global climate change, and increasingly a source of international conflict (e.g., Deffeyes, 2001; Heinberg, 2005; IPCC, 2007; Klare, 2004; Leggett, 2006; Roberts, 2005). A global shift in perspective is therefore occurring, toward a transition energy economy, with renewable and carbon-neutral sources of local energy being developed to supplement or replace imported fossil fuels.

Plants have been used since prehistoric times for energy, and firewood is still a major source of heat energy today. Now, with major changes in the energy economy looming, plant biomass is increasingly used to produce transportable fuels. For example, plant-derived alcohol is used to fuel automobiles in Brazil and other countries, and is used worldwide in mixtures to supplement gasoline supplies. Jerusalem artichoke is a promising candidate crop for direct combustion, the production of methane biofuel, and especially the manufacture of bioethanol.

7.1 BIOMASS

Biomass refers to total dry weight of living material expressed in terms of volume or area. This organic material can be harvested as a source of energy. Plants store energy from sunlight in their various parts, which can be accessed through several technologies. Plant biomass can be burnt to generate heat energy or electricity, converted to liquid and transportable fuels, or used as a feedstock for the production of chemicals. It can also be used as compost or green manure, and converted into building materials, fiber, or animal feed. Plants are the main source of biomass for energy, with crops that produce the greatest quantity of bulk material in the shortest possible time the most useful. The maximum biomass yield for energy crops is typically around 30 tonnes·ha^{-1} (White and Plaskett, 1981).

Biomass crops for energy have a number of disadvantages compared to fossil fuels, including a relatively modest thermal content, an often high moisture content that inhibits combustion, and a low density and high volume that necessitate large-scale equipment for handling and combustion. Procedures to improve the properties of biomass primarily involve drying and compaction. Biomass has advantages over fossil fuel in that it is renewable, releases less carbon dioxide into the atmosphere, and is readily obtainable, inexpensive, and not subject to unpredictable shortages or steep cost increases (White and Plaskett, 1981). As with all alternative energy strategies, the economic feasibility of energy crops depends on the cost of competing conventional fuels. As fossil fuel prices increase, the economic viability of plant biomass options is enhanced.

Jerusalem artichoke, with its rapid growth rate and ability to grow on marginal land, has great potential as a source of biomass for energy. It can yield well over 30 t·ha^{-1} under favorable conditions, is efficient in terms of water use, is a low-input crop with minimal external production costs, is rich in polysaccharides, and is among the group of plants that produce the highest total dry matter yield per hectare (Dambroth, 1984). Biomass production usually involves aerial plant parts, although all parts of Jerusalem artichoke can be utilized. The aerial parts are a feedstock for direct combustion and biogas production, while the tubers and stalks are used for alcohol production. The fructans in Jerusalem artichoke are temporarily stored in the stalks or stems prior to being translocated to the tubers. Therefore, harvesting aerial parts when they contain abundant sugar, before tuber filling occurs, is the best approach if they are to be used for alcohol or biogas

production. However, cutting the tops can impede tuber formation, thereby reducing the potential of Jerusalem artichoke as a multifunctional crop (Faget, 1993). Nevertheless, studies have shown that given the right timing of cutting, both aerial and belowground parts of Jerusalem artichoke can be utilized (e.g., Stauffer et al., 1981; Rawate and Hill, 1985). As plants can only assimilate a certain amount of carbon during a given period, whether tops, tubers, or both are ultimately harvested may make relatively little difference in terms of dry matter biomass in the long term.

A series of field trials in Europe in the late 1980s assessed the potential of Jerusalem artichoke as a multifunctional (food and nonfood) crop. Yields and growth characteristics were recorded from Ireland to Romania, and from Denmark to Spain and Italy, with the highest yields occurring in irrigated crops in Southern Europe (Grassi and Gosse, 1988). However, changing climatic conditions will influence energy crop distribution in Europe during the 21st century (Tuck et al., 2006). In a survey of 26 promising energy crops, Tuck et al. (2006) analyzed crop requirements against climate change models. Crop requirements for Jerusalem artichoke, for instance, included maximum and minimum rainfall of 1600 and 500 mm, and May to September temperatures averaging between 8 and 25°C. In 1990, most Jerusalem artichoke in Europe was grown in the latitudes 45 to 54° and 55 to 64° North. However, by 2050–2080, all the climate models tested predicted a substantial decline (up to 31 to 45%) in Jerusalem artichoke cultivation in latitudes 45 to 54° North (France and Germany), a small (5 to 15%) increase in cultivation in latitudes 55 to 64° North, and a large increase (up to 40 to 60%) in cultivation in the more northerly latitudes of 65 to 71° North. In this latter area, comprising Scandinavia and northern Russia, suitable land for Jerusalem artichoke cultivation will increase from 10% to around 80% of total cultivable land area. National Resources Canada is also modeling how climate change is likely to affect the range of *Helianthus tuberosus* in North America. In the models, by 2041 to 2070, the range has extended northward to Newfoundland (around St. John's) and westward over a large area of Alberta (centered on Edmonton); by 2071 to 2100, some areas of southern Alaska become suitable for growing Jerusalem artichoke (Canadian Forestry Service, 2006).

The cultivation of Jerusalem artichoke on marginal land for bioenergy can potentially be combined with a bioremediation function. The closely related sunflower (*Helianthus annuus* L.), which has a similar high biomass and rapid growth rate, is known to effectively accumulate cadmium (Cd), copper (Cu), lead (Pb), manganese (Mn), and nickel (Ni) from water contaminated with heavy metals (Brooks and Robinson, 1998; Dushenkov et al., 1995). Sunflower also removes cesium and strontium from radioactive environments, as shown in field tests around the damaged Chernobyl nuclear facility in Ukraine (Cooney, 1996; Dushenkov et al., 1999); after 10 days, roots of potted sunflowers had taken up so much radioactivity from comtaminated pools they could not be removed from the exclusion zone (Coghlan, 1997). Experimental studies have confirmed the considerable ability of Jerusalem artichoke to accumulate heavy metals, and its potential as a tool in the reclamation of land contaminated with heavy metals (Antonkiewicz and Jasiewicz, 2003; Antonkiewicz et al., 2004; Jasiewicz and Antonkiewicz, 2002). The metal content of Jerusalem artichoke tissue increases with the level of soil pollution with heavy metals. In descending order, the effectiveness of Jerusalem artichokes for accumulating heavy metals was Cd, Zn, Ni, Cu, and Pb (Antonkiewicz and Jasiewicz, 2003). Its potential as a combined energy crop and bioremediation tool, however, may be reduced by yield reductions in soils containing high levels of heavy metals (Jasiewicz and Antonkiewicz, 2002).

The environmental impact of growing energy crops over large land areas should be a consideration when assessing their potential. In Germany, 10 energy crops, including Jerusalem artichoke grown as a perennial (40,000 plants·ha^{-1}), were assessed on sandy soil under four fertilization regimes. Jerusalem artichoke was found to be a relatively good absorber of Pb, while having a relatively benign impact on soils and the environment compared to other energy crops. For instance, phosphorus levels in Jerusalem artichoke tops (haulms) were relatively low (0.05 to 0.15% dry matter), and the crop therefore does not require much phosphorus fertilizer, which is beneficial in terms of water eutrophication. Yields for Jerusalem artichoke tops were relatively low, however, in

this study (4.3 t dry matter·ha^{-1}), giving an energy balance of 62 GJ·ha^{-1}·year^{-1}. It was also noted that the stability of the stems diminished over the years when grown as a perennial, making the tops harder to harvest. Higher top yields occurred if the tubers were not harvested (Scholz and Ellerbrock, 2002).

Harvesting the tubers can lead to potential problems, as incomplete harvesting can cause crop resurgence in the following season, which makes Jerusalem artichoke difficult to fit into crop rotations. Better harvesting methods or control of volunteer plants needs to be developed if Jerusalem artichoke is to become an important biomass crop in rotations (Faget, 1993). However, when cultivated as an energy crop, Jerusalem artichoke has increasingly been grown as a perennial turning a potential harvesting problem into a virtue.

A pressing research need is the development of modern cultivars with improved characteristics for biomass and energy. In a Canadian study, a wide variation in forage composition was found among accessions, suggesting that composition could be readily improved through plant breeding (Stauffer et al., 1981). To fulfill its potential as an energy crop, Jerusalem artichoke will also require government support, for example, in the form of tax exemptions and research grants.

The total cost of producing biomass from a model tall broadleaf crop (sunflower) was estimated as 12.7 U.S.$·t^{-1}, given a whole plant yield of 15.0 t dry matter·ha^{-1}·year^{-1}. This was cheaper than the cost estimates for any other crop type, including tall grass (maize, 19.1 $·t^{-1}), short broadleaf (sugar beet, 77.1 $·t^{-1}), and legume (alfalfa, 20.9 $·t^{-1}) (Klass, 1998). Estimates for a Jerusalem artichoke biomass crop in Italy suggested that farmers would need to receive from 18 to 47 Ecu·t^{-1} (1990 prices) for tubers to gain an income comparable to more traditional energy crops (Bartolelli et al., 1991).

The two principal ways of obtaining energy from biomass are thermal (direct combustion) and biological (the conversion of organic matter to biofuel through microbial action). Biomass is also playing an increasingly important role as a feedstock for organic chemicals and materials. The utilization of inulin from Jerusalem artichoke as a feedstock for a range of industrial chemicals has been described in Chapter 5. The combustion and biological conversion of Jerusalem artichoke to produce energy is considered below.

7.2 DIRECT COMBUSTION

Direct combustion converts biomass to thermal energy. The removal of access moisture as a liquid (dewatering), the complete drying (dehydration), and the compaction or densification of biomass are critical processes to ensure efficient combustion. The energy expended in these processes must be compensated for by increased efficiency of conversion of biomass to energy, to make direct combustion economical. Combustion is carried out in incinerators, boilers, or furnaces under controlled conditions. The burning of biomass consists of a rapid chemical reaction; biomass components are oxidized, with the release of energy, carbon dioxide, and water. Chemical energy is released in the form of radiant and thermal energy, which can be used directly for drying purposes, or it can be converted into hot air, hot water, or steam, for instance, to generate electricity in turbines. Under perfect conditions, each reactant would be totally combusted, but in practice, this does not occur and considerable amounts of ash result. The removal of ash via grates is an important consideration for the efficient running of combustion systems. Plant biomass can be mixed with a range of other combustible materials in incinerators, including domestic and industrial biowastes. Crop biomass feedstocks are particularly suitable for use in combined heat and power (CHP) generators.

Although Jerusalem artichoke tops need extensive drying, they can be a useful source of biomass for direct combustion. Trials in Lithuania have confirmed Jerusalem artichoke's suitability as an energy crop. The bulk density of tops harvested in autumn was 78 kg·m^3, compared to 65 kg·m^3 in the spring, while the average net calorific value of dry biomass harvested in autumn was 18.0

$MJ \cdot m^{-2}$, compared to 18.5 $MJ \cdot m^{-2}$ in the spring. Harvesting in either spring or late summer provided dry matter with the best properties for combustion (Rutkauskas, 2005).

Jerusalem artichoke is unlikely to become a major biomass source for direct combustion because of the drying required. Zubr (1988) also noted that when the aim of energy generation by direct combustion is also the recycling of materials, then using Jerusalem artichoke might be hard to justify when biowastes are available. The crop is therefore more likely to become of greater significance as a wet feedstock in the production of biofuels.

7.3 BIOLOGICAL CONVERSION

7.3.1 Ethanol

Ethanol (ethyl alcohol) can be produced from a wide variety of feedstocks, including wood, wastepaper, and crop residues. Ethanol produced from plant biomass is also known as bioethanol. The production of bioethanol from plant biomass involves the fermentation of pulped, mashed, or juiced plant material by yeasts and bacteria (Wiselogel et al., 1996).

Bioethanol is a colorless, water-soluble, volatile liquid that can be utilized as a versatile fuel and fuel additive. It was recognized from the early days of the internal combustion engine that alcohol could be used as an alternative to fossil fuels, especially gasoline. During the 1920s in France and Germany, mixtures of ethanol and gasoline (e.g., 25% ethanol to 75% gasoline by volume) were used to extend motor fuel supplies and utilize agricultural surpluses. There was a revival of interest in ethanol as a motor vehicle fuel in the early 1970s, following the steep rise in oil prices imposed by OPEC. Bioethanol promised to reduce dependence on imported fossil fuel and extend gasoline supplies. The potential of bioethanol as a modern fuel for automobiles was first realized in Brazil in 1975, with the establishment of the National Alcohol Program. Initially the scheme used blends of gasoline with 10% and 20% bioethanol obtained from sugarcane. By 1995, 35% of passenger vehicles (4.2 million cars) were fueled by pure (100%) bioethanol (gasohol).

Bioethanol is being increasingly added to gasoline worldwide to improve engine performance through octane boosting. A fuel's octane number is a measure of the delay between fuel injection and self-ignition; the higher the octane number, the shorter the delay, and this reduces engine knocking. Lead was added to gasoline to enhance its octane rating but has been phased out, as it is a serious environmental pollutant. Ethanol provides an environmentally friendly alternative; with ethanol, gasoline blends effectively, raising octane rating. The use of ethanol in blends also helps to reduce exhaust emissions, such as carbon monoxide (CO) and volatile organic compounds (VOCs), thereby improving air quality. Many countries have moved toward ethanol and gasoline mixtures for these reasons, for example, 10% bioethanol to 90% gasoline (E10) (Bailey, 1996). Bioethanol can also be converted into ethyl tert-butyl ether (ETBE), which is used as a gasoline additive to enhance air quality. ETBE lowers the vapor pressure of gasoline, reducing the release of organic compounds that contribute to pollution and smog.

The production costs of liquid (transportable) fuels from biomass are generally higher than those from fossil fuel sources. For example, ethanol net production costs were $0.46 per energy equivalent of gasoline in the U.S. in 2005 (Hill et al., 2006). However, the costs of bioethanol are likely to fall due to biotechnological advances and economies of scale, while fossil fuel costs may rise due to future shortages and unpredictability of supplies. Energy content and energy conversion values for ethanol are also less favorable for biomass than fossil fuel feedstocks, with ethanol giving approximately 34% less energy than the equivalent quantity of gasoline. The lower heating value (LHV) for ethanol is around 21.1 $MJ \cdot l^{-1}$ (75,700 $Btu \cdot gallon^{-1}$) compared to 32.0 $MJ \cdot l^{-1}$ (115,000 $Btu \cdot gallon^{-1}$), while the higher heating values (HHVs) are 23.4 $MJ \cdot l^{-1}$ (84,000 $Btu \cdot gallon^{-1}$) for ethanol and 35.0 $MJ \cdot L^{-1}$ (125,000 $Btu \cdot gallon^{-1}$) for gasoline (Anon., 2006). Therefore, more ethanol

is required to do the same amount of work, which needs to be factored into the relative costs to the consumer.

However, bioethanol offers many environmental advantages over fossil fuels that are desirable for meeting the challenges of future energy production. Bioethanol is produced from renewable and sustainable resources, and theoretically makes no net contribution to greenhouse gas emissions. Its production and combustion reduce greenhouse gas emissions by around 12% relative to the fossil fuels it replaces (Hill et al., 2006). As a transport fuel (pure bioethanol or in mixtures with gasoline), it results in considerable reductions in emissions of pollutants (e.g., VOCs and CO). Bioethanol also contains no sulfur, and therefore does not contribute to acid rain. Therefore, demand for bioethanol is forecasted to rise, to enable environmental targets to be met and to stretch fossil fuel supplies. The development of domestically abundant and inexpensive biomass feedstocks will be required to meet future demand, particularly using wastes and biomass from agriculturally marginal land.

There has been a long history of converting Jerusalem artichoke into ethanol. The chemist Anselme Payen advised the French alcohol industry in the late 1800s, for example, to use Jerusalem artichoke tubers as a carbohydrate source for fermentation with yeasts, to produce a beer that could be distilled into pure ethanol. Fermented and distilled tuber extracts of Jerusalem artichoke have continued to be used in beer, wine, and spirit production. Beer made from Jerusalem artichoke tubers is said to have a sweet, fruity flavor; extracts of tubers or stalks can be added at various stages during the brewing process (Fritsche and Oelschlaeger, 2000; Zelenkov, 2000). In France and Germany, topinambur brandy has been made from tubers fermented by yeasts, especially *Saccharomyces cerevisiae* and *Kluyveromyces marxianus* (Benk et al., 1970; Hui, 1991). Vodka and sake can also be produced by the fermentation and distillation of Jerusalem artichoke extracts (e.g., Arbuzov et al., 2004; Ge and Zhang, 2005). The quality of spirits obtained from Jerusalem artichoke extracts is determined by their characteristic composition (e.g., inulin content), with esters produced during fermentation giving these spirits a distinctive aromatic quality (Szambelan et al., 2005). All systems that ferment Jerusalem artichoke stalks and tubers need to take into account the inulins present; the chemistry of inulin fermentation has been described in Chapter 5.

Ethanol from Jerusalem artichoke has been recognized as a promising biofuel since at least the 1920s. However, ambitious schemes in the 1930s and 1980s to promote Jerusalem artichoke as a source of fuel ethanol in the U.S. failed, primarily through lack of markets (Amato, 1993). The market for plant-derived ethanol is now growing, however, and improvements in the efficiency of production of ethanol from Jerusalem artichoke continue to be made (e.g., Baev et al. 2003; Filonova et al., 2001; Krikunova et al., 2001; Kobayashi et al., 1995).

Plant biomass feedstocks undergo a series of pretreatments before fermentation, including milling or grinding, and the separation of juice and pulp. Further treatments remove lignin and digest components such as cellulose and hemicellulose into fermentable compounds by partial or complete hydrolysis. Cellulose can be broken down, for example, using sulfurous acids, exogenous enzymes, or enzymes from cellulolytic strains of fungi or bacteria. The inulin present in Jerusalem artichoke can be converted to fermentable sugars by acidic or enzymatic hydrolysis (Figure 7.1a) prior to fermentation with yeasts or bacteria (van Bekkum and Besemer, 2003). This process is sometimes called separate hydrolysis and fermentation (SHF). Acid hydrolysis was the original method of obtaining fermentable sugars from plant feedstocks, using either high acid concentrations at low temperatures or low acid concentrations at high temperatures. A hot acid hydrolysis of pulped Jerusalem artichoke, for instance, was formerly the method of producing fructose and glucose from inulin, prior to fermentation with *S. cerevisiae* or other distillery yeasts (e.g., Boinot, 1942; Lampe, 1932; Underkofler et al., 1937). Subsequently, enzymic pretreatment has been used to hydrolyze inulin prior to fermentation (Combelles, 1981; Duvnjak et al., 1982; Sachs et al., 1981; Zubr, 1988). A process to produce ethanol from Jerusalem artichoke tubers was designed by Kosaric et al. (1982), for example, using a two-step tuber maceration to yield juice with a 12 to 15% carbohydrate content. This was heated and hydrolyzed enzymatically. After cooling, the juice was fermented in

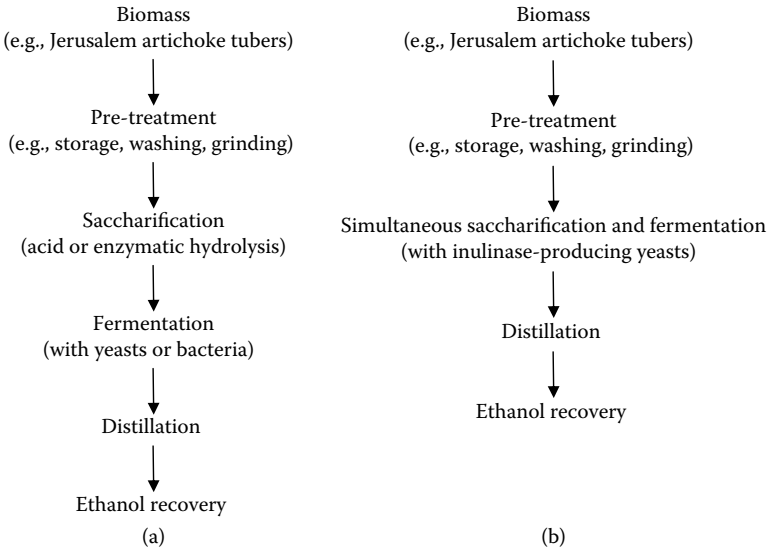

FIGURE 7.1 Stages in ethanol production from Jerusalem artichoke using (a) acid or enzymatic hydrolysis followed by fermentation with classical yeasts (e.g., *S. cerevisiae*) or the bacteria *Z. mobilis*, and (b) inulinase-producing yeast (e.g., *K. marxianus*).

batches, with yeast being recycled. An ethanol yield of about 90% of the theoretical maximum value was achieved after 28 h (Kosaric and Vardar-Sukan, 2001). Zubr assessed enzymatic pre-treatments of tuber pulp (cv. 'Urodny') prior to fermentation with *S. cerevisiae*; the highest ethanol yields were obtained in conjunction with the industrial enzyme 'Novo 230' (Zubr, 1988). Extracellular inulinase from *Aspergillus niger* can also be used in conjunction with *S. cerevisiae* to ferment tuber juice or pulp (Ohta et al., 2004).

Traditional fermentation yeasts, such as *S. cerevisiae*, are not adapted to utilize inulin. However, a number of yeast strains have been discovered with inulinase activity, which can both hydrolyze inulin and ferment the resulting sugars (Echeverrigaray and Tavares, 1985; Guiraud et al., 1981a, 1981b; Padukone, 1996). It is therefore possible to produce ethanol from Jerusalem artichoke juice using these yeasts in a single vessel, without prior hydrolysis or saccharification, in a process called simultaneous saccharification and fermentation (SSF) (Figure 7.1b). In practice, enzymatic hydrolysis may still be conducted under acidic conditions, for instance, to utilize the enzymes present in the plant material and to start saccharification prior to the addition of inulinase-producing yeasts. High rates of ethanol production from tuber extracts have been obtained with inulin-fermenting strains of *K. marxianus*, *K. fragilis*, *Candida pseudotropicalis*, *C. kefyr*, *C. macedoniensis*, *Saccharomyces fermentati, S. diasticus*, *Schwanniomyces castellii*, and *Torulopsis colliculosa* (Duvnjak et al., 1981; Ge and Zhang, 2005; Guiraud et al., 1986; Rosa et al., 1986). Improvements have been made to these yeasts to further increase the efficiency of ethanol production; for example, a strain of *K. fragilis* has been selected with improved ethanol tolerance (Rosa et al., 1988).

There are, in general, four types of ethanol production systems used by industry: batch, fed-batch, continuous, and semicontinuous processes. The batch process is the classical method of producing alcoholic beverages and is the method by which most ethanol is produced today. Batch processes are easily managed and flexible; their main disadvantage is unproductive downtime, though several bioreactors can be run at staggered intervals. Continuous processes have little downtime; microbial cells are born in the bioreactor, replacing those that are washed out. Continuous systems can produce more ethanol, of a more uniform quality, than batch processes and are better suited to large-scale production, but they are less flexible, have higher investment and operating costs, and have a higher risk of adverse microbial mutation due to longer culturing periods.

Fed-batch processing combines batch and continuous cultures, with feedstocks and microbial cultures added at regular intervals and effluent removed discontinuously. Semicontinuous production is effectively repeated fed-batch processing, with culture withdrawn at intervals, and new microbes and fresh medium added (Kosaric and Vardar-Sukan, 2001). The fermentation of Jerusalem artichoke extracts in experimental trials has been conducted using batch, semicontinuous, and continuous processes (e.g., Bajpai and Bajpai, 1991; GrootWassink and Fleming, 1980). Fermentation by all processes can be conducted with either free (e.g., Margaritis and Bajpai, 1982b) or immobilized (e.g., Margaritis and Bajpai, 1983; Margaritis and Merchant, 1984) yeast cells. Free cells are suspended in the culture medium and may aggregate through natural flocculation, while immobilized cells are held on surfaces or within particles. Immobilized cells can occur at higher cell concentrations, and the need for cell recycling systems to replace washed out cells is avoided, although free cells are less prone to inhibition due to the high levels of substrate or alcohol that can occur around immobilized cells.

Optimal rates of fermentation occur at acidic pH levels. In nonacidified conditions (e.g., over pH 6.4) more contaminants occur, which reduces the efficiency of fermentation. Guiraud et al. (1982) found that fermentation with inulin-fermenting strains of a range of yeast species occurred optimally at pH 3.5, with higher-grade alcohol produced after 7 days in a semicontinuous culture (Guiraud et al., 1982). In batch and continuous cultures, with free and immobilized cells, the optimal pH range is 3.5 to 6.0 (e.g., Bajpai and Margaritis, 1987; Margaritis and Bajpai, 1982a; Margaritis et al., 1983b). Fermentation with inulinase-containing yeasts occurs optimally at high temperatures. For instance, Rosa et al. (1987, 1992) reported that batch fermentation with *K. marxianus* proceeded efficiently at fermentation temperatures of 28 to 36°C and occurred up to 39 to 40°C, although at higher temperatures premature stoppage of fermentation is more likely due to a reduced ethanol tolerance of the yeast. Temperature affects the rate of ethanol production differently in free and immobilized yeast cell systems. Bajpai and Margaritis (1987) found that fermentation with free cells of *K. marxianus* occurred optimally at 25 to 35°C, while immobilized cells performed well over a wider temperature range of 25 to 45°C. However, Williams and Munnecke (1981) observed a lower optimum temperature for immobilized *S. cerevisiae* than for free cells, probably due to diffusional limitations arising from the support matrix, resulting in inhibitory levels of ethanol around the cells at higher temperatures.

In addition to yeasts, strains of the bacteria *Zymomonas mobilis* also efficiently and rapidly ferment Jerusalem artichoke juice. The bacteria do not contain inulinase, so fermentation must be in conjunction with acidic or enzymatic hydrolysis of inulin (Kim and Rhee, 1990). However, *Z. mobilis* has several properties that are suited to industrial applications. It has a natural tendency to flocculate, raising fermentation efficiency in batch production, and grows in both high sugar and ethanol concentrations without inhibition, while it has more favorable fermentation kinetics than yeasts such as *S. cerevisiae* (Ingram et al., 1989; Rogers et al., 1979; Toran-Diaz et al., 1983). Moreover, Szambelan et al. (2005) found that concentrations of components other than ethanol, which are potential contaminants, were fewer using *Z. mobilis* than when using strains of yeast (*S. cerevisiae* and *K. fragilis*). The optimal conditions for fermentation with *Z. mobilis* are typically 30 to 40°C and pH 4.0 to 5.0 (Kosaric and Vardar-Sukan, 2001). Fermentation of Jerusalem artichoke ('Albik' and 'Rubik') tubers by *Z. mobilis* gave theoretical yields of ethanol, after acid and enzymic inulin hydrolysis, of 86 and 90%, respectively (Szambelan and Chrapkowska, 2003). In a number of other studies with *Z. mobilis*, ethanol yields of 90 to 94% of the theoretical maximum have been obtained (Allias et al., 1987; Favela-Torres et al., 1986; Szambelan et al., 2005; Toran-Diaz et al., 1985). In continuous production systems, *Z. mobilis* consistently outperforms yeast strains in terms of ethanol yield (Kosaric and Vardar-Sukan, 2001). However, there is a need to sterilize the culture medium when using *Z. mobilis*, while yeast strains that produce inulinase may be preferable in economic terms when fermenting Jerusalem artichoke extracts. *Z. mobilis* can be used in mixtures with yeasts (e.g., *S. cerevisiae* and *K. fragilis*), and this can result in higher theoretical yields than obtained from single organisms alone (Szambelan et al., 2004b).

TABLE 7.1
Ethanol Yields from Jerusalem Artichoke

Plant Part	Yield per Wet Weight ($l \cdot t^{-1}$)[a]	Yield per Area ($l \cdot ha^{-1}$)	Reference
Tops (aboveground parts)	78	11,230	Judd, 2003
Tops	83	—	Klass, 1998
Tubers	—	11,000	Ercoli et al., 1992
Tubers	—	3,970 to 7,448	Schittenhelm, 1987
Tubers	80–100	—	Franke, 1985
Tubers		2,500–7,500	Guiraud et al., 1982
Tubers	—	2,610	El Bassan, 1998
Tubers	—	3,840–5,850	Kahnt and Leible, 1985
Tubers	—	6,400	Chabbert et al., 1983
Tubers	337 $ml \cdot kg^{-1}$	3,060	Zubr, 1988
	—	5,600	Williams and Ziobro, 1982
Tubers	77	1,500–3,100	Kaŕa et al., 2005
Tubers	—	4,169	Mays et al., 1990
Tubers	—	2,630–5,589	Stolzenburg, 2006
Tubers	—	5,708	Fernandez, 1998

[a] Unless otherwise noted.

Jerusalem artichoke mash, pulp, or juice provides a complete medium for cultures of yeasts and *Z. mobilis* bacteria; in addition to carbohydrate, it supplies the necessary minerals and vitamins needed for growth (Duvnjak et al., 1981; Toran-Diaz et al., 1985). Therefore, no additional nutrients need be added, although it is necessary to standardize the media for experimental studies. However, higher ethanol yields were obtained with juice than with mash or pulp, when fermentation proceeded with inulinase-producing yeasts (Szambelan et al., 2004a).

Ethanol yields of over 90% of the theoretical maximum (calculated from known carbohydrate content) are usually obtained from Jerusalem artichoke tubers (e.g., Bajpai and Bajpai, 1991; Barthomeuf et al., 1991; Duvjnak et al., 1981; Ge and Zhang, 2005; Guiraud et al., 1981a; Margaritis and Bajpai, 1982c; Margaritis et al., 1983a). Given average dry matter yields and the use of yeast strains with inulinase activity (e.g., *K. marxianus*), it has been estimated that ethanol yields of at least 8,500 $l \cdot ha^{-1}$ are readily obtainable (Bajpai and Bajpai, 1989, 1991; Guiraud et al., 1982). Yields of ethanol from Jerusalem artichoke reported in the literature are given in Table 7.1. Ethanol yields of at least 3,900 to 4,500 $l \cdot ha^{-1}$ are considered attainable under commercial production conditions (Hayes, 1981; Kosaric and Vardar-Sukan, 2001), while ethanol yields of up to 11,230 $l \cdot ha^{-1}$ can theoretically be achieved (Ercoli et al., 1992; Judd, 2003). Jerusalem artichoke could therefore become an important bioethanol feedstock, particularly when grown on marginal or set-aside land in regions with a temperate climate.

Both the tops and tubers of Jerusalem artichoke can be used for ethanol production. Although tubers have predominantly been used, levels of accumulating fructans in the stalks are sufficient in the late summer, prior to the final stage of tuberization, for them to be a good substrate for ethanol production (Bajpai and Margaritis, 1986; Caserta and Cervigni, 1991; Curt et al., 2005; Harris, 1985; Negro et al., 2006). Curt et al. (2005) found that the peak stalk content of soluble carbohydrates (43.9% of total stalk dry weight) coincided with the appearance of floral buds, although at that stage the yield of early maturing clones was relatively low due to lower stalk biomass. The highest overall productivity was recorded for late-maturing clones (i.e., 'Boniches,' 'China,' and 'Violet de Rennes'), which gain a favorable balance of stalk and tuber yields (Curt et al., 2005). Using a stalk extract containing 7.3% total sugars, Margaritis et al. (1983a) obtained an

ethanol yield of 97% of the theoretical maximum value. A strain of *K. marxianus* was the best of seven yeasts tested, although *K. fragilis*, *Debaryomyces* sp., and *Schizosaccharomyces pombe* also efficiently fermented stalk carbohydrates to ethanol. Stolzenburg (2006) reported highest ethanol yields (3,197 l·ha^{-1}) from tops harvested in September in Germany. Ethanol yields produced from the stalks have sometimes been discouraging (Zubr, 1987), although yields comparable with those obtained using tubers are possible (Judd, 2003). Negro et al. (2006) showed that both acid hydrolysis, followed by fermentation with *S. cerevisiae*, and direct fermentation with *K. marxianus* can efficiently produce ethanol from stalk fructans. It is also economically feasible to use whole plant (stalks and tubers) for bioethanol production, particularly if the residual solids are used as a protein-rich animal feed (Bajpai and Bajpai, 1989).

Inulin hydrolysis appears to be the limiting factor in the fermentation rate of Jerusalem artichoke pulp and juice. Variations in residual sugar composition observed during fermentation using a flocculating strain of *Saccharomyces diastaticus* (NCYC 625), for instance, were due to differences in the inulin polymer distribution of the tuber extracts. Hydrolysis due to enzymic activity and fermentation yield decreased when the fructose/glucose ratio of the extract increased (Schorr-Galindo et al., 2000). *S. diastaticus* NCYC 625 facilitates high overall productivity by converting monosaccharides and short-chain fructoligosaccharides efficiently to ethanol, while leaving the longer-chain fructooligosaccharides unmetabolized for use as a source of fructose (Schorr-Galindo et al., 1994, 1995a, 1995b).

The time of Jerusalem artichoke harvest was found to be critical for ethanol production by classical batch methods in the early 20th century; tubers harvested for fermentation in September and October generally gave poor results, while tubers harvested after overwintering or kept in cold storage were favored. This was because storage resulted in inulin being brokendown into abundant quantities of fermentable carbohydrates. Acid and enzymatic hydrolysis pretreatments were subsequently developed to optimize ethanol yields from tubers. Nevertheless, ethanol yields are related to the total amount of fermentable sugar present in the plant material at harvest. In a 2-year German study, for instance, ethanol yields of 3,840 and 5,850 l·ha^{-1} were obtained for tubers with 6.7 and 10.3 t fermentable sugar·ha^{-1}, respectively (Kahnt and Leible, 1985), sufficient to give ethanol yields of up to 5,600 l·ha^{-1} (Williams and Ziobro, 1982). In a more recent German study, peak ethanol production from tubers (6,179 l·ha^{-1}) coincided with peak fructose (8.7 t·ha^{-1}) in October, with ethanol yields remaining high until February, but with low yields prior to October (Stolzenburg, 2006). A partial inhibition of fermentation has been noted in early-harvested tubers that is not due to polymerization of sugars; this may be related to the presence of chlorogenic acid or similar fermentation inhibitors (Guiraud et al., 1982; Paupardin, 1965).

Cultivars differ in their ethanol yield potential (Chabbert et al., 1986); for instance, tuber extracts of 'Bianka,' 'Waldspindel,' and 'Medius' yielded 3,970, 7,448, and 7,086 l·ha^{-1} ethanol, respectively (Schittenhelm, 1987). Cultivars with the highest tuber yields produced the highest ethanol yields in a study with 17 cultivars, ranging from 'BS-86-17' (12.2 t·ha^{-1} and 5,589 l·ha^{-1} ethanol) to 'Henriette' (5.6 t·ha^{-1} and 2,630 l·ha^{-1} ethanol) (Stolzenburg, 2006).

The potential of Jerusalem artichoke as a feedstock for ethanol production has been assessed in many countries in recent years. In New Zealand, for instance, Jerusalem artichoke gave the highest potential ethanol yield (calculated from known crop yields and fermentable content) of a range of crops assessed. From three harvests of the tops a year, estimated ethanol production was 78 l·t^{-1} and 11,230 l·ha^{-1}. Although fodder beet (*Beta vulgaris* L.) remains a favored feedstock for ethanol production in New Zealand, Jerusalem artichoke has been recommended for further study (Judd, 2003).

High yields of fermentable sugars in Jerusalem artichoke have been reported in Canada. The sugar yields obtained from tubers of 6.2 to 8.6 t·ha^{-1} under prairie conditions compared favorably to the yield of 4.9 t·ha^{-1} obtained with sugar beet (Stauffer et al., 1981). Theoretical ethanol yields from Jerusalem artichoke grown in Manitoba were given as 4,580 kg·ha^{-1} (5,780 l·ha^{-1}) for tubers (of fresh weight 42,000 kg·ha^{-1} and carbohydrate content 7,088 kg·ha^{-1}) and 1,920 kg·ha^{-1} (2,423

l·ha^{-1}) for forage (of 12,000 kg·ha^{-1} dry matter). In comparison, theoretical yields of ethanol from sugar beet roots, corn (maize) grain, and wheat grain were 3,185, 2,680, and 1,447 kg·ha^{-1} or 4,019, 3,382, and 1,826 l·ha^{-1}, respectively (Stauffer et al., 1981). Studies in Quebec and western Canada on the economics of ethanol production from Jerusalem artichoke, however, showed that the cost advantage was greater for tops than for tubers (Baker et al., 1990).

In Taiwan, estimated yields of 46.2 and 52.3 l·t^{-1} were reported for fresh tubers and tops, respectively. Total alcohol production was calculated at U.S.$114.3 per hectare (1985 prices), which compared with U.S.$197 for sweetpotato (Lee et al., 1985). Jersualem artichoke was found to be superior to other crops, particularly *Amaranthus*, in terms of yield for bioenergy production in the Kaluga region of the Russian Federation (Bogomolov and Petrakova, 2001a). Yields of around 12.3 t·ha^{-1} dry weight of fodder gave 105 to 142 GJ·ha^{-1} of metabolizable energy (Bogomolov and Petrakova, 2001b). In a comparison of a range of crops, Jerusalem artichoke ('Mammoth French White') had the second highest alcohol production potential, after sweetpotato (*Ipomoea batatas* (L.) Lam). A tuber yield of 30.7 t·ha^{-1} produced 4,169 l·ha^{-1} ethanol (Mays et al., 1990). In a European Commission report of 1985 the estimated total costs of producing bioethanol from Jerusalem artichoke (72 Ecu·100 l^{-1}) compared favorably with a range of other crops, including potato (73), sugar beet (49), wheat (54), and maize (68) (Spelman, 1993). These costs took into account raw materials, transport, processing, and by-product value. However, mainstream crops like sugar beet, maize, and cereals have a level of policy support and subsidy not available to less conventional crops like Jerusalem artichoke. Therefore, initiatives involving Jerusalem artichoke have been difficult to launch.

Harvesting the tops at an optimum time for use as a leaf protein concentrate in Italy was compatible with using the tubers for ethanol production. Sugar in the tubers was over 15% of fresh matter in both the first and second years of the study, although tuber yields were lower in the second year (on average, 16.5 t·ha^{-1} cf. 9.4 t·ha^{-1}), when the crop was grown as a perennial for herbage. Ethanol production was up to 11,000 l·ha^{-1} in the first year and 7,200 l·ha^{-1} in the second year. Eight cultivars were compared, and they showed marked differences in tuber dry matter and ethanol yields over the 2 years. In the first year, the highest dry matter production was 23 t·ha^{-1}, for 'Violet de Rennes' and 'K8,' while the highest ethanol production (10,756 l·ha^{-1}) was with 'K8.' In the second year, 'Nahodka' gave the highest tuber yield (14.0 t·ha^{-1}) and the best ethanol yield (7,163 l·ha^{-1}), while also producing 15 t·ha^{-1} of aerial biomass for protein extraction (Ercoli et al., 1992). In central and south Italy, tuber dry matter yields of 68 to 72 t·ha^{-1} ('Violet de Rennes') have been obtained in trials aimed at bioethanol production, but irrigation is necessary in the dry climatic conditions of these regions (Mimiola, 1988). Even in a hot dry climate with relatively poor soils, however, if tubers comprise over 15% sugars by fresh weight, then ethanol yields of over 5,000 l·ha^{-1} can be achieved (Bartolelli et al., 1982; Bosticco et al., 1989; Zonin, 1987).

In the U.S., corn (maize; *Zea mays* L.) is the favored feedstock source for bioethanol production for transportation fuel, although some is produced from soybean (*Glycine max* L.). There were 101 bioethanol refineries in the U.S. in 2006, mainly located in the Midwest and California, with a total capacity of around 4,830 million gallons annually and a further yearly capacity of 2,880 million gallons under construction (RFA, 2006). These refineries predominantly utilized *Z. mays* and were of moderate size. The high cost of transporting energy crops favors farm-scale refineries that process locally harvested feedstock, with around 15 miles considered an upper limit in terms of a cost-effective energy balance. Utilizing corn for bioethanol has several drawbacks, however, including the need for large areas of land, which are consequently taken out of food production (Hill et al., 2006). As bioethanol production increases, more of the U.S. corn crop (possibly over a fifth by 2008) will be consumed for bioethanol production. As more bioethanol is used in automobile fuel, more agricultural land is required to grow energy crops. Although significant areas of agricultural land (up to 33 million ha in the early 1990s) have been practically idle in recent years (Putsche and Sandor, 1996), and agricultural residues and municipal wastes will also

contribute to biomass feedstocks, the diversion of increasing amounts of U.S. corn to bioethanol production has caused concern. As bioethanol production has become more profitable in the U.S., less corn has been available for feed and food applications, thereby driving up global grain prices, potentially leading to food insecurity in lower-income countries (e.g., Brown, 2006). Corn also has relatively high cultivation costs and high energy requirements in terms of inputs and conversion to ethanol. U.S. Department of Agriculture (USDA) studies have concluded that corn has a net energy balance of up to 1.34 (i.e., 34% more energy is gained than is consumed by biomass production) (Shapouri et al., 1995, 2002). This figure has been contested, however, with one analysis suggesting that little or no positive energy balance is evident, while if nitrogen fertilizers and other inputs are considered, then corn ethanol may contribute nearly as much to greenhouse gas emissions as fossil fuels (e.g., Pearce, 2006; Pimentel, 2002, 2003). It should be noted that energy balance figures vary considerably between different locations, while by-products must be taken into account as they contribute to a positive energy balance. If leftover biomass is used as a dry fuel or fed to animals, for example, a positive energy balance occurs and around 13% less greenhouse emissions overall are emitted than for the equivalent amount of gasoline, although this is not current practice (Farrell et al., 2006). The ongoing capacity expansion for bioethanol production is set to make an important contribution to stretching gasoline supplies in the U.S., especially within bioethanol–gasoline blends, while also improving air quality. However, the reliance on corn as a feedstock is proving problematic.

As demand for bioethanol increases in the U.S., in response to the Energy Security Act of 2005, environmental policy initiatives, and rising gasoline prices, additional low-cost feedstocks will be required that do not utilize high-grade agricultural land. Jerusalem artichoke is a promising alternative biomass source, with a number of advantages over other energy crops (e.g., Wieczorek and Kosaric, 1984). It can grow on marginal land and in nutrient-depleted soils, where corn and soybean cultivation is not successful, requires relatively little energy input in terms of fertilizer, pesticides, and irrigation, and has produced favorable ethanol yields (e.g., 83 $l \cdot t^{-1}$) in trials in the U.S. (Klass, 1998). It has been estimated that biofuels produced on marginal cropland could replace a fifth of U.S. transportation fuel by around 2020, given the right level of support (Lee Lynd of Dartmouth College, quoted in Roberts, 2004, p. 79). However, not all areas of the U.S. may be suitable for growing Jerusalem artichoke. Disease problems and relatively low yields, compared to other energy crops (e.g., 62 $kg \cdot t^{-1} \cdot day^{-1}$), were observed in trials in Florida, leading to the conclusion that the crop could not be recommended for biomass production in the southeastern U.S. (O'Hair et al., 1983, 1988).

The economic viability of using Jerusalem artichoke as a bioethanol feedstock depends on several factors. These include production, harvesting, and transport costs; the scale of biorefinery operations; the value of by-products (e.g., animal feed, protein concentrate); the type of end product (e.g., gasoline additives or pure bioethanol); and, especially, overall costs compared to competing energy crops and fossil fuels (Baker et al., 1990; Hill et al., 2006; Kosaric et al., 1982; Kosaric and Vardar-Sukan, 2001). Subsidies and tax breaks may be important in developing new biomass feedstocks such as Jerusalem artichoke (von Sivers and Zacchi, 1996). Financial incentives to expand biofuel production have been put into place, for example, as a means of reducing oil dependency and improving air quality. The market will increasingly drive bioethanol demand, as the rising price of oil makes bioethanol more profitable. Studies on the economics of producing bioethanol from Jerusalem artichoke are described in Chapter 14.

Jerusalem artichoke is a promising biomass crop for ethanol production. It is easily cultivated and relatively cheap to grow, requiring little input in terms of irrigation, weed and pest control, and fertilizer. Fewer inputs are environmentally beneficial, while lower input costs lead to a more favorable overall energy balance. However, the tubers of Jerusalem artichoke have potential disadvantages as an ethanol feedstock. They tend to be tightly attached to the crown, making it relatively difficult to harvest them cleanly, and it can be hard to retain sugar quality during storage (Fleming and GrootWassink, 1979). One proposed solution for better storage is to make a concentrated extract

that can be stored as syrup until needed (Bajpai and Bajpai, 1989). It is also important that appropriate cultivars are grown for biomass.

Ethanol and spirits made from Jerusalem artichoke have many applications in the food industry and as an industrial chemical feedstock. Ethanol, for instance, is a key raw material in the manufacture of plastics, lacquers, and many other industrial products. Therefore, alternative markets exist for bioethanol should surpluses occur as a liquid fuel. Ethanol fermentation from Jerusalem artichoke also results in a range of valuable by-products, including a pulp (7% protein) utilizable as animal feed, protein concentrates, and a liquid crop fertilizer (Guiraud et al., 1982). The economic value of animal feed by-products, in particular, is a key factor in the economic viability of using Jerusalem artichoke as an energy crop. The tuber residue remaining after ethanol distillation can be used as a feedstock for biogas production (see below). The crop has also been proposed as a dual source of ethanol and single-cell proteins, simultaneously produced using different groups of yeasts to ferment tuber extracts (Apaire et al., 1983; Bajpai and Bajpai, 1989). The cultivation of biomass for energy on underutilized land can furthermore create new livelihoods for farmers, contribute to farm diversification, and create jobs in rural areas with high unemployment.

7.3.2 Biogas (Methane)

Biogas is a fuel produced by the anaerobic decomposition of wet organic matter (biomass), through the action of bacteria. As with natural gas, the main fuel component is methane. Biogas occurs naturally, for example, in swamps and marshes, where a layer of water gives rise to the necessary anaerobic conditions, and biogas from such sources can be harnessed as a fuel. Important feedstocks for the production of biogas in commercial anaerobic digester systems include industrial and domestic biowastes, slaughterhouse waste, and livestock manures. Any biomass can theoretically be used for biogas or methane production, and many plant species are potential candidate feedstocks, especially those rich in easily biodegradable carbohydrates (El Bassan, 1998). However, plants with a high lignin content have a low biodegradability and are less suitable (Klass, 1998).

Biomass crops are harvested, transported, and subject to pretreatments prior to fermentation (Figure 7.2). Pretreatments may include chopping to reduce the unit size of biomass, ensilage, acid hydrolysis, the addition of cellulase enzymes, or the use of solvents to remove lignin (Gritzali et al., 1988; Hayes et al., 1988). Pretreatments help to break down polysaccharides and other compounds into fermentable sugars before digestion. Anaerobic digestion is a multistage process involving a diversity of microorganisms that digest particular plant components (e.g., carbohydrates,

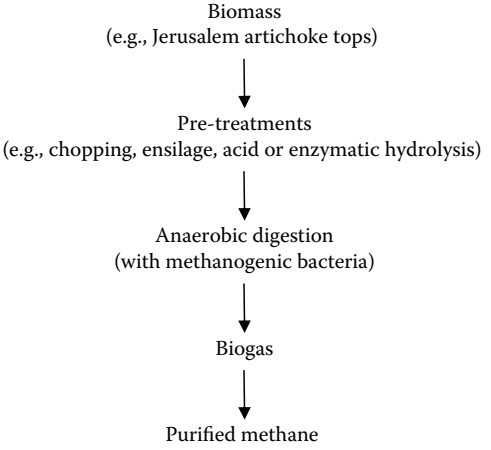

FIGURE 7.2 Stages in biogas and methane production from Jerusalem artichoke.

cellulose, and hemicellulose). The most important microorganisms involved are methanogenic bacteria, in the kingdom Archaebacteria. Three genera groupings of methanogenic bacteria are of particular importance: (1) *Methanobacterium* and *Methanobrevibacter* (e.g., *Methanobacterium formicum*); (2) *Methanococcus* (e.g., *Methanococcus vannielii*); and (3) *Methanomicrobium*, *Methanogenium*, *Methanospirillum*, and several other genera (e.g., *Methanomicrobium mobile*). All methanogenic bacteria are strictly anaerobic (Klass, 1998). Fermentation generally proceeds at pH 6.5 to 8.0 and usually within one of two optimal temperature ranges: a lower range (10 to 42°C) favorable to mesophilic bacteria and a higher range (50 to 70°C) favorable to thermophilic bacteria (White and Plaskett, 1981).

The biogas produced by anaerobic digestion mainly comprises methane (CH_4) and carbon dioxide (CO_2). For instance, the composition of a typical biogas from a pig manure is 65% methane and 35% carbon dioxide, with a thermal content of 26 $MJ \cdot m^{-3}$ (White and Plaskett, 1981). Methane content can range from 40 to 70% in biogas. Thermal values for biogas typically range from 15.7 to 29.5 $MJ \cdot m^{-3}$. In comparison, the energy values of dry natural gas and pure methane are 39.3 $MJ \cdot m^{-3}$ (Klass, 1998). For local use (e.g., on-farm heating of greenhouses or poultry sheds) biogas can be used without further processing. However, to obtain methane, for a more valuable and efficient biofuel, the carbon dioxide and minor components can be removed using several gas clean-up processes, such as alkali scrubbing or scrubbing with pressurized water. As the scale of energy-generating operations increases, so does the importance of removing carbon dioxide, which can be utilized as a by-product. The composition of minor components present in biogas depends on the type of feedstock deployed. Hydrogen sulfides, for instance, can occur at low levels (e.g., 0.1%) and lead to problems of corrosion and toxicity if not removed (White and Plaskett, 1981). Plant-derived feedstocks will generally give rise to fewer troublesome minor biogas components than biowastes and other types of feedstock. The nutrient-rich digestate remaining after biogas production can be fed back into the reactor, or it can be sold as a by-product, either as an animal feed or a crop fertilizer. The cleaned-up methane can be compressed and containerized, or distributed via pipelines. Methane is mainly used to generate heat and electricity.

Jerusalem artichoke is a suitable candidate energy crop for biogas production, and it amply fulfills many of the selection criteria. It has rapid growth and is easy to cultivate, has high energy and biomass yields with low-input requirements, a tolerance of a wide range of climatic conditions, resistance to pests and diseases, good overwintering ability, and an efficient convertibility to methane. The aerial parts of the crop are usually used, although tubers are also suitable. Nonstructural carbohydrates in the aerial parts are readily fermented, and the stems can contain large amounts of these carbohydrates. Converting Jerusalem artichoke tops to silage is an effective way of conserving aerial biomass, and enables it to be stored until required on a year-round basis. A number of studies, comparing the production of biogas (and methane purified from biogas) from fresh and ensiled tops, have demonstrated that the two types of feedstock give a similar productivity (Gunnarson et al., 1985; Lehtomäki, 2005; Mathisen and Thyselius, 1985; Zubr, 1986). It is better to harvest fresh green material for silage than to use material harvested during the stages of senescence (Zubr, 1985). Biogas and methane yields from Jerusalem artichoke, reported in the literature, are summarized in Table 7.2. For instance, the biogas yield from Jerualem artichoke tops after 20 days' retention time in a digester was 480 to 590 m^3 biogas$\cdot t^{-1}$ volatile solids (VS),* which was superior to six other crops (e.g., alfalfa, maize, and sugar beet) tested (El Bassan, 1998, quoting unpublished data from Weiland, 1997).

Feedstock chemical composition is important for biogas production. The low molecular weight sugars, inulin (fructans), hemicellulose, and cellulose present in Jerusalem artichoke are all digested in biogas fermentation. The highest proportions of most digestible components for the tops are found in the stem, and the inclusion of a high proportion of stems is therefore desirable for biogas production (Malmberg and Theander, 1986). Moreover, high levels of nitrogen in the substrate

* The quantity of solids in a sample that is lost by ignition of the dry solids at 600°C.

TABLE 7.2
Biogas and Methane Yields from Jerusalem Artichoke

Plant Part	Biogas ($l \cdot kg^{-1}$ VS)[a]	Methane per Wet Wt. ($l \cdot kg^{-1}$ VS)[z]	Biogas per Area ($m^3 \cdot ha^{-1}$)	Methane per Area ($m^3 \cdot ha^{-1}$)	Reference
Tops[b]	—	93 $m^3 \cdot t$	—	3,100–5,400	Lehtomäki, 2005
Tops	480–680	—	5,500	2,800	Gunnarson et al., 1985
Ensiled tops	468	315	—	—	Zubr, 1985
Tubers	595	411	—	—	Zubr, 1988
Tops	296	189	—	—	Zubr, 1988
Ensiled tops	331	229	—	—	Zubr, 1988
Tops	480–600	—	—	—	Mathisen and Thyselius, 1985
Ensiled tops	500–680	250–320	—	—	Mathisen and Thyselius, 1985
Tops	480–590 $m^3 \cdot t$	—	—	—	El Bassan, 1998

[a] Unless otherwise noted.

[b] Freshly harvested aerial parts (stem and leaves) unless otherwise stated.

are detrimental to biogas production, with nitrogen levels highest in the leaves of Jerusalem artichoke (Malmberg and Theander, 1986; Mathisen and Thyselius, 1985; Somda et al., 1999). Inulin hydrolysis is the rate-limiting step when using Jerusalem artichoke as a substrate in anaerobic digestion reactors.

Farm-scale biogas plants have been operating in Germany since 2000, and pilot plants are now being established worldwide. Energy crops are often used as a co-substrate with industrial and household biowastes and animal manures. Mixtures of ensiled plant biomass with cow or pig manures have been shown to produce high biogas yields (e.g., 350 to 540 $l \cdot kg^{-1}$ VS), with a mixture containing 70% silage giving the best biogas yields in one study (Mathisen and Thyselius, 1985). The anaerobic digestion of energy crops represents a renewable domestic energy source, which is amenable to decentralized farm-scale energy production in areas close to crop production. Plant biomass can be produced on set-aside land in crop rotations, or it can utilize crop overproduction and crop residues, creating new business opportunities in rural areas (Lehtomäki, 2005).

In a pilot anaerobic digestion system in Finland, the potential methane yields from Jerusalem artichoke were among the highest of a range of energy crops assessed, including timothy grass (*Phleum pratense* L.), lupine (*Lupinus polyphyllus* Lindl.), reed canary grass (*Phalaris arundinacea* L.), and nettle (*Urtica dioica* L.). Jerusalem artichoke had a methane production potential of 0.37 m^3 $CH_4 \cdot kg$ organic matter and 93 m^3 $CH_4 \cdot t$ wet weight. In trials, Jerusalem artichoke yielded an annual 9 to 16 t $dm \cdot ha^{-1}$ and 3,100 to 5,400 m^3 $CH_4 \cdot ha^{-1}$, equivalent to an annual gross energy potential of 30 to 50 $MWh \cdot ha^{-1}$ energy or 38,000 to 68,000 $km \cdot ha^{-1}$ of passenger car transport (Lehtomäki, 2005, 2006; Lehtomäki and Bjørnsson, 2006). For the crops with the highest methane potentials per hectare in Finland (Jerusalem artichoke, timothy grass, and reed canary grass) a hectare could potentially fuel one to three passenger cars (traveling an average distance of 20,000 to 30,000 km) for a year. Therefore, if the 2004 area of agricultural set-aside land in Finland had been used to produce biogas from energy crops, the methane could have potentially fueled 8 to 25% of the country's passenger cars (Lehtomäki, 2006).

Jerusalem artichoke had a similar methane production potential for repeated cuttings in the Finnish trials, whereas other leafy energy crops assessed, such as giant knotweed (*Reynoutria sachalinensis* F. Schmidt ex Maxim.) and sugar beet tops (*Beta vulgaris* L.), had methane potentials that increased at later harvests. Lignin levels were also unusually constant for the tops of Jerusalem artichoke, regardless of maturity, while nonstructural carbohydrates (fructans) increased in the stems

until mid-October. Therefore, the crop can be harvested late into the season without jeopardizing the efficiency of anaerobic digestion (Lehtomäki, 2006).

Zubr (1985) investigated the potential of 33 different raw materials, including silage from Jerusalem artichoke tops, for biogas production in Denmark. Anaerobic digestion was carried out under mesophilic conditions (35°C), using a series of batch system fermentation reactors. The production of biogas was registered daily. Retention times ranged from 26 to 82 days, depending on the material, with optimal retention time for Jerusalem artichoke being around 33 days. Jerusalem artichoke silage comprised 17.1% total solids (TS) and 15.4% volatile solids (VS), with 81.7% of VS being microbiologically decomposable. In general, the ratio VS/TS is a measure of organic matter content, which was found to be relatively high in Jerusalem artichoke silage. The silage contained 31.9% crude fiber, an indication of the presence of lignin. High levels of lignin lower the ability of microbes to decompose raw materials, with crude fiber varying between 44.2% (wheat straw) and 12.3% (sugar beet tops) for the material tested. Carbon and nitrogen in the silage were 42.0 and 2.48% of TS, with a C/N ratio of 17. Sulfur comprised 0.13% of TS, indicating that pollution of biogas by sulfur-containing contaminants is relatively unlikely using Jerusalem artichoke silage. The silage yielded 421 $l \cdot kg^{-1}$ TS, 468 l biogas$\cdot kg^{-1}$ VS, and 315 l methane$\cdot kg^{-1}$ VS, with the biogas comprising on average 67.4% methane (Zubr, 1985).

In Sweden, research to assess the potential of the aerial parts (stems and foliage) of Jerusalem artichoke as a feedstock for biogas production has been conducted at the Swedish University of Agriculture. Yields of aerial parts up to 20 $t \cdot ha^{-1}$ dry matter can be obtained in Sweden, where plants do not flower and instead produce strong vegetative growth (Wünsche, 1985). Gunnarson et al. (1985) found that the aerial dry matter yields for three clones ('Topinanca,' 'Variety No. 1927,' and 'Variety No. 1168,' the latter a hybrid of Jerusalem artichoke and sunflower) varied between 7 and 16 $t \cdot ha^{-1}$. 'Topinanca' had the highest dry matter content. Biomass digestion experiments were performed at mesophilic (37°C) conditions on a laboratory scale (Gunnarson et al., 1985; Mathisen and Thyselius, 1985). Biogas production was approximately equal with fresh and ensiled biomass, with a pH of around 7.5 in the digester in both cases. Fresh and ensiled material yielded 480 to 680 l biogas$\cdot kg^{-1}$ of organic material; the methane content of the biogas obtained was between 52 and 55%. The chemical composition of silage was determined before and after digestion for the production of biogas. The lignin part remained mostly unchanged, although cellulose, hemicellulose carbohydrates, and other extractable substances were much reduced after anaerobic digestion, with nonstructural carbohydrates (fructans) completely digested (Gunnarson et al., 1985). The authors concluded that under Swedish conditions it should be possible to obtain yields of around 5,500 m^3 biogas$\cdot ha^{-1}$ for Jerusalem artichoke. Given a methane concentration of 52%, the yield would be 2,800 m^3 methane$\cdot ha^{-1}$. The economics of biogas production are considered in Chapter 14.l.

Using the Swedish laboratory digester, Mathisen and Thyselius (1985) reported biogas yields from batch and semicontinuous digestion of fresh and ensiled Jerusalem artichoke tops. Batch digestion experiments were used to determine the highest possible yields from a range of energy crops, with substrate added in daily portions over a 3- to 4-week period. In batch digestion experiments, freshly chopped tops yielded 540 $l \cdot kg^{-1}$ VS after 1 week, 90% of the final value of 600 $l \cdot kg^{-1}$ VS. In two trials, ensiled tops yielded 470 and 510 $l \cdot kg^{-1}$ VS after 1 week, 72 and 76% of the final values of 660 and 680 $l \cdot kg^{-1}$ VS, respectively. The digestion rate for Jerusalem artichoke was a little slower than for fresh alfalfa (*Medicago sativa* L.), kale (*Brassica oleracea* L.), and grass (*Poa* spp.), but faster than for the woody biomass used: birch (*Betula* sp.) and sallow (*Salix* sp.). In the semicontinuous digestion experiments, chopped fresh material yielded 480 to 590 $l \cdot kg^{-1}$ VS (80 to 98% of final yield in batch experiments), while ensiled tops yielded 510 to 560 $l \cdot kg^{-1}$ VS (78 to 86% of final yield in batch experiments). The methane content of the biogas obtained from fresh and ensiled tops of Jerusalem artichoke under semicontinuous digestion was 50 to 55%, with organic loads of between 2.2 and 3.0 g $VS \cdot l^{-1} \cdot day^{-1}$ and a hydraulic retention time of between 43 and 59 days. The digestion of fresh material and silage was found to be a stable process, without

the need for pH adjustment. Fresh and ensiled material gave similar biogas yields with both batch and continuous digestion, which were among the highest of a range of crops and woody biomass tested. Although biogas production can proceed effectively via batch, semicontinuous, or continuous digestion, El Bassan (1998) suggested that production on a continuous long-term basis, using a homogeneous substrate, was the most cost-effective option.

The residue or sludge left after the pulp of Jerusalem artichoke tubers has been fermented and distilled to produce ethanol can be used to make biogas (methane). Tuber residue gave higher yields of biogas (595 $l \cdot kg^{-1}$ volatile solids) than fresh tops (296 $l \cdot kg^{-1}$) or ensiled tops (331 $l \cdot kg^{-1}$) (Zubr, 1988). Zubr concluded that using the tuber residue for further energy production was feasible, with yields of biogas being relatively high in comparison to other plant biomass materials. The combined exploitation of Jerusalem artichoke for bioethanol and methane yielded a gross energy of 159 $GJ \cdot ha^{-1}$, corresponding to 4,500 l oil equivalents $(EO) \cdot ha^{-1} \cdot year^{-1}$ (Zubr, 1988). However, the tops from Jerusalem artichoke did not appear particularly suitable for biogas production in this study, mainly because of the long retention time needed and the large amount of solid fermentation residue produced (Zubr, 1988).

Zubr (1988) analyzed the costs of producing Jerusalem artichoke for biofuel (ethanol and biogas) in Denmark. The total production costs, which included soil preparation, fertilizer, seed tuber purchase, cultivation, harvesting, and transport, were calculated as 8,843 $DKr \cdot ha^{-1}$. Seed tubers and fertilizer were the main expenses, with the total cost of raw materials accounting for around 50% of the production costs of ethanol. The study concluded that biofuels from Jerusalem artichoke were not competitive with fossil fuels in the market of 1988. However, the circumstances at the start of the 21st century are changing. A growing awareness of environmental problems linked to the burning of fossil fuels has resulted in subsidies, tax incentives, and regulations that favor renewable energy sources. Meanwhile, any steep rises in the price of gasoline will make plant biomass sources, such as Jerusalem artichoke, more competitive in relation to gasoline.

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8 Genetic Resources, Breeding, and Cultivars

The future of the Jerusalem artichoke as a crop hinges upon the introduction of critical genetic improvements via plant breeding. Existing commercial cultivars are closer in appearance to their wild ancestors than most crop species, due to the fact that the Jerusalem artichoke has not been subject to the same degree of genetic manipulation. Nevertheless, a great deal of diversity is evident. The tubers, for instance, occur in a range of shapes, sizes and colors. Selective breeding has been conducted since at least the 17th century, especially in Europe, although not in a particularly coordinated manner. A large number of cultivars and clones have been described, but duplication under different names may be commonplace. Breeding efforts have concentrated on increasing tuber yield and the inulin content of tubers. More recently, interest has focused on using Jerusalem artichoke as a multipurpose crop, for food and nonfood industry applications, as a feedstock for energy production, and as forage or concentrated animal feed.

8.1 BREEDING PROGRAMS

Growers have selected for desirable traits in Jerusalem artichokes since the early days of its cultivation, with the result that a large number of cultivars and clones have been described. The tubers have been the main focus of selection, with substantial variation occurring in size, shape, color, and yield (see Chapter 4). The first tubers taken to Europe were larger than wild tubers and have been continuously selected by growers since the 17th century. However, the first systematic breeding program for Jerusalem artichoke probably dates from the early 1900s, when it was realized that the tubers could be utilized for industrial products such as ethanol.

Considerable selection of Jerusalem artichoke has occurred since it was first brought to Europe from North America in 1607. Nevertheless, for much of the 20th century, the crop was considered only of value as animal feed, a food in time of scarcity, and a relatively minor industrial crop. However, after many years of neglect, breeding programs for Jerusalem artichoke intensified during the 1980s (van Soest, 1993). This was primarily due to increased demand for inulin and fructose by the food industry, although research was also aimed at maximizing biomass productivity and improving other traits. However, breeding as well as research on the crop remains highly cyclic. Increased fuel costs or demand for low-priced fructose or inulin triggers a new round of interest that to date has ebbed with changes in status of the initial stimuli. Each new cycle of interest invariably results in some repetition of previous research and genetic improvements, decreasing the overall efficiency of progress.

Jerusalem artichokes are largely bred by public service institutions. Clones are reproduced asexually, and so once released they are readily multiplied. Hence, commercial plant breeders have no way to enforce plant breeders' rights, minimizing the chances of recouping their breeding program investment. As tubers are so readily multiplied, there is no need for farmers to regularly buy seed, while limited markets for Jerusalem artichoke products have in the past deterred commercial interest in improving the crop. Public institutions today breed Jerusalem artichokes to suit local climatic and photoperiodic conditions, and for particular applications (e.g., high inulin content for food industry applications).

In Canada, Jerusalem artichoke research has centered on the Agriculture Canada Research Station in Morden, Manitoba. Research has been aimed at increasing tuber yields, and the fructose

and inulin content of tubers, in accessions adapted to the conditions of western Canada (Chubey and Dorrell, 1974). A number of Morden (M) accessions have been bred and selected in experimental trials (e.g., 'M5,' 'M6,' and 'M7'). Some of these have gone on to become commercially grown cultivars, including 'Columbia' (Chubey and Dorrell, 1982).

In the U.S., a number of small-scale breeding programs have aimed to improve Jerusalem artichoke for industrial applications, including one at the USDA-ARS, Northern Crop Science Laboratory, Fargo, ND, where research has focused on enhancing the crop's value for forage and silage (Seiler and Campbell, 2004).

In the European Union, support has been forthcoming for a number of initiatives on industrial crops, including Jerusalem artichoke; for example, the agroindustrial program of 1990 was established and co-financed by the European Community (van Soest, 1993). At the national level, several countries have institutions involved in the preservation of genetic resources and breeding of Jerusalem artichoke. European breeding programs have at one time or another been conducted in Austria, Denmark, France, Germany, Hungary, Italy, the Netherlands, Russia, Sweden, Ukraine, and other former USSR countries.

The Federal Centre for Breeding Research on Cultivated Plants, in Braunschweig, Germany, for instance, has been a major European center for Jerusalem artichoke genetic resource conservation and plant breeding since the 1980s (Küppers-Sonnenberg, 1952; Schittenhelm, 1987). Recent research has focused on breeding to maximize inulin yields from the tubers (e.g., Schittenhelm, 1999). In Hungary, research on Jerusalem artichoke was conducted in the 1950s at the Martonvásár Institute of the Hungarian Academy of Sciences (Pätzold, 1955, 1957). The main emphasis was on improved cultivation and tuber processing methods, for the production of alcohol and fructose concentrates. This research was suspended when the focus shifted to maize. However, research on Jerusalem artichoke has been revived in Hungary, particularly at the University of Horticulture and Food Industry, Budapest (Barta, 1993).

In France, research has been concentrated at Institut National de la Recherches Agronomique (INRA) institutions in Rennes, Clermont-Ferrand, and, more recently, Montpellier (Chabbert et al., 1983). Increased carbohydrate content for ethanol production has been one of the aims, and numerous crosses between cultivars held in the national germplasm collection have generated novel material for selection (Le Cochec and de Barreda, 1990). In Italy, breeding and field trials to select for enhanced tuber yields and inulin content have been conducted at ERSA (Entre Regionale di Svilippo Agricola della Regione Abruzzo). Clones selected to produce high yields in poor soils have been cultivated in Bari (Faget, 1993; De Mastro et al., 2004).

In the Netherlands, Jerusalem artichoke breeding research is conducted at the Centre for Plant Breeding and Reproduction Research–Dienst Landbouwkunding Onderzoek (CPRO-DLO) in Wageningen, where clones have been bred for increased inulin yields (Meijer et al., 1993; Mesken, 1988; Toxopeus et al., 1994; van Soest et al., 1993). In Sweden, Hilleshög AB Plant Breeding and the Swedish University initiated breeding programs to improve Jerusalem artichoke for bioenergy (Gunnarson et al., 1985).

Plant breeding in the Russian Federation, aimed at producing new cultivars and hybrids, has focused on clone selection from crosses between local populations (landraces), and between imported cultivars and local populations. Free pollination between clones has resulted in wide variation, while selection from the achenes (seed) of promising seedlings has enabled clonal lines to be established. Between 1966 and 1972, for example, at the Maikop Experimental Station, of the N.I. Vavilov Institute of Plant Industry (VIR), a program of intravarietal hybridization was carried out, which demonstrated favorable prospects for Jerusalem artichoke breeding. Established cultivars, including 'Blanc précoce' and 'Waldspindel,' were crossed with wild *Helianthus* material (e.g., *H. macrophyllus* Willd.) and other *H. tuberosus* material held in the VIR germplasm collection, with the aim of producing high-yielding cultivars adapted to local conditions. Among the seedlings produced from this breeding program, a large diversity of hybrid forms were noted with promising

characteristics (Pas'ko, 1974). One of the cultivars bred as a result was the drought-resistant and disease-tolerant 'Vostorg' (Pas'ko, 1976).

A breeding program for Jerusalem artichoke at the Institute of Biology, Ural Division of RAS, Syktyvkar, Komi Republic, Russian Federation, has selected tall, cold-resistant, locally adapted clones with high green biomass productivity (Kosmortov, 1966; Lapshina, 1983; Lapshina et al., 1980; Mishurov and Lapshina, 1993). A new cultivar with these traits ('Vylgortski') was released by the institute in 1999 and included in the state seed list (http://ib.komisc.ru/t/en/ir/in/11-nov.html). Jerusalem artichoke breeding has also been conducted at Odessa and Kharkov, in Ukraine. For example, in Kiev (SSR Nauk) during the 1960s, a group of high-yielding hybrid clones were obtained from Jerusalem artichoke × sunflower crosses (Marčenko, 1969).

The Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro, maintains many wild Jerusalem artichoke accessions, collected in the U.S. and Montenegro, as part of a sunflower breeding program. Research has focused on population variability and the analysis of meiosis and pollen viability for wild accessions. A number of interspecific hybrid lines have been produced by crossing wild *H. tuberosus* with cultivated sunflower (Atlagic et al., 1993, 2006; Dozet et al., 1993; Vasic et al., 2002). A breeding program at the Bulgarian Institute of Plant Industry has also investigated interspecific crosses with Jerusalem artichoke (Kalloo, 1993).

8.2 CYTOLOGY

The basic chromosome number in the genus *Helianthus* is 17. Diploid (2n = 34) species such as *H. annuus* and *H. debilis* are found, as are tetraploid (2n = 68) species, such as *H. divaricatus*, *H. eggertii*, *H. hirsutus*, and hexaploid (2n = 102) species, such as *H. rigidus*, *H. macrophyllus*, and *H. tuberosus* (Kihara et al., 1931; Kostoff, 1934, 1939; Wagner, 1932a; Watson, 1928; Whelan, 1978). Meiosis in *H. tuberosus* is irregular, with the second metaphase often varying in the number of chromosomes from 49 to 53 (Kostoff, 1934). Karyotype analysis of the chromosomes showed the total length of the pairs ranged from 3.90 to 2.05 μm and the arm ratios were from 2.54 to 0.52 (Pushpa et al., 1979). Twelve pairs of the chromosomes had median centromeres, 30 with submedian, and 9 with subterminal. The Xma frequencies per cell and bivalent were found to be 72.46 and 1.42, respectively.

8.3 INTERSPECIFIC HYBRIDS

New sources of insect and disease resistance, stress tolerance, and other advantageous traits can often be derived from other species. As a consequence, considerable interest has focused on interspecific crosses among *Helianthus* species as a means of obtaining such traits, in particular insect and disease resistance. Interspecific hybrids have been produced by crossing *H. tuberosus* with *H. annuus* (e.g., Davydoviĉ, 1947; Encheva et al., 2003; Heiser and Smith, 1964; Heiser et al., 1969; Mikhal'tsova, 1985; Pas'ko, 1980; Pustovoit, 1966; Pustovoit et al., 1976; Sĉibrja, 1938; Stchirzya, 1938), *H. hirsutus* (Heiser and Smith, 1964), *H. divaricatus* and *H. eggertii* (Heiser, 1976; Heiser et al., 1969), *H. strumosus* (Heiser and Smith, 1964; Heiser, 1965), *H. rigidus* (Clevenger and Heiser, 1963; Heiser et al., 1969), *H. resinosus* (Heiser and Smith, 1964), and *H. schweinitzii* (Heiser and Smith, 1964).

In most instances, the objective has been to move critical genes into *H. annuus*, the dominant commercial crop of the genus (Sackston, 1992). However, such crosses also provide improved traits for cultivated Jerusalem artichoke. For example, hybrid F_1 and F_2 plants from crosses of *H. tuberosus* and the 'Tjumen' sunflower cultivar had low tuber yields, but were more drought resistant than Jerusalem artichoke controls (Murzina, 1971, cited in Kalloo, 1993). Resistance to downy mildew (*Plasmopara halstedii* (Farl.) Berl. & de Toni) in cultivated sunflower can be traced to *H. tuberosus* and several additional wild *Helianthus* species (Miller and Gulya, 1988, 1991; Pustovoit and

Kroknin, 1978; Pustovoit et al., 1976; Tan et al., 1992). Two Russian sunflower cultivars ('Progress' and 'Novinka') developed by Pustovoit are based on wild *H. annuus* and *H. tuberosus* crosses (Pustovoit et al., 1976). Jerusalem artichoke also displays some resistance to Alternaria (Lipps and Herr, 1986) and has been a source of resistance to brown stem canker (*Phomopsis helianthi* Munt.-Cvet. et al.) (Skoric, 1985), head rot (*Sclerotinia sclerotiorum* (Lib.) de Bary) (Pustovoit and Gubin, 1974; Rönicke et al., 2004), and broomrape (*Orobanche cumana* Wallr.) (Pogorietsky and Geshele, 1976) in sunflower.

H. annuus and *H. tuberosus* crosses give hybrids with a chromosome number of 2n = 68 (Marčenko, 1952). *H. tuberosus* (♀) × *H. annuus* crosses should be made 7 days after stigma extension using fresh pollen (24 to 28°C) (Fedorenko et al., 1982). The pollen mother cells of the hybrid had 16.3% with 2n = 34, 27.2% with n = 33 and 43.6% with n = 32 (Kostoff, 1939). *H. tuberosus* × *H. annuus* hybrids have low fertility and are often sterile; pollen viability varied from 12 to 53% (Heiser and Smith, 1964; Le Cochec and de Barreda, 1990). Chromosome bridges have been observed, the frequency of which varies among studies (Kostoff, 1939; Heiser and Smith, 1964). Cauderon (1965) reported strongly asyndetic and weakly asyndetic meiosis, with both showing meiocytes with 34 bivalents. Aneuploid progeny can occur with *H. tuberosus* × *H. annuus* hybridization. Trisomic plants (2n + 1) were found in backcrosses that were resistant to downy mildew (Leclercq et al., 1970).

Inversions and other disturbances appeared to have resulted in the structural deviations. Wagner (1932a) crossed three hexaploid species (*H. rigidus*, *H. macrophyllus*, and *H. tuberosus*) with the diploid *H. cucumerifolius* as the female parent and obtained seed sets from 8 to 37%. Reciprocal crosses were unproductive. Hybrids between *H. rigidus* and *H. tuberosus* are common and fertile, and therefore allow gene flow between the two species (Pas'ko, 1975). Tuber formation was a dominant trait with 96% of the hybrids having tubers, though of 87 crosses, only 25 had Jerusalem artichoke-like tubers. The hybrids between *H. annuus* and *H. tuberosus* had lower tuber yields but higher drought tolerance than Jerusalem artichokes (Kalloo, 1993).

Large variations in pollen viability have been observed in F_1 hybrids; for instance, in a study with 15 F_1 hybrids it varied between 12.4 and 57.1%. Likewise, pollen viability of 180 *H. tuberosus* × *H. annuus* F_1 hybrids and 170 backcrosses (BC_1) was 17.2% (1.2 to 34.2% range) and 3% (0 to 11.6%), respectively (Cedendo et al., 1985). The maximum number of chromosome bridges was 6. The mean number of bivalents of the BC_1 progeny was 15.2 and trivalents 1.57 per cell. Heiser and Smith (1964) found pollen stainability (viability) ranged from 12 to 53%, though most of the F_1 hybrids were female sterile. Low pollen viability can be accounted for by irregularities in meiosis in the pollen of F_1 hybrids (Atlagic et al., 1993).

Measures to reduce the incompatibility between Jerusalem artichoke and sunflower have been investigated at the Bulgarian Institute of Plant Industry. F_1 hybrids from crosses showed great variability (e.g., in mode of branching), with some plants showing resistance to *Orobanche*, and others having high seed oil content. The best crossing results were obtained by pollinating with fresh sunflower pollen, at an air temperature of 24 to 28°C and 70% relative humidity (Encheva et al., 2004; Fedorenko et al., 1982; Georgieva-Todorova, 1957; Kalloo, 1993).

In many instances, the success of interspecific hybrid crosses is limited, although with embryo culture it can often be improved. In a range of crosses, the success rate was increased using a two-stage technique (Chandler and Beard, 1983). The embryos were initially developed on a solid medium, for germination, and then transferred to a liquid medium. Embryos were excised and cultured for 3 to 7 days.

A regenerating tissue culture system also facilitates somatic hybridization and somaclonal variation, expanding the potential for incorporating genetic variation. Immature embryos, approximately 12 mm^2 in area, have the capacity to regenerate (Witrzens et al., 1988). Initial culture used Murashige–Skoog medium salts and organics and 30 $g \cdot l^{-1}$ sucrose and 1 $mg \cdot l^{-1}$ 6-benzylaminopurine. After the third week, 0.5 $mg \cdot l^{-1}$ of indoleacetic acid was added. Problems encountered included the premature initiation of flowering and the occurrence of "vitreous" plantlets that could not be

successfully transplanted to a potting media. The addition of phloridzin (10 μ*M*), esculin (30 μ*M*), or naringin (100 μ*M*) to the culture medium improved success. See Section 9.3 for additional information.

8.4 CONTROLLED CROSSES

Selfing is seldom successful (Marčenko, 1939; Sĉibrja, 1937; Wagner, 1932b). Of 1028 selfed flowers, only three fertile egg cells were formed (0.29%) (Wagner, 1932b). The high self-incompatibility, however, means that emasculation is not necessary unless crosses are made using alternative species as the female parent (e.g., *H. annuus*). Is such cases, the tip of the flower is opened and the anthers very carefully excised using tweezers before the styles have opened (Oliver, 1910, as cited by Wagner, 1932b). Pollen grains adhering are gently removed using a fine spray of water. Four days after anther removal, the styles were dusted with fresh pollen, yielding from a 22 to 90% seed set.

Pollen collection and application methods are the same as for the sunflower. Generally, pollen from flowers that have been bagged to prevent contamination is collected using a cloth or cotton swab. Collection early in the day is preferred in that direct sunlight reduces the pollen viability (Gundaev, 1971). Fresh pollen gives the highest percentage seed set; however, it can be successfully stored for varying periods depending upon the conditions (i.e., 2 weeks at room temperature in stoppered vials (Putt, 1941); up to 4 weeks at 4 to 6°C and a humidity of <40 $g \cdot kg^{-1}$ (Frank et al., 1982; Miller, 1987); 4 years at –76°C (Frank et al., 1982); 6 years in liquid N (Roath, 1993)).

8.5 TRADITIONAL BREEDING

There is considerable genetic variability within the Jerusalem artichoke gene pool, such that a number of desirable traits can be potentially obtained from within the species. In a study of 63 populations of Jerusalem artichokes collected in Montenegro, the clones were evaluated for 31 morphological characteristics: leaf size, plant height, uniformity of flowering, flower head inclination, head size, head shape, branching, branching type, leaf shape, leaf color, anthocyanin in leaves, leaf glossiness, leaf margin, leaf cross-sectional shape, leaf base shape, angle of leaf lateral nerves, leaf length, petiole length, pubescence, internode length, bud openness, length of bracts, pubescence of bracts, bract shape, bract size, length of bract, number of ray flowers, shape of ray flowers, color of ray flowers, color of disk flowers, and stigma anthocyanin intensity (Dozet et al., 1993). The populations represent escapes from cultivation of material largely introduced during or after World War II and displayed considerable variation with geographical location. Similar divergence was found within 19 wild populations collected within the U.S. (Dozet et al., 1994). Clones can be separated based upon branching type into monopodial, sympodial, and intermediate forms. Sympodial branching was associated with earliness and seed production, while monopodial type gives earlier clones (Pas'ko, 1982). Similarly, crosses among 35 clones of *H. tuberosus* resulted in some F_1s with higher tuber yields and total fermentable sugars than controls (Frese et al., 1987), indicating the potential for genetic improvement.

8.6 BREEDING TECHNIQUES

Jerusalem artichoke is very easy to multiply vegetatively. Plants can have up to 50 tubers, while tuber pieces can be used for planting. However, although propagation is successfully achieved by planting tubers, clones produce little diversity for improving key traits. To produce improved lines, it is therefore necessary to propagate via sexual reproduction: by crossing to produce seed. A number of difficulties have to be overcome in crossing, including incompatibility and a reluctance to flower in the long-day photoperiods that occur in the more northern latitudes, where much Jerusalem artichoke is grown.

Seed sterility is a general problem in plants that are usually multiplied vegetatively. Past selection has focused on the vegetative organs, at the expense of the organs of sexual reproduction. Seed sterility has hampered crossing and hybridization. A high incidence of irregular chromosomes has been noted, which interferes with the efficiency of meiosis in the germ cells, resulting in sterile pollen (Kostoff, 1934).

There are three general approaches used in Jerusalem artichoke breeding: (1) controlled crosses conducted under greenhouse conditions, (2) natural open-pollinated crosses using polycross nurseries, and (3) a variation of the latter where isolated pairs are allowed to cross in the field. Each method has its advantages and disadvantages.

8.6.1 Controlled Crosses in the Greenhouse

A major problem with using open pollination in the field is that the genetic variability that can be generated is quite restricted due to distinct differences in flowering dates. Thus, early clones have completed flowering before late-season clones have begun, preventing crossing. As a consequence, breeding for certain traits (e.g., maturity date) generally necessitates some controlled greenhouse crosses. Pollen parents are grown in growth chambers under short-day conditions (14 h artificial light). Schittenhelm (1987) found that 10 m^2 of chamber area was sufficient to produce pollen for 600 to 700 crosses. In addition to expanding the genetic range of crosses that can be made, controlled crosses in the greenhouse produce substantially more seed per flower pollinated. This ranged from 0 to 5.7 seed per flower pollinated, with an average seed set of 2.68. A seed set with open-pollinated plants is much lower, owing in part to the more extreme conditions in the field. The total number of seeds that can be obtained, however, is generally far greater, and the cost per seed is substantially lower.

8.6.2 Natural Open-Pollinated Crosses Using Polycross Nurseries

Polycross nurseries involve placing selected parent clones in an isolated area with the plants positioned in a manner that facilitates all possible combinations. Crossing is by way of natural pollinators, and while the female parent is known, the pollen source is not. The primary advantage of the technique is that it requires minimal time and labor. Large numbers of seed can be produced, and the cost per seed is very low.

Open pollination produces seedlings with a great deal of genetic variation. Around 14,000 open-pollinated seeds were obtained from four early and medium–late flowering cultivars ('Columbia,' 'Bianka,' 'Précoce,' and 'Yellow Perfect') to obtain visually selected clones from over 8,000 seedlings, in a study in the Netherlands (van Soest et al., 1993). Eighty third-year clones were selected, on the basis of tuber yield and tuber composition, and from these four superior clones were selected for further field study. The tuber yields and inulin content of these clones were superior to those of the commercial cultivar 'Columbia,' demonstrating the potential for genetic improvement. The exceedingly low success rate (~0.02%) underscores the numerical advantage of breeding methods that produce large amounts of seed.

Open-pollinated flower heads from several clones were harvested and threshed to obtain seed in another Dutch study. Seed was obtained from the mainly early flowering cultivars 'Columbia,' 'Topinsol,' 'Bianka,' 'Topianka,' 'Yellow Perfect,' 'Rozo,' 'Cabo Hoog,' 'Précoce,' 'Sükössdi/Nosszu,' and 'D-2120.' Abundant yields (over 20,000 seeds in total) were recorded, so despite potential problems of meiotic disturbance, partial male sterility, and incompatibility, open pollination can produce high seed yields (Mesken, 1988). Seed dormancy was broken by storing for about 4 weeks at 2°C, and then treating with a 0.2% solution of KNO_3 for 1 week at 10°C. The seeds were then kept in boxes in a soil–sand mixture under a 28°C day and 18°C night regime. A germination rate of 60% was recorded for seed from open pollination, compared to 70% from controlled greenhouse crosses (Mesken, 1988).

8.6.3 Isolated Pair Crosses

Crosses between isolated clones can be made in southern production locations (e.g., Spain) where the plants are under natural short-day conditions (Le Cochec, 1988). Isolation distance is the same as for sunflower, 800 m (FAO, 1961). In crossing experiments with four established clones ('K8,' 'Nahodka,' 'Fuseau 60,' and 'Violet de Rennes'), sufficient seed was obtained for a subsequent experimental program. With a total of 13,663 plants in three locations over 3 years, 5,372 achenes in total were produced. Each seed has a unique genetic composition, unlike tubers produced via vegetative propagation, and can give rise to a new and distinctive clone (Le Cochec and de Barreda, 1990). The material has been tested in breeding programs in Germany, France, and Spain, with a view to raising inulin yields and enhancing disease resistance.

8.7 FLOWERING TIME MANIPULATION

For cross-pollination between clones, synchronous flowering is essential. Kays and Kultur (2005) assessed the flowering date and duration of 190 clones (Figure 8.1). Substantial genetic variation was observed, with the onset of flowering ranging from 69 to 174 days after planting, and flowering duration ranging from 21 to 126 days. The results suggested that flowering could be manipulated to some extent by planting date at lower latitudes. However, at higher latitudes growth under controlled conditions may be required to synchronize flowering.

Latitude has a considerable influence on the flowering time of particular Jerusalem artichoke cultivars. For 'Violet de Rennes,' for example, flowering date varied from June 20 to September 5 to September 30 for plants growing in Tenerife (28°N), Valencia (39°N), and Rennes (48°N), respectively, with the plants in Rennes failing to produce seed (Le Cochec, 1988). Valencia lies at the same latitude as the crop's center of origin in North America. In fact, most cultivars (excepting very early maturing ones) do not flower or set seed in Northern Europe. Therefore, flowering must be artificially induced in order to cross using these cultivars in Northern European countries.

Research in the Netherlands has involved exposing numerous clones to varying photoperiods and temperature conditions. Artificially shortening day length can induce flowering and therefore the production of seed. Mesken (1988) reported that:

- Short-day treatments of 11 hours induced flowering in most genotypes tested.
- For some clones a duration of 2 weeks was most effective; for others it was 4 weeks.
- For late-flowering genotypes given short-day treatments and grown in greenhouses, flowering was advanced by 3 weeks.

It was concluded that late-maturing clones should be given an 11-hour short-day treatment for 4 weeks. This induced nearly all the clones tested to flower in time to produce adequate pollen for crossing purposes (Mesken, 1988). To make crosses, pollen from the male parent is collected in a paper bag and pollination is carried out by hand using a small brush (Mesken, 1988).

8.8 IRRADIATION

Irradiation is used in plant breeding programs to induce mutations, whereby increasing the genetic variability with which to work. The primary disadvantage of this technique is that the percentage of beneficial mutations is generally exceedingly low.

The influence of radiation on Jerusalem artichoke was first studied during the 1950s, to assess its effects on tuber composition (Pätzold and Kolb, 1957). In the 1980s, radiation was assessed as a breeding tool. Tubers irradiated with 3 krad of gamma rays produced offspring showing abnormal leaf shapes and sizes. White-skinned tubers were obtained, whereas the parent cultivar ('Violet de Rennes') had red tubers. Four plants were developed from the white-skinned tuber material, having

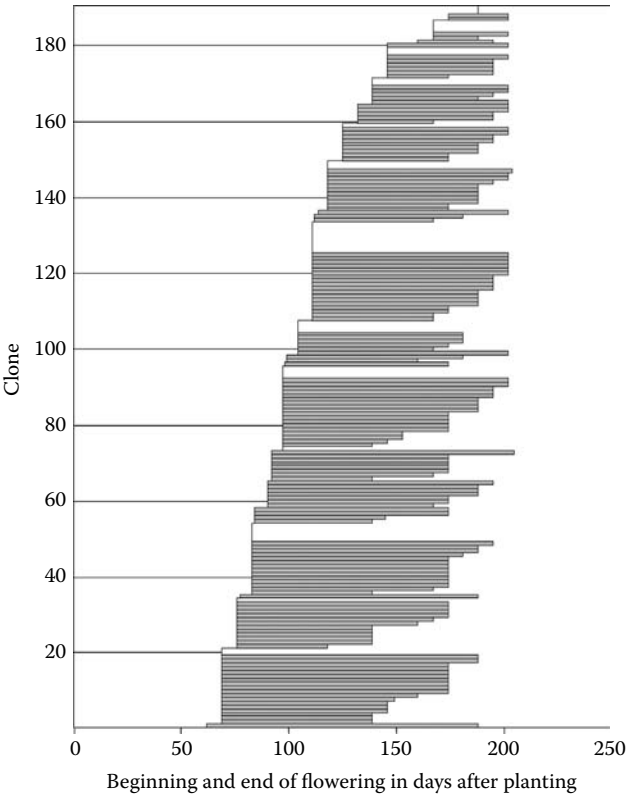

FIGURE 8.1 Timing of the onset and duration of flowering for individual Jerusalem artichoke clones. (From Kays, S.J. and Kultur, F., *HortScience*, 40, 1675–1678, 2005.) Individual clones are: 1. NC10-85, 2. NC10-8, 3. NC10-9, 4. NC10-15, 5. NC10-16, 6. NC10-18, 7. NC10-24, 8. NC10-25, 9. NC10-28, 10. NC10-32, 11. NC10-34, 12. NC10-35, 13. NC10-48, 14. NC10-88, 15. BBG 2, 16. 'Gute Gelbe,' 17. 'Waldspindel,' 18. 'Waldoboro Gold,' 19. 'Fuseau,' 20. 'Magenta Purple',[z] 21. 'Waldspindel',[z] 22. 'Jack's Copperskin,' 23. PI 547227, 24. NC10-5, 25. NC10-7, 26. NC10-14, 27. NC10-26, 28. NC10-41, 29. NC10-62, 30. NC10-78, 31. 'Mahlow rot,' 32. 'Bela,' 33. 2327, 34. 'Stampede',[z] 35. NC10-73, 36. 'Waldoboro Gold,' 37. PI 503276, 38. PI 503277, 39. 'Fuseau' (Idaho), 40. NC10-4, 41. NC10-6, 42. NC10-11, 43. NC10-13, 44. NC10-46, 45. 'Stampede,' 46. 'Remo,' 47. 'Columbia,' 48. 'Top,' 49. 'Novost,' 50. KWI 204,[z] 51. 12/84,[z] 52. 952-63,[z] 53. 'Dwarf Sunray',[z] 54. 'Orrington',[z] 55. 'Miles #1,' 56. 'Urodny,' 57. 'Nora,' 58. C 2071-63, 59. 'Nakhodka,' 60. PI 503269, 61. PI 503274, 62. NC10-52, 63. NC10-83, 64. NC10-84, 65. HEL 63 'Gibrid,' 66. 228-62, 67. 2071-63, 68. 'Leningrad,' 69. 'Dave's Shrine,' 70. 'Long Red McCann,' 71. 'Grem Red,' 72. 9, 73. 'Mari,' 74. PI 503272,[z] 75. PI 503279, 76. PI 503283, 77. NC10-29, 78. NC10-40, 79. NC10-70, 80. NC10-81, 81. 'Deutsche Waldspindel,' 82. 'Medius,' 83. 'Fuseau 60,' 84. 'Nahodka,' 85. 'Onta,' 86. D19-63-122, 87. D19-63-340, 88. 'Nakhodka,' 89. 'Grem White,' 90. 'Volga 2,' 91. 'Nescopeck,' 92. 'Southington Pink,' 93. 'Austrian Wild Boar',[z] 94. 'Fuseau',[z] 95. D 19,[z] 96. PI 503265, 97. 'Gold Nugget,' 98. 'Clearwater,' 99. NC10-44, 100. NC10-100, 101. BBG 1, 102. 'Mahlow Gelb', 103. 'Tambovski Krasnyi,' 104. 'Sachalinski Krasnyi,' 105. HEL 53,[z] 106. 'Rozo',[z] 107. 'CR Special,'[z] 108. 'Skorospelka,' 109. 'CR Special,' 110. PI 503262, 111. PI 503280, 112. NC10-75, 113. NC10-82, 114. Unknown, 115. 'Brazilian White,' 116. 'Sunchoke,' 117. D 19, 118. 'Violet de Rennes,' 119. 'Parlow Gelb,' 120. 'Gross Beeren,' 121. 'Neus,' 122. 'Maikopski,' 123. HEL 68, 124. 'Medius,' 125. BT3, 126. 'Castro',[z] 127. 'Totman',[z] 128. 'Cowell's Red',[z] 129. 'Olds',[z] 130. 'Skorospelko',[z] 131. 'Clearwater',[z] 132. 'Refla',[z] 133. 'Vanlig'[z], 134. 'Swenson,' 135. Hybrid 120, 136. 'Monteo,' 137. 'Freedom,' 138. 'Mulles Rose,' 139. NC10-22, 140. 'Challenger,' 141. BT4, 142. dwarf, 143. 'Drushba,' 144. 'Sunrise,' 145. 'Susan's Yard,' 146. 'Gurney's Red,' 147. 'Swenson,' 148. 'Wilton Rose',[z] 149. 'Reka',[z] 150. 'Coldy Mille,' 151. PI 503266, 152. NC10-94, 153. NC10-99, 154. 'Firehouse,' 155. 'Sodomka,' 156. 'Boston Red,' 157. 'Whitford,' 158. 'Jack's Copperskin,' 159. K 24,[z] 160. 'Leningrad,' 161. PI 503271, 162. 'Boyard,' 163. 'Jack's White,' 164. 'Silverskin,' 165. NC10-76, 166. 'Kierski Beli,' 167. 'Sugar Ball,' 168. 'Drown's Long Red,' 169. 'Flam,' 170. 'Draga',[z] 171. 'Sunchoke',[z] 172. 'Garnet,' 173. PI 503275, 174. NC10-90, 175. NC10-92, 176. 'Challenger,' 177. HEL 69, 178. Hybrid 120, 179. 'Beaula's,' 180. 'Karina,' 181. 'Bianca,' 182. 'Cross Bloomless,' 183. 'Vadim,' 184. 'Schmoll',[z] 185. J.A. 61[z], 186. PI 503264[z], 187. 'Roter Topinambur,' 188. 'Lucien's Painting,' 189. 'White Crop,' 190. 'Kiev White.' Superscript z indicates clones in which the duration of flowering is missing, having succumbed to *Sclerotium rolfsii* Sacc. before flowering was complete.

unbranched stems that were thinner than the controls; one had uniformly white tubers, the other three tubers with some pigmentation. The use of irradiation produced some plants that were capable of sexual reproduction, unlike untreated controls (Coppola, 1986).

8.9 SELECTION CRITERIA

Identification of critical traits to be selected for in a breeding program and estimates of their relative heritability are essential steps in the pragmatic development of new cultivars. For example, instability of inulin yields with location or year, susceptibility to leaf diseases, irregular tuber shape, and harvesting difficulties arising from the close attachment of the tubers to the base of the stalks are all factors that limit Jerusalem artichoke productivity (Le Cochec, 1988). However, high variability has been observed for most characteristics, suggesting that there is good potential for genetic improvement. The following are important breeding objectives (not necessarily listed in order of importance).

8.9.1 Yield

Increased tuber yield is a primary selection trait. Since production costs are largely fixed, net return per hectare is strongly influenced by yield. Yield is determined by genetics, in combination with environmental, climatic, and geographic factors. High-yielding cultivars may only be highly productive, for instance, in regions with the photoperiodic and temperature conditions under which the cultivar was selected. High tuber yields are desirable for high productivity of inulin and fructose.

Yield increases in most field crops come from shifting a greater percentage of photosynthate fixed into the plant part of interest rather than changes in photosynthetic efficiency per se. To this end, the Jerusalem artichoke represents a unique challenge in that a number of the traits that make wild clones successful are counterproductive for maximizing yield in an agricultural setting. A critical factor is the carryover from the species progenitors of a dry matter storage system in which the aerial plant parts store photosynthate and then recycle it upon flowering and tuber formation. This strategy has several negative aspects:

- It requires a far greater investment in a nonrecyclable aerial canopy at the expense of tuber yield. This differential is readily apparent when contrasting the harvest index between chicory roots and Jerusalem artichoke tubers (e.g., Schittenhelm, 1999).
- Flowering terminates the formation of new leaves (with the exception of small leaves on flowering branches). The photosynthetic efficiency of the existing leaves declines due to age and changes instigated by flowering. In addition, flowering and tuber formation trigger the onset of a senescence syndrome where mobile resources in the plant are recycled into the tubers.

While tuberization and flowering are both modulated by photoperiod, its control over flowering has been broken such that day-neutral cultivars are widely available. Early flowering generally results in earlier tuber formation, though tuberization remains responsive to short days in clones we have tested. If tuberization, however, could be induced early in the growing season and flowering delayed until much later, temporary storage of photosynthate in aerial plant parts might be circumvented. This would require plants that are day neutral for tuberization but short day for flowering, the precise day-length requirement for the latter being determined by geographical location and length of the growing season. Direct deposition of photosynthate in the tubers from the onset would decrease the metabolic costs required for recycling and allow substantial reduction of the stature of the plant, and therefore the amount of dry matter utilized for nonrecyclable components.

8.9.2 Tuber Size

The size of individual tubers greatly influences harvest efficiency in that small tubers generally drop through the lift chains on the harvester. Likewise, for tubers that are to be washed after harvest or peeled prior to cooking/processing, increased tuber size greatly increases the efficiency of the operation, in that volume increases by the third power while surface area by only the second power. Larger tubers are also less likely to wither during storage than small ones.

8.9.3 Smoothness of Tuber Surface

Surface topography influences the utility of a clone for use as a fresh vegetable in that tubers with irregular surfaces and branching are much more difficult to prepare for use. For industrial extraction of inulin, irregular surfaces make cleaning prior to grinding/slicing more difficult. Branched tubers are likewise less desirable for propagation purposes in that they tend to produce varying numbers of stems, decreasing the precision at which the plant population density can be controlled. The cultivar 'Fuseau,' for instance, has been selected for a smooth tuber surface.

8.9.4 Inulin Quantity and Quality

Inulin content is critical in cultivars grown for extraction. In addition, inulin quality, as reflected by the chain length (degree of polymerization), has a significant influence on the potential quality and use of the extracted product. Long chain lengths are desirable for a number of applications. For example, the longer the chain length, the higher the purity of fructose syrups derived from the inulin (fructose-to-glucose ratio). Long chain lengths are also essential for applications such as fat replacement in processed foods. While there are a number of uses for short-chain-length inulin, long-chain-length molecules can be readily shortened through controlled hydrolysis, while there has been little success achieved thus far in extending chain length.

8.9.5 Rhizome Length

Rhizome (stolon) length strongly influences harvest efficiency. Cultivars with long rhizomes have a greater percentage of tubers remaining in the field after harvest, because they are formed too far into row middles or too deep in the soil. If rhizomes are too short, however, tubers are formed in a tight clump at the base of the plant, which can inhibit their development and make separation during harvest difficult. In addition to genotypic differences between clones, the phenotypic expression of rhizome length is strongly modulated by production conditions, especially soil textural properties. Tight soil results in restricted rhizome length for most clones. In breeding programs in the Netherlands, for example, clones have been selected for medium rhizome length (Mesken, 1988).

Rhizome diameter and longevity are also important. Larger-diameter rhizomes have greater difficulty penetrating dense soils and require additional photosynthetic resources for production. Rhizomes that dissipate fairly readily after the death of the aerial plant parts are desirable in that their absence facilitates harvest.

8.9.6 Plant Height, Stem Number, and Branching

The height of the plant is important in that the aboveground parts (primarily the stems) serve as a temporary storage site for carbohydrates formed in the leaves. Likewise, stem height and architecture are important in leaf distribution and arrangement to maximize photosynthesis. However, allocation of dry matter into stem structure, above what is essential, reduces yield in that the structural carbohydrates are little recycled during tuber filling and top senescence. Clones of intermediate height, therefore, are generally selected in breeding programs. An exception to this is the Dutch breeding program, where dwarf cultivars were selected to influence the relative amount

of top-to-tuber growth (Pilnik and Vervelde, 1976; Mesken, 1988). The ideal height is also partly a function of the length of the growing season; typically shorter growing seasons require shorter stemmed clones. It is important to be cognizant of the fact that final height is strongly modulated by production conditions.

Stem number is partly determined by the size of the seed tuber (Barloy, 1988; Louis, 1985) and is closely related to the early canopy development and leaf area index (Baillarge, 1942; Cors and Falisse, 1980). Branching type is genetically controlled, although the number of branches is largely regulated by plant density.

8.9.7 Maturity Date

The ideal time interval for a clone to reach maturity will depend upon where the crop is to be grown. In more northern production zones, earlier maturity is highly desirable in that long-season cultivars do not adequately mature before the first frost. Conversely, if clones reach maturity too early, the length of the growing season is decreased, thereby decreasing the maximum tuber yield that can be achieved. Photoperiodic control over tuberization is a key factor modulating the plant's growth and potential productivity.

8.9.8 Disease Resistance

Disease resistance represents one of the more difficult traits for selection. The primary diseases impacting Jerusalem artichoke production are sclerotinia wilt/rot (*Sclerotinia sclerotiorum* (Lib.) de Bary), rust (*Puccinia helianthi* Schw.), southern wilt/blight/collar rot (*Sclerotium rolfsii* Sacc.), and powdery mildew (*Erysiphe cichoracearum* DC.) (see Chapter 11). The importance of each disease is dependent upon the production site. For example, in Europe, sclerotinia is a critical disease, while rust and southern wilt are important diseases in North American production areas. Powdery mildew tends to be less important, in that Jerusalem artichoke appears to have reasonable levels of endogenous resistance.

8.9.9 Forage Quality

The aboveground portion of the plant is of increasing interest for biomass and biofuel production, and for animal forage or silage. High biomass yields and high carbohydrate content are the main objectives when breeding for bioenergy productivity. High forage yields, accompanied by high levels of protein and carbohydrate, are the objective when breeding for animal feed.

8.10 SELECTION SEQUENCE

In a conventional Jerusalem artichoke breeding program, crosses are made between carefully selected parent lines and the progeny are screened for traits that are considered critical (e.g., yield; disease resistance; tuber color, size, and shape; tuberization photoperiodic response; inulin content; and degree of polymerization). With traits that have low heritabilities or are difficult to accurately quantify, progress is often very slow. Breeders generally progress through a predetermined sequence of selection traits with progeny being discarded that do not meet the minimum acceptable requirements. There is generally a trade-off between the importance of the trait for improvement and ease of selection. The first trait in the selection sequence has the greatest number of progeny; as members are discarded, the number remaining for subsequent traits in the sequence decreases rapidly. For example, while the degree of polymerization of inulin may be considered the most critical trait for improvement, the difficulty of measuring it often moves the trait much later in the selection sequence, such that 99% of the progeny have already been discarded before inulin chemistry is assessed. Therefore, if you start with 1,000 progeny, by the time you assess inulin chemistry there are probably only 10 remaining. The chance of finding one of these clones in which the degree of

polymerization is truly superior is exceedingly small. Hence, selection sequence can have a pronounced impact on breeding success. The numerical implications can be seen in selection for inulin yield by van Soest et al. (1993). From 8,000 seedlings derived from an open-pollinated nursery, the population was reduced to 80 by the third year, which produced only four clones with significantly improved inulin yield over 'Columbia' (i.e., 0.05% of the original population).

8.11 HERITABILITY OF IMPORTANT TRAITS

Breeding is to a large extent a numbers game. When making a single cross between n parent lines, the number of crosses required rapidly becomes unmanageable as the number of lines increases. With 120 lines crossed in all possible combinations $\{[n(n-1)]/2\}$, the number of progeny exceeds 7,000. As a consequence, it is highly desirable to identify which lines, when crossed with another parent, are the most likely to result in superior progeny. This is accomplished by crossing the lines with common parents (testers) and evaluating the hybrids produced for the traits in question. Differences in performance of a line in crosses with other parents are a measure of the general combining ability. In contrast, the specific combining ability is a measure of the performance of a line when crossed with a specific parent.

Schittenhelm (1990) utilized two testers and seven male lines to obtain estimates of the general and specific combining abilities for a cross section of traits (i.e., early vigor, plant height, stems per plant, rhizome (stolon) length, tuber knobbiness, tubers per plant, mean tuber weight, tuber yield, tuber percent dry matter, aboveground yield, aboveground percent dry matter, and the harvest index). The general combining ability of Jerusalem artichoke lines (M^2l) and testers (M^2t) and the specific combining ability (M^2lt) are given in Table 8.1 for each trait. Significance differences in the general combining ability for testers were found for all traits except tuber yield, tuber knobbiness, and harvest index.

Coefficients of variation for 15 traits in a study by Le Cochec (1990) are given in Table 8.2. Mid-point values for parents and crosses were similar for plant height, rhizome (stolon) length, and the percent tuber dry matter. There was a substantial increase in the number of tubers and stems per plant, both of which were considered to be undesirable traits. The fact that tuber number per plant increases while the mean tuber weight decreases indicates that obtaining new, large-tubered lines is going to be difficult.

Many economically important traits in cultivated sunflowers are under the genetic control of multiple genetic loci, with several unique combinations of these genes present in sunflower germplasm (Fick, 1978).

8.12 TRANSGENIC PLANTS

Jerusalem artichoke has been the source of genetic material for the transformation of other crop species. Numerous transformations have been conducted with cultivated sunflower, and some with sunflower–Jerusalem artichoke hybrids, but no attempt to date has been made to improve Jerusalem artichoke as a crop via genetic transformation. However, Jerusalem artichoke is a classic tissue culture species (see Section 9.3), while much of the experience gained with transgenic sunflower is applicable to Jerusalem artichoke. Therefore, the means of transforming Jerusalem artichoke are largely in place.

8.12.1 Jerusalem Artichoke as a Source of Genes

Inulin biosynthesis in Jerusalem artichoke occurs via the combined action of two enzymes: 1-sucrose:sucrose fructosyltransferase (1-SST) and 1-fructan:fructan fructosyltransferase (1-FFT). 1-SST catalyzes the synthesis of inulins of a low degree of polymerization, while 1-FFT catalyzes the synthesis of fructans of a degree of polymerization up to 50 (Sévenier et al., 2002a). High

TABLE 8.1
Estimates for Variance Components for Lines (M^2l), Testers (M^2t), Lines H Testers (M^2lt), and Experimental Error (M^2e)

Trait	(M^2l)	(M^2t)	(M^2lt)	(M^2e)
Early vigor (cm)	–0.74	31.67**	3.76	13.12
Plant height (cm)	–28.87	386.25*	221.77**	72.81
Stem per plant	0.14*	0.36**	–0.03	0.20
Stolon length[a]	0.08	0.22*	0.15*	0.09
Tuber knobbiness[b]	0.36*	–0.01	0.03	0.13
Tubers per plant	35.28*	13.57*	3.77	26.69
Mean tuber weight (g)	3.77	6.73*	5.63	6.13
Tuber yield (dt/ha)	563.62	7.79	1,499.27**	641.31
Tuber dry matter (%)	0.47*	3.29**	0.12	0.27
Stems + leaves (dt/ha)	1,253.24**	81.65	19.60	371.69
Stems + leaves (% dm)	2.31	3.11*	–0.08	8.18
Harvest index ($H10^2$)	11.24	–1.60	10.40**	2.42

Note: Significance probability: * = 0.05; ** = 0.01.

[a] Rating scale from very short (1) to very long (9).

[b] Rating scale from very smooth (1) to very knobby (9).

Source: Adapted from Schittenhelm, S., *Vorträge für Pflanzenzøchtung*, 15–16, 1990.

levels of expression for these genes occur in the tubers, with lower levels of expression in the stems and flowers. The genes encoding both 1-SST and 1-FFT have been isolated from Jerusalem artichoke tubers, purified, and characterized (Koops and Jonker, 1994, 1996; Luscher, 1993). Isolated cDNA clones of the two genes have been introduced into plants (e.g., *Petunia*) as constructs with a CaMV 35S promoter, where their expression has led to fructan biosynthesis in tissues previously incapable of producing fructans. Plants transformed with just a *35s-1-sst* construct accumulated 1-kestose (GF2), 1,1-nystose (GF3), and 1,1,1-fructosylnystose (GF4) (van der Meer et al., 1998). Plants transformed with just the *35s* construct did not accumulate fructans, but did so when low molecular weight fructans were present as a substrate. Crosses between *35s-1-sst*- and *35s-1-fft*-transformed *Petunia* plants produced progeny that accumulated high molecular weight fructans in their leaves (van der Meer et al., 1998). Therefore, two genes control the plant fructan biosynthesis pathway, and these are now available for transforming any plant species.

Sévenier et al. (2002b) advanced the idea of using certain crops as biofactories for the production of inulin and other chemicals sought by food and nonfood industries. The initial crop of choice in Europe was sugar beet (*Beta vulgaris* L.), which is an industrial crop with an established processing infrastructure for the production of sucrose. Diversification will aid sugar beet growers during times when demand for sugar falls. A key objective for transforming sugar beet by genetic modification is to get the crop to produce fructans, which (unlike sucrose) are increasingly in demand in both food and nonfood industries. Industrial usage of fructans is limited because there is currently no abundant and inexpensive crop source. Sugar beet does not naturally produce fructans (i.e., fructooligosaccharides and inulin), but by using genes from plants such as Jerusalem artichoke, it can be made to produce considerable amounts. Sugar beet accumulates high levels of sucrose in the vacuoles of its taproot, while the enzymes catalyzing the synthesis of fructans in Jerusalem artichoke are located in the vacuoles and use sucrose as a primary substrate.

Sugar beet has been successfully transformed using Jerusalem artichoke-derived *35s-1-sst* and *35s-1-fft* constructs, incorporating promoters and selection markers, with fructans accumulating in

TABLE 8.2
Coefficients of Variation and Phenotypic and Genotypic Variance, Heritability, and Genetic Gain Expected during Selection for 15 Traits in a Clonal Population

Characteristic and Units	Coefficient of Variation		Variance		Heritability (%)	Gain in Selection	Gain in Selection (% of mean)
	Phenotypic	Genotypic	Phenotypic	Genotypic			
Days to sprout (d)	18.6	9.2	18.15	4.48	24.7	2.20	9.5
Stem height in July (cm)	12.3	8.2	162.8	72.2	44.4	11.71	11.2
Days to flower (d)	11.0	10.8	291.0	279.6	96.1	33.77	21.8
Mildew susceptibility (0–9)	23.5	13.1	3.03	0.94	30.9	1.11	15.0
Leaf duration (d)	5.3	5.1	102.1	96.4	94.4	19.65	10.2
Vegetative cycle (d)	5.0	4.9	95.9	90.5	94.4	19.04	9.8
Number of stems	50.9	25.5	2.18	0.55	25.0	0.76	26.2
Plant height at harvest (cm)	18.8	16.7	2,846.8	2,252.1	79.1	86.93	30.7
Number of tubers	30.9	18.4	141.2	51.1	36.2	8.86	23.1
Dry weight of tops (g)	32.5	19.8	6,041.7	2,245.1	37.2	59.63	24.9
Dry weight of entire plant (g)	27.4	12.4	30,726	6,338	20.6	74.40	11.6
Dry weight of tubers/plant (g)	30.6	16.0	309,107	84,605	27.4	313.8	17.3
% dry matter of tubers	8.9	8.0	3.87	3.16	81.7	3.31	14.9
Average tuber dry weight (g)	29.6	13.1	13,964	2,726	19.5	47.47	11.9

Source: Adapted from Le Cochec, F., *Agronomie*, 90, 797–806, 1990.

the vacuoles as predicted. When the cDNA constructs were expressed in sugar beet, a dramatic change in the main type of storage carbohydrate was observed, with sucrose being nearly all converted into low molecular weight fructans. Around 90% of the sucrose imported into the taproot of the sugar beet was converted into fructans of a low degree of polymerization. The efficiency of fructan accumulation in sugar beet was higher with cDNA from Jerusalem artichoke than equivalent cDNA for fructosyl transferase from any other plant or microorganism (Sévenier et al., 1998, 2002a, 2002b; Smeekens, 1998).

Cytochrome P450 comprises a large family of heme-containing oxygenases that catalyze the introduction of oxygen into substrates, including foreign (xenobiotic) toxins. They play an important role in plants, for example, in the synthesis of phenolic compounds such as lignin, pigments, hormones, and plant chemical defenses (see Section 10.9). The first multifunction cytochrome P450 enzyme found in plant tissue, *trans*-cinnamate 4-hydroxylase (C4H), was from Jerusalem artichoke (Benveniste and Durst, 1974), and several inducible cytochrome P450s have since been isolated and cloned from Jerusalem artichoke (e.g., Teutsch et al., 1993). These are induced in response to wounding or chemical treatments and act to detoxify a range of foreign molecules, including certain herbicides (Batard et al., 1995; Cabello-Hurtado et al., 1998). For instance, an increase in the activity of C4H, the plant-specific cytochrome P450 encoded by the gene CYP73A in Jerusalem artichoke, occurs in response to physical and chemical stresses in the tubers (Batard et al., 1997). CYP73A1 has been expressed in transgenic yeast, and the C4H produced dealkylated the model xenobiotic compound 7-ethoxycoumarin (Batard et al., 1998; Schoch et al., 2003). Anti-C4H antibody from Jerusalem artichoke can be used as a tool in the characterization of cytochrome P450 in other plant species (e.g., Gabriac et al., 1991; Kochs et al., 1992; Menting et al., 1994; Ponnamperuma and Croteau, 1996; Werck-Reichhart et al., 1993).

When engineered into other species, P450 genes (e.g., CYP76B1, CYP81B1, CYP73A) originally isolated from Jerusalem artichoke have good potential as plant markers for chemical stress, for the biomonitoring of pollutants (e.g., as tools in the phytoremediation of contaminated sites), and for the control of herbicide tolerance (Batard et al., 1998). The inducible cytochrome P450 CYP76B1 from Jerusalem artichoke, for instance, catalyzes rapid oxidative dealkylation of various phenylurea herbicides to yield nonphytotoxic metabolites. The expression of CYP76B1 in tobacco (*Nicotiana tabacum* L.) and *Arabidopsis* conferred a 20-fold increase in tolerance to the herbicide linuron and a 10-fold increase in tolerance to isoproturon or chlortoluron (Didierjean et al., 2002; Robineau et al., 1998).

Lectins (agglutins) are plant-derived proteins that bind specifically to sugars or oligosaccharides, causing agglutination of certain cell types (Pusztai, 1992; Van Damme et al., 1998). Several lectins have been isolated and characterized from Jerusalem artichoke tubers and callus (Guillot et al., 1991; Nakagawa et al., 1996, 2000; Suseelan et al., 2002), including *H. tuberosus* agglutinin (HTA) or Heltuba (lectin classification code, LECp.HelTub.tu.Hmm1), a mannose-binding lectin (Barre et al., 2001; Bourne et al., 1999; Van Damme et al., 1999). The genes (*hta*) involved in expressing HTA in Jerusalem artichoke tubers have been isolated (HTA being encoded by a multigene family) and corresponding cDNA has been cloned (Van Damme et al., 1999). When *hta* homologous cDNAs were expressed in *E. coli*, HTA had trypsin-inhibiting activity (Chang et al., 2006). HTA agglutinates yeast cells and has potential application, for example, in sake production (Nakagawa et al., 2000).

Plant lectins play an important role in plant defense, conferring resistance to predators and pathogens. The *Galanthus nivalis* agglutinin (GNA) from snowdrop bulbs, for example, is an insect antifeedant (Hogervorst et al., 2006; Powell et al., 1995; Van Damme et al., 1987), and the gene encoding GNA confers resistance to insect pests when expressed in transgenic potato and rice (e.g., Down et al., 1996; Rao et al., 1998). cDNA (*hta*-b and *hta*-c) encoding *H. tuberosus* agglutinin, introduced into tobacco via *Agrobacterium tumefaciens* and expressed using the CaMV 35S promoter, similarly had deleterious effects on peach-potato aphid (*Myzus persicae*), a polyphagous crop pest. The average aphid population on transgenic tobacco after 11 days' feeding was decreased by 70% compared to the control, while aphid fecundity declined by around 50 to 65%. The results

suggested that *hta* was a promising candidate for plant transgenic engineering against Homoptera insect pests, due to its trypsin-inhibiting action (Chang et al., 2003).

cDNA libraries compiled for Jerusalem artichoke provide a useful resource for researchers involved in plant genetic modification. For example, an ATP/ADP transporter protein, encoded by a gene (*HtAATP*) from a *H. tuberosus* tuber cDNA library, has been cloned and characterized. The hydrophobic membrane protein is expressed in tuber sink tissues during different developmental stages and plays an active role in carbohydrate formation (Meng et al., 2005). Another cDNA sequence, isolated from a *H. tuberosus* tuber cDNA library, encoded a type 2 metallothionein-like protein (*htMT2*). In Jerusalem artichoke, the gene is predominantly expressed in internodes and nodes, with low levels of expression in the leaves, leafstalks, tubers, and young roots, and none in older roots. Different metal ion treatments changed the expression level, suggesting that *htMT2* may be involved in the transport or availability of Cu^{2+} and Zn^{2+} (Chang et al., 2004).

8.12.2 Transformation of Jerusalem Artichoke

Genetic transformation has been achieved for cultivated sunflowers (*Helianthus annuus* L.), and also with sunflower × Jerusalem artichoke hybrids. Callus, shoot, embryo, and other sunflower and hybrid tissues have been transformed and regenerated in tissue culture (e.g., Espinasse and Lay, 1989; Everett et al., 1987; Finer, 1987; Greco et al., 1984; Paterson and Everett, 1985; Pugliesi et al., 1993a, 1993b; Witrzens et al., 1988). Jerusalem artichoke is a model species for tissue culture studies, and therefore can be readily regenerated after genetic manipulation (see Section 9.3). The techniques used to transform sunflowers can be adapted for Jerusalem artichoke. Although sunflowers have predominantly been modified to improve seed properties (e.g., seed yield, oil content, high kernel-to-husk ratio, early and even ripening), which are of little concern to Jerusalem artichoke breeders, traits such as disease resistance are relevant to both crops (Hahne, 2002).

Transgenic sunflowers have been produced using direct gene transfer and *Agrobacterium*-mediated transformation. Direct gene transfer utilizes insertion into protoplasts via microinjection or particle guns. In a comparison of techniques, *Agrobacterium* co-culture was found to be the best method for producing stable transformations and the recovery of transformed plants (Laparra et al., 1995). A number of patents, for instance, owned by Pioneer Hi-Bred (U.S.) and Biocem (France), cover specific technology relevant to sunflower transformation (Hahne, 2002; http://www.derwent.com/). The characteristics engineering into transgenic sunflowers include improved seed quality, resistance to fungal disease (e.g., *Sclerotinia*), resistance to viral disease, resistance to insect pests (using genes encoding *Bacillus thuringiensis* toxins), and herbicide resistance. In addition, various marker genes, genes conferring male sterility, and genes to enhance drought tolerance have been incorporated into sunflower genomes (Hahne, 2002). Of these, genes for pest and disease resistance and drought tolerance would be of the most benefit in Jerusalem artichoke breeding programs.

A number of problems have been encountered in producing transgenic sunflowers. Callus has proved difficult to transform, while only a small proportion of cells in explants may take up foreign genes using direct transformation techniques. Regeneration may be low after selection, and low transformation efficiency has been reported (Everett et al., 1987; Hahne, 2002; Laparra et al., 1995; Schrammeijer et al., 1990). Therefore, plant breeders are already aware of the potential problems that may be encountered when producing transgenic Jerusalem artichoke, and the best approaches to try and overcome them.

In order to improve Jerusalem artichoke as a multipurpose crop through genetic transformation, tissue-specific promoters are being developed. A cDNA library of around 60,000 clones has been established in Canada, for instance, to search for gene promoters that enhance the crop's value as a bioreactor (Eldridge et al., 2005).

8.13 GENETIC RESOURCES

Plant genetic resource collections are vital to plant breeding efforts. In the early 1990s, one survey concluded that the Jerusalem artichoke gene pool available to plant breeding may not exceed 150 accessions (van Soest et al., 1993). However, even given duplications in different collections, this appears to be an underestimate. Many hundreds of accessions are today maintained in plant germplasm collections worldwide. These include wild and weedy accessions, landraces or traditional and obsolete cultivars, and advanced or improved cultivars.

Germplasm can be maintained (1) in "living collections" as tubers ("seed tubers"), which are propagated, dug, and replanted at regular intervals (e.g., every 2 years); (2) as seed in seedbanks, under controlled conditions for extended periods in a dormant state; or (3) in tissue culture. Propagation by tuber is relatively labor intensive and expensive, but is a simple and effective way of preserving cultivated and wild accessions of *H. tuberosus* for conservation, research, and breeding purposes. Under normal cultivation, Jerusalem artichoke is propagated by tuber, harvested as an annual, and does not set seed. However, sexual reproduction and the production of seed are essential for crossing. Seed is also desirable for long-term storage. Tissue culture requires extensive facilities and expertise, but is growing in importance as a means of preserving Jerusalem artichoke germplasm (e.g., Volk and Richards, 2006).

Jerusalem artichoke is native to North America, and therefore the preservation of wild biodiversity from North America is especially important for future plant breeding programs. The focus in North America has been on conserving wild, weedy, and landrace accessions. The selective breeding of advanced Jerusalem artichoke cultivars, however, has mainly been conducted in European institutions. The conservation of crop biodiversity generated by these breeding efforts has been the main focus of European gene banks, as a platform for further crop improvements. Frison and Servinsky (1995) listed 14 European Institutions holding *H. tuberosus* material available to plant breeders. Ideally, for a vegetatively propagated crop such as Jerusalem artichoke, it is important to complement germplasm collections with collaborative programs with growers, in areas where landraces originate, in order to conserve genetic resources *in situ* (Maxted et al., 1997).

8.13.1 Canada

The main repository for Jerusalem artichoke germplasm in Canada is Plant Gene Resources of Canada (PGRC), Saskatoon Research Centre, which maintains around 175 accessions (Dallas Kessler, personal communication; Volk and Richards, 2006). These comprise clones bred at the Agriculture Canada Research Station in Morden, Manitoba; wild-collected accessions of North American origin (native populations or populations derived from escapes); and cultivars from North America and Europe. All accessions are propagated from tubers, which are dug and replanted every 3 years (Ken Richards, personal communication). The accessions maintained at PGRC in 2006 are listed in Table 8.3. In addition, five wild-collected accessions ('CN32463,' 'CN31464,' 'CN31634,' 'CN52867,' and 'CN52868') were listed on the Germplasm Resources Information Network–Canadian (GRIN-CA) database (http://www.pgrc3.agr.ca/) in 2006.

Seeds of Diversity Canada (formerly the Heritage Seed Program) operates from Toronto and cultivates accessions of Jerusalem artichoke as part of a conservation program (MacNab, 1989). The program includes material from wild populations and populations established from material originally planted in gardens.

8.13.2 U.S.

In the U.S., the National Plant Germplasm System oversees crop genetic resources, while the Agricultural Research Service (ARS) of the U.S. Department of Agriculture (USDA) in Beltsville, near Washington, D.C., coordinates the Germplasm Resources Information Network (GRIN), including a searchable online database. The *H. tuberosus* collected is maintained at the North

TABLE 8.3
The 179 Accessions Maintained in the Collection of Plant Gene Resources of Canada (PGRC), Saskatoon, Canada, in 2006

Name of Accession	Code	Origin
7305	NC10-3	Canada (Manitoba)
7306	NC10-4	Canada (Manitoba)
7307	NC10-5	Canada (Manitoba)
7308	NC10-6	Canada (Manitoba)
7309	NC10-7	Canada (Manitoba)
7310	NC10-8	Canada (Manitoba)
7312	NC10-9	Canada (Manitoba)
7512	NC10-10	Canada (Manitoba)
7513	NC10-11	Canada (Manitoba)
HM Hybrid A	NC10-12	Canada (Manitoba)
HM Hybrid B	NC10-13	Canada (Manitoba)
HM Hybrid C	NC10-14	Canada (Manitoba)
HM-2	NC10-15	Canada (Manitoba)
HM-3	NC10-16	Canada (Manitoba)
HM-5	NC10-17	Canada (Manitoba)
HM-7	NC10-18	Canada (Manitoba)
HM-8	NC10-19	Canada (Manitoba)
HM-9	NC10-20	Canada (Manitoba)
HM-10	NC10-21	Canada (Manitoba)
HM-11	NC10-22	Canada (Manitoba)
HM-12	NC10-23	Canada (Manitoba)
HM-13	NC10-24	Canada (Manitoba)
DHM-3	NC10-25	Canada (Manitoba)
DHM-4	NC10-26	Canada (Manitoba)
DHM-5	NC10-27	Canada (Manitoba)
DHM-6	NC10-28	Canada (Manitoba)
DHM-7	NC10-29	Canada (Manitoba)
DHM-13	NC10-30	Canada (Manitoba)
DHM-31	NC10-31	Canada (Manitoba)
DHM-32	NC10-32	Canada (Manitoba)
DHM-18	NC10-33	Canada (Manitoba)
DHM-19	NC10-34	Canada (Manitoba)
DHM-21	NC10-35	Canada (Manitoba)
DHM-22	NC10-36	Canada (Manitoba)
W-97	NC10-37	Canada (Manitoba)
W-106	NC10-38	Canada (Manitoba)
Comber	NC10-40	Canada (Manitoba)
B.C. #1	NC10-41	Canada (Manitoba)
B.C. #2	NC10-42	Canada (Manitoba)
—	NC10-43	U.S. (USDA-P1)
Sunchoke-Fiesda's	NC10-44	U.S. (California)
75005	NC10-45	Canada
75004-52	NC10-46	Canada
A-3-6	NC10-48	Canada
HM Hybrid-A-4	NC10-49	Canada
DHM-14-3	NC10-52	Canada
DHM-14-6	NC10-53	Canada

TABLE 8.3 (CONTINUED)
The 179 Accessions Maintained in the Collection of Plant Gene Resources of Canada (PGRC), Saskatoon, Canada, in 2006

Name of Accession	Code	Origin
DHM-15	NC10-54	Canada
7513A	NC10-55	Canada
W-97	NC10-58	Canada
Comber Select #1	NC10-60	Canada
Comber Select #2	NC10-61	Canada
PRG-2367	NC10-63	Canada (PGR Ottawa)
—	NC10-65	U.S. (South Dakota)
—	NC10-67	U.S. (Michigan)
—	NC10-68	U.S. (Minnesota)
U-2U-2G	NC10-70	Former USSR
Rizskij	NC10-71	Former USSR
Intress	NC10-72	Former USSR
Volzskij-2	NC10-73	Former USSR
Jamcovskij Krashyj	NC10-74	Former USSR
Leningradskij	NC10-75	Former USSR
Vadim	NC10-76	Former USSR
—	NC10-77	Japan
—	NC10-78	Japan
W-3 × Branching 7611	NC10-79	Canada
W-3 × Branching 7701	NC10-80	Canada
Mammoth French White	NC10-81	U.S. (Washington)
Oregon White	NC10-82	U.S. (Minnesota)
—	NC10-83	Canada (British Columbia)
TUB-346 USDA-ARS	NC10-85	U.S. (Texas)
TUB-365 USDA-ARS	NC10-86	U.S. (Texas)
TUB-675 USDA-ARS	NC10-87	U.S. (Texas)
TUB-676 USDA-ARS	NC10-88	U.S. (Texas)
TUB-709 USDA-ARS	NC10-89	U.S. (Texas)
TUB-847 USDA-ARS	NC10-90	U.S. (Texas)
#2	NC10-92	Canada (Ontario)
#4	NC10-94	Canada (Ontario)
#5	NC10-95	Canada (Ontario)
Fuseau 60	NC10-96	France
(37 × 39) 1982	NC10-97	Canada (Manitoba)
Nahodka	NC10-101	Former USSR
Violet de Rennes	NC10-103	France
Rijskii	NC10-104	Former USSR
Vernet	NC10-105	France
D-19	NC10-106	France
Interess	NC10-107	Former USSR
79-62	NC10-108	France
242-63	NC10-109	France
Topinsol	NC10-110	Former USSR
Waldspindel	NC10-111	France
D-19-63-122	NC10-112	France
Kievskii	NC10-113	Former USSR
Industrie	NC10-114	Former USSR

TABLE 8.3 (CONTINUED)
The 179 Accessions Maintained in the Collection of Plant Gene Resources of Canada (PGRC), Saskatoon, Canada, in 2006

Name of Accession	Code	Origin
Leningradskii	NC10-116	Former USSR
Ellijay	NC10-118	Former USSR
Nachodka	NC10-119	Former USSR
D16	NC10-120	France
D19-63-340	NC10-121	France
242-62	NC10-122	France
29-65	NC10-123	France
105-62G2	NC10-125	France
1277-63	NC10-127	France
073-87	NC10-129	Germany
#1	NC10-130	Canada (Ontario)
#2	NC10-131	Canada (Ontario)
357303 Volga 2	NC10-140	Former USSR
83-001-1 (37 × 6)	NC10-143	Canada (Morden)
83-001-2 (37 × 6)	NC10-144	Canada (Morden)
83-001-3 (37 × 6)	NC10-145	Canada (Morden)
83-001-4 (37 × 6)	NC10-146	Canada (Morden)
83-001-5 (37 × 6)	NC10-147	Canada (Morden)
83-001-6 (37 × 6)	NC10-148	Canada (Morden)
83-001-7 (37 × 6)	NC10-149	Canada (Morden)
83-001-8 (37 × 6)	NC10-150	Canada (Morden)
83-001-9 (37 × 6)	NC10-151	Canada (Morden)
83-001-10 (37 × 6)	NC10-152	Canada (Morden)
83-001-11 (37 × 6)	NC10-153	Canada (Morden)
83-001-12 (37 × 6)	NC10-154	Canada (Morden)
83-001-13 (37 × 6)	NC10-155	Canada (Morden)
83-002-1 (69 × 6)	NC10-156	Canada (Morden)
83-003-1 (6 × 20)	NC10-157	Canada (Morden)
83-004-1 (6 × 20)	NC10-158	Canada (Morden)
83-004-2 (6 × 20)	NC10-159	Canada (Morden)
83-004-4 (6 × 20)	NC10-160	Canada (Morden)
83-004-5 (6 × 20)	NC10-161	Canada (Morden)
83-005-1 (39 × 40)	NC10-162	Canada (Morden)
83-005-2 (39 × 40)	NC10-163	Canada (Morden)
83-006-1 (40 × 39)	NC10-164	Canada (Morden)
83-006-3 (40 × 39)	NC10-165	Canada (Morden)
83-006-4 (40 × 39)	NC10-166	Canada (Morden)
83-006-5 (40 × 39)	NC10-167	Canada (Morden)
83-007-1 (69 × 3)	NC10-168	Canada (Morden)
83-007-2 (69 × 3)	NC10-169	Canada (Morden)
83-007-4 (69 × 3)	NC10-171	Canada (Morden)
83-007-5 (69 × 3)	NC10-172	Canada (Morden)
83-008-1 (69 × 39)	NC10-173	Canada (Morden)
83-009-1 (6 × 37)	NC10-174	Canada (Morden)
83-009-2 (6 × 37)	NC10-175	Canada (Morden)
88-3 (6 × 37)	NC10-176	Canada (Morden)
88-5 (6 × 37)	NC10-177	Canada (Morden)

TABLE 8.3 (CONTINUED)
The 179 Accessions Maintained in the Collection of Plant Gene Resources of Canada (PGRC), Saskatoon, Canada, in 2006

Name of Accession	Code	Origin
89-1 (6 × 37)	NC10-178	Canada (Morden)
89-2 (6 × 37)	NC10-179	Canada (Morden)
89-3 (6 × 37)	NC10-180	Canada (Morden)
89-4 (6 × 37)	NC10-181	Canada (Morden)
HM-1	NC10-182	Canada (Morden)
HM-2	NC10-183	Canada (Morden)
HM-4	NC10-184	Canada (Morden)
HM-5	NC10-185	Canada (Morden)
HM-6	NC10-186	Canada (Morden)
HM-7	NC10-187	Canada (Morden)
HM-8	NC10-188	Canada (Morden)
HM-9	NC10-189	Canada (Morden)
HM-11	NC10-190	Canada (Morden)
HM-14	NC10-192	Canada (Morden)
HM-15	NC10-193	Canada (Morden)
HM-16	NC10-194	Canada (Morden)
HM-17	NC10-195	Canada (Morden)
HM-18	NC10-196	Canada (Morden)
HM-20	NC10-198	Canada (Morden)
HM-21	NC10-199	Canada (Morden)
HM-23	NC10-201	Canada (Morden)
HM-25	NC10-202	Canada (Morden)
HM-26	NC10-203	Canada (Morden)
HM-27	NC10-204	Canada (Morden)
HM-28	NC10-205	Canada (Morden)
HM-29	NC10-206	Canada (Morden)
HM-30	NC10-207	Canada (Morden)
HM-31	NC10-208	Canada
HM-32	NC10-209	Canada (Morden)
HM-33	NC10-210	Canada (Morden)
HM-35	NC10-211	Canada (Morden)
HM-36	NC10-212	Canada (Morden)
HM-37	NC10-213	Canada (Morden)
SR	SR	—
Cambridge sunroot	Group 1	—
Usborne sunroot	Group 2	—
Mansell sunroot	Group 3	—
Jack's Copperclad	Group 4	—

Source: Dallas Kessler (PGRC), personal communication.

Central Regional Plant Introduction Station (NCRPIS), based at Iowa State University (ISU), Ames. In August 2006, NCRPIS held 112 accessions of *H. tuberosus* (Table 8.4). The first 22 rows of Table 8.4 ('TUB-33' to '3') were available to plant breeders in August 2006; the following 42 rows ('TUB-1765' to 'TUB-2089') were accessions in the field for seed increase, and therefore soon to be available; the next 37 rows ('TUB-1798' to '19') were unavailable and requiring seed increase; while the final 11 rows ('TUB-320' to 'TUB-1913') were accessions pending inactivation in August

TABLE 8.4
The 112 Accessions in the Collection of NCRPRIS, USDA-ARS, and ISU, Ames, ID, in 2006

Name of Accession	Accession Number	Origin
TUB-33	Ames 2714	South Dakota
TUB-1776	Ames 2722	South Dakota
TUB-1777	Ames 2723	South Dakota
TUB-49	Ames 2729	South Dakota
TUB-1783	Ames 2730	South Dakota
TUB-1786	Ames 2733	South Dakota
TUB-1789	Ames 2736	Iowa
TUB-1800	Ames 2746	South Dakota
TUB-1799	Ames 2747	South Dakota
Waldoboro Gold	Ames 8380	Maine
Jack's Copperskin	Ames 8383	Maine
TUB-2189	Ames 18010	Nebraska
TUB-2329	Ames 22229	Manitoba, Canada
Ames 22746	Ames 22746	North Dakota
No. 72196	PI 451980	North Dakota
TUB-1877	PI 503262	West Virginia
TUB-2047	PI 547230	Ohio
TUB-2050	PI 547232	Ohio
TUB-2051	PI 547233	Ohio
TUB-2061	PI 547237	Ohio
TUB-2066	PI 547241	Ohio
3	PI 613795	Iowa
TUB-1765	Ames 2711	South Dakota
TUB-1769	Ames 2715	South Dakota
TUB-1774	Ames 2720	South Dakota
TUB-1775	Ames 2721	South Dakota
TUB-64	Ames 2739	Iowa
TUB-1797	Ames 2744	South Dakota
TUB-1540	Ames 7318	Arkansas
Swenson	Ames 8376	Maine
Freedom	Ames 8378	Maine
Garnet	Ames 8379	Idaho
Beaula's	Ames 8381	Canada
Colby Miller	Ames 8382	Maine
Fuseau	Ames 8384	Idaho
Unity Firehouse	Ames 8386	Maine
Mulles Rose	Ames 8388	Maine
Clearwater	Ames 8390	Maine
Ames 22745	Ames 22745	North Dakota
Hybrid 120	PI 357297	Russian Federation
Kiev's White	PI 357298	Ukraine
Leningrad	PI 357299	Russian Federation
Nakhodka	PI 357300	Russian Federation
Vadim	PI 357302	Ukraine
Volga 2	PI 357303	Russian Federation
TUB-1880	PI 503263	West Virginia
TUB-1904	PI 503265	Virginia
TUB-1906	PI 503267	Maryland

TABLE 8.4 (CONTINUED)
The 112 Accessions in the Collection of NCRPRIS, USDA-ARS, and ISU, Ames, ID, in 2006

Name of Accession	Accession Number	Origin
TUB-1912	PI 503269	New Jersey
TUB-1928	PI 503272	Connecticut
TUB-1936	PI 503274	Vermont
TUB-1939	PI 503276	New York
TUB-1940	PI 503277	New York
TUB-1942	PI 503278	New York
TUB-1943	PI 503279	New York
TUB-2024	PI 547227	Wisconsin
TUB-2052	PI 547234	Ohio
TUB-2055	PI 547235	Ohio
TUB-2062	PI 547238	Ohio
TUB-2063	PI 547239	Ohio
TUB-2067	PI 547242	Ohio
TUB-2069	PI 547243	Indiana
TUB-2070	PI 547244	Indiana
TUB-2089	PI 547248	Illinois
TUB-1798	Ames 2745	South Dakota
Ames 3244	Ames 3244	Unknown
Ames 3245	Ames 3245	Unknown
TUB-571	Ames 6502	Oklahoma
TUB-870	Ames 6706	Alabama
TUB-1057	Ames 7141	North Dakota
TUB-1067	Ames 7151	Illinois
TUB-1078	Ames 7161	Illinois
TUB-1079	Ames 7162	Illinois
TUB-1080	Ames 7163	Illinois
TUB-1081	Ames 7164	Illinois
TUB-1609	Ames 7382	South Carolina
TUB-1610	Ames 7383	South Carolina
TUB-1632	Ames 7405	North Dakota
TUB-2278	Ames 22227	Manitoba, Canada
TUB-2282	Ames 22228	Manitoba, Canada
Ames 26006	Ames 26006	Missouri
TUB-821	PI 435758	Oklahoma
TUB-322	PI 435889	Texas
TUB-825	PI 435893	Oklahoma
TUB-1625	PI 468896	Tennessee
TUB-1892	PI 503264	Virginia
TUB-1905	PI 503266	Maryland
TUB-1090	PI 503268	New Jersey
TUB-1925	PI 503271	Connecticut
TUB-1937	PI 503275	Vermont
TUB-1946	PI 503280	New York
TUB-1959	PI 503283	Pennsylvania
TUB-2045	PI 547228	Ohio
TUB-2046	PI 547229	Ohio
TUB-2048	PI 547231	Ohio
TUB-2057	PI 547236	Ohio

TABLE 8.4 (CONTINUED)
The 112 Accessions in the Collection of NCRPRIS, USDA-ARS, and ISU, Ames, ID, in 2006

Name of Accession	Accession Number	Origin
TUB-2064	PI 547240	Ohio
TUB-2071	PI 547245	Indiana
TUB-2073	PI 547246	Indiana
TUB-2080	PI 547247	Indiana
19	PI 613796	Iowa
TUB-320	Ames 6303	Minnesota
TUB-321	Ames 6304	Minnesota
Gold Nugget	Ames 8377	Idaho
Wilder Hill	Ames 8387	Maine
Totman	Ames 8391	Maine
Skorospelka	PI 357301	Russian Federation
White Crop	PI 357304	Russian Federation
TUB-365	PI 435892	Texas
CR Special	PI 461518	Argentina
TUB-1628	PI 468897	Tennessee
TUB-1913	PI 503270	New Jersey

Source: NCPRIS database, http://www.ars-grin.gov/npgs/search-grin.html; Laura Marek (NCRPRIS), personal communication. (For further details on individual accessions, see Section 8.14.2.)

2006, and therefore no longer available (Laura Marek, personal communication). When available, accessions are usually supplied in the form of seed, in a quantity of up to 100 seeds.

The Jerusalem artichoke material held by NCPRIS mainly comprises wild or weedy accessions originating from within the U.S. A great many of these were originally collected by the USDA sunflower unit and held in Bushland, TX, prior to being transferred to Ames in 1986. Therefore, the collection date for these accessions is noted as pre-1988 in the accessions listing below (Section 8.14.2). Because this material was collected as part of a program involving the genetic improvement of cultivated sunflower, the data held for some of these accessions have detailed information on the seeds, including morphology and seed oil analysis (http://www.ars-grin.gov/npgs/search-grin.html). More recently, plant-collecting trips (e.g., conducted by Gerald Seiler and colleagues of USDA-ARS, Fargo, ND) have extended the range of wild-collected *H. tuberosus* accessions held at Ames. A range of landraces from the U.S. and material from Canada and the Russian Federation are also held at Ames.

When material first arrives at NCRPRIS in Ames, it is given an Ames number, which acts as an initial accession number. At some point, the accession is converted to a Plant Introduction (PI) number, generally when relevant plant passport data are deemed adequate (Laura Marek, personal communication). Therefore, NCRPIS material has either an Ames or a PI number, but not both, in addition to an accession name. The wild and weedy accessions generally have 'TUB-' accession names, although some accessions still have their Ames numbers for accession names (Table 8.4).

One of the most comprehensive sources of Jerusalem artichoke tubers in North America is maintained and available from the Scatterseed Project, part of the Seed Savers Exchange Members Network (Decorah, IA), run by Will Bonsall, Box 1167, Farmington, ME 04938, U.S. This collection includes an impressive range of landraces, and obsolete and traditional cultivars from around North America (see Section 8.14.2).

8.13.3 Central and South America

Little or no *H. tuberosus* material is maintained in Central and South American countries. The Estacion Experimental Agropecuaria, Belcare, Buenos Aires, Argentina, holds three wild or weedy accessions of U.S. origin; CENARGEN/EMBRAPA, Brasilia, Brazil, reportedly has one accession; while the Facultdad de Ciencias Agrarias, Universidad Austral de Chile, Valdivia, Chile, holds two old cultivar accessions collected in Chile (IPGRI, 2006). 'CR Special' (Argentina) is among the very few accessions in germplasm collections with a South American origin.

8.13.4 Germany, Austria, Slovenia, and Switzerland

In the past, the main repository for *H. tuberosus* (topinambur) genetic resources in Germany was at the Federal Centre for Breeding Research on Cultivated Plants (BAZ), in Braunschweig, Germany (Frison and Servinsky, 1995). Although BAZ remains a major institute for plant breeding, the national germplasm collection for *H. tuberosus* has been moved to the Genebank of the Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) in Gatersleben (Gatersleben, Germany). With 18 accessions listed in 1995 (Frison and Servinsky, 1995), Gatersleben held 115 accessions in 2006 after the movement of material from BAZ. All these accessions are maintained as tubers (Helmut Knuepffer, personal communication). In addition, the original 18 Gatersleben accessions are also in the *in vitro* collection and propagated by tissue culture (Joachim Keller and Khan, 1997). The complete listing of accessions held at Gatersleben is given in Table 8.5, with further details of individual accessions (including former Braunschweig BGRC numbers) given in Section 8.14.2.

A number of botanical gardens in Germany also hold a small amount of Jerusalem artichoke material, including gardens in Stuttgart, Bonn, Bayreuth, Frankfurt, Göttingen, Marburg, and Ülm (GBIF, 2006).

There are four institutes in Austria holding crop plant germplasm, two of them with Jerusalem artichoke accessions. The Research Station for Special Crops (Wies 88, Austria) makes available three cultivars of German origin: 'Bianka' (WIES-D16), 'RoZo' (WIES-D17), and 'Gute Gelbe' (WIES-D18). The Federal Office of Agrobiology Seed Collection (BVAL, Biologiezentrum Linz) maintains an Austrian accession ('BVAL-901') (Eurisco, 2003). Material from 38 wild *H. tuberosus* populations, collected between 2000 and 2003 from around Austria, is held by Biologiezentrum Linz (GBIF, 2006).

In Slovenia, the Agronomy Department (Oddelek za Agronomijo) at the University of Ljubljana (Ljubljana, Slovenia) holds 16 accessions of *H. tuberosus*, comprising 14 advanced cultivars and 2 landraces (Frison and Servinsky, 1995; IPRGI, 2006).

SAVE (Safeguard for Agricultural Varieties in Europe; St. Gallen, Switzerland) was reported as holding three accessions in 1995, but these were subsequently offered to Pro Specie Rara when the organization's show farm closed (Frison and Servinsky, 1995; Pavel Beco, personal communication). Pro Specie Rara (St. Gallen, Switzerland), a Swiss NGO, holds up to five accessions (IPGRI, 2006).

8.13.5 France and Spain

The diversity of Jerusalem artichoke clones has been recognized in France for many years (Meunissier, 1922; Tsvetoukhine, 1960). The national germplasm collection was first assembled at INRA–Rennes (Lefèvre, 1941) and then moved to INRA–Clermont Ferrand, where it remained for about 15 years. In 2005, the collection was moved to the INRA breeding station at Montpellier (UMR DGPC), an institute actively involved in the study of cultivated and wild *Helianthus* genetic resources. The *H. tuberosus* (topinambour) collection comprises 140 cultivated clones and about 30 wild accessions (with sexual propagation). The cultivated clones in the INRA collection are propagated as tubers, in 100-l pots, with an artificial substrate (vermiculite) and mineral fertilization, and with two replications of each accession. This system effectively prevents clone mixing in the

TABLE 8.5
The 115 Cultivated Clones Maintained in the Collection of IPK, Gatersleben, Germany, in 2006

Name of Accession	IPK Accession Number	Origin
—	HEL 51	Unknown
—	HEL 53	Germany
—	HEL 54	Germany
—	HEL 55	Germany
—	HEL 56	Germany
—	HEL 57	Germany
—	HEL 58	Germany
G-71-39	HEL 59	Unknown
Majkopskij 33-650	HEL 60	Russian Federation
Tambovskij Krasnyi	HEL 61	Russian Federation
Sachalinskij Krasnyi	HEL 62	Russian Federation
Gibrid 103	HEL 63	Russian Federation
—	HEL 64	Unknown
Sejanec 19	HEL 65	Russian Federation
Kievskij Belyj	HEL 66	Ukraine
M-24-2	HEL 67	Unknown
—	HEL 68	Unknown
—	HEL 69	Unknown
—	HEL 231	Germany
Bianka	HEL 243	Unknown
Waldspindel	HEL 244	Unknown
—	HEL 245	Unknown
—	HEL 246	Unknown
Topianka?	HEL 247	Unknown
Rote Zonenkugel	HEL 248	Unknown
—	HEL 249	Unknown
Medius	HEL 250	France
Novost	HEL 251	Russian Federation
—	HEL 252	Germany
—	HEL 253	Unknown
—	HEL 254	Unknown
—	HEL 255	Unknown
—	HEL 256	Unknown
—	HEL 257	Unknown
—	HEL 258	Unknown
Fuseau 60	HEL 259	France
Nahodka	HEL 260	Russian Federation
Violet de Rennes	HEL 261	France
KWI 204	HEL 262	Unknown
Sel. Aus Saemlingspop.	HEL 263	Canada
BT3	HEL 264	Hungary
BT4	HEL 265	Hungary
Bela	HEL 266	Former Yugoslavia
12/84	HEL 267	Former Yugoslavia
Onta	HEL 268	Canada
10562 G2	HEL 269	France
10562 G15	HEL 270	France
D19-63-122	HEL 271	France

TABLE 8.5 (CONTINUED)
The 115 Cultivated Clones Maintained in the Collection of IPK, Gatersleben, Germany, in 2006

Name of Accession	IPK Accession Number	Origin
D19-63-340	HEL 272	France
2327	HEL 273	France
228-62	HEL 274	France
952-63	HEL 275	France
2071-63	HEL 276	France
Dwarf	HEL 277	Netherlands
Voelkenroder Spindel	HEL 278	Unknown
BS-83-21	HEL 279	Unknown
BS-83-22	HEL 280	Unknown
BS-84-19	HEL 281	Unknown
BS-85-7	HEL 282	Unknown
BS-85-8	HEL 283	Unknown
Topstar	HEL 284	Unknown
BS-85-11	HEL 285	Unknown
BS-85-14	HEL 286	Unknown
Gigant	HEL 287	Unknown
RA1	HEL 288	Poland
RA2	HEL 289	Poland
RA3	HEL 290	Poland
RA4	HEL 291	Poland
RA7	HEL 292	Poland
RA9	HEL 293	Poland
RA10	HEL 294	Poland
RA14	HEL 295	Poland
RA24, Biala Kulista	HEL 296	Poland
—	HEL 297	Unknown
—	HEL 298	Unknown
—	HEL 299	Unknown
—	HEL 306	Unknown
—	HEL 307	Unknown
—	HEL 308	Unknown
—	HEL 309	Unknown
—	HEL 310	Unknown
—	HEL 311	Unknown
—	HEL 312	Unknown
—	HEL 313	Unknown
—	HEL 314	Unknown
—	HEL 315	Unknown
—	HEL 316	Unknown
—	HEL 317	Unknown
—	HEL 318	Unknown
—	HEL 319	Unknown
—	HEL 320	Unknown
—	HEL 321	Unknown
—	HEL 322	Unknown
—	HEL 323	Unknown
—	HEL 324	Unknown
—	HEL 325	Unknown

TABLE 8.5 (CONTINUED)
The 115 Cultivated Clones Maintained in the Collection of IPK, Gatersleben, Germany, in 2006

Name of Accession	IPK Accession Number	Origin
—	HEL 326	Unknown
—	HEL 327	Unknown
—	HEL 328	Unknown
—	HEL 329	Unknown
—	HEL 330	Unknown
—	HEL 331	Unknown
—	HEL 332	Unknown
—	HEL 333	Unknown
—	HEL 334	Unknown
—	HEL 335	Unknown
—	HEL 336	Unknown
BS-86-8	HEL 337	Unknown
BS-86-12	HEL 338	Unknown
BS-86-16	HEL 339	Unknown
BS-86-19	HEL 340	Unknown
BS-87-3	HEL 342	Unknown
BS-87-7	HEL 342	Unknown
BS-87-9	HEL 343	Unknown
BS-87-10	HEL 344	Unknown

Source: IPK database, http://gbis.ipk-gatersleben.de; Helmut Knuepffer (Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK), Corrensstrasse 3, Gatersleben, Germany), personal communication. (For further details on individual accessions, see Section 8.14.2.)

long term and limits the prevalence of soil disease. All the French accessions have very limited immediate availability and require additional multiplication before distribution (Hervé Serieys, personal communication). The names of the 140 cultivated clones are given in Table 8.6.

A collection of *H. tuberosus* accessions was previously held at the Escuela Tecnica Superior (ETS) de Ingenieros Agrónomes, Universidad Politénica de Madrid. Fernandez et al. (1988a, 1988b) listed 24 accessions held in the late 1980s (i.e., 'Blanca de Teruel,' 'Boniches,' 'C-13,' 'C-146,' 'C-34,' 'Campillo de Paravientos,' 'Ciudad Rodrigo,' 'D-19,' 'GUA-7,' 'Fuseau 60,' 'K-8,' 'Huertos de Moya-Rio,' 'Huertos de Moya-Tobares,' 'Huertos de Moya-Blanca,' 'Ibdes,' 'Karkowsky,' 'Medius,' 'Nahodka,' 'Rijskii,' 'Sepanetz-10,' 'Teruel,' 'Violet de Rennes,' 'Violeta de Teruel,' and 'Waldspindel'), some of which are Spanish in origin. The existence of this collection is absent from subsequent directories of European plant genetic resources (e.g., Frison and Servinsky, 1995).

8.13.6 Denmark, Finland, Iceland, Norway, and Sweden

The Nordic Gene Bank (NGB) was established in 1979 to act as a repository for genetic resources from Denmark, Finland, Iceland, Norway, and Sweden. The main institute is located in Alnarp, near Malmo, Sweden, and *H. tuberosus* (Jordskok) accessions have been maintained since 1995 at Forskningscenter Årslev [Danish Institute of Agricultural Research], in Denmark. The NGB holds 15 accessions of Jerusalem artichoke (Table 8.7). These include seven landraces or traditional cultivars and eight breeding or research clones. The accessions are propagated as tubers, with 20 plants per accession grown at any one time. Eight accessions were obtained from Denmark ('Bistr,' 'Columbia,' 'Flam,' 'Karina,' 'Mari,' 'Refla,' 'Reka,' 'Rema'), two in France ('C2071-63' and 'D

TABLE 8.6
The 140 Cultivated Clones in the Collection of INRA Breeding Station at Montpellier (UMG DGPC), France, in 2006

Name of Clone	INRA Code	Origin
1277.63 (48)[a]	MPHE001361	France
1992.63 (31)	MPHE001362	France
2071.63 (17)	MPHE001363	France
2088 (29)	MPHE001364	France
228.62 (15)	MPHE001365	France
23.27 (2)	MPHE001366	France
29.65 (54)	MPHE001367	France
342.62 (43)	MPHE001368	France
742.63 (51)	MPHE001369	France
79.62 (42)	MPHE001370	France
952.63 (21)	MPHE001371	France
AUTO105.62G.15 (7)	MPHE001372	France
AUTO105.62G.2 (8)	MPHE001373	France
CF.11 (56)	MPHE001374	France
CL2 (118)	MPHE001375	France
D13 (106)	MPHE001376	France
D16 (30)	MPHE001377	France
D18 (103)	MPHE001378	France
D19 (3)	MPHE001379	France
D19.6 (1)	MPHE001380	France
D19.63.122 (14)	MPHE001381	France
D19.63.340 (13)	MPHE001382	France
D.29 (96)	MPHE001383	France
D31 (37)	MPHE001384	France
D.42 (98)	MPHE001385	France
D5 (91)	MPHE001386	France
D8 (104)	MPHE001387	France
DL12 (100)	MPHE001388	France
H54.1 (102)	MPHE001389	France
I2.1044.344 (145) (I2)	MPHE001390	France
I3.2017 (146) (I3)	MPHE001391	France
K.4 (93)	MPHE001392	France
K.5 (94)	MPHE001393	France
L232 (108)	MPHE001394	France
MS.2.6 (47)	MPHE001395	France
MS81 (117)	MPHE001396	France
S3.1 (105)	MPHE001397	France
V102 (101)	MPHE001398	France
BERNO (131)	MPHE001399	France
CLONE ACP 1981 (125)	MPHE001400	France
CLONE DUVAL 1980.1 (122)	MPHE001401	France
CLONE DUVAL 1980.2 (123)	MPHE001402	France
CLONE PORCHERON 1980 (121)	MPHE001403	France
PORCHERON (120)	MPHE001404	France
EGMOND 1982 (129)	MPHE001405	France
FILIO (138)	MPHE001406	France
FUSEAU 60 (60)	MPHE001407	France
INDUSTRIE (35)	MPHE001408	France
JANTO (133)	MPHE001409	France

TABLE 8.6 (CONTINUED)
The 140 Cultivated Clones in the Collection of INRA Breeding Station at Montpellier (UMG DGPC), France, in 2006

Name of Clone	INRA Code	Origin
JAUNE DE ROUILLE (36)	MPHE001410	France
LACHO (139)	MPHE001411	France
MARONDO (141)	MPHE001412	France
MEDIUS (58)	MPHE001413	France
MONTEO (134)	MPHE001414	France
PATATE VILMORIN (27)	MPHE001415	France
PIEDALLU 8 (109)	MPHE001416	France
PIRIFORME ROUGE (95)	MPHE001417	France
SCOTT (99)	MPHE001418	France
TAIT (92)	MPHE001419	U.S.
VERNET (28)	MPHE001420	France
VIOLET COMMUN (57)	MPHE001421	France
VIOLET DE RENNES (69)	MPHE001422	France
(K8*VR) (353)	MPHE001423	France
(NK*F60).1 (219)	MPHE001424	France
(NK*F60).2 (220)	MPHE001425	France
(NK*F60).3 (222)	MPHE001426	France
(NK*F60).4 (226)	MPHE001427	France
(NK*F60).5 (234)	MPHE001428	France
(NK*F60).6 (259)	MPHE001429	France
(NK*F60).7 (273)	MPHE001430	France
(NK*F60).8 (276)	MPHE001431	France
(NK*F60).9 (279)	MPHE001432	France
(NK*F60).10 (281)	MPHE001433	France
(NK*K8) (336)	MPHE001434	France
(NK*VR).1 (321)	MPHE001435	France
(NK*VR).2 (327)	MPHE001436	France
(VR*F60).1 (215)	MPHE001437	France
(VR*F60).2 (217)	MPHE001438	France
(VR*F60).3 (218)	MPHE001439	France
(VR*NK).1 (297)	MPHE001440	France
FL83FC (151B) (ISSU DE FL)	MPHE001441	France
FL 83 NK (154.1) (FL NAHODKA)	MPHE001442	France
FL 84 EL1 (157.1) (FL ELLIJAY)	MPHE001443	France
FL 84 EL2 (157.2) (FL ELLIJAY)	MPHE001444	France
FL 85 JT1 (161) (FL JANTO)	MPHE001445	France
FL 85 JT2 (162) (FL JANTO)	MPHE001446	France
FL 85 K8 (163) (FL K8)	MPHE001447	France
FL 85 342.62.1 (164) (FL 342.62)	MPHE001448	France
FL 85 342.62.2 (165) (FL 342.62)	MPHE001449	France
FL 85 342.62.3 (166) (FL 342.62)	MPHE001450	France
ONTA (208)	MPHE001451	Belgium
WAGENINGSE DWARF (213)	MPHE001452	Netherlands
DORNBURGER (50)	MPHE001453	Germany
K8 (59)	MPHE001454	Germany?
KARNTNER LANDSORTE (211)	MPHE001455	Germany
ROZO (86)	MPHE001456	Germany
TOPIANKA (49)	MPHE001457	Germany
WALDSPINDEL (34)	MPHE001458	Germany

TABLE 8.6 (CONTINUED)
The 140 Cultivated Clones in the Collection of INRA Breeding Station at Montpellier (UMG DGPC), France, in 2006

Name of Clone	INRA Code	Origin
WALDSPINDEL (204)	MPHE001459	Germany
WALDSPINDEL (201)	MPHE001460	Austria
BT3 (202)	MPHE001461	Hungary
BT4 (203)	MPHE001462	Hungary
12/84 (206)	MPHE001463	Former Yugoslavia
BIANCA (142)	MPHE001464	Europe
OZOV (210)	MPHE001465	Europe
SUKOSTI (209)	MPHE001466	Europe
BART 70 JANEZ (67)	MPHE001467	Russian Federation
BELOSHIPKE (68)	MPHE001468	Russian Federation
DORNAISKII (66)	MPHE001469	Russian Federation
G71.39 (78)	MPHE001470	Russian Federation
HYBRIDE 103 (77)	MPHE001471	Russian Federation
INTERESS (85)	MPHE001472	Russian Federation
KIEVKII BLANC (90)	MPHE001473	Ukraine
KIRGNIZSKII BLANC (82)	MPHE001474	Russian Federation
KULISTY CREMONSKY (70)	MPHE001475	Russian Federation
LENINGRADSKII (74)	MPHE001476	Russian Federation
M24.29 (84)	MPHE001477	Russian Federation
MAIKOPSKII 33.650 (63) (TOP*TS)	MPHE001478	Russian Federation
NAHODKA (61)	MPHE001479	Russian Federation
RYSKII (89)	MPHE001480	Russian Federation
SEJANETZ 10 (76)	MPHE001481	Russian Federation
SEJENETZ 19 (81)	MPHE001482	Russian Federation
TAMBOVSKII ROUGE (64) (TOP*TS)	MPHE001483	Russian Federation
TOPINSOL 63 (39) (TOP*TS)	MPHE001484	Russian Federation
TOPINSOL VIR (62) (TOP*TS)	MPHE001485	Russian Federation
VADIM (73)	MPHE001486	Russian Federation
VORSTORG (79) (TOP*TS)	MPHE001487	Russian Federation
CHICAGO (24)	MPHE001488	U.S.?
ELLIJAY (87)	MPHE001489	U.S.
CHALLENGER (212)	MPHE001490	Canada
COLUMBIA (143)	MPHE001491	Canada
GUA 7 (144)	MPHE001492	Guadeloupe
SAKHALINSKII (65)	MPHE001493	Russian Federation
SAKHALINSKII ROUGE (83)	MPHE001494	Russian Federation
IRANIEN (80)	MPHE001495	Iran
MS.2.6 (46)	MPHE001496	France
HUGUETTE 93	MPHE001497	Morocco
CROIX LEONARDOUX	MPHE001498	France
ANTONIN	MPHE001499	France
99B	MPHE001500	France

[a] Numbers in parentheses after the accession names correspond to the initial collection number attributed by INRA–Rennes.

Source: Hervé Serieys (INRA, UMR Diversité des Plantes Cultivées, Laboratoire Tournesol, Domaine de Melgueil, F-34131, Mauguio, France), personal communication. (For further details on individual accessions, see Section 8.14.2.)

TABLE 8.7
The 15 Cultivated Clones in the Collection of the Nordic Gene Bank, Årslev, Denmark, in 2006

Name of Clone	Accession Number	Origin
Rema	DKHEL1	Denmark
Reka	DKHEL2	Denmark
Refla	DKHEL3	Denmark
K24	DKHEL4	Czech Republic
Karina	DKHEL5	Denmark
Flam	DKHEL6	Denmark
Vanlig	DKHEL7	Sweden
Bistr	DKHEL8	Denmark
Mari	DKHEL9	Denmark
Nora	DKHEL10	Norway
D19	DKHEL11	France
Columbia	DKHEL12	Denmark
C2071-63	DKHEL13	France
Urodny	DKHEL14	Czech Republic
Dwarf	DKHEL15	Netherlands

Source: The Nordic Gene Bank database, http://tor.ngb.se/sesto/. (For further details on individual accessions, see Section 8.14.2.)

19'), and one each in the Netherlands ('Dwarf'), Norway ('Nora'), Sweden ('Vanlig'), the Czech Republic ('K24'), and the Russian Federation ('Urodny') (http://tor.ngb.se/sesto/). A replica collection of the NGB accessions is held at Landbohøjskolen in Copenhagen, Denmark. In addition, two further accessions are held at the Danish Institute of Agricultural Science's horticultural research station at Årslev — 'Bianca' (HEL 16) and 'Draga' (HEL 17) — donated by the University of Agriculture in 2002 (Gitte Kjeldsen Bjørn, Forskningscenter Årslev, personal communication). The Hilleshög AB Plant Breeding Company in Sweden has also in the past maintained a small number of distinct clones, including 'No. 1168' — a Jerusalem artichoke × sunflower hybrid (Gunnarson et al., 1985).

8.13.7 Russian Federation

In the Russian Federation, the primary institute for the maintenance of genetic resources and breeding of Jerusalem artichoke is the N.I. Vavilov Institute of Plant Industry (VIR; St. Petersburg, Russian Federation). It houses one of the world's largest collections of plant germplasm. In addition to a large collection of sunflower (*H. annuus*) accessions, 324 advanced cultivars of *Helianthus* spp. were listed in the *European Directory of Plant Germplasm* in 1995 (Frison and Servinsky, 1995). Pas'ko (1982) studied 160 *H. tuberosus* accessions from the collection in the 1970s.

8.13.8 Ukraine and Azerbaijan

In 1992, the Ukrainian Academy of Sciences (UAAS) financed a program for plant genetic resources, including the creation of a new center in the Yurjev Plant Production Institute in Kharkov. The National Centre for Plant Genetic Resources of the Ukraine (Kharkov, Ukraine) holds 17 accessions of cultivated Jerusalem artichoke ('M-037,' 'K105,' and various 'TUB-' accessions; see

Section 8.14.2). Two wild-collected accessions, one of Ukrainian ('UM0600001') and one of U.S. ('UE0100253') origin, are also held in other Ukrainian germplasm collections (Eurisco, 2003).

In Azerbaijan, the Institute of Genetic Resources, Azerbaijan National Academy of Sciences, Baku, maintains two Jerusalem artichoke accessions ('Yeralmasi' and 'Yerarmudu gunebakhani'), both of Azerbaijan origin (Eurisco, 2003).

8.13.9 Bulgaria, Hungary, and Romania

In Bulgaria, the Institute of Plant Genetic Resources "K. Malkov" (Sadovo, Bulgaria) maintains seven Jerusalem artichoke accessions ('M-037,' 'M-053,' 'M-057,' 'M-108,' 'M-140,' 'M-146,' and 'M-169'), all originating from the U.S. (Eurisco, 2003).

Genetic resources activities in Hungary are supported by the Agriculture Fund, under the supervision of the Ministry of Agriculture. The Plant Introduction and Gene Bank section of the Institute for Agrobotany in Tápiószele (Agrobotanikai Intézet, Tápiószele, Hungary) is the main repository of *H. tuberosus* material in Hungary. The institute maintains 54 advanced cultivars and landraces of *H. tuberosus*, and numerous advanced cultivars, genetic stock, landraces, and wild/weedy species of *Helianthus* spp. (Frison and Servinsky, 1995; IPGRI, 2006). In addition, the Research Centre of Debrecen Agricultural University (Nyíregyháza, Hungary) is also recorded as holding breeding lines of *Helianthus* spp. (Frison and Servinsky, 1995).

The Research Institute for Cereals and Technical Plants, in Calarasi, Romania, has one *H. tuberosus* holding, a wild/weedy accession ('ROM023-6149') obtained from the former Yugoslavia in 1980. Two landraces (obsolete/traditional cultivars) originating in Romania are held by the University of Agricultural Sciences and Veterinary Medicine, in Timisoara, Romania: Gurahont ('ROM023-6150') and Sebis ('ROM023-6151'), collected in 1989 (IPGRI, 2006; Eurisco, 2003).

8.13.10 Czech Republic, Slovakia, and Serbia and Montenegro

The primary repository for Jerusalem artichoke germplasm in the Czech Republic is in Olomouc-Holice (Gene Bank Department, Research Institute of Crop Production, Olomouc-Holice, Czech Republic). Eight accessions have been maintained in recent years, including six landraces from the Czech Republic, one advanced cultivar from Poland, and one landrace from Germany (Frison and Servinsky, 1995; IPGRI, 2006). Five landraces or obsolete cultivars (LV accessions; see Section 8.14.2) have been propagated from tubers since their local collection in 1958 (Eurisco, 2003; Olomouc-Holice Genebank Database, 2006, http://genbank.vurv.cz/).

In Slovakia, the crop plant germplasm collection is stored in around 18 specialized research and breeding institutes. The Research Institute of Plant Protection in Piestany, Slovakia, holds six accessions (2002 data): four advanced cultivars and a landrace from Hungary, and an advanced cultivar from the Czech Republic (IPGRI, 2006).

The Institute of Field and Vegetable Crops in Novi Sad (IFVCNS), Serbia and Montenegro, maintains 155 wild accessions of *H. tuberosus*, originating from Montenegro and the U.S. (Table 8.8) (IPGRI, 2006; Jovanka Atlagi, personal communication). These accessions have primarily been collected as potential sources of disease resistance for cultivated sunflowers. Material originating from the U.S. has been exchanged with the participation of the USDA (in 1980, 1985, and 1991) and on a collaborative field trip (Marinkovic/Miller in North Dakota in 1984), while the material from Montenegro was mainly collected during an IFVCNS field trip in 1990 (Marinkovic/Dozet). In addition to the availability of many of these accessions in the form of either seed or tubers (Table 8.8), F_1 hybrids from some of the crosses between wild *H. tuberosus* and cultivated sunflower are available in the form of tubers (Jovanka Atlagic, personal communication).

TABLE 8.8
The 155 Wild-Collected *H. tuberosus* Clones Maintained in the Collection of the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro, in 2006

Accession	Origin	Availability
TUB 1540	U.S.	+
TUB 1609	U.S.	–
TUB 1610	U.S.	–
TUB 1623	U.S.	–
TUB 1625	U.S.	+
TUB 1628	U.S.	+
TUB 1633	U.S.	–
TUB 1634	U.S.	–
TUB 1634	U.S.	–
TUB 1635	U.S.	–
TUB 1636	U.S.	–
TUB 1877	U.S.	–
TUB 1880	U.S.	–
TUB 1892	U.S.	–
TUB 1904	U.S.	–
TUB 1905	U.S.	–
TUB 1906	U.S.	–
TUB 1909	U.S.	–
TUB 1912	U.S.	–
TUB 1913	U.S.	–
TUB 1925	U.S.	–
TUB 1928	U.S.	–
TUB 1933	U.S.	–
TUB 1936	U.S.	–
TUB 1937	U.S.	–
TUB 1939	U.S.	–
TUB 1940	U.S.	–
TUB 1942	U.S.	–
TUB 1943	U.S.	–
TUB 1945	U.S.	+
TUB 1946	U.S.	–
TUB 1947	U.S.	–
TUB 1954	U.S.	–
TUB 1959	U.S.	+
TUB 2024	U.S.	+
TUB 2045	U.S.	+
TUB 2046	U.S.	+
TUB 2047	U.S.	+
TUB 2048	U.S.	–
TUB 2050	U.S.	+
TUB 2051	U.S.	+
TUB 2055	U.S.	–
TUB 2057	U.S.	–
TUB 2061	U.S.	+
TUB 2062	U.S.	+
TUB 2064	U.S.	–

TABLE 8.8 (CONTINUED)
The 155 Wild-Collected *H. tuberosus* Clones Maintained in the Collection of the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro, in 2006

Accession	Origin	Availability
TUB 2067	U.S.	+
TUB 2069	U.S.	+
TUB 2070	U.S.	+
TUB 2071	U.S.	+
TUB 2080	U.S.	+
TUB 2089	U.S.	+
TUB 2052	U.S.	+
TUB 2073	U.S.	–
TUB 2066	U.S.	+
TUB 2063	U.S.	–
TUB-CG 1	Montenegro	–
TUB-CG 10	Montenegro	+
TUB-CG 11	Montenegro	+
TUB-CG 12	Montenegro	+
TUB-CG 13	Montenegro	+
TUB-CG 14	Montenegro	+
TUB-CG 15	Montenegro	+
TUB-CG 16	Montenegro	+
TUB-CG 17	Montenegro	+
TUB-CG 18	Montenegro	+
TUB-CG 19	Montenegro	+
TUB-CG 2	Montenegro	+
TUB-CG 20	Montenegro	+
TUB-CG 21	Montenegro	+
TUB-CG 22	Montenegro	+
TUB-CG 23	Montenegro	+
TUB-CG 24	Montenegro	+
TUB-CG 25	Montenegro	+
TUB-CG 26	Montenegro	+
TUB-CG 27	Montenegro	+
TUB-CG 28	Montenegro	+
TUB-CG 29	Montenegro	+
TUB-CG 3	Montenegro	+
TUB-CG 30	Montenegro	+
TUB-CG 31	Montenegro	+
TUB-CG 32	Montenegro	+
TUB-CG 33	Montenegro	+
TUB-CG 34	Montenegro	+
TUB-CG 35	Montenegro	+
TUB-CG 36	Montenegro	+
TUB-CG 37	Montenegro	+
TUB-CG 38	Montenegro	+
TUB-CG 39	Montenegro	–
TUB-CG 4	Montenegro	+
TUB-CG 40	Montenegro	+
TUB-CG 41	Montenegro	+

TABLE 8.8 (CONTINUED)
The 155 Wild-Collected *H. tuberosus* Clones Maintained in the Collection of the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro, in 2006

Accession	Origin	Availability
TUB-CG 42	Montenegro	+
TUB-CG 43	Montenegro	+
TUB-CG 44	Montenegro	+
TUB-CG 45	Montenegro	+
TUB-CG 46	Montenegro	+
TUB-CG 47	Montenegro	+
TUB-CG 48	Montenegro	+
TUB-CG 49	Montenegro	+
TUB-CG 5	Montenegro	+
TUB-CG 50	Montenegro	+
TUB-CG 51	Montenegro	+
TUB-CG 52	Montenegro	+
TUB-CG 53	Montenegro	+
TUB-CG 54	Montenegro	+
TUB-CG 55	Montenegro	+
TUB-CG 56	Montenegro	+
TUB-CG 57	Montenegro	+
TUB-CG 58	Montenegro	+
TUB-CG 59	Montenegro	+
TUB-CG 6	Montenegro	+
TUB-CG 60	Montenegro	–
TUB-CG 61	Montenegro	+
TUB-CG 62	Montenegro	+
TUB-CG 63	Montenegro	+
TUB-CG 64	Montenegro	–
TUB-CG 65	Montenegro	+
TUB-CG 66	Montenegro	+
TUB-CG 67	Montenegro	+
TUB-CG 68	Montenegro	–
TUB-CG 69	Montenegro	+
TUB-CG 7	Montenegro	+
TUB-CG 71	Montenegro	–
TUB-CG 72	Montenegro	–
TUB-CG 73	Montenegro	–
TUB-CG 74	Montenegro	–
TUB-CG 75	Montenegro	–
TUB-CG 76	Montenegro	–
TUB-CG 77	Montenegro	–
TUB-CG 78	Montenegro	–
TUB-CG 79	Montenegro	–
TUB-CG 8	Montenegro	+
TUB-CG 80	Montenegro	–
TUB-CG 81	Montenegro	–
TUB-CG 9	Montenegro	+
TUB 2189	U.S.	+
TUB 15	U.S.	+

TABLE 8.8 (CONTINUED)
The 155 Wild-Collected *H. tuberosus* Clones Maintained in the Collection of the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro, in 2006

Accession	Origin	Availability
TUB 16	U.S.	+
TUB 20	U.S.	+
TUB 26	U.S.	+
TUB 6	U.S.	+
TUB 7	U.S.	+
TUB 8	U.S.	+
TUB 1765	U.S.	–
TUB 1765	U.S.	–
TUB 1774	U.S.	–
TUB 1775	U.S.	–
TUB 1783	U.S.	–
TUB 1786	U.S.	–
TUB 1789	U.S.	–
TUB 1797	U.S.	–
TUB 1798	U.S.	–
TUB 1799	U.S.	–
TUB 825	U.S.	–

Source: Atlagic, J., Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro, personal communication. (For further details on individual accessions, see Section 8.14.2.)

8.13.11 Asia and Australasia

Wild-collected material in these regions is likely to be derived from cultivated material that has established in natural habitats. Eleven specimens of *H. tuberosus* have been deposited in the Herbarium of the Museum of Nature and Human Activities, Hyogo Prefecture, Japan, all collected in Honshu, Japan, between 1966 and 1998 (GBIF, 2006). Landcare Research, New Zealand, has eight recorded specimens of Jerusalem artichoke (between 1978 and 1996), collected from around the country, but mainly on the North Island (GBIF, 2006). The Australian National Herbarium has one wild-collected specimen, collected in 1963 from the east base of Black Mountain, Canberra; this plant was described as 2 m tall, with light green leaves and flowering (GBIF, 2006).

H. tuberosus is maintained in scattered collections across Asia and Australasia. The Australian Tropical Crops and Forages Genetics Resources Centre, Biloela, Queensland, maintains one wild/weedy accession, originating from the U.S. (IPGRI, 2006).

The Central Agricultural Research Institute (Gannoruwa, Peredeniya, Sri Lanka) has previously been recorded as holding one Jerusalem artichoke accession (Lawrence et al., 1986).

8.14 CULTIVARS AND CLONES

8.14.1 Synonyms, Duplication, and Confusion in Collections

Collections of Jerusalem artichoke cultivars and clones have tended to be scattered and poorly coordinated, resulting in duplication and naming confusions. The following section takes the form of a directory of cultivars, clones, and wild-collected material, giving information (where available)

on the country of origin, notes on plant and tuber appearance, earliness or lateness of maturity/flowering, and availability to researchers and plant breeders. Selected references are also given for sources containing data on yield, physiological parameters, or descriptions of appearance. Synonyms are noted in the listing, although further unrecognized duplication may occur with material appearing under different names.

It is important to be able to distinguish between individual clones as a cultivar spreads geographically. However, Jerusalem artichoke names (e.g., 'Mammoth French White,' 'French White Improved,' 'Blanc Commun') may not represent specific or well-defined cultivars or clones, but instead refer to general types. Cultivar names are also often translated into the language used in a new production location, subsequently to return to its original area with the new name, while mistranslation can occur between languages. This results in the duplication of material within germplasm collections under different names. For example, Schittenhelm (1990) found that the approximately 400 accessions in the German national collection, then at Braunschweig, could be reduced using electrophoresis and cluster analysis to 35 different genotypes. Conversely, some material held in collections having the same name may be different genetically, as found by Kays and Kultur (2005), who observed different flowering dates for the same cultivars obtained from different collections. Cultivar names are mixed up for a variety of other reasons, including loss of labels and mislabeling, and renaming for commercial purposes (a unique name being desirable for marketing purposes).

Although the following section has numerous entries, most of these are for research clones, obscure cultivars and landraces, or material collected from small wild populations, none of which are widely cultivated. A handful of cultivars or cultivar types may account for much of the production in any particular region. Heiser (1995) has gone as far as to suggest that all the Jerusalem artichokes commercially cultivated in the U.S. might have been derived from a single clone. The cultivar listing, however, gives an indication of the potential genetic diversity for Jerusalem artichokes held in germplasm collections. Unfortunately, there is not currently a single germplasm collection that can be used for reference purposes and preservation. Therefore, there is a pressing need to correctly identify clones, eliminate cultivar synonyms, and classify cultivars into genetically identical or similar groupings. This will enable plant breeders to more effectively create new clones without wasting time and resources crossing identical or closely related material. The genetic variability within *H. tuberosus* can then be more fully exploited.

A recent tool for marker-assisted backcross breeding involves the analysis of amplified fragment length polymorphisms (AFLPs) on a plant's chromosomes (Vos et al., 1995). AFLPs are molecular markers, obtained by selective polymerase chain reaction (PCR) amplification, of restricted DNA fragments. The AFLP® technique (AFLP is a registered trademark of Keygene N.V., Wageningen, The Netherlands) utilizes specialist image analysis software to compare the unique "genetic fingerprint" obtained from each cultivar and clone. The fingerprint takes the form of bands in a high-resolution gel image. Quantification of the relatedness of cultivars and clones can then inform crossing decisions. Research has shown that the majority of amplified restriction fragments obtained correspond to unique loci in the genome. Therefore, in conjunction with existing random amplified polymorphic DNA (RAPD) data, AFLP fingerprint analysis is enabling detailed linkage maps to be constructed for crop species, including sunflower (Langer et al., 2003; Peleman, 1999). The extension of this technique to Jerusalem artichoke would clarify the extent of genetic diversity and the genetic relationships of accessions held in germplasm collections.

Genetic techniques, including RAPD and AFLP, enable evolutionary relationships to be ascertained. A number of studies have constructed genetic maps and dendrograms for *Helianthus* species, which have become an important model species grouping for the study of the genetics of adaptation and speciation. For instance, Lai et al. (2005) used a quantitative trait locus (QTL) analysis to investigate the emergence of sterility barriers among *H. anomalus*, *H. deserticola*, and *H. paradoxus*, and compared the linkage maps of these three hybrid sunflower species with those of the parental species *H. annuus* and *H. petiolaris*. They found massive divergence from the parental species in

karyotype, with gene order differences in most of the linkage groups studied. Burke et al. (2004) compared linkage maps of *H. petiolaris* and *H. annuus* to investigate their evolutionary divergence, revealing that since these two annual sunflower species diverged, around 750,000 to 1,000,000 years ago, a high rate of 5.5 to 7.3 chromosomal rearrangements per million years of evolution had occurred — one of the highest rates reported for any taxonomic group. Quagliaro et al. (2001) analyzed the genetic diversity within and between populations of *H. argophyllus* and *H. argophyllus* × *H. annuus* hybrids, while Liu and Burke (2006) analyzed nucleotide polymorphisms in wild and cultivated sunflowers and concluded that sunflower is a product of a single domestication. Genetic studies (e.g., RAPD) can also help identify the most promising wild-collected *Helianthus* material for crossing with cultivated Jerusalem artichoke, and help select promising *Helianthus* hybrids generated in breeding programs (e.g., Encheva et al., 2004).

8.14.2 Directory of Cultivars, Clones, and Wild-Collected Material, with Synonyms, and Notes on Origin, Characteristics, Availability in Collections, and References to Relevant Studies, with Selected Yield Data (as Fresh Weight unless Specified as Dry Matter, DM)

A-A — *See* NC10-2.

A-3-6 — *See* NC10-48.

Abeillo — French origin. Red tubers. Late maturing. Ben Chekroun et al., 1996.

Abo — Unknown origin. Zubr, 1988a (tubers, 7.2 t/ha).

Albik — Polish origin. Cieslik et al., 2003; Sawicka and Michaek, 2005.

Ames 3244 — U.S. origin. Maintained (accession Ames 3244) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

Ames 3245 — U.S. origin. Maintained (accession Ames 3245) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

Ames 22745 — U.S. origin. Collected in North Dakota in 1995. Available (accession Ames 22745) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

Ames 22746 — U.S. origin. Collected in North Dakota in 1995. Available (accession Ames 22746) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

Ames 26006 — U.S. origin. Collected in Missouri in 1995. Maintained (accession Ames 26006) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

Antonin — French origin. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001499); limited immediate availability.

Austrian Wild Boar — Austrian origin? Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Auto105.62G.2 — French origin. White tubers, ovoid (oblong) shaped. Early maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001373); limited immediate availability.

Auto105.62G.15 — French origin. White tubers, very irregular shape. Early maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001372); limited immediate availability.

Bárdi — Hungarian origin. Kaŕa et al., 2005.

Bárdi 3 — Hungarian origin. Barta, 1996 (Average mass of large tubers, 216 g; small, 40 g.)

Bart 70 Janez — Russian Federation origin. Pink tubers, spherical or irregular pear shaped. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001467); limited immediate availability.

BBG 1 — German origin. Previously provided (to S.J. Kays) by Dr. B. Honermeier, Lehr- und Versuchsanatalt für Integrierten Pflanzenau e.V., Güterfelde, Germany. Kays and Kultur, 2005.

BBG 2 — German origin. Previously provided (to S.J. Kays) by Dr. B. Honermeier, Lehr- und Versuchsanatalt für Integrierten Pflanzenau e.V., Güterfelde, Germany. Kays and Kultur, 2005.

B.C. #1 — Canadian origin. Early maturing. Maintained (in Native American Collection) by Plant Gene Resources of Canada (PGRC), Saskatoon (NC10-41); acquired in 1976, from Dr. E.D. Putt. Kays and Kultur, 2005 (as NC10-41); Volk and Richards, 2006.

B.C. #2 — *See* Red I.B.C.

Beaula's — Canadian origin. Collected from wild in Quebec, Canada, by Richard Beaula, pre-1988. Available (accession Ames 8381) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Available (listed as Beauln) from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Beaver Valley Purple — U.S. origin. Purple/red tubers. Available from Darrell Merrell, 2208 W. 81st St. S, Tulsa, OK 74132-2623, U.S.

Bela — Former Yugoslavia origin. Early maturing. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 266; formerly Braunschweig 57361). Berenji, 1988; Kays and Kultur, 2005; Pekic and Kišgeci, 1984; Pejin et al., 1993 (tubers, 53 t/ha; tops, 7 t/ha); Schittenhelm, 1988 (mean, 15.6 tubers/plant); Stolzenburg, 2004.

Belaja — *See* Belyi.

Belaja Urozajnaja — *See* Belyi Urozhainyi.

Belhimer — U.S. origin?

Beľoslupké — Russian Federation origin. White, spherical tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001468); limited immediate availability. Kaŕa et al., 2005; Pas'ko, 1973; Votoupal, 1974; Zubr, 1988a (tubers, 4.5 t/ha).

Belyi Kievskii [White Kiev] — Ukrainian origin. Available (as Kievskij Belyj) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 66); donated by VIR (N.I. Vavilov Research Institute of Plant Industry), St. Petersburg, Russian Federation. Davydoviĉ, 1951; Lapshina, 1983; Mishurov et al., 1999; Ustimenko, 1958; Ustimenko et al., 1976; Votoupal, 1974; Zubr, 1988a, 1988b.

Belyi Rannii [White Early] — Russian Federation origin. White tubers. Early maturing. Lapshina, 1983; Mishurov et al., 1999; Vavilov et al., 1975; Votoupal, 1974.

Belyi Ulučšennyi [Improved White] — Russian Federation origin. Davydoviĉ, 1951.

Belyi Urozhainyi [White Productive] — Russian Federation or Latvian origin. Late maturing. Davydoviĉ, 1951; Lapshina, 1981; Marčenko, 1969; Meleškin, 1957; Ustimenko, 1958 (as synonym Belaja Urozajnaja); Ustimenko et al., 1976.

Berno — French origin. Pink or red tubers, irregular surface. Late maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001399); limited immediate availability. Ben Chekroun et al., 1996; Honermeier et al., 1996.

Biala Kulista — Polish origin. Available (also called RA24) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 296; formerly Braunschweig BGRC 57392).

Bianca — *See* Bianka.

Bianca precocé — French origin. Synonym of D19. Ercoli et al., 1992 (tubers, 31.4 t/ha); Gabini, 1988; Gabini and Corronca, 1988.

Bianco precocé — *See* Bianca precocé.

Bianka — German origin. Short stems, with weak branching. White, short-pear- or spherical-shaped tubers. Early maturing. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 243; formerly Braunschweig BGRC 57337). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001464); limited immediate availability. Available from Research Station for Special Crops, Wies 88, Austria (accession WIES-D16). Maintained by Forskningscenter Årslev, Denmark (DKHEL16). Frequently as 'Bianca' in literature. Berenji, 1988; Kaŕa et al., 2005; Kays and Kultur, 2005; Klug-Andersen, 1992 (tubers, 22 to 39 t/ha); Mesken, 1988; Pekic and Kišgeci, 1984; Pejin et al., 1993 (tubers, 52 t/ha; tops, 7 t/ha); Schittenhelm, 1988 (mean, 16.6 tubers/plant); Soja and Dersch, 1993; Soja and Haunold, 1991 (tubers, 5.5 t/ha); Soja et al., 1993; Stolzenburg, 2003 (tubers, 9.1 t/ha); Stolzenburg, 2004; Zubr, 1988a (tubers, 7.2 t/ha).

Bíly Kyjevský — *See* Belyi kievskii.

Bílý Raný — *See* Belyi rannii.

Bílý Výnosný — Russian Federation origin. Votoupal, 1974.

Bistr — Danish origin. Available from Nordic Gene Bank (accession DKHEL 8), a landrace; donated by (and named after) Birgit Strand, Ornebjerg, DK-4760 Vordingborg, Denmark. Zubr, 1988a (tubers, 7.6 t/ha).

Blanc Ameliore [White Improved] — U.S. origin? Tall spreading plants. White tubers, medium-smooth skins. Boswell et al., 1936; Underkofler et al., 1937 (tubers, 25 t/ha).

Blanc Commun [Common White] — French origin? White tubers. A cultivar type. Kaŕa et al., 2005.

Blanc Commun D-19 [Common White D-19] — French origin. Early maturing. Karolini, 1971.

Blanc précoca — *See* Blanc précoce.

Blanc précoce [Early White] — French origin. Short-stemmed plants (1.5 to 2.0m), with small leaves. White tubers, short pear shaped with irregular surface. Early maturing. Synonymous with D19 breeding/research clone. Barloy, 1988; Barloy and Le Pierres, 1988; De Mastro, 1988 (tubers, 71.6 t/ha, 20.6 t DM/ha); Gabini, 1988; Mesken, 1988; Mimiola, 1988; Pas'ko, 1973, 1974; Varlamova et al., 1996.

Blanc Sutton — *See* Sutton White.

Blanca de Teruel — Spanish origin. Fernandez et al., 1988b.

Blanco — Portuguese origin? Rosa et al., 1992.

Blandette — Unknown origin. Steinrücken and Grunewaldt, 1984.

Boijo — French origin. Early maturing. Ben Chekroun et al., 1996.

Boniches — Spanish or Portuguese origin. Curt et al., 2005; Fernandez et al., 1988a (tubers, 58 t/ha, 13 t DM/ha; tops, 14 t/ha, 11 t DM/ha); Fernandez et al., 1988b; Rosa et al., 1992.

Bonno — French origin. Red tubers. Late maturing. Ben Chekroun et al., 1996.

Bordo — French origin. Red tubers. Late maturing. Ben Chekroun et al., 1996.

Boston — *See* Boston Red.

Boston Red — U.S. origin. Large red tubers, with irregular (knobbly) surface. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Bouchard — U.S. origin? Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.)

Boyard — *See* Boynard.

Boynard — U.S. origin? Medium maturing. Previously provided (to S.J. Kays) by Dr. B. Honermeier, Lehr- und Versuchsanatalt für Integrierten Pflanzenau e.V., Güterfelde, Germany. Kays and Kultur, 2005; Honermeier et al., 1996; Stolzenburg, 2004.

Bragança — Portuguese origin. Rosa et al., 1992.

Bramo — French origin. Red tubers. Late maturing. Ben Chekroun et al., 1996.

Brazilian Red — U.S. origin. Shoemaker, 1927 (cites an 1879 Patent Office Report: "'Red Brazilian' Artichokes from Washington").

Brazilian White — U.S. origin. Kays and Kultur, 2005.

BS-83-6 — German origin. Late maturing. Schittenhelm, 1988 (mean, 40.5 tubers/plant).

BS-83-21 — German origin. Early maturing. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 279; formerly Braunschweig BGRC 57374). Schittenhelm, 1988 (mean, 23.1 tubers/plant).

BS-83-22 — German origin. Early maturing. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 280; formerly Braunschweig BGRC 57375). Schittenhelm, 1988 (mean, 28.1 tubers/plant).

BS-84-19 — German origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 281; formerly Braunschweig BGRC 57376).

BS-85-7 — German origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 282; formerly Braunschweig BGRC 57377).

BS-85-8 — German origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 283; formerly Braunschweig BGRC 57378).

BS-85-11 — German origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 285; formerly Braunschweig BGRC 57380).

BS-85-14 — German origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 286; formerly Braunschweig BGRC 57381).

BS-86-8 — Unknown origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 337; formerly Braunschweig BGRC 61723).

BS-86-12 — Unknown origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 338; formerly Braunschweig BGRC 61724).

BS-86-16 — Unknown origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 339; formerly Braunschweig BGRC 61725).

BS-86-17 — German origin. Stolzenburg, 2003 (12.2 t/ha); Stolzenburg, 2004.

BS-86-19 — Unknown origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 340; formerly Braunschweig BGRC 61726).

BS-87-3 — Unknown origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 341; formerly Braunschweig BGRC 61727).

BS-87-7 — Unknown origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 342; formerly Braunschweig BGRC 61728).

BS-87-9 — Unknown origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 343; formerly Braunschweig BGRC 61729).

BS-87-10 — Unknown origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 344; formerly Braunschweig BGRC 61730).

BT3 — Hungarian origin. Light violet tubers. Late maturing cultivar. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 264; formerly Braunschweig BGRC 57359). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001461); limited immediate availability. Kays and Kultur, 2005; Pejin et al., 1993 (tubers, 57 t/ha; tops, 49 t/ha); Schittenhelm, 1988 (mean, 13.5 tubers/plant); Stolzenburg, 2004.

BT4 — Hungarian origin. White tubers, round or short pear shaped. Improved cultivar. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 265; formerly Braunschweig BGRC 57360). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001462); limited immediate availability. Kays and Kultur, 2005; Kaŕa et al., 2005; Pejin et al., 1993 (tubers, 63 t/ha; tops, 62 t/ha).

Bujo — French origin. White tubers. Late maturing. Ben Chekroun et al., 1996.

Büki 20 — Hungarian origin. Barta, 1996 (average mass of large tubers, 97 g; small, 48 g).

BVAL-901 — Austrian origin. Collected from wild in 2003. Available as seed from the Federal Office of Agrobiology Seed Collection, BVAL, Linz, Austria (no accession name, accession BVAL-901).

C-13 — French origin? Late maturing. Synonymous with D19.63.340. Barloy and Le Pierres, 1988 (tubers, 14 t DM/ha); De Mastro, 1988 (tubers, 72 t/ha, 14 t DM/ha); Fernandez

et al., 1988a (tubers, 70 t/ha, 15 t DM/ha; tops, 14 t/ha, 10 t DM/ha); Fernandez et al., 1988b; Gabini, 1988 (tubers, 50 t/ha); Gabini and Corronca, 1988.

C-34 — German origin? White tubers. Late maturing. Synonymous with/part of Waldspindel cultivar grouping. Barloy and Le Pierres, 1988 (tubers, 16.3 t DM/ha); De Mastro, 1988 (tubers, 67.5 t/ha, 13.4 t DM/ha); Gabini, 1988 (tubers, 44 t/ha).

C-76 — Unknown origin. Barloy and Le Pierres, 1988 (tubers, 14 to 16 t DM/ha); Kaŕa et al., 2005. In Fernandez et al. (1988a, 1988b) C-76 and Sepanetz-10 are synonymous; C76 and Sepanetz are synonymous in De Mastro (1988).

C-89 — *See* Rijskii.

C-122 — French origin. White tubers. Late maturing. Ben Chekroun et al., 1996.

C-146 — German origin. Late maturing. Synonymous with K-8. De Mastro, 1988 (tubers, 79.9 t/ha, 17.2 t DM/ha); Fernandez et al., 1988b; Gabini, 1988 (tubers, 72 t/ha); Gabini and Corronca, 1988.

C2071-63 — French origin. Available from Nordic Gene Bank (accession DKHEL 13), a breeding/research clone; donated by INRA–Rennes.

Cabo Hoog — Dutch origin. Mesken, 1988.

Cambridge sunroot — Unknown origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada; acquired 2004.

Campillo de Paravientos — Spanish origin. Fernandez et al., 1988b.

Castel Giubileo — Unknown origin. Ercoli et al., 1992 (tubers, 63 t/ha).

Castro — Unknown origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Ceglédi — Hungarian origin. Kaŕa et al., 2005; Pátkai and Barta, 2002.

Cervene — Unknown origin. Zubr, 1988a (tubers, 3.8 t/ha).

CF.11 — French origin. White tubers, spherical (short pear) shaped and indented (irregular). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001374); limited immediate availability.

Challenger — Canadian origin. Selected at the Agriculture Canada Research Station, Morden, Manitoba. White tubers, somewhat pear shaped. Medium to late maturing. Relatively tall plants. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-39); not 2006 listing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001490); limited immediate availability. Available from Mapple Farm, 129 Beech Hill Rd., Weldon, New Brunswick E4H 4N5, Canada. Hay and Offer, 1992; Kays and Kultur, 2005; Kiehn and Chubey, 1993 (tubers, 37 to 67 t/ha); Kiehn and Chubey, 1985 (tubers, 32 to 51 t/ha); Laberge and Sackston, 1987; Modler et al., 1993.

Changins — Unknown origin. Kaŕa et al., 2005.

Chicago — U.S. origin. Medium to tall plants, with light brown or white oval tubers. Early maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001488); limited immediate availability. Boswell et al., 1936; Underkofler et al., 1937 (tubers, 25 t/ha).

China — Unknown origin. Late maturing. Curt et al., 2005.

Ciudad Rodrigo — Spanish origin. Fernandez et al., 1988b; Rosa et al., 1992.

CL2 — French origin. White, elongated tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001375); limited immediate availability.

Clearwater — U.S. origin. Slight brownish, rough-skinned tubers, quite large and long with very little knobbing or branching. Tubers reportedly keep well. Collected in Industry, Maine, in 1988. A local variety/landrace. Available from Will Bonsall (Scatterseed

Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Available (accession Ames 8390) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Kays and Kultur, 2005.

Clone ACP 1981 — French origin. Violet, pear-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001400); limited immediate availability.

Clone Duval 1980.1 — French origin. Violet, spherical (short-pear) tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001401); limited immediate availability.

Clone Duval 1980.2 — French origin. White, spherical (short-pear) tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001402); limited immediate availability.

Clone Porcheron 1980 — French origin. White, spherical (short-pear) tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001403); limited immediate availability.

CN19152 — Canadian origin. Wild-collected material. Maintained and available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada.

CN31462 — Canadian origin. Wild-collected material. Maintained and available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada.

CN31463 — Canadian origin. Wild-collected material from Manitoba, Canada. Received as seed from W. Dedio, Morden Research Station, in 1978. Maintained and available (PGR2642) from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada.

CN31464 — Canadian origin. Wild-collected material from Manitoba, Canada. Maintained and available (PGR2643) from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada.

CN31634 — Romanian origin. Wild-collected material from Romania. Donated by N. Balcescu, Jardin Botanique de l'Institut Agronomique in 1978. Maintained and available (PGR2892) from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada.

CN52867 — Russian Federation origin. White tubers. Wild-collected material (var. *alba*) from Russia. Donated by Vavilov Institute of Plant Industry, Leningrad, Russian Federation, in 1977. Likely parent of wild population is cultivar Vengerskij (Vengerskii). Maintained and available (PGR2367) from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada.

CN52868 — Russian Federation origin. Purple tubers. Wild-collected material (var. *purpurellus*) from Russia. Donated by Vavilov Institute of Plant Industry, Leningrad, Russian Federation, in 1977. Likely parent of wild population is cultivar Goro-Altajskij. Maintained and available (PGR2368) from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada.

Colby Miller — U.S. origin. Tubers with yellowish skin, some rose eyes. Collected in Wilton, Maine, pre-1988. Available (accession Ames 8382) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Kays and Kultur, 2005.

Columbia — Canadian origin. Selected at the Agriculture Canada Research Station, Morden, Manitoba (Chubey and Dorrell, 1982). Highly branched, bushy appearance. White to tan tubers (white flesh); large, elongated with irregular surface. Early or medium maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-69). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001491); limited immediate availability. Material of Danish provenance in Nordic Gene Bank

(accession DKHEL 12), a landrace; donated by Danisco Seed, Højbygaardvej 31, DK-4960 Holeby, Denmark (contact: Steen Bisgaard). Cassells and Deadman, 1993; Cassells and Walsh, 1995; Chubey and Dorrell, 1982 (tubers, 40 to 60 t/ha); Cosgrove et al., 2000 (tubers, 22,398 lb/acre); Frappier et al., 1990 (tubers, 41.4 t/ha); Hay and Offer, 1992; Honermeier et al., 1996; Kaŕa et al., 2005; Kays and Kultur, 2005; Kiehn and Chubey, 1993 (tubers, 45 to 77 t/ha); Laberge and Sackston, 1987; Meijer et al., 1993; Modler et al., 1993; Seiler, 1993; Spitters et al., 1988 (tubers, 46 t/ha); Stauffer et al., 1981; Stolzenburg, 2004; Zubr and Pedersen, 1993 (tubers, 11.4 t DM/ha).

Comber — Canadian origin (Manitoba). Red tubers. Medium or late maturing. Relatively tall plants. Available from Plant Gene Resources of Canada (PGRC), Saskatoon (NC10-40); acquired in 1974, from Dr. C. Walkof. Kays and Kultur, 2005 (as NC10-40); Kiehn and Chubey, 1993 (tubers, 14 to 39 t/ha); Volk and Richards, 2006.

Comiikus iaresviacus — Russian Federation origin. Late maturing. Varlamova et al., 1996.

Commun Blanc — *See* Blanc Commun. Gagnon, 2005.

Commun Rouge — *See* Rouge Commun.

Cowell's Red — U.S. origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

CParvie — Unknown origin. Rosa et al., 1992.

CR Special — Argentinean origin. Donated in 1981 by N.D. Vietmeyer, Commission on International Relations, NAS, Washington, DC, U.S. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Pending inactivation in 2006 (accession PI 461518) at USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Kays and Kultur, 2005.

Croix Leonardoux — French origin. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001498); limited immediate availability.

Cross Bloomless — U.S. origin? Late maturing. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

D5 — French origin. White tubers, spherical (short pear) shaped. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001386); limited immediate availability.

D8 — French origin. Cream (white-yellow) tubers, spherical (short pear) shaped. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001387); limited immediate availability.

D9 [D-9] — French origin.

D13 — French origin. Light violet tubers, ovoid (oblong) shaped. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001376); limited immediate availability.

D16 — French origin. Light violet tubers, ovoid (oblong) and rather smooth (regular). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001377); limited immediate availability. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-120); acquired in 1984 from F. Le Cochec.

D18 — French origin. White, elongated tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001378); limited immediate availability.

D19 [D-19] — French origin. White tubers, clumped. Low plants, with skinny, abundantly branched (bushy) tops. Early maturing. Synonymous with Blanc précoce (e.g., De Mastro,

1988). *See also* Blanc Commun D-19 (Karolini, 1971). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001379); limited immediate availability. Available from Nordic Gene Bank (accession DKHEL 11), a breeding/research clone; donated by INRA–Rennes. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-106); acquired in 1984. Allirand et al., 1988; Barloy and Le Pierres, 1988 (tubers, 12 to 17 t DM/ha); Cassells and Deadman, 1993; De Mastro, 1988 (tubers, 72 t/ha, 15 t DM/ha); Fernandez et al., 1988a (tubers, 66 t/ha, 13 t DM/ha; tops, 6 t/ha, 5 t DM/ha); Gabini, 1988 (tubers, 83 t/ha); Gendraud, 1975; Hay and Offer, 1992; Honermeier et al., 1996; Kays and Kultur, 2005; Klug-Andersen, 1992 (tubers, 41 to 53 t/ha); Lee et al., 1985; Zubr and Pedersen, 1993 (tubers, 12 t DM/ha).

D19.6 — French origin. White tubers, ovoid and indented (irregular). Early maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001380); limited immediate availability.

D19.63.122 [D19-63-122] — French origin. White tubers, ovoid and somewhat indented (irregular). Semiearly maturing. Relatively tall plants. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001381); limited immediate availability. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 271; formerly Braunschweig BGRC 57366). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-112); acquired in 1984 (contact: Larry Tieszen). Cassells and Deadman, 1993; Kays and Kultur, 2005.

D19.63.340 [D19-63-340] — French origin. White tubers, ovoid and indented (irregular). Semiearly maturing. Synonymous with C-13. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001382); limited immediate availability. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 272; formerly Braunschweig BGRC 57367). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-121); acquired in 1984, from F. Le Cochec. De Mastro, 1988 (*see* C13); Kays and Kultur, 2005.

D.29 — French origin. Cream (white-yellow) tubers, spherical (short pear) shaped. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001383); limited immediate availability.

D31 — French origin. White tubers, pear shaped and irregular surfaced. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001384); limited immediate availability.

D.42 — French origin. White tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001385); limited immediate availability.

D-2120 — French origin? Mesken, 1988.

Dagnitral — Unknown origin. Early maturing. Varlamova et al., 1996.

Danforth — U.S. origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.)

Dave's Shrine — U.S. origin. Fat tubers (8 to 12 cm long) with bronzy purple skins and ivory-colored internal flesh. High dry matter content gives the tubers a saltier and meatier taste than other Jerusalem artichokes (Watson, 1996). Collected by Dave Briars of Craftsbury, VT, U.S. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME

04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005; Watson, 1996.

Deutsche Waldspindel — German origin. Part of the Waldspindel cultivar grouping (*see* Waldspindel). Previously provided (to S.J. Kays) by Dr. B. Honermeier, Lehr- und Versuchsanatalt für Integrierten Pflanzenau e.V., Güterfelde, Germany. Kays and Kultur, 2005.

DHM-3 — Canadian origin (Manitoba). Early maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-25); acquired in 1970 (contact: H.H. Marshall). Kays and Kultur, 2005 (as NC10-25).

DHM-4 — Canadian origin (Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-26); acquired in 1970 (contact: H.H. Marshall). Kays and Kultur, 2005 (as NC10-26).

DHM-5 — Canadian origin (Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-27); acquired in 1970 (contact: H.H. Marshall).

DHM-6 — Canadian origin (Manitoba). Early maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-28); acquired in 1970 (contact: H.H. Marshall). Kays and Kultur, 2005 (as NC10-28).

DHM-7 — Canadian origin (Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-29); acquired in 1970 (contact: H.H. Marshall). Kays and Kultur, 2005 (as NC10-29).

DHM-13 — Canadian origin (Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-30); acquired in 1970 (contact: H.H. Marshall).

DHM-14 — Canadian origin. White tubers. Early maturing. Short- to medium-height plants. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-31). Kiehn and Chubey, 1993 (tubers, 9 to 24 t/ha).

DHM-14-3 — Canadian origin. White tubers. Early maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-52); acquired in 1976 (contact: H.H. Marshall). Kays and Kultur, 2005 (as NC10-52); Kiehn and Chubey, 1993 (as DHM-143; tubers, 12 to 22 t/ha).

DHM-14-6 — Canadian origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-53); acquired in 1976 (contact: H.H. Marshall).

DHM-15 — Canadian origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-54); acquired in 1976 (contact: H.H. Marshall).

DHM-16 — Canadian origin (Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-32); acquired in 1970 (contact: H.H. Marshall). Kays and Kultur, 2005 (as NC10-32).

DHM-18 — Canadian origin (Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-33); acquired in 1970 (contact: H.H. Marshall).

DHM-19 — Canadian origin (Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-34); acquired in 1970 (contact: H.H. Marshall). Kays and Kultur, 2005 (as NC10-34).

DHM-21 — Canadian origin. White tubers. Early maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-35). Kays and Kultur, 2005 (as NC10-35); Kiehn and Chubey, 1993 (tubers, 10 to 27 t/ha).

DHM-22 — Canadian origin (Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-36); acquired in 1970 (contact: H.H. Marshall).

Dietichesky [Dieticheskii] — Russian Federation or Ukrainian origin. Late maturing. Bogomolov and Petrakova, 2001; Varlamova et al., 1996.

DL12 — French origin. Pink tubers, spherical (short pear) shaped. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001388); limited immediate availability.

Dornaiskii — Russian Federation origin. Pink or brown tubers, spherical or pear shaped, with variable indentation. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001469); limited immediate availability.

Dornburg — *See* Dornburger.

Dornburger — German origin. White tubers, round (short-pear)-shaped tubers, somewhat irregular surface. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001453); limited immediate availability. Galan and Filipescu, 1958; Galan, 1960; Löhrke, 1956; Mesken, 1988; Stolzenburg, 2003 (8.3 t/ha); Stolzenburg, 2004.

Draga — Unknown origin. Tall plants, slightly branching. White tubers. Maintained by Forskningscenter Årslev, Denmark (DKHEL17). Kays and Kultur, 2005; Klug-Andersen, 1992 (tubers, 25 to 47 t/ha).

Drillo — French origin. Early maturing. Ben Chekroun et al., 1996.

Drown's Long Red — *See* Long Red Drowns.

Drushba — Unknown origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Dubo — French origin. Red tubers. Medium maturing. Previously provided (to S.J. Kays) by Dr. B. Honermeier, Lehr- und Versuchsanatalt für Integrierten Pflanzenau e.V., Güterfelde, Germany. Ben Chekroun et al., 1996; Honermeier et al., 1996; Stolzenburg, 2004.

Dwarf — Dutch origin. Deep-violet-colored tubers, elongated or spindle shaped. Research clone. Available from Nordic Gene Bank (accession DKHEL 15), a breeding/research clone; donated by SVP-Wirrsum, Wageningen, The Netherlands. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 277; formerly Braunschweig BGRC 57372). Maintained (as Wageningse Dwarf) by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001452); limited immediate availability. Kays and Kultur, 2005; Pilnik and Vervelde, 1976 (tubers, 23 to 35 t/ha); Zubr and Pedersen, 1993 (tubers, 6.4 t DM/ha).

Dwarf Sunray — North American origin. Short plants (1.5 to 2 m tall), freely flowering. Tender and crisp tubers that do not need peeling when used as a vegetable. Promoted as an ornamental. Originally commercialized by Thompson and Morgan, marketed as shorter plants with higher tuber productivity. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Facciola, 1990; Hay and Offer, 1992; Kays and Kultur, 2005.

Egmond 1982 — French origin. Violet-colored, spherical (short-pear)-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001405); limited immediate availability.

Eigen Nabouw — Dutch or German origin. Selected to be late maturing. Pilnik and Vervelde, 1976 (tubers, 29 t/ha).

Elligay — *See* Ellijay.

Ellijay — Diverse origin. White spherical tubers. Late maturing. Maintained (U.S. origin) by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001489); limited immediate availability. Available (Russian Federation origin) from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-118); acquired in 1976 (contact: Larry Tieszen). Ben Chekroun et al., 1996 (French INRA origin); Mesken, 1988.

Faucho — French origin. Early maturing. Ben Chekroun et al., 1996.

Fiano — French origin. Red tubers. Late maturing. Ben Chekroun et al., 1996.

Filio — French origin. White, spherical (short-pear)-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001406); limited immediate availability.

Firehouse — U.S. origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Flam — Danish origin. White tubers. Tall plants, weakly branching. Late maturing. Plants rarely or never flower in Denmark, with moderate/average tuber yields. Available from Nordic Gene Bank (accession DKHEL 6), a breeding/research clone; donated by KVL, the Royal Veterinary and Agricultural University, Denmark. Henriksen and Bjørn, 2003 (tubers, 8.6 t/ha); Kays and Kultur, 2005; Klug-Andersen, 1992 (tubers, 31 to 34 t/ha); Zubr, 1988a (tubers, 7.5 t/ha).

FL 83 FC — French origin. White, spherical- or short-pear-shaped tubers. Descended from FL. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001441); limited immediate availability.

FL 83 NK — French origin. White, spherical- or short-pear-shaped tubers. From NL and Nahodka. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001442); limited immediate availability.

FL 84 EL1 — French origin. White, ovoid- or oblong-shaped tubers. From FL and Ellijay. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001443); limited immediate availability.

FL 84 EL2 — French origin. White, round- or pear-shaped tubers. From FL and Ellijay. Violet pear-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001444); limited immediate availability.

FL 85 JT1 — French origin. White, spherical- or pear-shaped tubers. From FL and Janto. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001445); limited immediate availability.

FL 85 JT2 — French origin. White, round- or oblong-shaped tubers. From FL and Janto. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001446); limited immediate availability.

FL 85 K8 — French origin. White, spindle-shaped tubers. From FL and K8. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001447); limited immediate availability.

FL 85 342.62.1 — French origin. Pink, pear-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001448); limited immediate availability.

FL 85 342.62.2 — French origin. White, round- or short-pear-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001449); limited immediate availability.

FL 85 342.62.3 — French origin. Violet pear-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001450); limited immediate availability.

Fonto — French origin. Red tubers. Late maturing. Ben Chekroun et al., 1996.

Freedom — U.S. origin. Collected pre-1988 in Maine. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Available (accession Ames 8378) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Kays and Kultur, 2005.

French Mammoth Hybrid — French origin. General type. Available from Blüm Seed Company, Idaho, U.S.

French Mammoth White — U.S. origin. Possible synonym of Mammoth French White, and may sometimes be used to refer to a general type rather than a cultivar. Maintained by Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-81); acquired in 1981 (Washington State), from Mohawk Oil. Available from Gene Forster, 217 IL Highway 1, Norris City, IL 62869, U.S. Gagnon, 2005; Kays and Kultur, 2005 (as NC10-81).

French White Improved — French origin. A general type rather than a cultivar.

Fuseau — French origin, although now a cultivar grouping of diverse origin rather than a distinct cultivar. Compact vegetative growth. Tubers cream-yellow, with sometimes purple tinge, and rather large and elongated (e.g., 10 to 12 cm long and up to 4 cm wide); smooth (knob-free) and often tapering, crescent or spindle shaped. Medium to late maturing. Available for many years from Vilmorin-Andrieux (Paris). Available (material of U.S. provenance; accession Ames 8384) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Also available from Organic Seed catalog (U.K.), www.organiccatalogue.com; CV Seeds Blüm, Boise, ID; and many other seed companies. Fuseau has been grown in many field studies, including Shoemaker, 1927; Facciola, 1990; Kays and Kultur, 2005; Klug-Andersen, 1992 (tubers, 16 to 23 t/ha); Rosa et al., 1992; Soja and Dersch, 1993; Soja and Haunold, 1991 (tubers, 8 t/ha); Soja et al., 1993.

Fuseau Red — French origin? Red (maroon) tubers, elongated, straight and smooth (knob-free). Early maturing. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Available from Garden City Seeds, Victor, MT, U.S.

Fuseau 60 — French origin. Cream-colored, spindle-shaped tubers, with netted surface (storage reduces tuber-to-tuber contact and therefore rot). Late maturing. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 259; formerly Braunschweig BGRC 57353). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001407); limited immediate availability. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-96); acquired in 1983, by B.B. Chubey. Fuseau 60 has been grown as part of many field studies, including Ben Chekroun et al., 1996; Cassells and Deadman, 1993; Ercoli et al., 1992 (tubers, 50.6 t/ha); Fernandez et al., 1988b; Hay and Offer, 1992; Hergert, 1991; Kays and Kultur, 2005; Kaŕa et al., 2005; Le Cochec and de Barreda, 1990; Lee et al., 1985 (tubers, 31.5 t/ha; tops, 16.3 t DM/ha); Stolzenburg, 2003 (8.9 t/ha); Stolzenburg, 2004.

Fuseau Vilmorin — French origin. Tsvetorukhine, 1960.

Fusil — Unknown origin. Modler et al., 1993.

G71.39 — Russian Federation origin. White-pink, spherical tubers, with slightly indented surface. Medium to late maturity. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001470); limited immediate availability. Available (as G-71-39) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 55); donated by VIR (N.I. Vavilov Research Institute of Plant Industry), St. Petersburg, Russian Federation.

G 120 — Russian Federation origin. Good tuber productivity in Grondo province, Russia. Kovalenko, 1969.

Garnet — U.S. origin. Dark red (ruby), sometimes pink, tubers with smooth surface and few knobs. Quite round shape, except when stem is elongated. Off-white internal flesh. Branching common under some conditions. Has been selected for a smooth tuber surface. Collected in Ohio, from population of 100 plants in roadside ditch, pre-1988. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Available (accession Ames 8379) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Available from CV Seeds Blüm, Boise, Idaho, U.S. Kays and Kultur, 2005; Watson, 1996.

Gatersleben — German origin. In literature, for an accession obtained from IPK, Gatersleben, Germany.

Gerrard — U.K. origin? Available from Edwin Tucker & Sons Ltd., Brewery Meadow, Stonepark, Ashburton, Devon TQ13 7DG, U.K.

Gibrid — *See* Gibrid 103.

Gibrid 103 — Russian Federation origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 63); donated by VIR (N.I. Vavilov Research Institute of Plant Industry), St. Petersburg, Russian Federation. Kays and Kultur, 2005 (as HEL 63 'Gibrid').

Gigant [Giant] — Unknown origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 287; formerly Braunschweig BGRC 57382). Praznik et al., 2002; Schittenhelm, 1999; Stolzenburg, 2003 (tubers, 7 t/ha); Stolzenburg, 2004.

Gigant 549 [Giant 549] — Russian Federation origin. Pas'ko, 1976, 1977.

Gold Nugget — U.S. origin. Tapering, carrot-like or spindle-shaped tubers. Collected in Maine, pre-1988. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Pending inactivation in 2006 (accession Ames 8377) at USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Available (as Golden Nugget) from Blüm Seed Company, ID, U.S. Kays and Kultur, 2005.

Golden Nugget — *See* Gold Nugget.

Gorno-Altaisk — Unknown origin. Pas'ko, 1974.

Gorno-Altajskij — *See* Gorno-Altaisk.

Grando — French origin. Early maturing. Ben Chekroun et al., 1996.

Grem Red — Unknown origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Grem White — Unknown origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Gross Beeren — German origin. Previously provided (to S.J. Kays) by Dr. B. Honermeier, Lehr- und Versuchsanatalt für Integrierten Pflanzenau e.V., Güterfelde, Germany. Kays and Kultur, 2005.

Gua — Guadeloupe origin. Probably synonymous with GUA 7. Mesken, 1988.

GUA 7 [Gua] — Guadeloupe origin. White spherical tubers. Early maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001492); limited immediate availability. Barloy and Le Pierres, 1988 (tubers, 16 t DM/ha); De Mastro, 1988 (tubers, 41 t/ha, 10 t DM/ha); Fernandez et al., 1988b.

Gurahont — Romanian origin. Available from the University of Agricultural Science (UAS), Timisoara, Romania (accession ROM023-6150); collected in Arad, Garahont, Romania, in 1989.

Gurney's Red — U.S. origin? Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Gute Gelbe — German origin. Late maturing. Available from Research Station for Special Crops, Wies 88, Austria (accession WIES-D18). Honermeier et al., 1996; Kays and Kultur, 2005; Stolzenburg, 2003 (tubers, 10 t/ha); Stolzenburg, 2004.

Gyöngyvér — Hungarian origin. Barta, 1996 (average mass of large tubers, 218 g; small, 44 g).

H54.1 — French origin. White, elongated tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001389); limited immediate availability.

HEL 51 — Unknown origin. Available (no accession name) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 51); donated by Dr. Crotogino, Löderburg b. Stassfurt.

HEL 53 — German origin. Available (no accession name) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 53); collected on expedition DDR 1975. Kays and Kultur, 2005.

HEL 54 — German origin. Available (no accession name) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 54); collected on expedition DDR 1975 (in Eisenberg, Thüringen).

HEL 55 — German origin. Available (no accession name) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 55); collected on expedition DDR 1975 (in Eisenberg, Thüringen).

HEL 56 — German origin. Available (no accession name) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 56); collected on expedition DDR 1975 (in Dresden).

HEL 57 — German origin. Available (no accession name) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 57); collected on expedition DDR 1975 (in Hedersleben).

HEL 58 — German origin. Available (no accession name) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics

and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 58); collected on expedition DDR 1975.

HEL 63 — *See* Gibrid.

HEL 64 — Unknown origin. Available (no accession name) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 64); donated by VIR (N.I. Vavilov Research Institute of Plant Industry), St. Petersburg, Russian Federation.

HEL 68 — Unknown origin. Available (no accession name) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 68). Kays and Kultur, 2005.

HEL 69 — Unknown origin. Late maturing. Available (no accession name) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 69). Honermeier et al., 1996; Kays and Kultur, 2005.

HEL 231 — German origin. Available (no accession name) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 231); donated by Dr. J. Keller, IPK Gatersleben.

HEL 245 — Unknown origin. Available (under 'Topinambur' for accession name) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 245; formerly Braunschweig BGRC 57339).

HEL 246 — Unknown origin. Available (under 'Topinambur' for accession name) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 246; formerly Braunschweig BGRC 57340).

HEL 249 — Unknown origin. Available (under 'Topinambur' for accession name) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 249; formerly Braunschweig BGRC 57343).

HEL 252 — German origin. Available (under 'Topinambur' for accession name) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 252; formerly Braunschweig BGRC 57346).

HEL 253 — Unknown origin. Available (under generic 'Topinambur' for accession name) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 253; formerly Braunschweig BGRC 57347).

HEL 254 — As HEL 253 (formerly Braunschweig BGRC 57348).

HEL 255 — As HEL 253 (formerly Braunschweig BGRC 57349).

HEL 256 — As HEL 253 (formerly Braunschweig BGRC 57350).

HEL 257 — As HEL 253 (formerly Braunschweig BGRC 57351).

HEL 258 — As HEL 253 (formerly Braunschweig BGRC 57352).

HEL 297 — As HEL 253 (formerly Braunschweig BGRC 57393).

HEL 298 — As HEL 253 (formerly Braunschweig BGRC 57394).

HEL 299 — As HEL 253 (formerly Braunschweig BGRC 57395).

HEL 306 — As HEL 253 (formerly Braunschweig BGRC 57396).

HEL 307 — As HEL 253 (formerly Braunschweig BGRC 57397).

HEL 308 — As HEL 253 (formerly Braunschweig BGRC 57398).

HEL 309 — As HEL 253 (formerly Braunschweig BGRC 57399).
HEL 310 — As HEL 253 (formerly Braunschweig BGRC 57400).
HEL 311 — As HEL 253 (formerly Braunschweig BGRC 57401).
HEL 312 — As HEL 253 (formerly Braunschweig BGRC 57402).
HEL 313 — As HEL 253 (formerly Braunschweig BGRC 57403).
HEL 314 — As HEL 253 (formerly Braunschweig BGRC 57404).
HEL 315 — As HEL 253 (formerly Braunschweig BGRC 57405).
HEL 316 — As HEL 253 (formerly Braunschweig BGRC 57406).
HEL 317 — As HEL 253 (formerly Braunschweig BGRC 57407).
HEL 318 — As HEL 253 (formerly Braunschweig BGRC 57408).
HEL 319 — As HEL 253 (formerly Braunschweig BGRC 57409).
HEL 320 — As HEL 253 (formerly Braunschweig BGRC 57410).
HEL 321 — As HEL 253 (formerly Braunschweig BGRC 57411).
HEL 322 — As HEL 253 (formerly Braunschweig BGRC 60282).
HEL 323 — As HEL 253 (formerly Braunschweig BGRC 60283).
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HEL 331 — As HEL 253 (formerly Braunschweig BGRC 60291).
HEL 332 — As HEL 253 (formerly Braunschweig BGRC 60292).
HEL 333 — As HEL 253 (formerly Braunschweig BGRC 60293).
HEL 334 — As HEL 253 (formerly Braunschweig BGRC 60294).
HEL 335 — As HEL 253 (formerly Braunschweig BGRC 60295).
HEL 336 — As HEL 253 (formerly Braunschweig BGRC 60296).
Henriette — German origin? Stolzenburg, 2003 (tubers, 6.4 t/ha); Stolzenburg, 2004.
HM-1 — Canadian origin (Morden, Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-182).
HM-2 — Canadian origin (Morden, Manitoba). White tubers. Early or medium maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accessions NC10-15 and NC10-183); originally acquired in 1970 (contact: H.H. Marshall/F.A. Kiehn). Kays and Kultur, 2005 (NC10-15); Kiehn and Chubey, 1993 (tubers, 9 to 31 t/ha).
HM-3 — Canadian origin (Morden, Manitoba). Early maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-16); acquired in 1970 (contact: H.H. Marshall). Kays and Kultur, 2005 (NC10-16); Volk and Richards, 2006.
HM-4 — Canadian origin (Morden, Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-184).
HM-5 — Canadian origin (Morden, Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accessions NC10-17 and NC10-185); originally acquired in 1970 (contact: H.H. Marshall/F.A. Kiehn).
HM-6 — Canadian origin (Morden, Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-186).
HM-7 — Canadian origin (Morden, Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accessions NC10-18 and NC10-187); originally acquired in 1970 (contact: H.H. Marshall/F.A. Kiehn). Kays and Kultur, 2005 (NC10-18); Stauffer et al., 1981 (forage, 7.3 t DM/ha).

HM-8 — Canadian origin (Morden, Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accessions NC10-19 and NC10-188); originally acquired in 1970 (contact: H.H. Marshall/F.A. Kiehn).

HM-9 — Canadian origin (Morden, Manitoba). White tubers. Relatively tall plants. Late maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accessions NC10-20 and NC10-189); originally acquired in 1970 (contact: H.H. Marshall/F.A. Kiehn). Kiehn and Chubey, 1993 (tubers, 24 to 38 t/ha).

HM-10 — Canadian origin (Morden, Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-21).

HM-11 — Canadian origin (Morden, Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accessions NC10-22 and NC10-190); originally acquired in 1970 (contact: H.H. Marshall/F.A. Kiehn). Kays and Kultur, 2005 (NC10-22).

HM-12 — Canadian origin (Morden, Manitoba). White tubers. Early maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-23). Kiehn and Chubey, 1993 (tubers, 6 to 27 t/ha).

HM-13 — Canadian origin (Morden, Manitoba). White tubers. Early or medium maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-24). Kays and Kultur, 2005 (NC10-24); Kiehn and Chubey, 1993 (tubers, 7 to 28 t/ha).

HM-14 to HM-37 (20 accessions in total) — Canadian origin (Morden, Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accessions NC10-192 to NC10-213; see Table 8.3).

HM Hybrid A [HMHYA] — *See* NC10-12.

HM Hybrid A-4 — *See* NC10-49.

HM Hybrid B [HMHYB] — *See* NC10-13.

HM Hybrid C [HMHYC] — *See* NC10-14.

HMR-1 — Canadian origin. Chubey and Dorrell, 1974.

HMR-2 — Canadian origin. Chubey and Dorrell, 1974.

HMR-3 — Canadian origin. Chubey and Dorrell, 1974.

Hradecké Běloslupké [White-skinned Hradec] — Russian Federation origin? Votoupal, 1974.

Huertos — Spanish origin. Schorr-Galindo and Guiraud, 1997.

Huertos de Moya — Spanish origin. Kaŕa et al., 2005.

Huertos de Moya-Blanca — Spanish origin. White tubers. Fernandez et al., 1988a (tubers, 70 t/ha, 14 t DM/ha; tops, 16 t/ha, 13 t DM/ha); Fernandez et al., 1988b.

Huertos de Moya-Rio — Spanish origin. Red tubers. Fernandez et al., 1988b.

Huertos de Moya-Roja — Spanish origin. Red tubers. Fernandez et al., 1988b.

Huertos de Moya-Tobares — Spanish origin. Fernandez et al., 1988b.

Huguette 93 — Moroccan origin. White tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001497); limited immediate availability.

Hybrid 103 — Russian Federation origin. Spherical, slightly indented tubers. Maintained (as Hybride 103) by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001471); limited immediate availability.

Hybrid 120 — Russian Federation origin. Available (accession PI 357297) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.; donated in 1971 by V. Lekhnovitch, VIR (N.I. Vavilov Institute of Plant Industry), Russian Federation. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005; Seiler, 1993; Usanova, 1967; Ustimenko, 1958.

I2.1044.344 — French origin. White tubers, irregular surface. Early maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001390); limited immediate availability.

I3.2017 — French origin. White tubers, spherical (short pear) shaped. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001391); limited immediate availability.

Ibdes — Spanish origin. Fernandez et al., 1988b; Rosa et al., 1992.

IGV — Unknown origin. Previously provided (to S.J. Kays) by Dr. B. Honermeier, Lehr- und Versuchsanatalt für Integrierten Pflanzenau e.V., Güterfelde, Germany.

Improved White — Unknown origin. A general type rather than a cultivar. Probably synonymous with Blanc Ameliore. Sprague et al., 1935 (tubers, 18 to 22 t/ha).

Industrie — Russian Federation origin. White tubers, oblong and fairly smooth. Maintained by Plant Gene Resources of Canada (PGRC), Saskatoon (NC10-114); acquired in 1984. Maintained (clone of French provenance) by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001408); limited immediate availability. Tsvetorukhine, 1960. Volk and Richards, 2006.

Interess [Interes] — Russian Federation origin (Odessa region). White tubers. Medium to late maturing. Moderate resistance to *Sclerotinia sclerotiorum*. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001472); limited immediate availability. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accessions NC10-72 and NC10-107); acquired in 1979 and 1984 (contact: M.D. Stauffer and Larry Tieszen, respectively). Bogomolov and Petrakova, 2001; Kiehn and Chubey, 1993 (tubers, 36 to 53 t/ha); Mikhal'tsova, 1985; Poljanskij et al., 2003; Varlamova et al., 1996 (Odessa, Ukraine; tubers, 17 to 27 g; growth period, 87 days; yields, 39.4 t/ha green matter, 6.4 t/ha dry matter, 5.9 t/ha tubers).

Iranien — Iranian origin. Pink-colored, ovoid- and irregular-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001495); limited immediate availability.

Ivanova Red — Russian Federation origin. Red tubers. Late maturing. Lapshina, 1981.

JA2 — Korean origin. White tubers. Code used by Lee et al., 1985 (tubers, 21.7 t/ha; tops, 13.8 t DM/ha).

JA3 — Korean origin. Violet tubers. Code used by Lee et al., 1985 (tubers, 29.6 t/ha; tops, 11.1 t DM/ha).

JA5 — Japanese origin. White tubers. Code used by Lee et al., 1985 (tubers, 22.1 t/ha; tops, 11.3 t DM/ha).

JA6 — U.S. origin (Kansas). Code used by Lee et al., 1985 (tubers, 15.8 t/ha; tops, 10.8 t DM/ha).

Jack's Copperclad — U.S. origin. Tall plants (over 3 m), with coppery-purple tubers. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada; acquired 2004.

Jack's Copperskin — U.S. origin. Collected in Maine as tubers, by Jack Kertesz of Freedom, ME, pre-1988. Available (accession Ames 8383) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Jack's White — U.S. origin. White tubers. Late maturing. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange

Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Jamcovskij Krashyj — Russian Federation origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC19-74); acquired in 1979 (contact: M.D. Stauffer).

Janno — French origin. Red tubers. Late maturing. Ben Chekroun et al., 1996.

Janto — French origin. Violet tubers. Late maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001409); limited immediate availability. Ben Chekroun et al., 1996.

Jaune de Rouille — French origin. Cream (yellow-white) tubers, pear shaped, semiflattened with irregular surface. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001410); limited immediate availability.

Judy's Red — *See* Dave's Shrine (Watson, 1996).

K105 — Russian Federation origin? Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (accession UE0100768).

K105 (Sort Interes) — Russian Federation origin? Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (accession UE0100769).

K.4 — French origin. Pink tubers, pear shaped. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001392); limited immediate availability.

K.5 — French origin. Deep violet tubers, spherical (short pear) shaped. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001393); limited immediate availability. Mesken, 1988 (as K5).

K 8 [K-8] — German origin. White, short-pear-shaped, irregular-surfaced tubers. Tall plants. Medium to late maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001454); limited immediate availability. Barloy and Le Pierres, 1988 (tubers, 16 to 17 t DM/ha); Ben Chekroun et al., 1996; Cassells and Deadman, 1993; Ercoli et al., 1992 (tubers, 94.6 t/ha); Fernandez et al., 1988a (tubers, 69 t/ha, 15 t DM/ha; tops, 15 t/ha, 12 t DM/ha); Fernandez et al., 1988b; Gabini, 1988; Hay and Offer, 1992; Honermeier et al., 1996; Le Cochec and de Barreda, 1990; Lee et al., 1985 (tubers, 32.7 t/ha; tops, 17.5 t DM/ha); Rosa et al., 1992; Soja and Haunold, 1991 (tubers, 9.6 t/ha); Soja et al., 1993. Also listed as C-146 (De Mastro, 1988).

K 24 — Czech Republic origin. White tubers, pear shaped. Late maturing. Available from Nordic Gene Bank (accession DKHEL 4), a breeding/research clone; donated by UKZUZ, Havlickuv Brod, Czech Republic. Kays and Kultur, 2005; Klug-Andersen, 1992 (tubers, 32 to 41 t/ha); Zubr and Pedersen, 1993 (tubers, 9.0 t DM/ha); Zubr, 1988b.

Karina — Danish origin. White tubers, pear shaped. Tall plants, with weakly branched tops. Late maturing. Rarely or never flower in Denmark, with moderate/average tuber yields. Available from Nordic Gene Bank (accession DKHEL 5), a landrace or local variety; donated by Harald Nielson, Nyby, DK-4653 Karise, Denmark. Henriksen and Bjørn, 2003 (tubers, 8.1 t/ha); Kays and Kultur, 2005; Klug-Andersen, 1992 (tubers, 25 to 35 t/ha); Zubr and Pedersen, 1993 (tubers, 8.5 t DM/ha); Zubr, 1988a (tubers, 6.7 t/ha).

Karkowsky — Russian Federation origin. Early maturing. Cassells and Deadman, 1993; Fernandez et al., 1988b; Rosa et al., 1992.

Kärntner Landsorte — German origin. White tubers. Spherical (short-pear)-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001455); limited immediate availability. Soja and Haunold, 1991 (tubers, 7.1 t/ha); Soja et al., 1993.

Kharkov — Russian Federation origin. Large white tubers. Late maturing. Ben Chekroun et al., 1996; Fernandez et al., 1988; Kaŕa et al., 2005; Marčenko, 1969, Pas'ko, 1973.

Khar'kovskii Krupnoklubnevyi [Khar'kov Large Tubered] — Russian Federation origin.

Kharkowskii — *See* Karkowsky.

Kierski Beli — Russian Federation origin? Previously provided (to S.J. Kays) by Dr. B. Honermeier, Lehr- und Versuchsanatalt für Integrierten Pflanzenau e.V., Güterfelde, Germany. Kays and Kultur, 2005.

Kierskij Belyi — *See* Belyi Kievskii.

Kiev — *See* Kiev's Kievskii.

Kievskii — Ukrainian origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-113); acquired in 1984 (contact: Larry Tieszen).

Kievskii Belyi [Kievskij Belyi] — *See* Belyi Kievskii.

Kievskii Blanc — *See* Kiev's White.

Kievskii Rannii — Ukrainian origin. Bogomolov and Petrakova, 2001.

Kiev's White — Ukrainian origin. White spherical tubers. Late maturing. Maintained (as Kievskii Blanc) by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001473); limited immediate availability. Available (accession PI 357298) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Ben Chekroun et al., 1996; Kays and Kultur, 2005; Lapshina, 1981; Seiler, 1993.

Kiev White — *See* Kiev's White.

Kijevsky — Ukrainian origin. Synonym of Kievskii? Zubr, 1988a.

Kirgnizskii Blanc — Russian Federation origin. White pear-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001474); limited immediate availability. Mesken, 1988.

Krasnaja [Red] — Russian Federation origin.

Krasnyi rannii — Russian Federation origin. Bogomolov and Petrakova, 2001.

Kulista Biaa — Polish origin. Gutmanski and Pikulik, 1994; Kaŕa et al., 2005; Sawicka, 2004.

Kulista Czerwona — Polish origin. Kaŕa et al., 2005; Sawicka, 2004.

Kulisty Cremonsky — Russian Federation origin. Pink, pear-shaped, and irregular-surfaced tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001475); limited immediate availability.

KWI 204 — Unknown origin. Cultivar. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 262; formerly Braunschweig BGRC 57356). Kays and Kultur, 2005.

L232D19.6 — French origin. Violet-brown tubers, spindle shaped. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001394); limited immediate availability.

Lacho — French origin. Violet tubers, short pear or round shaped. Late maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001411); limited immediate availability. Ben Chekroun et al., 1996.

Landsorte Rot — German origin. Stolzenburg, 2003 (8.6 t/ha); Stolzenburg, 2004.

Landsorte Weiss — German origin. Stolzenburg, 2003 (8.9 t/ha); Stolzenburg, 2004.

Leningrad — Russian Federation origin. Cream/white tubers. Late maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001476); limited immediate availability. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accessions

NC10-75 and NC10-116). Available (accession PI 357299) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005; Kiehn and Chubey, 1993 (tubers, 15 to 42 t/ha); Lapshina, 1981; Seiler, 1993.

Leningradskii [Leningradskij] — *See* Leningrad.

Lina — Unknown origin. Mesken, 1988.

'Local' — Egyptian origin. Yellow (cream) tubers, with irregular shape and white flesh. Name used by Ragab et al. (2003) for a clone obtained from the Department of Vegetable Crops, Faculty of Agriculture, Cairo University, Giza, Egypt.

Lola — German origin? Stolzenburg, 2003 (7.4 t/ha); Stolzenburg, 2004.

Long Red — North American origin. Elongated, tapering tubers, knob-free. Available from Glen Drowns, 1878 230th St., Calamus, IA 52729, U.S. Facciola, 1990.

Long Red Drowns — U.S. origin? Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Long Red McCann — U.S. origin? Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Long Red Sun Roots — U.S. origin? Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.)

Lucien's Painting — Unknown origin. Late maturing. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

LV (CSK1) — Czech origin. A landrace/obsolete cultivar, collected in 1958. Maintained by the Genebank Department, RICP Prague Vegetable Section, Olomouc-Holice, Czech Republic (accession 09H5400002); not available due to damage.

LV (CSK2) — Czech origin. A landrace/obsolete cultivar, collected in 1958. Maintained by the Genebank Department, RICP Prague Vegetable Section, Olomouc-Holice, Czech Republic (accession 09H5400003); not available due to damage.

LV (CSK3) — Czech origin. A landrace/obsolete cultivar, collected in 1958. Maintained by the Genebank Department, RICP Prague Vegetable Section, Olomouc-Holice, Czech Republic (accession 09H5400004); not available due to damage.

LV (red skin from Brun) — Czech origin. A landrace/obsolete cultivar, collected in 1958. Maintained by the Genebank Department, RICP Prague Vegetable Section, Olomouc-Holice, Czech Republic (accession 09H5400006); freely available.

LV (red skin from Hradek) — Czech origin. A landrace/obsolete cultivar, collected in 1958. Maintained by the Genebank Department, RICP Prague Vegetable Section, Olomouc-Holice, Czech Republic (accession 09H5400001); freely available.

M5 — Canadian origin. A research/breeding line (Morden accession); maintained at Agriculture Canada Research Station, Morden, Manitoba, Canada. Dorrell and Chubey, 1977 (tubers, 6 t/ha); Stauffer et al., 1981 (as Morden #5).

M6 — Canadian origin. A research/breeding line (Morden accession); maintained at Agriculture Canada Research Station, Morden, Manitoba, Canada. Dorrell and Chubey, 1977 (tubers, 46 t/ha).

M7 — Canadian origin. A research/breeding line (Morden accession); maintained at Agriculture Canada Research Station, Morden, Manitoba, Canada. Dorrell and Chubey, 1977 (tubers, 33 t/ha).

M-24-2 — Russian Federation origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 67); donated by VIR (N.I. Vavilov Research Institute of Plant Industry), St. Petersburg, Russian Federation.

M24.29 — Russian Federation origin. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001477); limited immediate availability.

M-037 — U.S. origin. Maintained by the Institute of Plant Genetic Resources "K. Malkov," Str. Drujba 2, 4122, Sadovo, Bulgaria (accession 20003-HEL-TU-2); donated in 2003 by USDA/ARS. Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (accession UE0100820).

M-053 — U.S. origin. Maintained by the Institute of Plant Genetic Resources "K. Malkov," Str. Drujba 2, 4122, Sadovo, Bulgaria (accession 20003-HEL-TU-6); donated in 2003 by USDA/ARS.

M-057 — U.S. origin. Maintained by the Institute of Plant Genetic Resources "K. Malkov," Str. Drujba 2, 4122, Sadovo, Bulgaria (accession 20003-HEL-TU-1); donated in 2003 by USDA/ARS.

M-108 — U.S. origin. Maintained by the Institute of Plant Genetic Resources "K. Malkov," Str. Drujba 2, 4122, Sadovo, Bulgaria (accession 20003-HEL-TU-5); donated in 2003 by USDA/ARS.

M-140 — U.S. origin. Maintained by the Institute of Plant Genetic Resources "K. Malkov," Str. Drujba 2, 4122, Sadovo, Bulgaria (accession 20003-HEL-TU-4); donated in 2003 by USDA/ARS.

M-146 — U.S. origin. Maintained by the Institute of Plant Genetic Resources "K. Malkov," Str. Drujba 2, 4122, Sadovo, Bulgaria (accession 20003-HEL-TU-3); donated in 2003 by USDA/ARS.

M-169 — U.S. origin. Maintained by the Institute of Plant Genetic Resources "K. Malkov," Str. Drujba 2, 4122, Sadovo, Bulgaria (accession 20003-HEL-TU-7); donated in 2003 by USDA/ARS.

Magenta Purple — Unknown origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Mahlow Gelb — Unknown origin. Previously provided (to S.J. Kays) by Dr. B. Honermeier, Lehr- und Versuchsanatalt für Integrierten Pflanzenau e.V., Güterfelde, Germany. Kays and Kultur, 2005.

Mahlow Rot — Unknown origin. Previously provided (to S.J. Kays) by Dr. B. Honermeier, Lehr- und Versuchsanatalt für Integrierten Pflanzenau e.V., Güterfelde, Germany. Kays and Kultur, 2005.

Maikopskii [Maikopski] — *See* Majkopskij.

Maine Giant — U.S. origin. From Maine. Tubers are creamy-white, knobby, and dense. Described as very productive. Formerly offered by Pinetree Garden Seeds (Maine). Available through Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S. Watson, 1996.

Majkopskij — Russian Federation origin. White pear-shaped tubers. Available (as Majkopskij 33-650) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 60); donated by VIR (N.I. Vavilov Research Institute of Plant Industry), St. Petersburg, Russian Federation. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier,

France (INRA MPHE001478); limited immediate availability. Honermeier et al., 1996; Kays and Kultur, 2005.

Majkopskij 33-560 — *See* Majkopskij (Pas'ko, 1973).

Malveira — Portuguese origin. Rosa et al., 1992.

Mammoth — Synonymous with Mammoth French White. Cosgrove et al., 2000 (tubers, 8,628 and 11,159 lb/acre).

Mammoth French White — French origin? Large white tubers. A general type rather than a single cultivar; therefore, now of diverse origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kaŕa et al., 2005; Lee et al., 1985 (tubers, 31.2 t/ha; tops, 17.7 t DM/ha); Mays et al., 1990; Sprague et al., 1935.

Mansell sunroot — Unknown origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada; acquired 2004.

Mari — Danish origin. White tubers. Low-growing plants, with abundantly branched tops. Early maturing. Flowers in northern Europe (Denmark), with relatively high tuber yields. Available from Nordic Gene Bank (accession DKHEL 9), a landrace; donated by Danisco Seed, Højbygaardvej 31, DK-4960 Holeby, Denmark (contact: Steen Bisgaard). Henriksen and Bjørn, 2003 (tubers, 9.4 t/ha); Kays and Kultur, 2005; Klug-Andersen, 1992 (tubers, 47 to 62 t/ha); Zubr and Pedersen, 1993 (12.5 t DM/ha).

Markizovsky — Ukrainian origin? Medium maturing. Varlamova et al., 1996.

Marondo — French origin. Red or pink tubers. Late maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001412); limited immediate availability. Ben Chekroun et al., 1996.

Maroudo — *See* Marondo.

Marso — French origin. Red tubers. Late maturing. Ben Chekroun et al., 1996.

Maurico — French origin. Red tubers. Late maturing. Ben Chekroun et al., 1996.

McMinnville White — Unknown origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.)

Medius [Médius] — French origin. White tubers, round (short pear) shaped. Medium maturing. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 250; formerly Braunschweig BGRC 57344). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001413); limited immediate availability. Ben Chekroun et al., 1996; Kays and Kultur, 2005; Fernandez et al., 1988b; Lee et al., 1985 (tubers, 35 t/ha; tops, 15 t DM/ha); Mesken, 1988; Rosa et al., 1992; Schittenhelm, 1988 (mean, 36.5 tubers/plant); Soja and Haunold, 1991 (tubers, 8.6 t/ha); Soja et al., 1993; Stolzenburg, 2003 (tubers, 9.7 t/ha); Stolzenburg, 2004.

Meillo — French origin. Red tubers. Late maturing. Ben Chekroun et al., 1996.

Mestnyi SKhI [Local SKhI] — Russian Federation origin?

Mile's #1 — U.S. origin? Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005 (as Miles #1).

MN-5 — Canadian origin. Chubey and Dorrell, 1974.

Montco — *See* Monteo.

Monteo — French origin. Violet or red tubers, round (short pear) shaped. Medium maturing. Pink, pear-shaped and irregular-surfaced tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001414); limited immediate availability. Ben Chekroun et al., 1996; Honermeier et al., 1996; Kays and Kultur, 2005; Stolzenburg, 2004.

Moure — French origin. White tubers. Late maturing. Ben Chekroun et al., 1996.

MS.1 — French origin? Dorrell and Chubey, 1977 (tubers, 7 to 9 t/ha).

MS.2.5 — French origin. White tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001496); limited immediate availability.

MS.2.6 — French origin. White tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001395); limited immediate availability.

MS81 — French origin. White tubers, spherical (short pear) shaped. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001396); limited immediate availability.

Mulles Rose — U.S. origin. Large off-white tubers, with roseate eye zones (rose-purple eyes). Collected in Maine, at Mulles Homestead in Stacyville, northwest of Mt. Katahdin, on open, wind-swept ridge top, in 1905. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Available (accession Ames 8388) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Kays and Kultur, 2005.

Münchener — German origin. Grown for tops. Küppers-Sonnenberg, 1955.

Nachodka [Discovery] — *See* Nahodka.

Nagykállói — Hungarian origin. Kaŕa et al., 2005; Pátkai and Barta, 2002.

Nahodka — Russian Federation origin. White, oval-shaped, knobbly tubers. Tops with bushy appearance. Medium to late maturing. Resistance to *Sclerotinia*. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 260; formerly Braunschweig BGRC 57354). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001479); limited immediate availability. Available (accession PI 357300) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accessions NC10-101 and, Nachodka, NC10-119); both acquired in 1984 (contact: Larry Tieszen). Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Nahodka has been used in numerous experimental studies, including Bagautdinova and Fedoseeva, 2000; Barloy and Le Pierres, 1988 (tubers, 11 t DM/ha); Ben Chekroun et al., 1996; Cassells and Deadman, 1993; Cassells and Walsh, 1995; Conde et al., 1988; Ercoli et al., 1992 (tubers, 59.6 t/ha); Fernandez et al., 1988a (tubers, 67 t/ha, 15 t DM/ha; tops, 16 t/ha, 13 t DM/ha); Fernandez et al., 1988b; Honermeier et al., 1996; Kays and Kultur, 2005; Kaŕa et al., 2005; Lapshina, 1981; Le Cochec and de Barreda, 1990; Lee et al., 1985 (tubers, 36.9 t/ha; tops, 18.3 t DM/ha); Mikhal'tsova, 1985; Rosa et al., 1992; Ustimenko et al., 1976; Varlamova et al., 1996; Zubr, 1988a.

Nakhodka — *See* Nahodka.

Navazio — Unknown origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.)

NC10-2 — Canadian origin. White tubers. Early maturing. A breeding/research clone. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession A-A); not 2006 listing. Kiehn and Chubey, 1993 (tubers, 17 to 24 t/ha).

NC10-3 — Canadian origin (Manitoba). White tubers. Early maturing. A breeding/research clone. Available from Plant Gene Resources of Canada (PGRC), Saskatoon,

Saskatchewan S7N 0X2, Canada (accession 7305); acquired in 1970 (contact: H.H. Marshall). Kiehn and Chubey, 1993 (tubers, 7 to 38 t/ha).

NC10-4 — Canadian origin (Manitoba). White tubers. Late maturing. A breeding/research clone. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 7306); acquired in 1970 (contact: H.H. Marshall). Kays and Kultur, 2005; Kiehn and Chubey, 1993 (tubers, 9 to 44 t/ha).

NC10-5 — Canadian origin (Manitoba). A breeding/research clone. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 7307); acquired in 1970 (contact: H.H. Marshall). Kays and Kultur, 2005; Stauffer et al., 1981 (forage, 9.8 t DM/ha).

NC10-6 — Canadian origin (Manitoba). A breeding/research clone. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 7308); acquired in 1970 (contact: H.H. Marshall). Kays and Kultur, 2005.

NC10-7 — Canadian origin (Manitoba). A breeding/research clone. Early maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 7309); acquired in 1970 (contact: H.H. Marshall). Kays and Kultur, 2005.

NC10-8 — Canadian origin (Manitoba). White tubers. Early maturing. A breeding/research clone. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 7310); acquired in 1970 (contact: H.H. Marshall). Kays and Kultur, 2005; Kiehn and Chubey, 1993 (tubers, 11 to 24 t/ha); Stauffer et al., 1981 (forage, 31.8 t DM/ha).

NC10-9 — Canadian origin (Manitoba). Early maturing. A breeding/research clone. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 7312); acquired in 1970 (contact: H.H. Marshall). Kays and Kultur, 2005; Stauffer et al., 1981 (forage, 8.4 t DM/ha).

NC10-10 — Canadian origin (Manitoba). A breeding/research clone. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 7512); acquired in 1970 (contact: H.H. Marshall).

NC10-11 — Canadian origin (Manitoba). White tubers. Early maturing. A breeding/research clone. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 7513); acquired in 1970 (contact: H.H. Marshall). Kays and Kultur, 2005; Kiehn and Chubey, 1993 (tubers, 15 to 28 t/ha).

NC10-12 — Canadian origin (Manitoba). White tubers. Early maturing. A breeding/research clone. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession HM Hybrid A); acquired in 1970 (contact: H.H. Marshall). Kiehn and Chubey, 1993 (tubers, 18 to 32 t/ha).

NC10-13 — Canadian origin (Manitoba). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession HM Hybrid B); acquired in 1970 (contact: H.H. Marshall). Kays and Kultur, 2005; Stauffer et al., 1981 (forage, 14.7 t DM/ha).

NC10-14 — Canadian origin (Manitoba). A breeding/research clone. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession HM Hybrid C); acquired in 1970 (contact: H.H. Marshall). Kays and Kultur, 2005.

NC10-15 — *See* HM-2.

NC10-16 — *See* HM-3.

NC10-17 — *See* HM-5.

NC10-18 — *See* HM-7.

NC10-19 — *See* HM-8.

NC10-20 — *See* HM-9.

NC10-21 — *See* HM-10.

NC10-22 — *See* HM-11.
NC10-23 — *See* HM-12.
NC10-24 — *See* HM-13.
NC10-25 — *See* DHM-3.
NC10-26 — *See* DHM-4.
NC10-27 — *See* DHM-5.
NC10-28 — *See* DHM-6.
NC10-29 — *See* DHM-7.
NC10-30 — *See* DHM-13.
NC10-31 — *See* DHM-14.
NC10-32 — *See* DHM-16.
NC10-33 — *See* DHM-18.
NC10-34 — *See* DHM-19.
NC10-35 — *See* DHM-21.
NC10-35 — *See* DHM-22.
NC10-37 — Canadian origin (Morden). White tubers. Medium maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession W-97); acquired in 1970 (contact: H.H. Marshall). Kiehn and Chubey, 1993 (tubers, 4 to 21 t/ha).
NC10-38 — Canadian origin. White tubers. Early maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession W-106); acquired in 1970 (contact: H.H. Marshall). Kiehn and Chubey, 1993 (tubers, 12 to 22 t/ha).
NC10-39 — *See* Challenger.
NC10-40 — *See* Comber.
NC10-41 — *See* B.C. #1.
NC10-42 — *See* Red I.B.C.
NC10-43 — U.S. origin. White tubers. Late maturing. Synonymous with P-4 and USDA-P1. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession USDA P-1); acquired from USDA in 1976. Kiehn and Chubey, 1993 (as PI-4; tubers, 13 to 39 t/ha); Volk and Richards, 2006.
NC10-44 — *See* Sunchoke-Fiesda's.
NC10-45 — Canadian origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 75005); acquired in 1976 (contact: H.H. Marshall).
NC10-46 — Canadian origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 75004-52); acquired in 1976 (contact: H.H. Marshall). Kays and Kultur, 2005.
NC10-48 — Canadian origin. White tubers. Medium maturing. A breeding/research clone. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession A-3-6); acquired in 1976 (contact: H.H. Marshall). Kays and Kultur, 2005; Kiehn and Chubey, 1993 (tubers, 9 to 18 t/ha).
NC10-49 — Canadian origin. A breeding/research clone. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession HM Hybrid-A-4); acquired in 1976 (contact: H.H. Marshall).
NC10-50 — Canadian origin. Low yielding, leafy and fine stemmed. High percentage of DM protein in forage. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada; not 2006 listing. Stauffer et al., 1981 (2.3 t DM/ha).
NC10-52 — *See* DHM-14-3.
NC10-53 — *See* DHM-14-6.
NC10-52 — *See* DHM-15.

NC10-55 — Canadian origin. White tubers. Early maturing. A breeding/research clone. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 7513A); acquired in 1976. Kiehn and Chubey, 1993 (tubers, 21 to 29 t/ha).

NC10-58 — Canadian origin. White tubers. Medium maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession W-97-K1A). Kiehn and Chubey, 1993 (tubers, 8 to 29 t/ha).

NC10-59 — Canadian origin. White tubers. Early maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession W-1061); not 2006 listing. Kiehn and Chubey, 1993 (tubers, 17 to 33 t/ha).

NC10-60 — Canadian origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession Comber Select #1). Stauffer et al., 1981 (forage, 26 t DM/ha).

NC10-61 — Canadian origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession Comber Select #2).

NC10-62 — Canadian origin. White tubers. Mid-season maturing. A breeding/research clone (accession 266). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada. Kays and Kultur, 2005; Kiehn and Chubey, 1993 (tubers, 13 to 18 t/ha).

NC10-63 — Canadian origin (Ottawa). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession PRG-2367).

NC10-65 — U.S. origin (South Dakota). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-65); acquired in 1978, from Gurney Seeds, South Dakota.

NC10-67 — *See* Yankton-1.

NC10-68 — U.S. origin (Minnesota). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada; acquired in 1978.

NC10-69 — *See* Columbia.

NC10-70 — Former USSR origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession U-2U-2G); acquired in 1979 (contact: M.D. Stauffer). Kays and Kultur, 2005.

NC10-71 — *See* Rizskij.

NC10-72 — *See* Interess.

NC10-73 — *See* Volzskij-2.

NC10-74 — *See* Jamcovskij Krashyj.

NC10-75 — *See* Leningradskij.

NC10-76 — *See* Vadim.

NC10-77 — Japanese origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada; acquired in 1979 (contact: B.B. Chubey).

NC10-78 — Japanese origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada; acquired in 1979 (contact: H.H. Marshall). Kays and Kultur, 2005.

NC10-79 — Canadian origin. Maintained by Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession W-3X Branching 7611); acquired in 1979 (contact: H.H. Marshall). Volk and Richards, 2006.

NC10-80 — Canadian origin. Maintained by Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession W-3X Branching 7701); acquired in 1979 (contact: H.H. Marshall).

NC10-81 — *See* French Mammoth White.

NC10-82 — *See* Oregon White.

NC10-83 — Canadian origin (British Columbia). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada; acquired in 1982, from Bob Harris. Kays and Kultur, 2005.

NC10-84 — Canadian origin? Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada; not in 2006 listing. Kays and Kultur, 2005.

NC10-85 — U.S. origin (Texas). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession TUB-346 USDA-ARS-SR); acquired in 1983, from Gerald Seiler. Kays and Kultur, 2005.

NC10-86 — U.S. origin (Texas). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession TUB-365 USDA-ARS-SR); acquired in 1983, from Gerald Seiler.

NC10-87 — U.S. origin (Texas). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession TUB-675 USDA-ARS-SR); acquired in 1983, from Gerald Seiler. Kays and Kultur, 2005.

NC10-88 — U.S. origin (Texas). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession TUB-676 USDA-ARS-SR); acquired in 1983, from Gerald Seiler. Kays and Kultur, 2005.

NC10-89 — U.S. origin (Texas). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession TUB-709 USDA-ARS-SR); acquired in 1983, from Gerald Seiler.

NC10-90 — U.S. origin (Texas). Late maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession TUB-847 USDA-ARS-SR); acquired in 1983, from Gerald Seiler. Kays and Kultur, 2005.

NC10-92 — Canadian origin (Ontario). Late maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession #2); acquired in 1983, from Richard Thomas. Kays and Kultur, 2005.

NC10-94 — Canadian origin (Ontario). Late maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession #4); acquired in 1983, from Richard Thomas. Kays and Kultur, 2005.

NC10-95 — Canadian origin (Ontario). Late maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession #5); acquired in 1983, from Richard Thomas. Kays and Kultur, 2005.

NC10-96 — *See* Fuseau 60.

NC10-97 — Canadian origin (Manitoba). Breeding/research clone. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession (37X39) 1982); acquired in 1984.

NC10-99 — Canadian origin? Late maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada; not in 2006 listing. Kays and Kultur, 2005.

NC10-100 — Canadian origin? Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada; not in 2006 listing. Kays and Kultur, 2005.

NC10-101 — *See* Nahodka.

NC10-103 — *See* Violet de Rennes.

NC10-104 — *See* Rijskii.

NC10-105 — *See* Vernet.

NC10-106 — *See* D-19.

NC10-107 — *See* Interess.

NC10-108 — French origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 79-62); acquired in 1984 (contact: Larry Tieszen).

NC10-109 — French origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 242-63); acquired in 1984 (contact: Larry Tieszen).
NC10-110 — *See* Topinsol 63.
NC10-111 — *See* Waldspindel.
NC10-112 — *See* D-19-63-122.
NC10-113 — *See* Kievskii.
NC10-114 — *See* Industrie.
NC10-118 — *See* Ellijay.
NC10-119 — *See* Nachodka.
NC10-120 — *See* D16.
NC10-121 — *See* D19-63-340.
NC10-122 — French origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 242-62); acquired in 1984, from F. Le Cochec.
NC10-123 — French origin. *See also* 29.65. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 29-65); acquired in 1984, from F. Le Cochec.
NC10-125 — French origin. *See also* 10562 G2. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 105-62G2); acquired in 1984, from F. Le Cochec.
NC10-127 — French origin. *See also* 1277.63. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 1277-63); acquired in 1984, from F. Le Cochec.
NC10-129 — German origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession 073-87); acquired in 1988, from J. Reckin.
NC10-130 — Canadian origin (Ontario). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession #1); acquired in 1988, from Wolf Hettgen. Volk and Richards, 2006.
NC10-131 — Canadian origin (Ontario). Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession #2); acquired in 1988, from Wolf Hettgen.
NC10-140 — *See* Volga 2.
NC10-143 to NC10-181 (37 accessions in total) — Canadian origin (Morden, Manitoba). Breeding/research clones. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (see Table 8.3 for individual accessions); mainly acquired in 1983 (contact: F.A. Kiehn).
NC10-182 to NC10-213 (29 accessions in total) — Canadian origin (Morden, Manitoba). Breeding/research clones. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accessions HM-1 to HM-37; see Table 8.3 for individual accessions); acquired in 1991 (contact: F.A. Kiehn).
Nescopeck — Unknown origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.
Neus — German origin. Previously provided (to S.J. Kays) by Dr. B. Honermeier, Lehr- und Versuchsanatalt für Integrierten Pflanzenau e.V., Güterfelde, Germany. Kays and Kultur, 2005.
Niederösterreichische Landsorte — German origin. Soja and Haunold, 1991 (tubers, 10.8 t/ha); Soja et al., 1993.
NIIZh10 — Ukrainian origin. Marčenko, 1969.

NIIZh10-39 — Ukrainian origin. Marčenko, 1969.
NIIZh72 — Ukrainian origin. Marčenko, 1969.
NIIZh155 — Ukrainian origin. Marčenko, 1969.
No. 1 [#1] — *See* NC10-130.
No. 2 [#2] — *See* NC10-92 and NC10-131.
No. 4 [#4] — *See* NC10-94.
No. 5 [#5] — *See* NC10-95.
No. 9 — Unknown origin. A breeding/research clone. Kays and Kultur, 2005; Klug-Andersen, 1992 (tubers, 39 t/ha).
No. 1168 — Swedish origin. Hybrid of cultivated sunflower and Jerusalem artichoke. Supplied to Gunnarson et al. (1985) by Hilleshög AB Plant Breeding Company, Sweden (tops, 9 to 15 DM/ha); Wünsche, 1985.
No. 1927 — Swedish origin. Jerusalem artichoke × sunflower hybrid. Supplied to Gunnarson et al. (1985) by Hilleshög AB Plant Breeding Company, Sweden (tops, 7 to 12 t DM/ha).
No. 72196 — U.S. origin. Collected in North Dakota in 1974. Available (accession PI 451980) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.
Nora — Norwegian origin. White tubers. Low-growing plants, with abundantly branched tops. Early maturing. Flowers in northern Europe (Denmark), with relatively high tuber yields. Available from Nordic Gene Bank (accession DKHEL 10), a landrace or local variety; donated in 1985 by Dirk Janson Smith, St. Magleby, Dragør, Denmark. Henriksen and Bjørn, 2003 (tubers, 9.3 t/ha); Kays and Kultur, 2005; Klug-Andersen, 1992 (tubers, 45 to 53 t/ha); Zubr and Pedersen, 1993 (12 t DM/ha).
Novost — Russian Federation origin. Hybrid between *H. tuberosus* cv. Sottip and *H. annuus* cv. Gigant 549. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 251; formerly Braunschweig BGRC 57345). Kays and Kultur, 2005; Kshnikatkina and Varlmov, 2001; Mikhal'tsova, 1985 (green matter, 39.4 t/ha; tubers, 24.2 t/ha).
Olds — Unknown origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.
Ongai — *See* Ongui.
Ongui — Hungarian origin? Kaŕa et al., 2005; Pátkai and Barta, 2002.
Onta — Canadian or Belgian origin. White tubers, spherical (short pear) shaped. Early maturing. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 268; formerly Braunschweig BGRC 57363). Maintained (Belgian clone) by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001451); limited immediate availability. Honermeier et al., 1996; Kays and Kultur, 2005.
Oregon — U.S. origin. Possibly synonymous with Oregon White. Cosgrove et al., 2000 (tubers, 12,477 lb/acre).
Oregon White — U.S. origin. Has been grown for its abundant tops. Maintained by Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-82); acquired in 1981 (Minnesota) from Mohawk Oil. Frappier et al., 1990 (tops, 40.5 t/ha); Kays and Kultur (as NC10-82); Laberge and Sackston, 1987.
Orrington — U.S. origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.
Ozor — Unknown origin. Berenji, 1988.

Ozov — European origin. Early to intermediate maturing. Light violet-colored, fusiform, or spindle-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001465); limited immediate availability.

Parlow — German origin. Assessed for biomass production. Scholz and Ellerbrock, 2002.

Parlow Gelb — German origin. Yellow-white tubers. Previously provided (to S.J. Kays) by Dr. B. Honermeier, Lehr- und Versuchsanatalt für Integrierten Pflanzenau e.V., Güterfelde, Germany. Kays and Kultur, 2005.

Parlow Rot — German origin. Red tubers. Late maturing. Honermeier et al., 1996.

Patate Vilmorin [Vilmorin Potato] — French origin. White tubers, oblong or semiflat shape with rather smooth surface. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001415); limited immediate availability. Gaudineau and Lafon, 1958; Mesken, 1988; Pas'ko, 1971, 1973, 1974.

Perron — Canadian origin. Dorrell and Chubey, 1977 (tubers, 20 t/ha); Stauffer et al., 1981.

PI-4 — *See* NC10-43.

PI 458544 — German origin. *H. annuus* × *H. tuberosus* hybrid, with reportedly high tuber yields.

Piedallu 8 — French origin. Cream-colored, elongated tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001416); limited immediate availability.

Piriforme Rouge — French origin. Purple, pyriform (pear-shaped) tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001417); limited immediate availability. Mesken, 1988.

Porcheron — French origin. Violet, spherical (short-pear) tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001404); limited immediate availability.

Potate Vilmorina — *See* Patate Vilmorin.

Précoce — French origin? Early maturing. Possibly a synonym of Précoce Commun. Mesken, 1988; van Soest et al., 1993.

Précoce Commun [Common Early] — French origin? Selected to be early maturing. Pilnik and Vervelde, 1976 (tubers, 35 t/ha).

Progrès — Unknown origin. Tsvetorukhine, 1960.

Quakertown — U.S. origin? Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.)

RA1 — Polish origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 288; formerly Braunschweig BGRC 57383).

RA2 — Polish origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 289; formerly Braunschweig BGRC 57384).

RA3 — Polish origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 290; formerly Braunschweig BGRC 57385).

RA4 — Polish origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection],

Correnssstrasse 3, 06466 Gatersleben, Germany (accession HEL 291; formerly Braunschweig BGRC 57386).

RA7 — Polish origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Correnssstrasse 3, 06466 Gatersleben, Germany (accession HEL 292; formerly Braunschweig BGRC 57387).

RA9 — Polish origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Correnssstrasse 3, 06466 Gatersleben, Germany (accession HEL 293; formerly Braunschweig BGRC 57389).

RA10 — Polish origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Correnssstrasse 3, 06466 Gatersleben, Germany (accession HEL 294; formerly Braunschweig BGRC 57390).

RA14 — Polish origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Correnssstrasse 3, 06466 Gatersleben, Germany (accession HEL 295; formerly Braunschweig BGRC 57391).

RA24 — *See* Biala Kulista.

Rayno — French origin. Red tubers. Late maturing. Ben Chekroun et al., 1996.

Red — Unknown origin. Available from Paul Simon, Box 323, Rt. 2, Mulvane, KS 67110, U.S.

Red Fuseau — *See* Fuseau Red.

Red I.B.C. — Canadian origin. Red tubers. Late maturing. Available (as B.C. #2) from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-42); acquired in 1976, from Dr. E.D. Putt. Kiehn and Chubey, 1993 (tubers, 6 to 54 t/ha).

Red Skinned Garnet — Unknown origin. Possibly available from Seeds Blüm, Idaho.

Refla — Danish origin. Red tubers. Late maturing. Plants rarely or never flower in Denmark, with average or relatively low tuber yields. Available from Nordic Gene Bank (accession DKHEL 3), a breeding/research clone; donated by the Royal Veterinary and Agricultural University, Denmark. Henriksen and Bjørn, 2003 (tubers, 8.4 t/ha); Kays and Kultur, 2005; Klug-Andersen, 1992 (tubers, 23 to 42 t/ha); Zubr, 1988a (tubers, 8.2 t/ha); Zubr and Pedersen, 1993 (tubers, 6.5 t DM/ha).

Reka — Danish origin. Smooth-skinned red tubers. Plants rarely or never flower in Denmark, with average or relatively low tuber yields. Available from Nordic Gene Bank (accession DKHEL 2), a landrace or local variety; donated pre-1980 by Harald Nielson, Nyby, DK-4653 Karise, Denmark. Henriksen and Bjørn, 2003 (tubers, 8.3 t/ha); Kays and Kultur, 2005; Klug-Andersen, 1992 (tubers, 28 to 37 t/ha); Zubr, 1988a (tubers, 7.3 t/ha); Zubr and Pedersen, 1993 (tubers, 6.3 t DM/ha).

Relikt — Russian Federation origin. Selected for alcohol production. Arbuzov et al., 2004.

Rema — German origin. Available from Nordic Gene Bank (accession DKHEL 1), a landrace or local variety; donated in 1986 by Danisco Seed, Højbygaardvej 31, DK-4960 Holeby, Denmark (contact: Steen Bisgaard).

Remo — French origin. Early maturing. Previously provided (to S.J. Kays) by Dr. B. Honermeier, Lehr- und Versuchsanatalt für Integrierten Pflanzenau e.V., Güterfelde, Germany. Ben Chekroun et al., 1996; Honermeier et al., 1996; Kays and Kultur, 2005.

Rennes — French origin. Kaťa et al., 2005.

Resom — Unknown origin. Zubr, 1988a (tubers, 7.7 t/ha).

Revan — Unknown origin. Zubr, 1988a (tubers, 7.3 t/ha).

Rico — French origin. Red tubers. Late maturing. Previously provided (to S.J. Kays) by Dr. B. Honermeier, Lehr- und Versuchsanatalt für Integrierten Pflanzenau e.V., Güterfelde,

Germany. Barta, 1996 (average mass of large tubers, 167 g; small, 42 g); Ben Chekroun et al., 1996; Honermeier et al., 1996; Kaŕa et al., 2005; Pátkai and Barta, 2002; Stolzenburg, 2004.

Rijskii — Russian Federation origin. White tubers. Late maturing. Synonymous with C-89. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-104); acquired in 1984 (contact: Larry Tieszen). Barloy and Le Pierres (as C89; tubers, 15 t DM/ha); De Mastro, 1988 (as C89; tops, 78 t/ha, 17 t DM/ha); Fernandez et al., 1988b (as C-89).

Rika — *See* Rico.

Rio — Unknown origin. Possible synonym of Huertos de Moya-Rio. Rosa et al., 1992.

Rizskij — Russian Federation origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-71); acquired in 1979 (contact: M.D. Stauffer). Kiehn and Chubey, 1993 (tubers, 23 to 47 t/ha).

ROM023-6149 — Former Yugoslavia origin. Maintained by the Research Institute for Cereals and Technical Plants, Calarasi, Romania (no accession name); collected in former Yugoslavia in 1980.

Rose Ordinaire [Ordinary Pink] — French origin. Küppers-Sonnenberg, 1953.

Roter Topinambur — German origin? Late maturing. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Rote Zonenkugel — German origin. Noted for good yields when cultivated as a perennial. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 248; formerly Braunschweig BGRC 57342). Conti, 1957; Küppers-Sonnenberg, 1955 (as synonym Zonenkugel); Soja and Haunold, 1991 (tubers, 8.6 t/ha); Soja et al., 1993; Stolzenburg, 2003 (tubers, 9 t/ha); Stolzenburg, 2004.

Rouge Commun — French origin. Red tubers. Cultivar type? Gagnon, 2005.

Roumo — French origin. Red tubers. Late maturing. Ben Chekroun et al., 1996.

Rozo [RoZo] — German origin. Pink tubers. Short-pear to round tubers, variably indented. Early maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001456); limited immediate availability. Available from Research Station for Special Crops, Wies 88, Austria (accession WIES-D17). Kays and Kultur, 2005; Kahnt and Leible, 1985; Mesken, 1988; Steinrücken and Grunewaldt, 1984.

Rubik — Polish origin. Cieslik et al., 2003; Sawicka and Michaek, 2005.

Ryskii — Russian Federation origin. White, irregular, and somewhat indented tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001480); limited immediate availability.

S3.1 — French origin. White, elongated tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001397); limited immediate availability.

Sachalinski Krasni — *See* Sachalinski Krasnyi.

Sachalinski Krasnyi — Russian Federation origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 62); donated by VIR (N.I. Vavilov Research Institute of Plant Industry), St. Petersburg, Russian Federation. Kays and Kultur, 2005.

Sachalinski Krasnyj — *See* Sachalinski Krasni.

Sakhalinskii — Russian Federation origin. White tubers, with spherical and indented shape. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001493); limited immediate availability.

Sakhalinskii Rouge — Russian Federation origin. Light-purple-colored and pear-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001494); limited immediate availability. Mesken, 1988 (as Sekhalenskii rouge).

Saratov — Russian Federation origin. Ustimenko, 1958.

Saratov 1 — Russian Federation origin. Ustimenko, 1958.

Schmoll — Unknown origin. Late maturing. Kays and Kultur, 2005.

Scott — French origin. Light violet, elongated (spindle) tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001418); limited immediate availability.

Sebis — Romanian origin. Available from the University of Agricultural Science (UAS), Timisoara, Romania (accession ROM023-6151); collected in Arad, Sebes, Romania, in 1989.

Sejanec — Russian Federation origin. Late maturing. Honermeier et al., 1996; Kovalenko, 1969.

Sejanec 1 [Seedling 1] — Russian Federation origin. Usanova, 1967.

Sejanec 19 [Sejenetz 19] — Russian Federation origin. White tubers, spherical or pear shaped. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 65); donated by VIR (N.I. Vavilov Research Institute of Plant Industry), St. Petersburg, Russian Federation. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001482); limited immediate availability.

Sejanetz 10 [Sejanec 10] — Russian Federation origin. White tubers, spherical or pear shaped. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001481); limited immediate availability.

Sejenetz — *See* Sejanec.

Sejenic — *See* Sejanec.

Sekhalenskii rouge — *See* Sakhalinskii Rouge.

Sel. Aus Saemlingspop. — Canadian origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 263; formerly Braunschweig BGRC 57358).

Sepanetz [Sépanetz] — Unknown origin. Synonymous with C-76. Late maturing. De Mastro, 1988 (tubers, 73 t/ha, 17 t DM/ha); Fernandez et al., 1988b.

Sepanetz-10 — *See* Sepanetz.

Seyanets — *See* Sejanec.

Silver Skin — *See* Silverskin.

Silverskin — U.S. origin? Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Hay and Offer, 1992; Kays and Kultur, 2005.

Sinleo — French origin. Red tubers. Late maturing. Ben Chekroun et al., 1996.

Skorospelka [Early or Early Ripener] — Russian Federation origin. Early maturing. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Pending inactivation in 2006 (accession PI 357301) at USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Bagautdinova and Fedoseeva, 2000; Kays and Kultur, 2005; Usanova, 1967; Ustimenko et al., 1976; Varlamova et al., 1996.

Smooth Garnet — *See* Garnet.

Sodomka — Unknown origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Solskocka — *See* Sunchoke [Swedish].

Sottip — Russian Federation origin. Mikhal'tsova, 1985.

Southington Pink — U.S. origin? Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Spindel — German origin. Early maturing. Possible synonym/part of Waldspindel cultivar group. Previously provided (to S.J. Kays) by Dr. B. Honermeier, Lehr- und Versuchsanatalt für Integrierten Pflanzenau e.V., Güterfelde, Germany. Honermeier et al., 1996. Kays and Kultur, 2005.

SR — Unknown origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession SR). Volk and Richards, 2006.

Stampede — U.S. origin. Short plants (up to 1.8 m tall). Large white tubers, selected for smooth surface. Early maturing (flowering by July in the U.S.). Tolerant of extreme cold. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Available from Garden City Seed, Victor, MT, U.S. Available from Mapple Farm, 129 Beech Hill Rd., Weldon, New Brunswick E4H 4N5, Canada. Facciola, 1990; Kays and Kultur, 2005.

Sugar Ball — Hungarian origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Sugárka — Hungarian origin. Barta (average mass of large tubers, 173 g; small, 50 g).

Sükössdi/Nosszu — Unknown origin. Early maturing. Mesken, 1988.

Sukosti — European origin. Round- or short-pear-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001466); limited immediate availability.

Sun Choke — *See* Sunchoke.

Sunchoke — Swedish origin. Short rhizomes (stolons) and large tubers, with reportedly high productivity as a vegetable crop. A sunflower × Jerusalem artichoke hybrid, originating in 1950 Swedish plant breeding program (Sachs et al., 1981). Now mainly available in U.S., from Californian seed merchants (e.g., Turlock, CA). Grown in California, where it is recommended as a vegetable with a fresh nutty flavor. Kays and Kultur, 2005; McLaurin et al., 1999; Sachs et al., 1981 (tubers, 27 to 34 t/ha); Seiler, 1993; Williams et al., 1982 (tubers, 33 t/ha). Sunchoke is also sometimes used as an alternative name for Jerusalem artichoke.

Sunchoke-Friesda's — U.S. origin (California). Maintained by Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (NC10-44); donated in 1976. Stauffer et al., 1981 (forage, 23 t DM/ha); Volk and Richards, 2006.

Sunrise — U.S. origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Sunroot — Unknown origin. Modler et al., 1993. Generally used as a generic term rather than a distinct cultivar or cultivar type.

Susan's Yard — U.S. origin. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Sutton White — U.K. origin. Ex-catalog of Sutton Seeds, Suffolk, U.K. Garcia-Rodriguez and Gautheret, 1976.

Swenson — U.S. origin. Originally collected in Maine, from Swenson homestead site in New Sharon, ME, in 1905, from patch of plants growing on floodplain of Sandy River. Reportedly good tuber size and yield. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Available (accession Ames 8376) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Kays and Kultur, 2005.

Swojecka — Polish origin. Gutmanski and Pikulik, 1994; Kaŕa et al., 2005.

Swojecka Czerwona — Polish origin. Sawicka, 2004.

Sysol'skii — Russian Federation origin. Mishurov et al., 1999.

Szolosnyaraloi — Hungarian origin? Kaŕa et al., 2005; Pátkai and Barta, 2002.

Tait — U.S. origin. White, spherical (short-pear)-shaped tubers with some indentations. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001419); limited immediate availability.

Tambov [Tamboy] — Russian Federation origin. Pas'ko, 1973; Usanova, 1967.

Tambovskii Krasnyi [Tambov Red] — Russian Federation origin. Late maturing. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 61); donated by VIR (N.I. Vavilov Research Institute of Plant Industry), St. Petersburg, Russian Federation. Kays and Kultur, 2005; Honermeier et al., 1996; Pas'ko 1974. Probably synonymous with Tambovskii Rouge.

Tambovskii Rouge — Russian Federation origin. Violet-red, oval-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001483); limited immediate availability. Possible synonym of Tambovskii Krasnyi.

Tambowski Krasnyi — *See* Tambovskii Krasnyi.

Tapioi korai — Unknown origin. Nemeth and Izsaki, 2006.

Teruel — Spanish origin. Fernandez et al., 1988b.

Teta — Unknown origin. Zubr, 1988a (6.1 t/ha).

Thoumo — French origin. White tubers. Late maturing. Ben Chekroun et al., 1996.

Tombowski Krasni — *See* Tambovskii Krasnyi.

Top — Unknown origin. Medium maturing. Previously provided (to S.J. Kays) by Dr. B. Honermeier, Lehr- und Versuchsanatalt für Integrierten Pflanzenau e.V., Güterfelde, Germany. Honermeier et al., 1996; Kays and Kultur, 2005.

Topianca — *See* Topianka.

Topianka — German origin. Light-violet tubers, short pear shaped, somewhat indented. Early flowering. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 247; formerly Braunschweig 57341). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001457); limited immediate availability. Anon., 1959; Berenji, 1988; Gunnarson et al., 1985 (tops, 12 to 15 t DM/ha); Malmberg and Theander, 1986 (tops, 11 to 16 t DM/ha); Mesken, 1988; Soja and Haunold, 1991 (6.6 t/ha); Soja et al., 1990, 1993; Stolzenburg, 2003 (tubers, 8.8 t/ha); Stolzenburg, 2004.

Topinambour Fuseau — *See* Fuseau. Gagnon, 2005.

Topinambour Patate — Canadian origin? White tubers. Historical type? Gagnon, 2005.

Topinanca — *See* Topianka.

Topine — A contraction of 'Topinambur' in German literature. Nash, 1985.

Topino — Italian origin? Ercoli et al., 1992 (tubers, 59.4 t/ha); Masoni et al., 1993.

Topinsol — Russian Federation origin. Probably synonymous with Topinsol VIR (N.I. Vavilov Research Institute of Plant Industry). Masoni et al., 1993; Mesken, 1988.

Topinsol 63 — Russian Federation origin. White spherical tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001484); limited immediate availability. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-110); acquired in 1984 (contact: Larry Tieszen). Mesken, 1988.

Topinsol VIR — Russian Federation origin. White, elongated oval and indented tubers. Probably synonymous with Topinsol. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001485); limited immediate availability. Pas'ko, 1973.

Topstar — German origin? Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 284; formerly Braunschweig BGRC 57379). Schittenhelm, 1987; Stolzenburg, 2003 (tubers, 8 t/ha); Stolzenburg, 2004.

Torpedo — German origin? Küppers-Sonnenberg, 1955.

Totman — U.S. origin. Large, white, knobby tubers. Late maturing. Noted as a good keeper. Collected in Maine by Caroline Totman of Waldoboro, ME, pre-1988. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Pending inactivation in 2006 (accession Ames 8391) at USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Kays and Kultur, 2005.

Traube Vollbehang — German origin. Grown for tops. Küppers-Sonnenberg, 1955.

TUB-6 — U.S. origin. Collected in North Dakota (Pembina River) in 1984. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (available).

TUB-7 — U.S. origin. Collected in North Dakota (Lake Astabul) in 1984. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (available).

TUB-8 — U.S. origin. Collected in North Dakota (north of Valley City) in 1984. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (available).

TUB-15 — U.S. origin. Collected in North Dakota (Abercrombie) in 1984. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (available).

TUB-16 — U.S. origin. Collected in North Dakota (Valley City) in 1984. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (available).

TUB-20 — U.S. origin. Collected in North Dakota (Fort Ransom) in 1984. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (available).

TUB-26 — U.S. origin. Collected in North Dakota (Wild Rice River) in 1984. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (available).

TUB-33 — U.S. origin. Collected in South Dakota (Union County), from roadside ditch in 1982. Available (accession Ames 2714) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-49 — U.S. origin. Collected in South Dakota (Clay County), from roadside ditch in 1982. Available (accession Ames 2729) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-64 — U.S. origin. Collected in Iowa (Sioux County), from roadside ditch in 1982. Available (accession Ames 2739) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-320 — U.S. origin. Collected in Minnesota in 1972. Pending inactivation in 2006 (accession Ames 6303) at USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-321 — U.S. origin. Collected in Minnesota in 1975. Pending inactivation in 2006 (accession Ames 6304) at USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-322 — U.S. origin. Collected in Texas in 1905. Maintained (accession PI 435889) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-346 — *See* NC10-85.

TUB-365 — U.S. origin. *See* NC10-86. Collected in Texas in 1976. Pending inactivation in 2006 (accession PI 435892) at USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-571 — U.S. origin. Collected in Oklahoma in 1976. Maintained (accession Ames 6502) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-675 — *See* NC10-87.

TUB-676 — *See* NC10-88.

TUB-709 — *See* NC10-89.

TUB-821 — U.S. origin. Collected in Oklahoma in 1977. Maintained (accession PI 435758) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-825 — U.S. origin. Collected in Oklahoma, on Coal Creek, west of Stewart, in 1977. Maintained (accession PI 435893) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1241).

TUB-847 — *See* NC10-90.

TUB-870 — U.S. origin. Collected in Alabama in 1977. Maintained (accession Ames 6706) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-1057 — U.S. origin. Collected in North Dakota in 1979. Maintained (accession Ames 7141) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-1067 — U.S. origin. Collected in Illinois in 1979. Maintained (accession Ames 7151) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-1078 — U.S. origin. Collected in Illinois in 1905. Maintained (accession Ames 7161) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-1079 — U.S. origin. Collected in Illinois in 1905. Maintained (accession Ames 7162) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-1080 — U.S. origin. Collected in Illinois in 1905. Maintained (accession Ames 7163) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-1081 — U.S. origin. Collected in Illinois in 1905. Maintained (accession Ames 7164) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-1540 — U.S. origin. Collected from wild in Arkansas in 1980. Available (accession Ames 2718) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (accession UE0100767). Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1061).

TUB-1609 — U.S. origin. Collected in South Carolina in 1980. Maintained (accession Ames 7382) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1124).

TUB-1610 — U.S. origin. Collected in South Carolina in 1980. Maintained (accession Ames 7383) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1125).

TUB-1625 — U.S. origin. Collected in Tennessee in 1980. Maintained (accession PI 468896) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (accession UE0100755). Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1140).

TUB-1628 — U.S. origin. Collected in Tennessee in 1980. Pending inactivation in 2006 (accession Ames 6303) at USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1143).

TUB-1632 — U.S. origin. Collected in North Dakota in 1980. Maintained (accession Ames 7405) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-1633 — U.S. origin. Collected in 1980. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1148).

TUB-1634 — U.S. origin. Collected in 1980. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1149).

TUB-1635 — U.S. origin. Collected in 1980. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1150).

TUB-1636 — U.S. origin. Collected in 1980. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1151).

TUB-1698 — U.S. origin. Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (accession UE0100756).

TUB-1699 — U.S. origin. Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (accession UE0100757).

TUB-1700 — U.S. origin. Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (accession UE0100758).

TUB-1701 — U.S. origin. Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (accession UE0100759).

TUB-1703 — U.S. origin. Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (accession UE0100760).

TUB-1705 — U.S. origin. Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (accession UE0100761).

TUB-1765 — U.S. origin. Collected in South Dakota (Union County), from roadside ditch in 1982. Available (accession Ames 2711) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1302).

TUB-1769 — U.S. origin. Collected in South Dakota (Union County), from roadside ditch in 1982. Available (accession Ames 2715) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-1774 — U.S. origin. Collected in South Dakota (Clay County), from roadside ditch in 1982. Available (accession Ames 2720) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1303).

TUB-1775 — U.S. origin. Collected in South Dakota (Clay County), from roadside ditch in 1982. Available (accession Ames 2721) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1304).

TUB-1776 — U.S. origin. Collected in South Dakota (Clay County), from roadside ditch in 1982. Available (accession Ames 2722) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-1777 — U.S. origin. Collected in South Dakota (Clay County), from beside railroad in 1982. Available (accession Ames 2723) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-1783 — U.S. origin. Collected in South Dakota (Clay County), from beside roadside in 1982. Available (accession Ames 2730) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1305).

TUB-1786 — U.S. origin. Collected in South Dakota (Union County), roadside in 1982. Available (accession Ames 2733) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1306).

TUB-1789 — U.S. origin. Collected in Iowa (Plymouth County), roadside ditch in 1982. Available (accession Ames 2736) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1307).

TUB-1797 — U.S. origin. Collected in South Dakota (Clay County), from the banks of the Missouri River in 1982. Available (accession Ames 2744) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1308).

TUB-1798 — U.S. origin. Collected in South Dakota in 1982. Maintained (accession Ames 2745) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1309).

TUB-1799 — U.S. origin. Collected in South Dakota (Clay County), from roadside in 1982. Available (accession Ames 2747) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1310).

TUB-1800 — U.S. origin. Collected in South Dakota (Union County), from roadside in 1982. Available (accession Ames 2746) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-1877 — U.S. origin. Collected as seed from plants growing in rock soil near a creek in West Virginia in 1965 (assigned PI number in 1986). Available (accession PI 503262) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1317). Kays and Kultur, 2005.

TUB-1880 — U.S. origin. Collected from population of six plants in West Virginia (Greenbrier County), in wild near stream, by G. Seiler and D. Skoric, in 1985. Available (accession PI 503263) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1320).

TUB-1892 — U.S. origin. Collected in Virginia in 1985. Maintained (accession PI 503264) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1331). Kays and Kultur, 2005.

TUB-1904 — U.S. origin. Collected in Virginia (Northhampton County), from population scattered alongside railroad, by G. Seiler and D. Skoric, in 1985. Available (accession PI 503265) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1341). Kays and Kultur, 2005.

TUB-1905 — U.S. origin. Collected in Maryland in 1985. Maintained (accession PI 503266) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1342). Kays and Kultur, 2005.

TUB-1906 — U.S. origin. Collected in Maryland (Wicomico County), from steep bank of drainage ditch by G. Seiler, W. Roath, and D. Skoric, in 1985. Susceptibility to rust. Available (accession PI 503267) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1343).

TUB-1909 — U.S. origin. Collected in New Jersey in 1985. Maintained (accession PI 503268) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1344).

TUB-1912 — U.S. origin. Red tubers. Collected in New Jersey (Mercer County), from large population near habitation, therefore probably garden escapee, by G. Seiler, W. Roath, and D. Skoric, in 1985. Some rust. Available (accession PI 503267) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1347). Kays and Kultur, 2005.

TUB-1913 — U.S. origin. Collected in New Jersey in 1985. Pending inactivation in 2006 (accession PI 503270) at USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1348).

TUB-1925 — U.S. origin. Collected in Connecticut in 1985. Maintained (accession PI 503271) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1358). Kays and Kultur, 2005.

TUB-1928 — U.S. origin. Collected in Connecticut (Litchfield County), from roadside by G. Seiler, W. Roath, and D. Skoric, in 1985. Alternaria and insect damage noted. Available (accession PI 503272) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1361). Kays and Kultur, 2005.

TUB-1933 — U.S. origin. Collected in Massachusetts in 1985 (PI 503273). Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1362).

TUB-1936 — U.S. origin. Tall plants, up to 3 to 3.6 m, with large, long, and narrow tubers. Collected in Vermont (Caledonian County), probable garden escapee, by G. Seiler, W. Roath, and D. Skoric, in 1985. Some rust reported. Available (accession PI 503274) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1364). Kays and Kultur, 2005.

TUB-1937 — U.S. origin. Collected in Vermont in 1985. Maintained (accession PI 503275) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1365). Kays and Kultur, 2005.

TUB-1939 — U.S. origin. Red tubers. Small plants, 1.5 to 1.8 m tall. Collected in New York (Saratoga County), on roadside verge, by G. Seiler, W. Roath, and D. Skoric, in 1985. Susceptibility to rust. Available (accession PI 503276) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1367). Kays and Kultur, 2005.

TUB-1940 — U.S. origin. Small, red tubers. Collected in New York (Saratoga County), on shaded roadside verge, by G. Seiler, W. Roath, and D. Skoric, in 1985. Powdery mildew reported. Available (accession PI 503277) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1368). Kays and Kultur, 2005.

TUB-1942 — U.S. origin. White tubers, elongated like wild *H. tuberosus*. Tall plants, 3 to 3.6 m high. Collected in New York (Saratoga County), from population of 20 plants in small thicket near stream, by G. Seiler, W. Roath, and D. Skoric, in 1985. Considerable rust noted. Available (accession PI 503278) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1370).

TUB-1943 — U.S. origin. Large, white, elongated tubers. Plants 1.5 to 2.1 m tall. Collected in New York (Schoharie County), from population of 25 plants by stream near woods, by G. Seiler, W. Roath, and D. Skoric, in 1985. Insect and rust damage noted. Available (accession PI 503279) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1371). Kays and Kultur, 2005.

TUB-1945 — U.S. origin. Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (accession UE0100762). Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1373).

TUB-1946 — U.S. origin. Collected in New York in 1985. Maintained (accession PI 503280) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1374). Kays and Kultur, 2005.

TUB-1947 — U.S. origin. Collected in New York in 1985 (PI 503281). Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1375).

TUB-1954 — U.S. origin. Collected in Pennsylvania in 1985 (PI 503282). Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1382).

TUB-1959 — U.S. origin. Collected in Pennsylvania in 1985. Maintained (accession PI 503283) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1387). Kays and Kultur, 2005.

TUB-2024 — U.S. origin. Collected in Wisconsin (Columbia County) from roadside in 1989. Few, small tubers and severe rust recorded. Available (accession PI 547227) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1516). Kays and Kultur, 2005.

TUB-2045 — U.S. origin. Collected in Ohio in 1989. Maintained (accession PI 547228) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1537).

TUB-2046 — U.S. origin. Collected in Ohio in 1989. Maintained (accession PI 547229) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1538).

TUB-2047 — U.S. origin. Branching plants, up to 2.5 m tall, with large leaves (largest in USDA-ARS collection) and red/purple stems. Collected in Ohio, from population of 100 plants in roadside ditch in 1989. Available (accession PI 547230) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (accession UE0100763). Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1539).

TUB-2048 — U.S. origin. Collected in Ohio in 1989. Maintained (accession PI 547231) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1540).

TUB-2050 — U.S. origin. Tall plants, up to 2.5 m tall, with hirsute stems; rust present. Collected in Ohio, from population of 50 plants at edge of cornfield in 1989. Available (accession PI 547232) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (accession UE0100764). Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1542). Kays and Kultur, 2005.

TUB-2051 — U.S. origin. Plants 2 m tall, with large lower leaves. Collected from isolated population of 25 plants in Ohio (Holmes County), in roadside ditch, in 1989. Available (accession PI 547233) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1543).

TUB-2052 — U.S. origin. Collected in Ohio (Wayne County), near woodland edge, as seed in 1989. Available (accession PI 547234) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1544).

TUB-2055 — U.S. origin. Collected in Ohio in 1989. Available (accession PI 547235) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1547).

TUB-2057 — U.S. origin. Collected in Ohio in 1989. Maintained (accession PI 547236) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1549).

TUB-2059 — U.S. origin. Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (accession UE0100765).

TUB-2061 — U.S. origin. Purple stems, with very large lower leaves (up to 12.5 cm wide). Collected in wild from population of 75 plants in Ohio in 1989. Available (accession PI 547237) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (accession UE0100766). Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1553).

TUB-2062 — U.S. origin. Collected in Ohio in 1989. Available (accession PI 547238) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1554).

TUB-2063 — U.S. origin. Collected in Ohio in 1989. Available (accession PI 547239) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1555).

TUB-2064 — U.S. origin. Collected in Ohio in 1989. Maintained (accession PI 547240) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1556).

TUB-2066 — U.S. origin. Collected from population of 45 plants in Ohio (Clinton County), on roadside near cornfield, in 1989. Available (accession PI 547241) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1558).

TUB-2067 — U.S. origin. Collected in Ohio in 1989. Available (accession PI 547242) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1559).

TUB-2069 — U.S. origin. Collected in Indiana in 1989. Available (accession PI 547243) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1561).

TUB-2070 — U.S. origin. Collected in Indiana in 1989. Available (accession PI 547244) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1562).

TUB-2071 — U.S. origin. Collected in Indiana in 1989. Maintained (accession PI 547245) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1563).

TUB-2073 — U.S. origin. Collected in Indiana in 1989. Maintained (accession PI 547246) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1565).

TUB-2080 — U.S. origin. Collected in Indiana in 1989. Maintained (accession PI 547247) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1572).

TUB-2089 — U.S. origin. Collected in Illinois in 1989. Available (accession PI 547248) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1581).

TUB-2189 — U.S. origin. Plants 1. 5 to 2 m tall. Large-diameter, thick leaves. Collected in Nebraska, from population of 38 plants by G. Seiler in 1991. Available (accession Ames 18010) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Maintained by (available) the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro (Cat. 1681).

TUB-2278 — Canadian origin. Collected in Manitoba, Canada, in 1994. Maintained (accession Ames 22227) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-2282 — Canadian origin. Collected in Manitoba, Canada, in 1994. Maintained (accession Ames 22228) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-2329 — Canadian origin. Collected in Manitoba, near Lake Metigoshe, in 1994. Available (accession Ames 22229) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

TUB-CG 1 to TUB-CG 81 (81 accessions in total) — Montenegro origin. All collected in 1990, from wild populations. Maintained by the Institute of Field and Vegetable Crops, Novi Sad, Serbia and Montenegro.

Turuel — *See* Teruel.

Tuscarora #1 — U.S. origin? Available from Doug Egeland, Maple Leaf Housing, Apt. A-4, St. Regis Falls, NY 12980, U.S.

Tuscarora #2 — U.S. origin? Available from Doug Egeland, Maple Leaf Housing, Apt. A-4, St. Regis Falls, NY 12980, U.S.

Tyumen' 2 — Russian Federation origin. Ustimenko et al., 1976.

U-2U-2G — *See* NC10-70.

UE0100253 — U.S. origin. Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (no accession name); collected/donated U.S., 2001 (noted as subspecies *subcanescens* A. Gray).

UE0100822 — Unknown origin. Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (no accession name).

Ukr. 1 — Ukrainian origin. Berenji, 1988.

Ukr. 2 — Ukrainian origin. Berenji, 1988.

Ukr. 3 — Ukrainian origin. Berenji, 1988.

UKR 4/82 — Ukrainian origin. Kaŕa et al., 2005.

Ukrainian 30 — Ukrainian origin (Odessa). Marčenko, 1969.

Ukrainskii 108 — *See* Ukrainian 108.

Ukranian 108 — Ukrainian origin. Early to mid-season maturing. Lapshina, 1981; Lapshina et al., 1980; Mishurov et al., 1999.

UM0600001 — Ukrainian origin. Maintained by the National Centre for PGR of Ukraine, Moskovs'kyi pr. 142, 61060, Kharkov, Ukraine (no accession name); collected in Poltavs'ka, Ukraine, in 1998.

Unity Firehouse — U.S. origin. Collected beside roadway, opposite firehouse in Unity, ME, and donated by Jack Kertesz of Freedom, ME, pre-1988. Available (accession Ames 8386) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

Urodny — Russian Federation origin. White tubers. Low-growing plants, abundantly branching tops. Early maturing. Flowers in northern Europe (Denmark), with relatively high tuber yields. Material of Czech Republic provenance in Nordic Gene Bank (accession DKHEL 14), a breeding/research clone; originally donated in 1959 by UKZUZ, Havlickuv Brod, Czech Republic. Henriksen and Bjørn, 2003 (tubers, 9.0 t/ha); Kays and Kultur, 2005; Klug-Andersen, 1992 (tubers, 39 to 50 t/ha); Zubr and Pedersen, 1993 (tubers, 12 t DM/ha); Zubr, 1988a (tubers, 8.4 t/ha).

Usborne sunroot — Unknown origin. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada; acquired 2004.

USDA-P1 — *See* NC10-43.

V71 — French origin. Experimental clone, with resistance to *Sclerotinia*. Gaudineau and Lafon, 1958.

V102 — French origin. Very light violet tubers, spindle shaped. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001398); limited immediate availability.

Vadim — Ukrainian origin (Odessa). Late maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001486); limited immediate availability. Available (accession PI 357302) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.; donated in 1971 by VIR (N.I. Vavilov Institute of Plant Industry), Russian Federation. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-76); acquired in 1979 (contact: M.D. Stauffer). Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Davydoviĉ, 1951; Kays and Kultur, 2005 (as Vadim and NC10-76); Meleškin, 1957; Seiler, 1993; Usanova, 1967; Ustimenko et al., 1976; Vavilov et al., 1975 (tubers, 11 t/ha); Varlamova et al., 1996; Zubr, 1988a.

Vanlig — Swedish origin. White tubers. Tall plants, weakly branching. Late maturing. Plants rarely or never flower in Denmark, with moderate/average tuber yields. Available from Nordic Gene Bank (accession DKHEL 7), a breeding/research clone; donated by Sveriges Landbrugsuniversitet (SLU), Alnarp, Sweden. Henriksen and Bjørn, 2003 (tubers, 8.0

t/ha); Kays and Kultur, 2005; Klug-Andersen, 1992 (tubers, 24 to 43 t/ha); Zubr, 1988a (tubers, 7.7 t/ha).

Vengerskii — Hungarian origin. Pas'ko, 1971, 1974.

Verbesserte Gelbe — German origin? Küppers-Sonnenberg, 1955.

Vernet — French origin. Violet tubers, with smooth (regular) surface, and spherical (short pear) shaped. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001420); limited immediate availability. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-105); acquired in 1984, from Larry Tieszen. Mesken, 1988.

Verona 1 — Italian origin. Ercoli et al., 1992 (tubers, 63.0 t/ha).

Vilmorin Potato — *See* Patate Vilmorin.

Violeta de Teruel — Unknown origin. Fernandez et al., 1988b.

Violet Commun [Common Purple] — French origin. Purple tubers, pear- to oblong-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001421); limited immediate availability. Berenji, 1988; Küppers-Sonnenberg, 1955; Pekic and Kišgeci, 1984 (as Violet Communes); Pas'ko, 1973, 1974, 1977; Chabbert et al., 1983.

Violet Communes — *See* Violet Commun.

Violet de Rennes [Rennes Purple] — French origin (Brittany). Red-purple, pear-shaped tubers. Late maturing. Intermediate plant height (2 to 3 m), one or two stems. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 261; formerly Braunschweig BGRC 57355). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001422); limited immediate availability. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-103); acquired in 1984. This cultivar has been used in numerous studies, often as a control to compare with new clones, including Allirand et al., 1988; Berenji, 1988; Cassells and Deadman, 1993; Baldini et al., 2004; Barloy, 1988; Barloy and Le Pierres, 1988; Curt et al., 2005; De Mastro, 1988 (tubers, 70 t/ha, 15 t DM/ha); De Mastro et al., 2004; Ercoli et al., 1992 (tubers, 75.6 t/ha); Gabini, 1988 (tubers, 80 t/ha); Garcia-Rodriguez and Gautheret, 1976; Fernandez et al., 1988a (tubers, 71 t/ha, 16 t DM/ha; tops, 12 t/ha, 8 t DM/ha); Fernandez et al., 1988b; Kaŕa et al., 2005; Le Cochec and de Barreda, 1990; Lee et al., 1985 (tubers, 40.2 t/ha; tops, 8.8 t DM/ha); Meijer et al., 1993; Mesken, 1988; Pasquier and de Valbray, 1981 (tubers, 60 to 90 t/ha); Pejin et al., 1993 (tubers, 70 t/ha; tops, 60 t/ha); Rosa et al., 1992; Schittenhelm, 1988 (mean, 17.5 tubers/plant); Soja and Dersch, 1993; Soja and Haunold, 1991; Soja et al., 1990, 1993; Spitters et al., 1988; Stolzenburg, 2003 (tubers, 9 t/ha).

Violett de' Rennes — *See* Violet de Rennes.

Voelkenroder Spindel — Unknown origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 278; formerly Braunschweig BGRC 57373). Stolzenburg, 2003 (tubers, 7.6 t/ha); Stolzenburg, 2004.

Volga 2 — Russian Federation origin. Derived from an interspecific cross between Jerusalem artichoke and sunflower. Available (accession PI 357303) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.; donated in 1971 by VIR (N.I. Vavilov Institute of Plant Industry), Russian Federation. Available (as Volzskij-2 and Volga 2) from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accessions NC10-73 and NC10-140); acquired in 1979 and 1989, from M.D. Stauffer and USDA-ARS, Ames, IA, respectively. Available from Will Bonsall

(Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Available (as Volgo 2) Mapple Farm, 129 Beech Hill Rd., Weldon, New Brunswick E4H 4N5, Canada. Kays and Kultur, 2005; Kiehn and Chubey, 1993 (tubers, 17 to 45 t/ha); Lavrühin, 1954.

Volgo 2 — *See* Volga 2.

Volzskaja 2 — *See* Volga 2.

Volzskij-2 — *See* Volga 2.

von Hagens Standard — German origin. Conti, 1957.

Vorstorg — *See* Vostorg.

Vostorg [Rapture] — Russian Federation origin. White spherical tubers. Bred at the Maikop experimental station (Russian Federation), by crossing the sunflower Violet Commun [Common Purple] with the Jerusalem artichoke Gigant 549 [Giant 549]. Resistant to drought and most pests and diseases, except *Sclerotinia sclerotiorum*. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001487); limited immediate availability. Pas'ko, 1976, 1977, 1980.

VR — *See* Violet de Rennes. Shortened to VR in Ben Chekroun et al., 1996; De Mastro, 1988.

Vyl'gortskii [Vylgortski] — Russian Federation origin. Bred for cold resistance, tall plant height, and productivity of green mass, by Institute of Biology, Komi Science, Ural Division of RAS, Komi Republic, Russian Federation (into State Seed List 1999). Mishurov et al., 1999.

W-97 — *See* NC10-37.

W-97-K1A — *See* NC10-58.

W-106 — *See* NC10-38.

W-1061 — *See* NC10-59.

W-3X Branching 7611 — *See* NC10-79.

W-3X Branching 7701 — *See* NC10-80.

Waldoboro Gold — U.S. origin. Very distinctive yellow tubers, very long and slender, twisted and convoluted. Yellow internal flesh. Early maturing. Reportedly poor yielding and difficult to clean. Collected in Maine, beside Route 1, Waldoboro, from an old patch growing wild, by Ken Steward of Damariscotta, ME, pre-1988. Available (accession Ames 8380) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Waldspindel — German origin, although now a cultivar grouping (of diverse origin). Medium to late maturing. Synonymous with C34 research/breeding clone. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 244; formerly Braunschweig BGRC 57338). Three clones maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001458, German origin, violet ovoid tubers; MPHE001459, German origin, violet, fusiform/spindle tubers; and MPHE001460, Austrian origin, violet, ovoid to round tubers); very limited immediate availability. Available (French origin) from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-111); a cquired in 1984 (contact: Larry Tieszen). Barta, 1996 (average mass of large tubers, 83 g; small, 48 g); De Mastro, 1988 (C34); Fernandez et al., 1988b (C-34); Gabini, 1988; Gabini and Corronca, 1988; Kaŕa et al., 2005; Kays and Kultur, 2005; Pas'ko, 1974; Pátkai and Barta, 2002; Pejin et al., 1993 (tubers, 47 t/ha; tops, 39 t/ha); Schittenhelm, 1988 (mean, 28.5 tubers/plant); Soja and

Dersch, 1993; Soja and Haunold, 1991 (tubers, 3.8 t/ha); Soja et al., 1993; Stolzenburg, 2003 (tubers, 9.2 t/ha); Stolzenburg, 2004.

Walspindel — *See* Waldspindel.

Waterer — U.S. origin. Boswell et al., 1936.

White Crop — Russian Federation origin. Late maturing. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Pending inactivation in 2006 (accession PI 357304) at USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S. Kays and Kultur, 2005.

White Early — *See* Belyi Rannii.

White Mammoth — Unknown origin. Large white tubers, purplish tinge. A cultivar type/grouping? Available from David Laverine, 517 S. Brush, Graton, CA 95444, U.S.

White Productive — *See* Belyi Urozhainyi.

Whitford — U.S. origin? Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Wilder Hill — U.S. origin. Medium-large, white tubers. Collected in Maine, by Arthur Wilder of Norridgewock, Maine, in 1988, from patch of plants several decades old. Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Pending inactivation in 2006 (accession Ames 8387) at USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

Wilton Rose — U.S. origin? Available from Will Bonsall (Scatterseed Project), Box 1167, Farmington, ME 04938, U.S. (The Seed Savers Exchange Members Network, 3076 North Winn Rd., Decorah, IA 52101, U.S.) Kays and Kultur, 2005.

Wolcottonian Red — *see* Dave's Shrine. Watson, 1996.

Yankton-1 — U.S. origin (Michigan). White tubers. Late maturing. Available from Plant Gene Resources of Canada (PGRC), Saskatoon, Saskatchewan S7N 0X2, Canada (accession NC10-67); acquired in 1978 from Burgess Seed Company. Kiehn and Chubey, 1993 (tubers, 15 to 46 t/ha).

Yellow Perfect — Unknown origin. Early maturing. Mesken, 1988; van Soest et al., 1993.

Yeralmasi — Azerbaijan origin. Maintained by Institute of Genetic Resources (accession 151-he), Azerbaijan National Academy of Sciences (155-Azadlii Ave., 1106, Baku, Azerbaijan); collected in 2005 from Ganja, Azerbaijan.

Yerarmudu gunebakhani — Azerbaijan origin. Maintained by Institute of Genetic Resources (accession aze DER-384), Azerbaijan National Academy of Sciences (155-Azadlii Ave., 1106, Baku, Azerbaijan); collected in 1973 in Azerbaijan.

Zeleneckii — Russian Federation origin. Mishurov et al., 1999.

Zonenkugel — *See* Rote Zonenkugel.

3 — U.S. origin. Collected from population of 100 plants in Iowa (Woodbury County), in roadside ditch, by Mary Brothers in 1999. Available (accession PI 613795) from USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

12/84 — Former Yugoslavia origin. Cultivar. Violet tubers, short pear shaped. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 267; formerly Braunschweig BGRC 57362). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001463); limited immediate availability. Kays and Kultur, 2005.

19 — U.S. origin. Collected in Iowa in 1999. Maintained (accession PI 613796) by USDA, ARS, National Genetic Resources System, NCRPIS, Ames, IA 50011, U.S.

23.27 — French origin. White tubers, elongated ovoid (oblong) and indented (irregular surface). Early maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001366); limited immediate availability. Available (as 2327) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Correnssstrasse 3, 06466 Gatersleben, Germany (accession HEL 273; formerly Braunschweig BGRC 57368). Kays and Kultur, 2005 (as 2327).

29.65 — French origin. *See also* NC10-123. White tubers, round/short pear or pear shaped, somewhat indented (irregular). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001367); limited immediate availability.

79.62 — French origin. White tubers, ovoid and indented (irregular). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001370); limited immediate availability.

99B — French origin. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001500); limited immediate availability.

228.62 — French origin. White tubers, ovoid and fairly indented (irregular). Early maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001365); limited immediate availability. Available (as 228-62) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Correnssstrasse 3, 06466 Gatersleben, Germany (accession HEL 274; formerly Braunschweig BGRC 57369). Kays and Kultur, 2005 (as 228-62).

266 — *See* NC10-62.

342.62 — French origin. White tubers, ovoid and very indented (irregular). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001368); limited immediate availability.

742.63 — French origin. White tubers, spindle shaped and indented (irregular). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001369); limited immediate availability.

952.63 — French origin. White tubers, spherical (short pear) shaped and somewhat indented (irregular). Early maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001371); limited immediate availability. Available (as 952-63) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Correnssstrasse 3, 06466 Gatersleben, Germany (accession HEL 275; formerly Braunschweig BGRC 57370). Kays and Kultur, 2005 (as 952-63).

1277.63 — French origin. *See also* NC10-127. White tubers, ovoid and very indented (irregular). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001361); limited immediate availability.

1999.63 — French origin. White tubers, ovoid and somewhat indented (irregular). Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001362); limited immediate availability.

2071.63 [2071-63] — French origin. White tubers, variable and irregular in shape. Early maturing. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001363); limited immediate availability. Available (as 2071-63) from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Correnssstrasse 3, 06466 Gatersleben, Germany (accession HEL 276; formerly Braunschweig BGRC 57371). Hay and Offer, 1992; Kays and Kultur, 2005; Schittenhelm, 1988 (mean, 18.3 tubers/plant); Stolzenburg, 2004; Zubr and Pedersen (clone 2071-63; 12.2 t DM/ha).

2088 — French origin. Pink tubers, irregular surface. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001364); limited immediate availability.

7305 — *See* NC10-3.

7306 — *See* NC10-4.

7307 — *See* NC10-5.

7308 — *See* NC10-6.

7309 — *See* NC10-7.

7310 — *See* NC10-8.

7312 — *See* NC10-9.

7512 — *See* NC10-10.

7513 — *See* NC10-11.

7513A — *See* NC10-55.

10562 G2 — French origin. *See also* NC10-125. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 269; formerly Braunschweig BGRC 57364).

10562 G15 — French origin. Available from Genbank, Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) [Leibniz Institute of Plant Genetics and Crop Protection], Corrensstrasse 3, 06466 Gatersleben, Germany (accession HEL 270; formerly Braunschweig BGRC 57365).

75004-52 — *See* NC10-46.

75005 — *See* NC10-45.

(K8*VR) — French origin. Cross between K8 and Violet de Rennes. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001423); limited immediate availability.

(NK*F60).1 to (NK*F60).10 (10 accessions in total) — French origin. Crosses between Nahodka and Fuseau 60. Varied tuber color and shape. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (see Table 8.6 for INRA code); limited immediate availability.

(NK*K8) — French origin. Cross between Nahodka and K8. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001434); limited immediate availability.

(NK*VR).1 — French origin. Cross between Nahodka and Violet de Rennes. Deep violet tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001435); limited immediate availability.

(NK*VR).2 — French origin. Cross between Nahodka and Violet de Rennes. Light violet, pear- or spindle-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001436); limited immediate availability.

(VR*F60).1 — French origin. Cross between Violet de Rennes and Fuseau 60. Pink, spherical (short-pear)-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001437); limited immediate availability.

(VR*F60).2 — French origin. Cross between Violet de Rennes and Fuseau 60. White or pink, spindle- or pear-shaped tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001438); limited immediate availability.

(VR*F60).3 — French origin. Cross between Violet de Rennes and Fuseau 60. White, ovoid-(oblong) to spindle-shaped tubers. Maintained by Institut National de la Recherches

Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001439); limited immediate availability.

(VR*NK) — French origin. Cross between Violet de Rennes and Nahodka. Violet, ovoid (oblong) tubers. Maintained by Institut National de la Recherches Agronomique (INRA), UMR-DGPC, Montpellier, France (INRA MPHE001440); limited immediate availability.

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9 Propagation

Jerusalem artichokes can be propagated using tubers, rhizomes, slips, stem cuttings, tissue culture, and seeds. Tubers represent the primary choice for commercial production of the crop. While rhizomes are important in the regeneration of wild populations, rhizomes, slips, and stem cuttings represent secondary methods of asexual propagation that are occasionally used to expand the numbers of a particular clone when tubers are not available. Tissue culture is used for long-term storage of clones in germplasm repositories and for the production of transgenic plants. Unlike sunflower (*Helianthus annuus* L.), where seed represents the primary means of propagation, seed is not a viable method for the production of Jerusalem artichokes and is used only in breeding programs to obtain the progeny from crosses.

9.1 TUBERS

Jerusalem artichokes are propagated from tubers or tuber pieces typically 45 to 60 g in size; large tubers can be cut into smaller pieces that sprout under normal conditions as well as intact tubers (Baillarge, 1942; Milord, 1987). An individual piece must include at least one bud from which a new stem develops. Additional buds (two or three) are sometimes recommended (e.g., Wood, 1979). The size of the tuber/tuber piece is important in that pieces less than ~40 g have reduced emergence (Delbetz, 1867; Morrenhof and Bus, 1990), number of stems (Boswell et al., 1936), and eventual yield (Boswell, 1959; Kovac et al., 1983). Additional stems per tuber or tuber piece increase the leaf area index early in the development of the plant (Baillarge, 1942; Cors and Falisse, 1980). Intact tubers are thought to be superior to tuber pieces if the soil is dry during planting.

Emergence generally occurs within 3 to 5 weeks of planting (Baillarge, 1942; Zubr, 1988) if the dormancy requirement has been adequately fulfilled (see Section 9.1.1). Timing of emergence is dictated largely by temperature (Tsvetoukhine, 1960), and treatments that warm the soil (e.g., film plastic) hasten emergence (Morrenhof and Bus, 1990). The threshold temperature for emergence is thought to be between 2 and 5°C (Barloy, 1984; Kosaric et al., 1984). Presprouting of the tubers can have a positive effect on emergence, early growth, and yield (Morrenhof and Bus, 1990; Spitters and Morrenhof, 1987), though care must be taken to prevent mechanical damage during planting.

The quantity of tubers required to plant a hectare depends upon their size and the plant population density. Using 50 g of seed pieces, plant spacings of 30×100, 50×100, 50×70, and 100×100 cm require a minimum of 1,666, 1,428, 1,000, and 500 kg, respectfully.

9.1.1 Tuber Dormancy

Jerusalem artichoke tubers have a dormancy period where development is suspended even though environmental conditions may be suitable for growth. Dormancy allows the plants to synchronize subsequent growth with desirable environmental conditions (Kays and Paull, 2004). In their native geographical range, Jerusalem artichoke tubers remain dormant during the winter months when sprouts would have a very low probability of survival. The length of the dormant period can vary among tubers from a single clone/cultivar, an adaptation that serves to enhance the long-term survival potential of the clone.

Of the three general types of dormancy (Lang, 1987), Jerusalem artichokes display what is termed endodormancy, where an internal mechanism prevents sprouting even though the external

conditions may be ideal. The mechanism leading to fulfillment of dormancy involves the perception by the tubers of an environmental signal, in this case exposure to low temperatures. After exposure to the appropriate temperature for a sufficient length of time (generally temperatures near 0°C* and below a specific maximum), the dormancy mechanism is fulfilled, and when environmental conditions are conducive, the cells within the tuber begin to divide and the tuber sprouts.

In addition to its biological role, tuber dormancy also has significant agricultural implications. Production of the crop in regions that do not have a cold period sufficient to fulfill the dormancy requirement can be greatly exasperated by the lack of or uneven sprouting in the spring. Likewise, insufficient cold can result in only part of the tubers sprouting, with a significant percentage remaining dormant. When this occurs during the first crop rotation following Jerusalem artichokes, the carryover of unsprouted weed tubers into the following season makes eradication more difficult.

The tubers become dormant in the fall, prior to the actual completion of their development. For example, Steinbauer (1939) found the onset of dormancy (two cultivars) to be between August 28 and September 7 in the U.S. After this time, freshly dug tubers did not sprout even under suitable environmental conditions. The exact timing of the onset of dormancy varied between individual tubers on the same plant and with production location, cultivar, and other factors. Interestingly, the larger, more mature tubers were the last to enter into dormancy. Dormancy was initially established in the rhizomes and small, younger tubers and well before the completion of the maturation process and the first frost. The onset of dormancy appeared to be a gradual process; thus, not all of the tubers on a plant became dormant simultaneously.

The depth or degree of dormancy varies considerably among cultivars and within an individual cultivar such that one tuber will sprout while others are delayed considerably. In a study of 145 cultivars, Boswell (1932) found that the time required for 50% of the tubers to sprout when not subjected to a cold treatment to fulfill the dormancy requirement ranged from 54 to 200 days, with 5 to 6 months typical for most cultivars. Likewise, the degree of dormancy varied between seasons. Cutting the tubers did not alter the dormancy. Treatment with certain chemicals (e.g., ethylene chlorohydrin), however, could shorten the dormancy period, although a number of the chemicals tested also slowed the subsequent growth of the sprout (Steinbauer, 1939).

The optimum temperature for fulfilling the dormancy requirement is between 0 and 5°C. Higher temperatures, such as 10°C, result in very slow breaking of dormancy (Steinbauer, 1939), a higher incidence of rotting (Steinbauer, 1932), and rapid loss of moisture (Traub et al., 1929). Likewise, at the higher temperature, the emerging sprouts were less vigorous. Fluctuating low temperatures (–1.1 to 4.4°C) were less effective than a constant 0°C. Typically 30 to 45 days was a sufficient cold (0°C) treatment to break dormancy in the two cultivars tested ('Chicago' and 'Blanc Ameliore').

9.1.1.1 Control of Dormancy

The large number of tubers available and the ease in which dormancy can be maintained or broken have made the Jerusalem artichoke an attractive model for studying the control of dormancy in tubers. The tubers possess a mechanism by which the duration of the exposure to cold is quantified, and once sufficient exposure has occurred, it instigates a signaling mechanism that sets off a cascade of reactions leading to sprouting. A number of hypotheses concerning the control mechanism have been put forward based on correlative changes occurring within the cells. However, it is extremely difficult to delineate the mechanism controlling dormancy from subsequent biochemical alterations.

Tuber dormancy studies can be separated into three general types based upon the tuber material used and whether the dormancy requirement is fulfilled naturally or via an artificial induction of cell division. Each method has distinct advantages and disadvantages. The tuber material includes intact tubers, tuber slices in which cell division is induced using an auxin analogue in an aqueous

* The highest freezing point of the tubers is –2.2°C (Whiteman, 1957).

medium, and excised segments (i.e., a portion of the tuber containing the apical bud and a wedge of subtending parenchyma cells). The difficulty with each of the methods is in discerning exactly when dormancy is fulfilled, thus identifying the point from which prior and subsequent physical and chemical alterations are fixed chronologically.

Of the three methods, the apical bud with excised parenchyma cells technique has been useful in that it allows studying the interrelationship between the bud and its subtending parenchyma cells. If the excised tuber segment is held under conditions that maintain dormancy (i.e., warm temperatures (e.g., 24°C) in the dark), the tubers undergo an interesting phenomenon. The apical bud on the tuber begins to slowly grow, forming a new tuber (also called filiate, secondary, or neotuber) (Courduroux, 1963; Hanover, 1960). The development of the new tuber involves the reallocation of dry matter and moisture from the existing tuber and continues until the reserves are exhausted. Any treatment that breaks the dormancy during this period (e.g., 4°C for 12 to 16 weeks) results in modification of the apical bud and its conversion into a shoot that elongates (Courduroux, 1967; Tort et al., 1985). When conditions (e.g., 28°C in the dark) are created that stimulate the parenchyma cells in the nodes subtending the apical bud, organogenesis in the apical meristem is repressed. Conversely, when growth of the internodes is inhibited, the apical bud is stimulated. Therefore, a complex interrelationship exists between the apical bud and the subtending internodes.

The role of polyamines in tuber dormancy has been studied using slices of tuber parenchyma cells that are pharmacologically triggered to divide. Polyamines are small aliphatic amines, of which putrescine, spermidine, and spermine are prevalent. They are synthesized from ornithine, arginine, and s-adenosylmethionine, and there are hundreds of papers reporting correlations between polyamine level within tissues and a diverse cross section of developmental and physiological events in plants (for reviews see Malmberg et al., 1998; Kuehn and Phillips, 2005; Kumar et al., 1997; Walden et al., 1997). The initial demonstration that polyamines could help break the dormancy and stimulate cell proliferation in tuber slices of Jerusalem artichoke (Bagni, 1966) led to a series of papers on their possible role (Bagni et al., 1971, 1978, 1980, 1981; Bagni and Serafini-Fracassini, 1985; Bagni and Seperanza, 1971; Bertossi et al., 1965; Bogen Ottoko, 1977; Courduroux et al., 1972; Cionini and Serafini-Fracassini, 1972; Del Duca and Serafini-Fracassini, 1993; Gendraud and Lafleuriel, 1985; Serafini-Fracassini and Filiti, 1976; Serafini-Fracassini et al., 1980; Serafini-Fracassini and Alessandri, 1983). There is a rapid increase in polyamine level that peaks 24 h after excision and induction of the tuber tissue. The addition of an inhibitor (difluoromethylornithine) of ornithine decarboxylase, a key enzyme in the polyamine synthesis pathway, suppressed cell division. Torrigiani et al. (1987) found that ornithine decarboxylase, arginine decarboxylase, and s-adenosylmethionine carboxylase activities (critical enzymes in the polyamine synthesis pathway) and polyamine level increased before and during the S phase of the initial cell cycle induced by auxin, and subsequently declined during cell division. A rise in polyamine content and synthesis before and during nuclear DNA synthesis has been demonstrated elsewhere in the plant kingdom.

The polyamines putrescine, spermidine, and spermine have been identified in Jerusalem artichoke tubers (Serafini-Fracassini et al., 1980), though Phillips et al. (1987) found spermidine, diaminopropane, and cadaverine during the initial 24-h activation and onset of mitosis. Both research groups found a correlation between polyamine levels and early cell division, and that polyamines could induce a limited pattern of cell division.

The precise role of polyamines in the control of dormancy and the onset of cell division in Jerusalem artichoke tubers, and for that matter in plant development per se, remains in question. Evidence from arginine decarboxylase mutants of *Arabidopsis* does indicate a possible role in root meristem function (Watson et al., 1998).

9.1.1.2 Initial Events after the Fulfillment of Dormancy

Parenchyma cells go into dormancy in the DNA presynthetic phase (G_1) (Adamson, 1962; Mitchell, 1967), and when these cells are held on a culture media containing 2,4-dichlorophenoxyacetic acid

(2,4-D) to break or circumvent the dormancy, the cells enter mitosis (Bennici et al., 1982). The first and second divisions are well synchronized (Serafini-Fracassini et al., 1980); however, with further divisions, synchrony is gradually lost (Yeoman et al., 1965). Likewise, there are marked changes in the timing of the first and second cell cycles with the progression of dormancy (Bennici et al., 1982).

As mentioned previously, when dormant there are low amounts of polyamines in the tubers; however, they are synthesized rapidly when dormancy is broken (Del Duca and Serafini-Fracassini, 1993; Serafini-Fracassini et al., 1984), the onset of which occurs very early in the G_1 phase. Likewise, immediately after the fulfillment of the dormancy, there was a marked decrease in arginine and glutamine (precursors of polyamines) and a corresponding increase in polyamines (Durst and Duranton, 1966; Serafini-Fracassini et al., 1980).

With the onset of development, there is an increase in the rate of protein synthesis (Masuda, 1965, 1967), a shift in the metabolism of purine nucleotides (Le Floc'h et al., 1982; Le Floc'h and Lafleuriel, 1983a, 1983b), and an increase in overall metabolism. With sprouting, ribosomes present almost exclusively as monosomes, decreased considerably (Bagni et al., 1972). There is an increase in RNA synthesis (Gendraud, 1975a, 1975b; Gendraud and Pre'vôt, 1973), a greater incorporation of amino acids as dormancy is broken (Cocucci and Bagni, 1968; Duranton and Maille, 1963), and alterations in free and bound amino acids (Scoccianti, 1983). In addition, with the onset of development, there are significant alterations in the activity of certain enzymes, for example, phosphoenolpyruvate carboxylase activity increases four-fold (Dubost and Gendraud, 1987).

The interrelationship between the apical bud and subtending cells has stimulated studies on a possible membrane mechanism controlling the reallocation of internal constituents (Gendraud and Lafleuriel, 1985; Petel and Gendraud, 1986, 1988). During the formation of a neotuber, dry matter from the existing tuber is recycled into the new cells (Gendraud and Lafleureil, 1983). Control over the transfer is postulated to be via an ATPase mechanism on the plasma membrane (Petel and Gendraud, 1986). It is proposed that there is a shift in the plasmalemma's ATPase activity between before and after the fulfillment of the dormancy requirement, i.e., qualitative alterations in membrane proteins that correlate with the onset and release of dormancy (Petel and Gendraud, 1988). Changes in membrane proteins have been shown to be induced by exposure to cold (Ishikawa and Yoshida, 1985).

As the neotuber develops, there is a significant alteration in the water and nutrient status of the mother tuber in that without external sources, the requisites for growth must be recycled from within the tuber (Sueldo et al., 1991). When dormancy is maintained, a neotuber develops and the water content near the bud initially increases (15 days), while in the basal region of the mother tuber it decreases. Likewise, after a cold treatment (9 to 10 weeks at 4°C) that induces sprout formation, significant changes in water status also occur within the tuber with water moving from subtending regions into the growing bud. The reallocation of existing materials is supported by the fact that in dormant tubers the parenchyma cells more readily took up sucrose and tetraphenylphosphonium and the intercellular pH was higher than in nondormant cells (Gendraud and Lafleuriel, 1983). This was interpreted to indicate the possibility that the H^+-sucrose co-transport mechanism is involved in dormancy. In addition, there are changes in the uptake of abscisic acid between dormant and nondormant (faster) tubers (Ottono and Charnay, 1986).

9.2 RHIZOMES

Rhizomes are specialized underground stems that arise from belowground portions of the aerial stem. They facilitate dispersal in that they can form new vegetative shoots as far as 50 cm outward from the parent plant (Swanton, 1986). Rhizomes are generally white, vary in length, and have nodes that possess axillary buds from which branches and vegetative shoots may arise. Most undisturbed rhizomes are found in the upper 10 to 15 cm of the soil. Rhizome length varies with plant type, clone, and growing conditions (e.g., soil type). For example, at high plant population densities, rhizome appearance is delayed and the number per plant reduced, as is the average length,

node number, and amount of branching (Korovkin, 1985), suggesting that factors that limit carbohydrate supply inhibit rhizome formation.

Jerusalem artichoke clones can be separated into two general types based upon morphology, habitat preference, and phenology: wild clones with smaller, spindle-shaped tubers formed at the ends of long rhizomes, and cultivated clones with round tubers on short rhizomes clustered at the base of the main stem. The two types differ in rhizome number, length, total dry weight, and number of buds/rhizomes, with wild clones being substantially greater than cultivated ones (Swanton, 1986). There is also substantial variation among clones in the longevity of the rhizomes in the soil after the tops die in the late fall. The rhizomes of some clones decompose at the end of the growing season or during the winter, while others survive and produce plants in the spring. The longer rhizomes of wild clones function not only as conduits for the transport of photosynthates from the aerial plant parts to the developing tubers, but also as carbon storage sites, reproductive propagules, and a means of dispersal. In general, rhizomes are fragile and readily fragment via cultivation and animal feeding and, as a consequence, can become a weed control problem.

Regeneration of plants via rhizomes is substantially less than that for tubers; however, their reproductive potential is significant and varies depending upon a number of factors (e.g., clone, age, depth in the soil, size, environmental conditions). Immediately after harvest in the fall, most of the rhizomes were capable of regeneration (Konvalinková, 2003); if cut into 1-, 2-, and 4-cm lengths, 85 to 95% sprouted. The longer the rhizome piece, the greater the number and size of the shoots produced (Konvalinková, 2003). Tubers tend to produce larger shoots than rhizomes (i.e., 2.5 to 3 times), apparently due to the availability of substantially more stored carbon. Timing of rhizome sprouting (wild type) varied with planting time (July 23, September 1, October 15) and depth in the soil. Earlier planting resulted in shoot formation in 25 days when the rhizomes were planted 5, 10, or 20 cm in depth (Swanton, 1986); rhizomes planted 30 cm below the surface required ~300 days for emergence. Later planting dates also resulted in much delayed sprout formation (i.e., 214 to 258 days after planting). At 5- and 10-cm planting depths emergence was ~100%, at 20 cm this dropped to 80%, and at 30 cm, only 57%.

The basic developmental physiology of root formation in rhizomes (i.e., cell proliferation, differentiation of phloem and tracheids, organization of cambiums and formation of root primordia from the cambiums), and factors affecting it, has been detailed by Gautheret (1961a, 1961b, 1965, 1966a, 1966b, 1967, 1968, 1969; Spanjersberg and Gautheret, 1962, 1963a, 1963b; Tripathi and Gautheret, 1969) and several other scientists (Goris, 1968; Nitsch and Nitsch, 1956; Paupardin, 1966; Rücker and Paupardin, 1969; Tripathi, 1968) in a series of papers in the 1960s using an *in vitro* model. "Rhizogenesis" was modulated by minerals, salts, sugar, auxin, temperature, and light. Temperature and carbohydrate supply probably are the most relevant of these parameters under *in vivo* conditions.

9.3 TISSUE CULTURE

Plant tissue culture is the culturing of cells, tissues, or organs from plants under aseptic conditions. The material cultured ranges from cells or cell aggregates in suspension to mature or immature embryos, segments, or explants of plant organs, and isolated plant organs, shoot, or root tips. *Helianthus* species have been raised from diverse material, although Jerusalem artichoke has been predominantly micropropagated through the culturing of tuber tissue explants.

In the appropriate culture medium, tissue explants give rise to callus tissue. Callus tissue is comprised of large, thin-walled parenchyma cells. It is similar to the undifferentiated tissue produced by plants as a repair mechanism when they are injured. In tissue culture, dedifferentiated callus can be induced to form plantlets that grow into normal plants. The induction of callus occurs when a sterile explant is brought into contact with a nutrient medium, which contains substances that initiate cell division and support growth. An explant may be a uniform piece of tissue or tissue derived from different cell types (Yeoman, 1973). Storage parenchyma tissue from Jerusalem

artichoke tubers has a high degree of similarity among its constituent cells, in terms of DNA, RNA, and protein content (Mitchell, 1968, 1969). Therefore, it gives rise to a particularly uniform callus, which develops in a synchronous manner. The tubers of Jerusalem artichoke, along with storage organs of potato, carrot, and parsnip, were used in the studies that established the basic procedures for callus cultures (e.g., Steward et al., 1958; Yeoman et al., 1965). These are now regarded as classical plant culture systems.

To create explants, dormant Jerusalem artichoke tubers are typically cut into 25-mm-thick slices, from which cylinders of tissue are fashioned. Cylindrical shapes are favored because they can be uniformly reproduced and have a high ratio of surface area to volume that optimizes gas and nutrient exchange, and facilitates callus formation. A small size is desirable to maximize the number of explants obtained from the same tissue source. Jerusalem artichoke tuber explant size is typically around 2.4 by 2.0 mm. The minimum size is usually 8 mg and approximately 20,000 cells (Yeoman, 1973), although some reports have used smaller explant sizes (e.g., Caplin, 1963).

The growth medium used in plant tissue culture consists of a defined mixture of mineral salts, macro- and microelements (e.g., trace elements and an iron source), a source of sugar (usually sucrose), vitamins, amino acids, growth regulators (e.g., auxin, gibberellin, cytokinin), a chelating agent to remove unwanted metal ions (e.g., ethylene diamine tetra-acetic acid (EDTA)), and natural extracts such as coconut milk (Yeoman, 1973). Variations on the Murashige and Skoog (MS) medium tend to be favored for *H. tuberosus* tissue culture (Murashige and Skoog, 1962). Dormant Jerusalem artichoke tubers require media containing an auxin or related growth regulator, while cytokinin may not always be necessary (Yeoman, 1973). The medium can be liquid or solidified with agar. Cassells and Collins (2000) ranked 23 gelling agents, using a variety of growth parameters, for performance with Jerusalem artichoke explants, finding that a commercial agar (Sigma) performed best. Bacterial contamination can be a problem, but it can be prevented using antibiotics. Philips et al. (1981) tested six antibiotics and found that rifampicin was the most effective at controlling bacterial contamination, without affecting growth parameters, in cultured Jerusalem artichoke tuber explants.

Auxins and related growth factors commonly used to maintain callus tissue cultures are IAA (indole-3-acetic acid), NAA (naphthalene acetic acid), and 2,4-D (2,4-dichlorophenoxyacetic acid). Gibberellic acid and N^6-benzylaminopurine (BAP), a synthetic cytokinin, are also frequently used in Jerusalem artichoke growth medium. All growth regulators are used at low concentrations (e.g., around 10 μM). The optimum concentration of 2,4-D for cell division and fresh weight increase of Jerusalem artichoke tuber explants is around 10^{-6} M; little growth occurs in the absence of 2,4-D, while high concentrations inhibit growth completely (Finer, 1987; Yeoman and Aitchison, 1973). A dramatic increase in RNA synthesis occurs soon after the addition of 2,4-D to quiescent tissue. The nucleolus is the most important site of action for growth-regulating substances, and ^{14}C-labeled 2,4-D accumulates in the nucleoli of dividing cells of Jerusalem artichoke tuber explants (Yeoman and Mitchell, 1970; Zwar and Brown, 1968). A rapid rise in cell DNA follows the RNA peak, as protein synthesis escalates.

Only cells on the outer layer of explants are induced to divide, resulting in an active periphery surrounding a central nondividing core. It was observed that when Jerusalem artichoke tuber explants were excised in the light, only about half of the peripheral cells divided immediately after induction. However, if explants were prepared in low-intensity green light, practically all the periphery cells divided soon after induction (Yeoman and Davidson, 1971). In light conditions, resources are divided between cell division and structural growth; therefore, relatively more cell division occurs under darker conditions. The degree of peripheral cell division can be improved by the addition of amino acids to the growth media (Yeoman and Aitchison, 1973). Low-intensity white light enhances the rhizogenic effect of auxin, with a positive effect on the production of rhizome tissue in Jerusalem artichoke tuber explants (Gautheret, 1971).

After the induction of tuber explants, cell division proceeds quickly. The cell number for a Jerusalem artichoke tuber explant increased 1000% over 7 days at 25°C (Yeoman et al., 1965).

Alternating temperatures (e.g., 26°C day and 20° night) may optimize callus growth (Capite, 1955). Individual cell size decreases markedly over the first 2 weeks of culture, as cell division outstrips cell growth. Growth media composition affects cell size in Jerusalem artichoke explants; cells were smaller in media containing 2,4-D and coconut milk than in media containing 2,4-D alone (Yeoman and Aitchison, 1973). The balance between cell division and cell expansion can be manipulated by pretreating tuber explants (Setterfield, 1963).

Different procedures and growth media composition can be used to determine the type of Jerusalem artichoke tissue that predominantly grows in culture (e.g., Minocha and Halperin, 1974; Roche and Cassells, 1996). Different media compositions, for instance, favor either shoot or root development. A number of protocols have successfully promoted adventitious shoot formation in seedling explants of sunflower (*H. annuus* L.), Jerusalem artichoke (*H. tuberosus*), and *H. annuus* × *H. tuberosus* hybrids (e.g., Espinasse and Lay, 1989; Espinasse et al., 1989; Greco et al., 1984; Pugliesi et al., 1993a; Witrzens et al., 1988). The addition of growth regulators (e.g., BAP, IAA) or ethylene inhibitors (e.g., 10 μ*M* AVG), for example, increased the number of adventitious shoots formed from callus (e.g., Robinson and Adams, 1987; Witrzens et al., 1988). Somatic embryos (i.e., embryos produced from nonreproductive plant cells rather than reproductive germ cells) were produced in some reports of adventitious shoot formation, in media containing large amounts of sucrose (e.g., Pugliesi et al., 1993a). To optimize embryo production and conversion into plants, a number of stages are necessary in which growth regulators and cultural conditions are varied (Pélissier et al., 1990).

Root formation in *Helianthus* callus can be induced in certain media without growth regulators (Espinasse et al., 1989). However, inducing root formation can be more difficult than inducing shoot formation. Rhizome and root formation was induced in Jerusalem artichoke callus by the presence of specific amounts of auxin and sugar, and a particular balance of light and temperature (Gautheret, 1966c, 1969). Devi and Rani (2002) used transformation with a strain of *Agrobacterium rhizogenes* carrying an Ri plasmid to induce rooting in *H. annuus* × *H. tuberosus* hybrids micropropagated from immature embryos, in an MS basal media containing the growth substances 2,4-D and IBA. The transformed plants produced prolific callus and shoots, but only sparse roots.

Electron microscopy (EM) has been used to study the development of Jerusalem artichoke explants in tissue culture. Tulett et al. (1969) described procedures for preparing tuber explants and callus tissue for EM to look at cell structure. Small pieces of callus were fixed in 6% glutaraldehyde in 0.1 *M* phosphate buffer at pH 6.9, at room temperature for 2 h, and then at 5°C overnight. After fixing, tissue was washed in several changes of phosphate buffer. Postfixation treatments involved immersion in a 1 to 2% buffered osmium solution for 1 h or a 2% aqueous solution of potassium permanganate for 1 to 2 h.

Two distinct membrane-bound systems have been described for Jerusalem artichoke plastids in tissue cultures under EM: an electron-dense sac-like central system (*corpo opaco*) and a peripheral system (Gerola and Dassu, 1960). The central system is morphologically variable and likely to store proteins. The peripheral system consists of irregular tubules and cisternae, with plastids occurring in clusters, especially near the nucleus (Tulett et al., 1969). The peripheral system may be involved in the transport of materials through the plastid envelope (Yeoman and Street, 1973).

Callus cultures derived from Jerusalem artichoke tubers are initially quiescent and have to be induced to divide. The induction of division is accompanied by a transformation in cell structure, which reflects changes in metabolism (e.g., Gamburg et al., 1999). Within an hour of the excision of Jerusalem artichoke tuber explants, ribosomes increase in abundance. They take the form of helices when scattered in the cytoplasm, and spirals when associated with the endoplasmic reticulum, and increase in frequency over time in line with the rate of protein synthesis (Yeoman and Street, 1973). Electron-dense bodies appear soon after in cell vacuoles, and to a lesser extent in the cytoplasm (Bagshaw et al., 1969), while crystal-containing bodies form in cells, which may contain hydrolytic enzymes (Bagshaw et al., 1969; Gerola and Bassi, 1964). Dormant Jerusalem artichoke tuber explants contain a variety of mitochondrial profiles, including distinctive cup-shaped

mitochondria (Yeoman and Street, 1973); during growth in tissue culture mitochondria display a wider range of forms, including complex bell shapes, long cylindrical rods, and branched and plate structures (Bagshaw et al., 1969). As the cells approach division, the nucleus becomes more rounded, with dense aggregations of chromatin around it and elongated structures that may extend into the cytoplasm (Yeoman et al., 1970). The nucleoli become less compact, within an electron-dense region of granular particles (Jordan and Chapman, 1971). The dissolution of the nuclear envelope is followed by mitosis and cell division, as described by Bagshaw et al. (1969) and Yeoman and Street (1973).

Following division, considerable anatomical and biochemical changes occur, with the resulting callus differing from the originating tissue. Callus derived from Jerusalem artichoke tuber cells, for instance, can even lack inulin (Kaneko, 1967). Tracheary elements (xylem) form rapidly in callus. Factors affecting xylem differentiation include levels of auxin, cytokinin, and nitrogen in the growth media, and temperature (Minocha and Halperin, 1974; Philips and Dodds, 1977).

Plant tissue culture is an important tool in plant breeding programs and in the conservation of genetic resources. Jerusalem artichoke breeders can draw directly upon the experience and techniques developed for sunflower micropropagation, as reported in numerous publications (e.g., Alissa et al., 1986; Bergounioux et al., 1988; Espinasse and Lay, 1989; Finer, 1987; Freyssinet and Freyssinet, 1988; Greco et al., 1984; Hendrickson, 1954; Lupi et al., 1987; Paterson and Everett, 1985; Pélissier et al., 1990; Power, 1987; Pugliesi et al., 1991; White, 1938; Wilcox et al., 1989). Sunflower plantlets have been regenerated from zygotic and immature embryos, seedling hypocotyls and cotyledons, and stem and root apices, using protocols and growth media that are also suitable for Jerusalem artichoke. To complement this, Jerusalem artichoke tuber explants are a model tissue culture system.

Crosses between sunflower and Jerusalem artichoke have been exploited in *Helianthus* breeding programs (Davydoviĉ, 1947; George, 1993). Jerusalem artichoke cultivars have also been produced by crosses with sunflower (e.g., 'Sunchoke'). Jerusalem artichoke and wild *Helianthus* can provide the germplasm needed to enhance resistance of cultivated sunflowers to pests and diseases. For instance, resistance to rust (*Puccinia helianthi* Schw.) has been incorporated from wild *H. annuus* (Putt and Sackston, 1963); resistance to *Alternaria helianthi* (Hansf.) Tubaki & Nishih. has been found in Australian populations of silverleaf sunflower *H. argophyllus* Torr. & Gray (Kochman and Goulter, 1983); and *H. tuberosus* carries potentially useful genes for resistance to *Sclerotinia sclerotiorum* (Lib.) de Bary (Orellana, 1975). However, reproductive barriers limit hybridization between *Helianthus* species, with low seed production and F_1 sterility in hybrids being common. These sterility barriers can be overcome using plant tissue culture techniques. Regenerated plants show a high degree of nonhomologous gene translocation (Pugliesi et al., 1993a). Hybrid embryos can therefore be regenerated and multiplied in large numbers, to greatly increase the chances of fertile hybrids being produced.

Methods for the culture and regeneration of interspecific Jerusalem artichoke and sunflower hybrids have been described by Witrzens et al. (1988) and Pugliesi et al. (1993a). Witrzens et al. (1988) found that immature embryos were the only explant type to give consistently regenerable cultures, although one genotype was regenerated from tuber tissue. Around 30% of shoots produced capitula (inflorescences) if the growth medium contained 30 $g \cdot l^{-1}$ sucrose, while flowering was even more premature if the sucrose was replaced by 40 $g \cdot l^{-1}$ glucose. The addition of gibberellic acid (GA_3) to the growth media assisted in stem elongation (Witrzens et al., 1988).

Pugliesi et al. (1993a) regenerated plantlets from cotyledon explants of *H. tuberosus*, *H. annuus* × *H. tuberosus* crosses, and backcrosses of hybrids with *H. annuus*. Cotyledons were cultured on MS basal medium supplemented with IAA and 6-furfurylaminopurine (kinetin) or BAP. Shoot regeneration occurred on most media tested, but was best on a medium with a high concentration of cytokinin (BAP or kinetin, 0.2 $mg \cdot l^{-1}$) and lower concentrations of auxin (IAA, 0.1 $mg \cdot l^{-1}$). Prolonged culture, with successive subculture on MS medium without growth regulators, resulted in embryo formation and shoot differentiation, with plantlets successfully transplanted into soil.

Tissue culture facilitates the screening of *in vitro* germplasm for desirable traits, such as *Sclerotinia* resistance or cold and salt tolerance (Cassells and Walsh, 1995; Escandon and Hahne, 1991). Culture techniques will become increasingly important if gene transfer and genetic manipulation techniques are widely applied to Jerusalem artichoke. Sunflower in tissue culture has been routinely transformed using direct gene transfer (gene guns), *Agrobacterium*-mediated gene transfer, and other genetic manipulation techniques (e.g., Grayburn and Vick, 1995; Knittel et al., 1994; Laparra et al., 1995; Moyne et al., 1989; Rao and Rohini, 1999; Shin et al., 2000). *H. annuus* × *H. tuberosus* hybrids have also been genetically transformed (e.g., Pugliesi et al., 1993b). Therefore, the techniques are in place for the genetic manipulation of Jerusalem artichoke (see also Section 8.12).

Tissue culture enables germplasm of Jerusalem artichoke to be preserved in biodiversity conservation programs. Once established in tissue culture, Jerusalem artichoke cultures can be stored for extended periods at low temperatures. *In vitro* cultures of nine cultivars, for example, were maintained in a Canadian study as a backup to a field germplasm collection (Volk and Richards, 2006). Survival was highest for plants kept for 3 months at 5°C, while after 6 months 52% of cultures remained healthy.

Cryopreservation (the nonlethal storage of biological tissue at ultra-low temperatures) is increasingly used with tissue culture to conserve plant material for long periods (Benson, 1994). Excised shoot tips from *in vitro* tuber-derived Jerusalem artichoke cultures were cryopreserved using a plant vitrification solution containing ethylene glycol, dimethyl sulfoxide, glycerol, and sucrose. Vitrification prevents ice crystals from forming as the plant material freezes. The Jerusalem artichoke material could be revived and grown after 30 min at 0°C (Volk and Richards, 2006). Jerusalem artichoke accessions can therefore be preserved at low temperatures in tissue culture, and potentially be stored for longer periods using cryopreservation techniques.

9.4 SLIPS

Slips (transplants), derived from sprouted tubers, can be used to increase the plant population of a clone over what would be realized via direct field planting of the tubers. To obtain slips the tubers are planted 4 to 6 cm deep in warm beds or within a greenhouse using standard potting media. The tubers should be spaced such that they are not touching but otherwise tightly arranged. Individual slips are harvested by carefully detaching them at the tuber when they are 20 to 30 cm tall and have four or more fully expanded leaves. Less mature slips have few if any roots, have small-diameter stems that are more likely to be broken or damaged, and grow more slowly than larger, more robust slips. Smaller slips should be left for a subsequent harvest. The slips can not be transplanted directly into the field without substantial losses and should first be placed in potting media under mist for 10 to 12 days before transplanting into the field. Removal from the mist to harden off for several days is recommended, especially if hot and dry conditions prevail during field planting. The slips, therefore, are collected in a succession of harvests every 4 to 6 days; as a consequence, it takes 4 to 5 weeks to produce the maximum number of slips plus additional time for rooting.

The number of sprouts produced per tuber varies with tuber size; small tubers (i.e., 30 g) produce fewer slips (~7) than larger tubers (50 to 70 g), which produce 13 to 15 plants each (Kays, unpublished data). Generally the slips from the larger tubers have thicker stems, are more robust, and are less inclined to droop. If the objective is to significantly increase the plant population, direct planting of a "seed tuber" in the field results in only one plant, while approximately 15 plants per tuber can be produced using slips. Slips may also be used for earlier field stand establishment; however, the disadvantages of this method are sufficient that it is seldom used. For example, it greatly increases labor costs, and the time interval required to obtain the maximum number of sprouts per tuber significantly staggers the age of the stand in the field. However, when only a small number of tubers of a cultivar are available and the objective is to increase the propagation material for the following year, the use of slips is effective.

9.5 CUTTINGS

Stem cuttings from several *Helianthus* species (e.g., *H. tomentosum* Michx., *H. debilis* Nutt.) can be readily rooted under appropriate conditions (Norcini and Aldrich, 2000; Phillips, 1985). A number of studies have also been conducted using *H. annuus* hypocotyls as a rooting model (Liu et al., 1995; Wample and Reid, 1979), though they have only limited relevance to rooting stem cuttings. While stem cuttings do not represent a normal reproductive mechanism for *Helianthus*, they can be used to rapidly expand clonal material when seeds are not available. For *H. debilis*, best results were obtained using subapical cuttings trimmed to distal leaves and rooted in a well-drained medium with frequent misting (e.g., 9 sec/2.5 min) and under partial shade (i.e., 30% shade) (Norcini and Aldrich, 2000). Survival was best without the use of a rooting hormone (1 *H*-indole-3-butyric acid solution). Nontreated cuttings had 100% survival and were sufficiently rooted for transplanting in 17 to 21 days. For both *H. tomentosum* (Phillips, 1985) and *H. debilis*, a well-drained medium is desirable (e.g., sand and peat moss, 3:1).

The potential of using stem cuttings for the propagation of *H. tuberosus* was tested (single clone; Kays, unpublished data). Cuttings of two lengths (15 and 25 cm), two stem diameters (medium and large), two positions (apical and subapical), and with and without hormone (100 ppm IBA talc) were placed in an artificial medium (2:1 perlite and peat moss) under mist and evaluated (1 to 5 rating) after 45 days. All cuttings rooted. However, there was considerable variation in the number of roots formed within and between treatments. Propagation of Jerusalem artichoke via stem cuttings does not appear to be a viable option for two reasons: (1) the time required for the stock plants to attain a sufficient size for cuttings plus the time required for rooting of the cuttings would make the production season too short for most locations, and (2) plants derived from rooted cuttings produced few tubers. The latter problem appears to be due to the fact that rhizomes normally arise from the underground portion of the stem and not the roots. They seldom formed on the underground portion of the rooted aerial stems, though the potential to do so may vary among clones.

9.6 SEED

Seed reproduction is important in wild populations and is an essential part of Jerusalem artichoke plant breeding programs. Jerusalem artichoke is an obligate outcrosser that exhibits a high level of self-incompatibility (Toxopeus, 1991; van de Sande Bakhuyzen and Wittenrood, 1950). Plants do, however, readily outcross with other clones and produce seed (Swanton and Cavers, 1989; Le Cochec, 1985). The seeds are considerably reduced in size compared to cultivated sunflower and, in general, have a substantially lower germination rate. Mature seeds also display a strong dormancy that can be suppressed with various treatments (Toxopeus, 1991).

Seed yield per plant varies widely with genotype, location, and production conditions. Wild populations tend to flower more and have higher achene viability than cultivated clones (Westley, 1993). In general, low seed production for the species may be in part related to the late flowering and cooler temperatures in the fall. The number of seeds per flower, number of seeds per plant, and mean seed size of six clones representing three ecotypes (two cultivated, two weedy, and two wild) varied substantially (Swanton, 1986). Weedy clones produced ~5 seeds per flower while the cultivated clones had from 0.08 to 2 seeds. Variation in the mean seed weight among clones was relatively small (3.5 to 4.8 mg), though individual seed weights ranged from 0.8 to 10.8 mg. The number of seeds per plant varied from 5.6 to 78. In contrast, the seed yield from five commercial cultivars allowed to outcross ranged from 88 to 1,058 seeds per plant (Lim and Lee, 1989).

A common problem in a number of wild *Helianthus* species is the presence of a seed coat dormancy mechanism. Though at a much lower level, some inhibition can also be seen in cultivated sunflowers. Kamar and Sastry (1974) found that 20-day-old seeds had a substantially higher germination than did more mature seeds (i.e., 30 and 40 days old), indicating the presence of a dormancy mechanism. The onset of dormancy early in seed development is typical of many seed-

bearing species in that it prevents premature germination (vivipary) during development (Kays and Paull, 2004). Seed dormancy of varying levels is found in all of the wild species of *Helianthus* but is particularly strong in the annual desert species *H. deserticola* Heiser, *H. anomalus* Blake, and *H. niveus* ssp. *tephrodes* (A. Gray) Heiser (Heiser et al., 1969).

Several methods to facilitate germination have been tested, such as planting the seed in pots that are placed outside during the winter for 3 to 4 weeks, where they are exposed to varying temperatures and freezing and thawing (Heiser et al., 1969). While germination improved, it was seldom over 50% and was not effective for xerophytic annual species. Chemical treatment of the seed with 2-chloroethyl phosphonic acid, an ethylene-releasing compound (Kamar and Sastry, 1974, 1975; Zimmerman, 1977), gibberellic acid (GA_3), and benzyladenine (Kamar and Sastry, 1974, 1975) has been shown to increase the germination of freshly harvested, cultivated sunflower seed. Likewise, dehulling facilitates germination (Harada, 1982; Kamar and Sastry, 1974, 1975). Tests on four difficult-to-germinate species (*H. bolanderi* A. Gary, *H. petiolaris* Nutt., *H. anomalus*, and *H. niveus* ssp. *tephrodes*) showed that the single most effective treatment was to remove the hull and seed coat (i.e., 90% germination) (Chandler and Jan, 1985). This could be improved with additional treatments (i.e., mechanical scarification, a 1-h soak in a 100 $mg \cdot l^{-1}$ solution of GA_3, and hull removal). Jerusalem artichoke seed germination is also substantially improved with the removal of the seed coat (Lim and Lee, 1990).

The following technique, utilizing sterile conditions at each step, is routinely used for facilitating the germination of wild *Helianthus* species (Seiler, personal communication). The seeds are first surface sterilized for 15 to 20 min using a 1% (w/v) solution of sodium hypochlorite, rinsed with distilled water, and then scarified by cutting a small portion of the seed coat from the wide end of the seed. The seeds are then treated with GA_3 at 100 $mg \cdot l^{-1}$ in distilled water for 1 h and subsequently placed on moist filter paper in a petri dish and held in the dark overnight (21°C). The following day the seed coat is carefully removed and the seedling rinsed with water, placed in a new petri dish with moist filter paper, and returned to dark storage for 2 days. A fungicide such as benomyl can be used to reduce the possibility of fungi contamination. After 2 days, the petri dishes are placed under fluorescent lighting until the seedlings are of sufficient size for transplanting.

Jerusalem artichoke seeds are not used as reproductive propagules for commercial production of the crop since the plants have relatively high levels of male sterility and incompatibility and the seed, when present, generally represents crosses between the mother plant and an unknown pollen donor. Thus, the genetic makeup of the seed is unknown, and with many polyploid species, the propensity for the offspring to be superior to the parent lines is generally extremely low. For example, from around 8,000 seedlings in a Jerusalem artichoke breeding program, only 17 were saved for evaluation from clonal material in the subsequent year (Mesken, 1988). In addition, Jerusalem artichokes derived from seed typically are less vigorous than the plants emerging from tubers. Hence, plants from tubers grow much more rapidly and establish a closed canopy more quickly. Finally, Jerusalem artichoke seeds typically have a low germination rate, decreasing their potential utility as a commercial means of propagation. Thus, while there have been occasional reports of successful production of the crop from seed (Lim and Lee, 1990), the potential of seed at this point in the genetic manipulation of the crop remains remote.

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10 Developmental Biology, Resource Allocation, and Yield

To understand the developmental biology of the Jerusalem artichoke, it is important to be cognizant of the fact that wild, domesticated, and intermediate clones are found and, while similar, differ significantly. Due to the very limited investment in breeding over the past 100+ years (Schittenhelm, 1987a; Toxopeus et al., 1994), especially when contrasted with rice, corn, or wheat, cultivated clones are generally not too far removed from their wild ancestors. Wild populations are frequently found in disturbed habitats such as roadsides, old fields, meadows, moist river and stream banks, and waste areas (Alex and Switzer, 1976; Gleason and Cronquist, 1963), not only around what is believed to be the general center of origin of the species, but as escapes in other areas of the world (Balogh, 2001; Konvalinková, 2003; Řehořek, 1997).

As an indigenous North American species, Jerusalem artichoke is a successful colonizer, readily invading open areas and land occupied by a cross section of native and cultivated species. Its success as a plant is in large measure due to its very effective and efficient resource acquisition and allocation. The plant invests substantial carbon and nutrients early in its development into stem, branch, and leaf growth, facilitating the exploitation of aboveground resources. Later in the developmental cycle carbon and nutrients are allocated to rhizomes and tubers, enabling the species to spread laterally outward, colonizing new areas. The plant thereby creates a zone of captured resources above- and belowground that makes it difficult for other species to penetrate or survive.

The Jerusalem artichoke can reproduce by two primary means. It can reproduce and colonize an area by the allocation of photosynthate and nutrients into both asexual (tubers and, to a lesser extent, rhizomes) and sexual (seed) reproductive organs. Flexibility in the amount of resources allocated between sexual and asexual means of reproduction confers a selective advantage in that conditions that inhibit or block sexual production (lack of pollen, herbivory of floral structures, undesirable weather) allow increased allocation to asexual reproduction. Artificially reduced allocation of resources to sexual reproduction, for example, results in a substantial increase in those allocated to asexual means. With flower bud removal, more (82 vs. 69) and larger (4.4 vs. 3.8 g) tubers were formed per plant than those with unlimited sexual reproduction (Westley, 1993). Total biomass was not altered, potentially indicating a relatively complete diversion of resources to asexual reproduction when sexual reproduction is blocked. From a reproductive standpoint, the risk of making it to the next season is high with sexual reproduction and relatively low with asexual reproduction. Increased investment in tubers increases the opportunity for sexual reproduction in the future.

Through natural selection, wild clones have developed favorable energy allocation cost–benefit ratios for the environmental conditions under which they evolved. With domestication, however, humans have altered this allocation pattern. Both wild and cultivated clones exhibit rapid increases in height and number of leaves early in their developmental cycle. In a study characterizing the morphological variation among six populations of Jerusalem artichokes (two cultivated clones, two found as weeds in cultivated crops, and two from river banks), the attributes that varied the most were leaf number and tuber dry weight (Swanton, 1986; Swanton and Cavers, 1989) (Table 10.1). Cultivated clones had much reduced rhizome length and seed development, and increased leaf number and dry matter allocated to tubers. Short rhizomes allow increased assimilate allocation for tuber enlargement; the long rhizomes of wild clones have adaptive significance for survival and dispersion, while small tubers increase the probability of escape from predators. Seed production

TABLE 10.1
Morphological Variation among Wild and Domesticated Clones of Jerusalem Artichokes Grown under Uniform Conditions (i.e., Two Cultivated and Two Wild Clones Gathered from River Banks and Two Found as Weeds in Crop Fields)

Plant Part	Morphological Parameters (mean/plant)	Range
	Plant height	102–186 cm[a]
Leaves	Number per plant	372–953
	Leaf dry weight per plant	55.4–175.2 g·plant^{-1}
	Number of dead leaves per plant	2.5–491.0
	Dry weight of dead leaves per plant	0.3–72.2 g·plant^{-1}
Stems	Stem diameter	1.6–2.4 cm
	Stem dry weight per plant	31.9–99.3 g·plant^{-1}
	Dry weight of underground stem per plant	13.1–39.0 g·plant^{-1}
Branches	Number of branches per plant	30.1–52.6
	Dry weight of branches per plant	31.0–131.2 g·plant^{-1}
Roots	Dry weight of roots per plant	6.1–19.5 g·plant^{-1}
Rhizomes	Number of rhizomes per plant	1.0–76.0
	Longest rhizome	1.0–47.6 cm
	Number of rhizome buds per plant	1.0–10.5
	Dry weight of rhizomes per plant	2.0–98.1 g·plant^{-1}
Tubers	Number of tubers per plant	35.1–90.1
	Mean tuber length	10.6–18.9 cm
	Mean tuber diameter	1.3–7.3 cm
	Dry weight of tubers per plant	2.0–98.1 g·plant^{-1}
Flowers	Number of flowers per plant	5.6–78.0
	Number of flower buds per plant	1.8–10.8
	Dry weight of flowers per plant	1.9–17.1 g·plant^{-1}
	Number of seeds per 100 flowers	8.0–536.0
	Flower head diameter	1.30–1.80 cm
	Dry weight of flower buds per plant	0.01–0.75 g·plant^{-1}
	Dry weight of seeds per 100 flowers	0.04–1.82 g·100 flowers^{-1}
	Mean seed dry weight	3.45–4.81 mg
	Range in seed dry weight	0.78–10.79 mg

[a] Canopy heights of cultivated clones from others ranged from 119 to 164 cm (9 cultivars; Hay and Offer, 1992) to 115 to 275 cm (30 clones; Kiehn and Chubey, 1993).

Source: Adapted from Swanton, C.J., Ecological Aspects of Growth and Development of Jerusalem Artichoke (*Helianthus tuberosus* L.), Ph.D. thesis, University of Western Ontario, London, 1986.

in wild clones is also much greater than in cultivated clones, increasing the opportunity for genetic variation and dispersal to new sites. Seed number was positively correlated with rhizome length and inversely related to tuber dry matter per plant.

While this chapter focuses upon cultivated clones, differences between domesticated and wild clones will be noted when appropriate.

10.1 DEVELOPMENTAL STAGES

The onset of "seed tuber" sprouting sets in motion a dramatic series of interdependent developmental processes that result in the three-dimensional morphology of a Jerusalem artichoke plant. Development is highly plastic, with the final structural morphology a function of the genetic makeup of the clone and the conditions under which the plant develops. While the final morphology will therefore vary due to many factors, its makeup is critical to the performance of the plant, and as a consequence, a general understanding of the sequence of development of individual components of the plant and factors that affect them is advantageous.

Development can be separated into five primary stages: emergence and canopy development, rhizome formation, flowering, tuberization, and senescence. The numerical development of plant parts within each stage of the developmental sequence is illustrated in Figure 10.1 for a long-season cultivar (McLaurin et al., 1999). While the temporal relationships among the components of the plant will vary with the clone in question and environmental factors (e.g., soil and air temperature, soil moisture level), the general developmental sequence is similar.

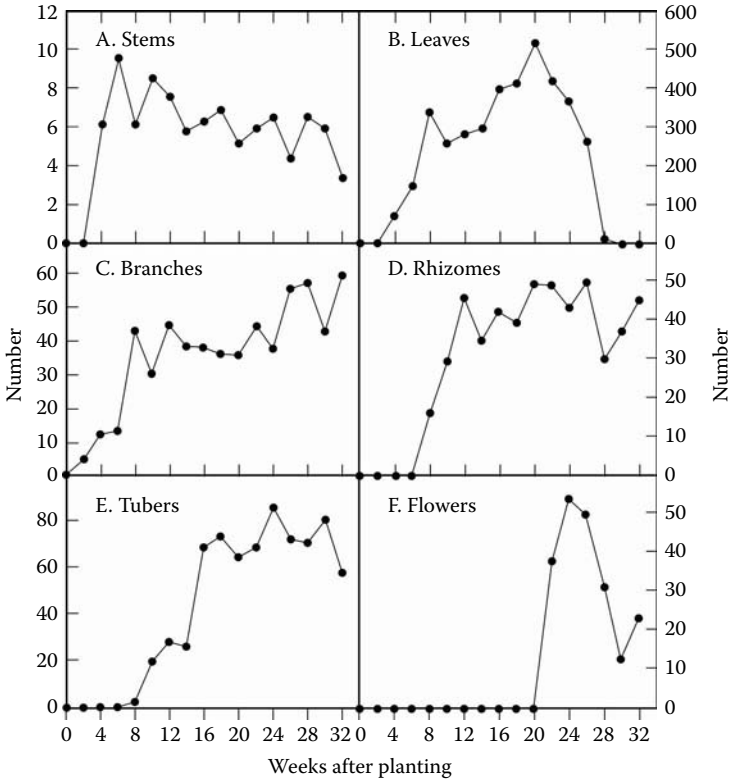


FIGURE 10.1 Changes in the number of (a) stems, (b) leaves, (c) branches, (d) rhizomes, (e) tubers, and (f) flowers per plant (cv. 'Sunchoke') during the growing season (30°57'N). (After McLaurin, W.J. et al., *J. Plant Nutr.*, 22, 1303–1313, 1999.)

10.1.1 Emergence and Canopy Development

10.1.1.1 Stems*

A new cycle of growth and development begins with sprouting of the seed tuber and the emergence of individual sprouts (shoots) that form the stems upon which the aerial canopy develops. Stem size, number, and position have a pronounced influence on canopy architecture in that they represent the scaffolding for the primary branches. The three-dimensional positioning of primary and secondary branches is critical in maximizing light reception and photosynthesis.

If the seed tubers are not dormant, under favorable conditions emergence is generally 98 to 100% (Hay and Offer, 1992). In warmer locations in which the dormancy requirement has not been completely fulfilled or under dry conditions (Mezencev, 1985), sprouting and shoot formation may be lower. For example, seed tubers stored at 20°C required 140 days for emergence, while at 1.3°C, 45 to 64.5 days were required (Stelzner, 1942). Threshold temperatures for sprouting are 2 to 5°C (Barloy, 1984; Kosaric et al., 1984), with higher temperatures accelerating the process (Tsvetoukhine, 1960). Film plastic over the bed, for example, generally results in warmer soil temperatures and earlier sprouting (Morrenhof and Bus, 1990), while low-soil-oxygen conditions delay sprouting (Barloy, 1984; Kosaric et al., 1984). Generally emergence in the spring begins 3 to 5 weeks after planting (Figure 10.1a), with most clones falling into this period (Baillarge, 1942; Bacon and Edelman, 1951; McLaurin et al., 1999); however, with warm conditions or the use of presprouting they can emerge within 7 to 10 days.

The number of stems per plant reported in various studies depend upon how they are counted, i.e., emerging from the ground or emerging directly from the seed tuber. In either case, the number is strongly modulated by cultivar (Gallard, 1985; Lemercier, 1987) and tuber size, with larger seed tubers or tuber pieces yielding more sprouts and therefore stems (Delbetz, 1867; Morrenhof and Bus, 1990), significantly impacting the subsequent canopy architecture. The recommended seed tuber or tuber piece size is around 40 to 60 g fwt (Kosaric et al., 1984), with a diameter larger than 35 mm (Morrenhof and Bus, 1990). Increases in seed tuber size can increase final yield, though above a certain size, yield increases do not compensate for the increased cost of propagation material (Barloy, 1984; Cors and Falisse, 1980). Tuber age can also alter the number of stems per plant (Gallard, 1985).

As illustrated by Figure 10.1a, approximately nine stems** were formed by the fourth week after planting; however, stem number is not static. The number declined to an average of four to six by the end of the season, with losses typically caused by shading of smaller, less vigorous stems.

The size of stems (length and diameter) is modulated by a number of factors. High plant population density results in accelerated elongation early in the season and taller plants; however, at very high plant populations the final height and number of internodes are lower (Hogetsu et al., 1960; Korovkin, 1985). The number of internodes on the stems tends to be more constant in early, rather than in late, cultivars (Milord, 1987). Short photoperiods result in reduced stem length, stem dry matter, and leaf growth, while long day lengths promote stem and leaf growth (Soja and Dersch, 1993).

10.1.1.2 Branches***

The presence and degree of branching vary with clone, plant population density, and photoperiod (Pas'ko, 1982). Individual clones (160) differed in their branching habit (e.g., nonbranched, intermediate, extensive). The absence of branches on the main stem is relatively rare. In branched clones, lateral branches are formed, starting at the base of the plant, in the axils of the leaves, generally

* The main ascending axes of the plant that emerge from the belowground seed tuber.

** The number emerging from the ground and not directly from the seed tuber.

*** A secondary stem emerging from an aboveground primary stem.

two at each node when the leaves are opposite. From these, secondary branches may be formed depending upon the distance of the node from the base of the primary branch, the position of the primary branch on the stem, and its photosynthetic potential. By the 39th day after planting, a typical plant (cv. 'Sunchoke,' ~50 cm tall) has ~33 lateral branches and 15 secondary branches (Figure 10.1c). There were a total of 171 nodes on lateral branches.

The number of branches formed is strongly influenced by cultivar, growing conditions, and plant population density (Korovkin, 1985; Mezencev, 1985). As the plant population increases, branch number decreases. Branches begin forming on the stems shortly after emergence and continue to form throughout much of the growing season (Figure 10.1c) (McLaurin et al., 1999). Initially there is a rapid increase in branching, predominantly at the base of the plant (Tsvetoukhine, 1960), which terminates toward the middle of the growing season. Branches are formed toward the top of the plant later in the growth cycle (Ustimenko et al., 1976), and shortly after the onset of flowering, branch formation again increases, as axillary buds developed into flowering branches (Garner and Allard, 1923; Zubr and Pedersen, 1993). Flower bud formation at the apex of the stems terminates vertical development and is followed by the induction of numerous small lateral branches with flowers.

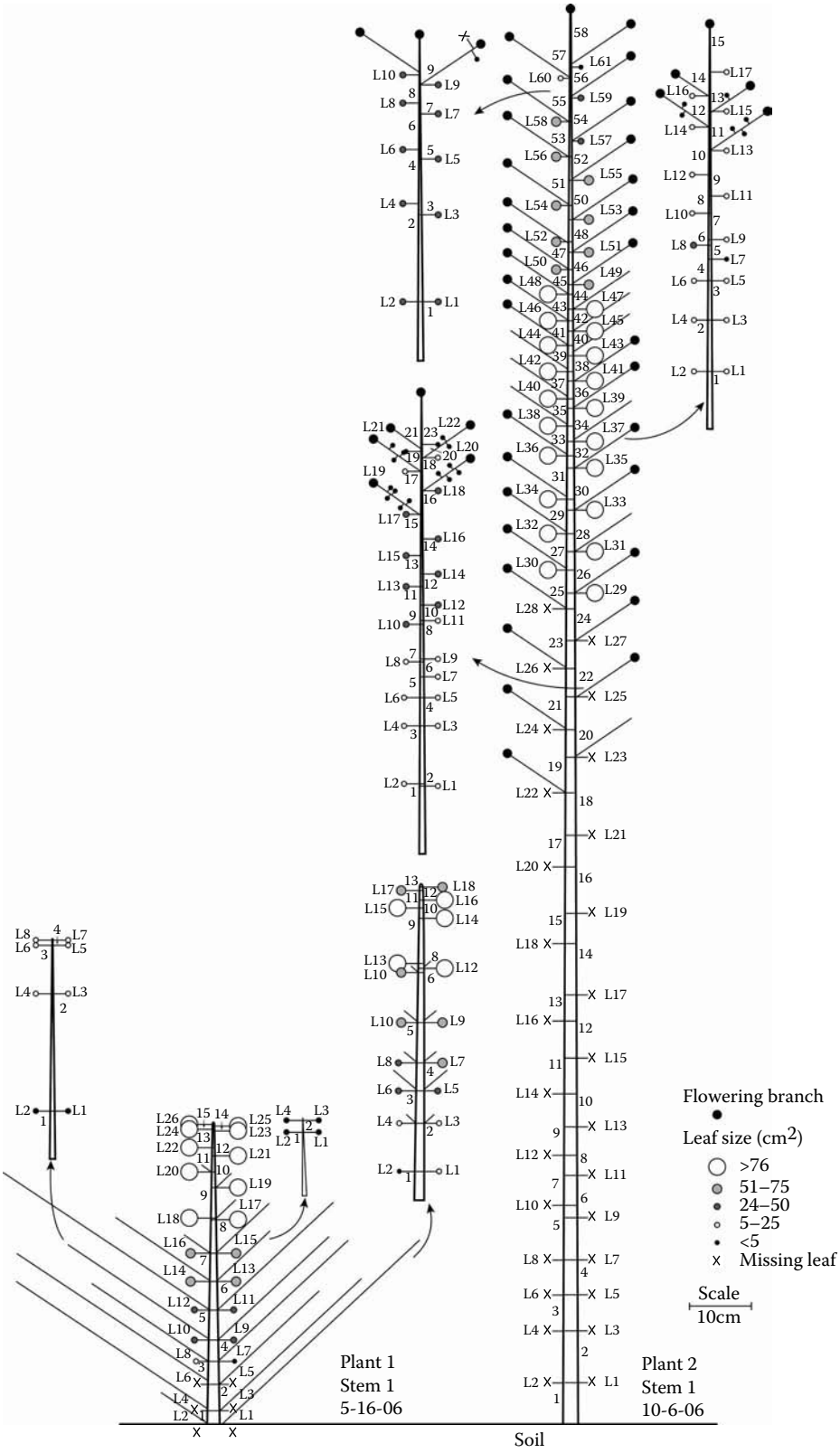
10.1.1.3 Leaves

Leaf size varies with position on the plant. Early leaves tend to be much smaller than those formed later (Figure 10.2). Typical leaves are 10 to 20 cm long, though the size varies among clones. For example, the average leaf fresh weight of 14 clones ranged from 1.9 to 5.0 g (0.34 to 0.93 g dwt), and their leaf area from 73.8 to 152 cm^2 (Berenji and Kisgeci, 1988). The position of the leaf on the plant also influences size. The size initially increases with height on the stem or branch, but then subsequently decreases toward the apex. For example, initial leaf blades on the first branch (Figure 10.2) were 8.7 × 2.3 cm, with a petiole length of 1.8 cm and a leaf area of 17 cm^2, while the 13th leaf on the branch was 13 × 8.7 cm, with a petiole length of 5.4 cm and a leaf area of 86 cm^2. The shape also changes with increasing size, as indicated by the change in the length-to-width ratio (i.e., 3.8→1.8).

The first leaves are arranged opposite on the stem, but by the 19th or 20th node (Hogetsu et al., 1960; Wittenrood, 1954) the plant has switched to alternate. Plant population density does not appear to alter the pattern (Hogetsu et al., 1960). Occasionally some plants will have a stem/branch with three leaves at each node, while leaves elsewhere on the plant are opposite. The location of the shift from opposite to alternate appears to vary with cultivar and position on the plant. For example, in the clone illustrated in Figure 10.2, the change in orientation on the stems was around node 9. There is a transition region for several nodes before emerging in a 3/8 phyllotaxy. Like the stems, leaves on branches are also initially opposite but eventually change to an alternate phyllotaxy. The chronological and developmental timing of the shift appears to vary depending upon the branch in question; therefore, the shift in leaf orientation is not uniform throughout the plant. On lateral branches it may occur earlier (e.g., node 4 on lower primary branches) than on the stems, such that leaves with both opposite and spiral phyllotaxies can be formed simultaneously on the plant. In some instances, for example, when a lateral branch is in a poor light reception position, the leaf pattern may shift to alternate for several nodes and then revert back to opposite.

There is a rapid increase in the number of leaves per plant. For example, at 39 days after planting (~50 cm high; Figure 10.2) there were 335 leaves: 44 on stems, 271 on primary branches, and 20 on secondary branches. The number of leaves per plant increases progressively until the onset of flowering (~20 weeks after planting), reaching a mean of ~500 leaves·$plant^{-1}$ (Figure 10.1b) (McLaurin et al., 1999).

Leaf area per plant increases rapidly early in the season. For example, a young plant 39 days after planting and approximately 50 cm high (Figure 10.2) had a leaf area of 2,816 cm^2 on its stems and 6,887 cm^2 on its branches. The final number of leaves and leaf area vary with plant population


Flowering branch
Leaf size (cm2)
>76
51–75
24–50
5–25
<5
Missing leaf
Scale
10cm
Plant 1
Stem 1
5-16-06
Plant 2
Stem 1
10-6-06
Soil

density and other factors. For example, the maximum leaf area was 390 cm^2 at very high (10 × 10 cm), 2,640 cm^2 at intermediate (20 × 20), and 4,510 cm^2 at lower (30 × 30) densities (Hogetsu et al., 1960). When expressed as leaf area per unit of soil surface area (leaf area index), during the early stages of plant development, the leaf area index increases exponentially. A leaf area index of 4 to 6 is considered optimum. The length of time required for attaining a maximum leaf area index and the magnitude of the index differ substantially with plant population density. Often the maximum leaf area index eventually begins to decline due to mutual shading and the subsequent leaf shedding. High plant populations very rapidly reach a point where 100% of the soil surface is covered, with lower densities reaching this point later in their development.

The light extinction coefficient (generally 0.78 to 1.01) varies due to leaf arrangement, direction, and light transmissibility (Hogetsu et al., 1960; Moule et al., 1967; Zubr, 1986). The percent leaf cover varies during the growing season. The very rapid development of leaf cover and the height of the plant are primary factors allowing Jerusalem artichoke to outcompete many other species. Under a perfect leaf distribution at a leaf area index of 1, there should be complete coverage of the soil surface; however, due to variation in leaf orientation within the canopy, this does not occur. For example, comparing three plant population densities Hogetsu et al. (1960) found that at a leaf area index of 1, the degree of cover of the highest population density (10 × 10 cm) was only 68%; the intermediate (20 × 20), 65%; and the lowest (30 × 30), 56%. At a leaf area index of 2, the percent coverage was 98, 90, and 73%, respectively.

After the onset of flowering, leaf number begins to decline appreciably (Figure 10.1b) as assimilates are translocated from the leaves into the developing tubers. The plant eventually is completely defoliated after frost. Likewise, leaf shedding occurs within individual plants throughout the growing season and well before low-temperature-induced death of the aboveground plant parts. Prior to canopy closure there is generally only a small amount of shedding, e.g., ~2% on a numerical basis for plants 50 cm tall at a 30 × 100 cm spacing or about 1.2% of the total leaf area, and the leaves tend to be at the base of the plant in the least advantageous light reception position. Leaf shedding accelerates after canopy closure and again shortly after the transition to the reproductive phase. Late in the developmental cycle programmed leaf dismantling and death appear to be operative.

Senescence of the lower leaves during development is caused by shading (Zubr, 1988a), which is exacerbated by high temperatures (Meijer et al., 1993) and high plant population density (Hogetsu et al., 1960). At high population densities, there is an increase in leaf shedding and a decrease in photosynthesizing leaves. The cumulative weight of individual leaves lost per plant was 2.1, 10.0, and 4.3 g for the high (10 × 10 cm), medium (20 × 20 cm), and low (30 × 30 cm) populations, and total leaf losses were 211, 250, and 48 $g \cdot m^{-2}$, respectively (Hogetsu et al., 1960).

While leaf loss begins very early in the developmental cycle, numerically these early losses are often masked by the rapid increase in the number of leaves present on the plant. Toward the base of the plant, however, nodes with missing leaves are readily evident. Lower leaves are at a competitive disadvantage in the light reception hierarchy, and their photosynthetic efficiency declines to a point that triggers the controlled disassembly and recycling of many of the cellular constituents, followed by death and shedding of the organ. In addition to fixed CO_2, the magnitude of respiratory losses is critical in that the respiratory rate of the leaves is substantially higher than

FIGURE 10.2 Schematic of a representative stem from a young (left, 37 days after planting (DAP)) and a mature (right, 143 DAP) Jerusalem artichoke plant. In plant 1 (one of two stems), stem diameter, internode lengths, and lateral branch lengths are drawn to scale with two lateral branches drawn in detail; leaf areas are separated into five size categories and the arrangement of individual leaves (opposite vs. alternate) indicated. Leaves (L) and internodes are numbered sequentionally; × indicates a missing leaf. Plant 2 had three stems and eight laterals that emerged from belowground. The lengths of the lateral branches on the stem (indicated as lines) are not drawn to scale, with the exception of the three branches indicated; solid circles indicate a branch with one or more flowers.

that for other plant parts, and the carbon balance within the leaf has a direct impact on leaf shedding. As the light reception for an individual leaf decreases due to increasing height of the canopy, lower leaves eventually drop below their light compensation point and either become a net importer of carbon or are shed from the plant. Shedding serves to reduce the number of older, less efficient leaves in the canopy and their corresponding maintenance costs to the plant.

10.1.2 Rhizome Formation

Individual tubers are formed at the ends of rhizomes, specialized underground stems that arise from belowground portions of the stem. Some confusion exists as to the appropriate terminology — stolon vs. rhizome. In general, the Jerusalem artichoke ecological literature has used the term *rhizome* while agriculturalists have preferred *stolon*. Both are modified plagiotropic stems but differ in their position relative to the soil surface, somewhat in morphology, and in function and physiology. These differences are clearly evident in *Cynodon dactylon* (L.) Pers., where both stolons and rhizomes are formed (Dong and de Kroon, 1994). Stolons are found on the soil surface, are generally thin, contain chlorophyll, and have scale leaves. Rhizomes, in contrast, are formed underground, white, and generally thickened. Both have nodes that possess axillary buds from which branch rhizomes/stolons may arise. Stolons function in a foraging capacity, establishing new plants in open areas. To this end they display considerable morphological plasticity in response to available resources (light, nutrients). Rhizomes have predominantly a storage function. They represent a source of buds and resources that allow the plant to regenerate after habitat disturbance (Grime, 1979). Their formation is repressed by low levels of assimilate, and they exhibit much less morphological plasticity than stolons (Dong and de Kroon, 1994). Based upon these differences, it is evident that Jerusalem artichoke tubers are formed on rhizomes.

Rhizome formation begins early in the developmental cycle, from 1.5 to 8 weeks after emergence (Dambroth et al., 1992; Gallard, 1985; Swanton and Cavers, 1989; Tsvetoukhine, 1960) and is enhanced by short-day conditions (Soja and Dersch, 1993). At high plant population densities, rhizome appearance is delayed and the number per plant reduced, as is the average length, node number, and degree of branching (Korovkin, 1985), suggesting that factors limiting carbohydrate supply inhibit rhizome formation. They emerge from the underground portion of the stem, 4 to 5 cm below the soil surface, and grow in a slight downward angle. Internode length is typically 3 to 4 cm, and the diameter 2 mm, but varies substantially among clones. If the tip is damaged, the rhizome branches at the first node back from the tip. If exposed to light due to erosion or the plant lodging, the exposed portion of the rhizome synthesizes chlorophyll, forms rudimentary green leaves at the tip, and alters subsequent growth in a vertical orientation as a sprout. Even underground branches of the exposed rhizome well back from the tip and in the dark begin to grow vertically.

When grown in tight or compacted soil, rhizome elongation is impeded, shortening the internode length with increasing physical resistance. In tight soils, the tubers are often tightly clustered around the underground portion of the stem, an undesirable trait in that the tubers are often misshapen and difficult to separate from the stem at harvest. In moist, sandy soils, the rhizomes may extend into the next row, 70 to 100 cm from the base of the plant.

In Figure 10.1d, the first rhizomes emerged prior to the 8th week after planting; by the 12th week there were approximately 40 rhizomes per plant (McLaurin et al., 1999). While the number of rhizomes reached a plateau around the 12th week after planting, tuber number did not level off until the 24th week (Figure 10.1e), indicating rhizome branching. The timing of rhizome formation, however, varies widely with cultivar, geographical location, and production conditions. The rhizomes persist in the soil after the aboveground plant parts have been killed by frost. Eventually the rhizomes of cultivated clones decompose prior to tuber sprouting the following spring. The interval before decomposition varies widely among clones and soil conditions. In wild clones, however, the rhizomes generally not only survive until the next growing season, but may also form new plants.

10.1.3 Tuberization

Jerusalem artichoke tubers vary in size and shape, with the latter ranging from round, to long and slender, to irregular, knobby clusters that are formed at the tip of the rhizome (Alex and Switzer, 1976). The shape can vary with growing conditions and time of development; e.g., the first tubers are often elongated and on long rhizomes, while the last formed tend to be rounder and on short rhizomes (Barloy, 1984). The tubers also vary in skin color, from white through pink to red/purple (Wyse and Wilfahrt, 1982), and to a lesser extent in interior color, as well as a cross section of other chemical and physical traits. For example, cultivated clones produce large tubers clustered near the main stem, whereas wild types produce smaller tubers typically at the end of long rhizomes.

Tuberization is a complex developmental process in which the distal end of the rhizome differentiates into a specialized reproductive storage organ. Tuberization can be separated into at least four general developmental stages: initiation, tuber formation, tuber bulking, and the acquisition of dormancy and cold tolerance. During bulking, much of the dry matter, in the form of fructans and storage proteins, accumulates and the organ becomes a viable reproductive propagule.

10.1.3.1 Initiation

During cellular, tissue, and plant development, gene expression is spatially and temporally coordinated in a very precise manner. Developmental and environmental changes are recognized, assessed, and integrated by the Jerusalem artichoke in such a manner that the appropriate genes from the estimated 25,000 to 30,000 present are up- or downregulated. For many regulated genes, the timing, location, and level of expression are critical. Environmental signals such as photoperiod are passed from receptors through signal transduction pathways that lead to expression of the appropriate genes. The Jerusalem artichoke integrates both environmental and developmental signals before tuber initiation. As a consequence, it is not surprising that a number of environmental factors may have an impact on tuberization, creating a less than clear picture of the relative role of each in the overall process. The molecular mechanisms controlling tuberization in the species are largely unknown, and our understanding is substantially behind that of crops such as potato (*Solanum tuberosum* L.), where tuber-specific promoters have been identified (e.g., *Stgan* (Bachem et al., 2001; Trindade et al., 2003)).

Sugars provide energy and carbon skeletons for the synthesis of the diverse range of chemical components in plants. They also function as regulatory molecules controlling metabolism, the cell cycle, development, and gene expression (Sheen et al., 1999). In potato tuber induction, sucrose appears to regulate gene expression beginning with a switch in assimilate phloem unloading in the subapical region of the developing stolons (Viola et al., 2001). High sucrose concentrations have been shown to induce the transcription of several genes involved in tuber storage metabolism. For example, high sucrose induces *StCDPK1*, which encodes a calcium-dependent protein kinase that is expressed in the stolon tip at the onset of swelling (Raíces et al., 2003). While the ability to sense the concentration of sucrose would appear to be a logical mechanism for controlling tuber initiation in Jerusalem artichoke, such a system has yet to be established, although several lines of evidence point in that direction.

Perhaps one of the most widely studied and least clearly understood environmental signals modulating tuberization in the Jerusalem artichoke is photoperiod (Czajlachian, 1937; Garner and Allard, 1923, 1931; Hackbarth, 1937; Schiebe and Müller, 1955; Wagner, 1932). This is due in part to the fact that tuberization involves multiple developmental processes, only part of which are modulated by photoperiod. Adding to the complexity of interpretating the role of photoperiod is the fact that it has multiple effects on the plant, e.g., both flowering and certain aspects of tuberization are photoperiodically controlled. In addition, photoperiod has also been shown to influence vegetative growth, the termination of vegetative growth, and tuber maturation (Hackbarth, 1937). Short day lengths decrease the amount of carbon assimilated by virtue of the shortened

period available for photosynthesis and reduce stem length, stem dry matter, and leaf growth, while rhizome induction and tuber growth are positively affected. Long days, in contrast, promote leaf and stem growth. Short days also signal the onset of flowering in short-day clones, setting off a pronounced alteration in carbon allocation, which in turn influences tuber formation.

Photoperiodic control over tuberization in short-day clones is not absolute. In the absence of the appropriate photoperiodic signal, tuber formation is not irretrievably blocked. Under suitable conditions, tuberization can be partially fulfilled even though the critical day length has not been met. For example, high light intensity can promote tuberization under noninducing conditions (Courduroux, 1966); even under long-day conditions, most clones eventually form tubers (Soja and Dersch, 1993). Likewise, cool night temperatures can also induce tuber initiation, and in some clones, the response is not only more effective than short day length exposure, but also translocatable (Courduroux, 1966; Soja and Dersch, 1993). Conversely, conditions conducive to high respiratory rates that result in lower carbohydrate availability delay or prevent tuber formation, as does leaf shading. This suggests that carbohydrate supply is a critical factor in the tuberization response. Tubers formed on short-day clones under long-day conditions, however, develop at a slower rate and are smaller (Meijer and Mathijssen, 1991) than those formed under short-day conditions. Due to the effect of carbohydrate availability and plant size on tuberization, cumulative degree days (≥520 degree days) can be used for predicting the onset of tuberization (Spitters et al., 1988a) and tuber number, which is linearly related to a cumulative temperature.

The complexity of the relationship between photoperiod and tuberization is also indicated by the numerical development of tubers in short-day clones (Figure 10.1e). Initial tuber formation in the cultivar 'Sunchoke' began 14 weeks prior to flower formation, with tuber number essentially stabilizing by the 16th week after planting. Therefore, the date of tuber initiation is relatively early in the growing season (July 1, Figure 10.1e) and well before the photoperiod changes appreciably from the maximum. Typically initiation begins from 5 to 13 weeks after emergence (Hay and Offer, 1992; McLaurin et al., 1999; Swanton and Cavers, 1989); however, this varies with cultivar, geographical location, and growing conditions. The formation of additional tubers, however, can continue significantly longer (Gallard, 1985; McLaurin et al., 1999; Milord, 1987).

There are several lines of evidence establishing the stimulation of tuberization by short days:

- Artificially imposed short days enhance tuberization and, in many instances, significantly increase yield even though the length of exposure to photosynthetically active radiation is decreased (Hackbarth, 1937).
- Grafting experiments where an induced scion (sunflower or a day-neutral- or short-day-induced Jerusalem artichoke) is grafted on a short-day stock enhancing tuberization (Daniel, 1934; Schiebe and Müller, 1955; Sibrja, 1937; van de Sande Bakhuyzen and Wittenrood, 1951; Wagner, 1932).
- The decreasing time interval between planting and tuberization as the planting date shifts progressively later in the growing season (Figure 10.3).

As indicated previously, the effect of short days on tuberization is not obligatory. Tubers will eventually form even in the absence of short days, indicating that other factors are operative. The dominance of photoperiod differs between flower and tuber initiation. Flowering is strongly modulated by photoperiod, and day-neutral, intermediate, and short-day clones have been selected (Figure 10.3). Tuberization in the same clones, however, is normally modulated by short days, although a day-neutral clone was reported by Hackbarth (1937). The length of time required for tuber initiation decreases progressively as the day length becomes shorter during the growing season; however, the fact that initial tuber formation often occurs substantially before reaching the appropriate photoperiod reiterates the role of additional factors modulating the response.

Jerusalem artichoke germplasm varies in its photoperiodic tuberization response from short day to day neutral (Hackbarth, 1937), the latter being relatively rare. Some clones display a 1.5- to

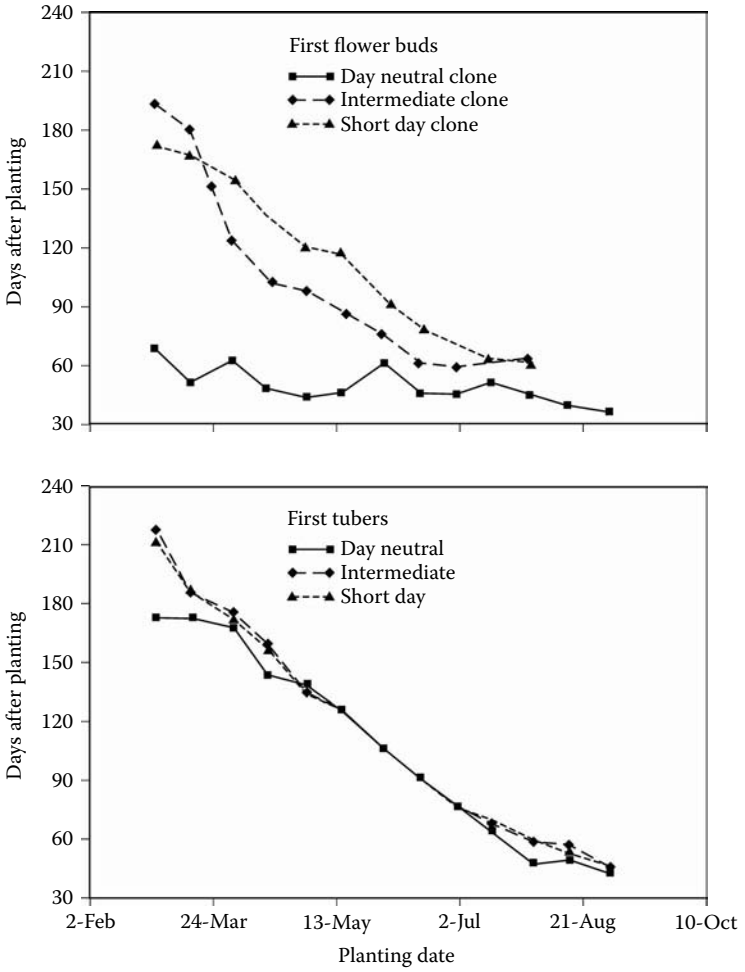


FIGURE 10.3 Number of days until first flower (A) and the onset of tuber formation (B) in a short-day (NC10-92), intermediate ('Parlow gelb'), and day-neutral (NC10-9) clone. Tubers were planted at 2-week intervals throughout the summer. (From Kays, S.J., unpublished data.)

4-fold increase in tuber yield under short days, while others display little or no effect. Tuber induction in short-day clones is facilitated by the appropriate photoperiodic stimulus (Courduroux, 1967; Ke-Fu, 1984; Nitsch, 1965). Once perceived by the leaves, a signal is translocated to the base of the plant, instigating the developmental changes required for tuber formation (Nitsch, 1965). Early-flowering (day-neutral) clones, in contrast, are always in an induced state. When a day-neutral clone is grafted on the stock of a short-day clone (DN/SD), tuberization is induced (van de Sande Bakhuyzen and Wittenrood, 1951); the absence thereof in the recipical graft (SD/DN) implies that a stimulus is translocated to the base of the plant and that the system for the assessment of photoperiod in the leaves is the same for flowering and tuberization.

Fulfillment of the photoperiodic requirement and the onset of tuber bulking involve a major shift in the dry matter allocation pattern in short-day clones. Initially carbon is stored primarily in the stems (Incoll and Neales, 1970). With the induction of tuberization, the tubers are initially formed, and with the onset of tuber bulking, carbon stored in aboveground organs, along with new photosynthates, is now directed to the rapidly developing tubers (McLaurin et al., 1999). When grown under very short day conditions, it is possible to bypass stem storage, with the sucrose transported directly into the tubers (Dickerson and Edelman, 1966). Day-neutral clones begin

allocating a substantial amount of assimilates to their tubers much earlier than short-day clones (Spitters et al., 1988a). In addition, less of the final tuber dry weight is comprised of assimilates recycled from the stem, indicating that substantial amounts of photosynthates are translocated directly to the developing tuber, bypassing transient storage in the stems.

The Jerusalem artichoke is capable of assessing the photosynthate status within the plant that appears, along with other factors, to determine the number of tubers set (Barloy, 1988b; Barloy and Fernandez, 1991). Not all of the tubers are set simultaneously, but are spread over a significant portion of the growing season. For example, the most rapid increase in number of tubers occurred between the 14th (24 tubers) and 16th (68 tubers) weeks and peaked 24 weeks after planting (i.e., 85.5 tubers·plant^{-1}) (Figure 10.1e).

The timing and number of tubers vary among clones. In addition, plant population density, depth and timing of planting, and photoperiod can also affect the number of tubers formed (Gallard, 1985; Moule et al., 1967; van de Sande Bakhuyzen and Wittenrood, 1952). Typically, tuber number and size are inversely related; small tubers (i.e., <15 g fwt) are generally lost during harvest (Barloy, 1988; Zonin, 1986). The difference between rhizome number and tuber number (Figure 10.1d and e) reflects rhizome branching and the presence of multiple tubers per individual primary rhizome emerging from the base of the plant.

10.1.3.2 Tuber Formation

The onset of tuberization entails rapid cell division and expansion, during which time the initial structural framework required for assimilate storage is established, a developmental step that occurs well before the influx of carbon during tuber bulking. While tuber initiation appears to be in part controlled by carbohydrate supply, bulking is strongly modulated by photoperiod, even in clones that are day neutral for flowering.

Tuber structure in cross section from exterior to interior can be separated into the epidermis, cortex, outer medulla, inner medulla, and pith (Mazza, 1985). Relatively little is known about the temporal sequence of cell division and differentiation leading up to bulking. Sink capacity is a function of the combined vacuolar volume of the tubers, the location of fructan synthesis and storage within the cells (Darwen and John, 1989; Keller et al., 1988; Pollock, 1986). Vacuolar volume is a function of cell size and number. The size of individual cells within the tuber varies with tissue type: cortex (286 cells per 10 mm^2), extension zone (145 cells per 10 mm^2), storage tissue (85 cells per 10 mm^2), and pith (149 cells per 10 mm^2) (Schubert and Feuerle, 1997). The extent that cell number and size increases after the initial formation of the tuber has not been adequately documented.

The tuber is composed largely of storage parenchyma cells interspersed with a small number of vascular traces (Fowke and Setterfield, 1968). The parenchyma cells at maturity are relatively large, thin walled, and highly vacuolated. Typically there is only a thin layer of cytoplasm, which varies in thickness (i.e., generally less than 5 μm), appressed to the cell wall. It displays very few cytoplasmic strands transversing the vacuole. Along the thin, linear portions of the cytoplasm adjacent to the cell wall, the cytoplasmic area is only 0.30 μm^2 per μm length of wall. The cytoplasm contains a nucleus, plastids, mitochondria, spherosomes, a few microtubules, and virtually no dictyosomes. Also within the cytoplasm are ovoid crystal-containing bodies 0.5 to 1.0 μm in diameter and bound by a single membrane, and round or oval bodies that contain finely granular, electron-dense material. The latter are up to 1.5 μm in diameter and have an irregular striated appearance. Nuclei were generally flattened against the cell wall, have an oblate spheroid shape, and contain one or more nucleoli (Figure 4.6). Ribosomes appear to be randomly scattered in the cytoplasm and seldom associated with the endoplasmic reticulum. Mitochondria are found clustered in thicker regions of the cytoplasm, especially so around the nucleus. The mitochondria are enclosed within well-developed double membranes and display tabular cristae and electron-dense material within the stroma.

10.1.3.3 Tuber Bulking

There is a progressive increase in dry matter accumulation within the parenchyma cells once bulking begins. Interestingly, the degree of polymerization peaks well before the tubers reach their maximum dry weight (Praznik and Beck, 1987); the biological rationale for this is not clear. The greatest percentage of high molecular weight inulin (degree of polymerization > 30) was found on August 30, but declined appreciably thereafter, even though the percent dry matter in the tubers continued to increase.

The deposition of dry matter, fructans, protein, and sugars is not uniformly distributed across the various tissue types of the tuber (Mazza, 1985). The highest concentration of each is in the cortex and progressively decreases inward, with the pith having the lowest concentration. The distribution of assimilates, however, is relatively equal from the proximal to distal ends of the tuber.

The inulin-containing vacuoles also often contain vesicles (Kaeser, 1983), more so in cells adjacent to the interfascicular cambium, and decreasing in number with increasing distance from the cambium. The largest are localized within the vacuole and contain fibrous or granular material. It is thought that the vesicles form in the cytoplasm and function in the transport of sucrose into the vacuole (for additional details, see Section 10.8).

10.1.3.4 Dormancy

The tubers become dormant in the early fall prior to completion of their development (Steinbauer, 1939), after which they will not sprout even under favorable conditions. The exact timing of the onset of dormancy varies among individual tubers on the plant and with production location, clone, and other factors. Large, more mature tubers are the last to enter into dormancy, with dormancy initially established in the rhizomes and smaller, younger tubers. The onset of dormancy appears to be a gradual process, such that not all of the tubers become dormant simultaneously.

The degree of dormancy varies considerably among clones and within individual clones, such that one tuber will sprout while others may be delayed considerably. Boswell (1932) found that the time required for 50% of the tubers to sprout (145 clones), when not subjected to a cold treatment to fulfill the dormancy requirement, ranged from 54 to 200 days, with 5 to 6 months typical for most cultivars.

The possible role of polyamines in tuber dormancy has been studied using slices of tuber parenchyma cells that are pharmacologically induced to divide. Polyamines are small aliphatic amines that are synthesized from ornithine, arginine, and s-adenosylmethionine. A number of studies have reported correlations between polyamine level and a diverse cross section of developmental and physiological processes in plants (for reviews, see Kuehn and Phillips, 2005; Kumar et al., 1997; Malmberg et al., 1998; Walden et al., 1997). Bagni (1966) first demonstrated that polyamines could help break the dormancy and stimulate cell proliferation in tuber slices of Jerusalem artichoke; this led to a series of papers on their possible role (Bagni et al., 1971, 1972, 1978, 1980, 1981; Bagni and Serafini-Fracassini, 1985; Bagni and Speranza, 1977; Bertossi et al., 1965; Bogen Ottoko, 1977; Courduroux et al., 1972; Cionini and Serafini-Fracassini, 1972; Del Duca and Serafini-Fracassini, 1993; Gendraud and Lafleuriel, 1985; Serafini-Fracassini and Filiti, 1976; Serafini-Fracassini et al., 1980; Serafini-Fracassini and Alessandri, 1983; Torrigiani et al., 1987). The evidence for polyamines is largely circumstantial. There is a rapid increase in polyamine level that peaks 24 h after excision and induction of the tuber tissue. Putrescine, spermidine, and spermine have been identified in the tubers (Serafini-Fracassini et al., 1980), though Phillips et al. (1987) found spermidine, diaminopropane, and cadaverine during the initial 24-h activation and onset of mitosis. Likewise, an inhibitor of ornithine decarboxylase, a key enzyme in the polyamine synthesis pathway, suppressed cell division. To date, the precise role of polyamines in the control of dormancy and the onset of cell division in the tubers remains in question (for additional information, see Section 9.1.1.1).

10.1.3.5 Initial Events after the Fulfillment of Dormancy

Parenchyma cells go into dormancy in the DNA presynthetic phase (G_1) (Adamson, 1962; Mitchell, 1967), and when these cells are held on a culture medium containing 2,4-dichlorophenoxyacetic acid to break or circumvent the dormancy, the cells enter mitosis (Bennici et al., 1982). The first and second divisions are well synchronized (Serafini-Fracassini et al., 1980); however, with further division, synchrony is gradually lost (Yeoman et al., 1965). Likewise, there are marked changes in the timing of the first and second cell cycles with the progression of dormancy (Bennici et al., 1982).

As mentioned previously, when dormant there are low levels of polyamines in the tubers; however, they are synthesized rapidly when dormancy is broken (Del Duca and Serafini-Fracassini, 1993; Serafini-Fracassini et al., 1984), the onset of which occurs very early in the G_1 phase. Likewise, immediately after the fulfillment of the dormancy, there was a marked decrease in arginine and glutamine (precursors of polyamines) and a corresponding increase in polyamines (Durst and Duranton, 1966; Serafini-Fracassini et al., 1980).

10.1.3.6 Cold Tolerance

The tubers start to become freeze tolerant (LD_{50} at –5°C) toward the end of October, prior to leaf senescence (Ishikawa and Yoshida, 1985). Tolerance increases to –11°C by mid-December. Increased low temperature tolerance did not appear to be due to changes in tuber moisture content; the role of inulin depolymerization in increased cold tolerance has not been assessed.

10.1.4 Flowering

10.1.4.1 Flower Initiation

The ability to reproduce is an essential requisite for all organisms, and in the plant kingdom, reproduction typically occurs via flower and seed production. The shift from the vegetative to reproductive phase is a critical period in the overall developmental cycle of plants; thus, control over the timing of the reproductive phase in many species tends to be tied to an internal mechanism that allows synchronizing reproduction with the appropriate time during the growing season. Photoperiodism, the length of the daily light and dark periods, is one of the most common mechanisms by which the timing of the reproductive phase is controlled. Photoperiodism is typically associated with flowering, with species separated into three very general categories (short day, long day, and day neutral).* In some species that reproduce asexually (e.g., Jerusalem artichokes, potatoes), photoperiod may also be involved in the induction or development of the reproductive propagules (e.g., tubers). In the Jerusalem artichoke, both flower and, to a lesser extent, tuber formation is modulated by photoperiod. It is interesting to note that some of the early basic research on photoperiodism by Garner and Allard (1923) utilized Jerusalem artichoke. Since then there has been a wide assortment of basic and applied photoperiodic studies on the crop (Allard and Garner, 1940; Czajlachian, 1937; Hackbarth, 1937; Hamner and Long, 1939; Nitsch, 1965; Schiebe and Müller, 1955; Tincker, 1925; van de Sande Bakhuyzen and Wittenrood, 1950, 1951; Wagner, 1932).

Jerusalem artichoke flower formation involves temporal, in addition to spatial, information that restricts flower initiation to a specific location on the plant (i.e., stem and branch apices). A cross section of genes must then be activated at the apex for the formation of the various structures comprising the flower. Photoperiodic plants perceive day length in the leaves and then translocate the signal (florigen) to the shoot apex, the location of flower formation. The presence of a translocatable substance from the leaves causing flowering at the shoot apex was demonstrated years ago by the fact that a photoperiodically induced leaf could be grafted on a noninduced plant causing

* The original classification of plants into three categories is now known to be more complex (i.e., there are also short-long-day and long-short-day plants).

flower formation. The quest for this elusive substance has been ongoing since the work of the Russian scientist M.H. Chailakhyan in the late 1930s. Recent data from Arabidopsis indicate that several genes interact in the flowering induction process. Perception of day length in the leaves is controlled through a transcription factor encoded by the gene *CONSTANS* (*CO*), the expression of which oscillates in a circadian manner (Velverde et al., 2004). In short-day plants, *CO* mRNA accumulation peaks in the leaf during the night. Under the appropriate photoperiod, it induces transcription of the *FLOWERING LOCUS T* (*FT*) gene (An et al., 2004; Ayre and Turgeon, 2004), the protein of which is translocated in the phloem to the shoot apex (Lifschitz et al., 2006; Wigge et al., 2005). FD, a transcription factor present in the shoot apex, is thought to physically interact with the FT protein, triggering expression of the floral identity gene (*APETALA 1*), which results in flower formation (Abe et al., 2005; Wigge et al., 2005).

The critical day length is the length of the photoperiod that must be met or exceeded to induce the reproductive phase, and a short-day plant is one that responds to a photoperiod shorter than the critical day length. For example, if the critical day length is 12 h, a photoperiod shorter than 12 h of light is required for induction. Long-day plants, in contrast, are induced by photoperiods longer than the critical day length. While day length is typically described, the length of the dark period is actually critical. For example, in short-day plants, interruption of the dark period with an artificial light period of sufficient duration results in inhibition of the induction of the reproductive phase even though the daytime light period is shorter than the critical day length.

Fulfilling the photoperiodic response for both flower and tuber induction is a function of the number and position of the leaves receiving the photoperiodic stimulus and the number of days the leaves are exposed to the stimulus. Even a single leaf exposed to short days is capable of triggering the induction of tuber development (Hamner and Long, 1939). The greater the number of leaves exposed, the shorter the duration of exposure required (Mesken, 1988; van de Sande Bakhuyzen and Wittenrood, 1950). Below the critical day length, the duration of exposure (days) is proportional to the day length (the shorter the day length, the shorter the exposure duration required) and inversely proportional to the number of leaves treated (van de Sande Bakhuyzen and Wittenrood, 1950, 1951). The upper and middle leaves are the receptive organs (Hamner and Long, 1939; van de Sande Bakhuyzen and Wittenrood, 1950, 1951), not the stem apex (Zimmerman and Hitchock, 1936), with the middle leaves appearing to be more critical (van de Sande Bakhuyzen and Wittenrood, 1950). Likewise, the longer the exposure, the greater the number of flowers initiated per plant (Mesken, 1988; van de Sande Bakhuyzen and Wittenrood, 1950).

The critical day length for a significant cross section of the Jerusalem artichoke germplasm is between 13 and 13.5 h (Allard and Garner, 1940; Hamner and Long, 1939; Zhou et al., 1984). Short-day clones exposed to photoperiods of 14 or more hours stay vegetative. Data on the minimum length of exposure to inductive conditions vary, though by a relatively short duration (16 to 17 days) (Hamner and Long, 1939; Zhou et al., 1984), and appear to be more likely than longer periods that have been proposed (Scheibe and Müller, 1955).

The photoperiodic requirement for Jerusalem artichoke is not consistent across all clones. Both short-day and day-neutral clones are found (Hackbarth, 1937), in addition to what appears to be a range in the critical day length for the short-day response. As a consequence, when a diverse cross section of the germplasm is assessed (Figure 10.4), a wide range of flowering dates are found (Kays and Kultur, 2005). Flowering in day-neutral (i.e., early-flowering) clones appears to be controlled by the stage of development of the plant. In contrast, short-day (late-flowering) clones are dependent upon receiving the appropriate photoperiodic response (Hackbarth, 1937; Steinrücken, 1984; van de Sande Bakhuyzen and Wittenrood, 1950; Zhou et al., 1984). Variability in the photoperiodic requirement has contributed some confusion to our understanding of the response since conclusions derived with only one or a small number of clones are not universally applicable across the germplasm. Likewise, day-neutral clones, whose flowering is largely dictated by their stage of development, also complicate interpretation. Young plants will not initiate flowers until reaching a certain minimum developmental stage even under an inductive photoperiod.

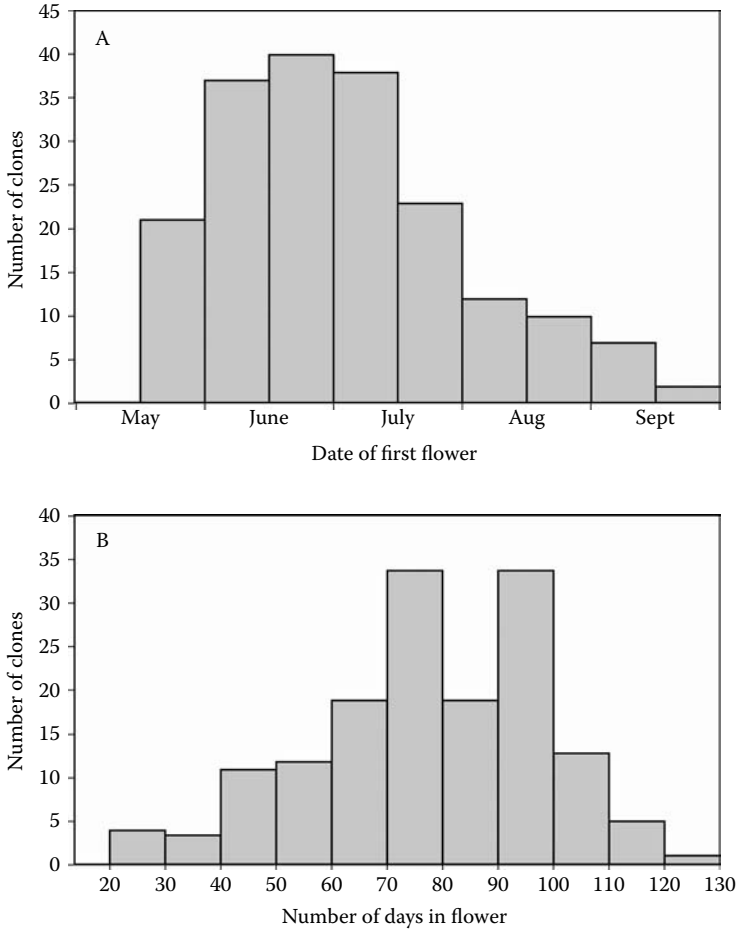


FIGURE 10.4 Date of first flower (A) and the duration of flowering (B) for 190 Jerusalem artichoke clones grown at 30°57'N (after Kays and Kultur, 2005).

Helianthus tuberosus originated in the more northern latitudes of the U.S., where the photoperiod is favorable for extensive stem growth during the summer (long days) and is followed by photoperiods conducive to flower and tuber formation in the fall. Thus, the location where the crop is grown has a significant impact of its development since long-day conditions favor development of aerial plant parts, of which the stem acts as a temporary sink for carbon. At mid-June the photoperiod at 60°N is >18 h, while at 40°N, 15 h; 26°N, 13.5 h; and the equator, 12 h. However, by October the light period has decreased to only 9.5 h at 60°N (10.5 at 40°N; 11 h at 26°N) but remains 12 h at the equator. Therefore, as the production location moves progressively away from the equator, the amount of photosynthetic irradiation during summer days increases while the length of the growing season decreases. As a consequence, short-season cultivars that have been selected for higher latitudes are not necessarily ideal for lower latitudes.

Another requisite for the induction of flowering is that the plants must be a certain minimal size/age (Meijer and Mathijssen, 1991; Steinrücken, 1984). Thus, during the juvenile phase the plants are not sensitive to environmental conditions that would otherwise induce the appropriate photoperiodic response (Wittenrood, 1954). This prevents young plants from shifting to a reproductive stage during the short days of early spring (Garner and Allard, 1923). Relatively small differences in planting date and rate of early growth can significantly influence the flowering date of some cultivars (Kays and Kultur, 2005).

10.1.4.2 Flower Development

Jerusalem artichoke is an obligate outcrosser and produces seed only when cross-pollinated. When in cultivation in homogenous stands, few seeds are produced. A high level of autoincompatibility (Toxopeus, 1991), irregular meiosis (van de Sande Bakhuyzen and Wittenrood, 1950), and differences in pollen viability among clones (i.e., 47 to 99%) (Atlagic et al., 1993) contribute to the low fertility. The absence of seed may also occur due to climatic reasons in some locations (Lohmeyer and Sukopp, 1992).

Development of an inflorescence, the opening of its individual flowers, and their eventual death occur over an extended period, the general sequence of which can be seen in Figure 10.5. The precise timing of an infloresence's life cycle varies among clones and with production conditions. Each inflorescence is comprised of a number of small disk flowers in the center, surrounded by 10 to 20 sterile, yellow ray flowers, the ligules of which are often thought of as the petals. Initially the ligules of the ray flowers are tightly closed but move to a more vertical position as the flower head begins to open, at which time they are one third to one half their final length. Within days the outer whorl of disk flowers begins to elongate and open with their stigmas emerging; anthesis moves progressively inward until all of the corollas have opened. Eventually the ligules wither and abscise, followed by the corollas of the disk flowers, and in most instances the ovary aborts.

Flower and seed production in wild populations represents a means of increasing genetic variation and enhancing dispersal and establishment in sites more distant from the parent plant, compared to what can be achieved via asexual means. When compared under uniform conditions, wild clones produced an average of 67 flower heads and 1,025 achenes per plant. However, 56% of the seeds failed to germinate and only 33% reproduced sexually during their first season (Westley, 1993). Hence, the risk of reestablishment the following season via seeds is disproportionately high when compared to tubers. Flowering generally coincides with a shift in the allocation of resources within the plant and represents a loss of resources that would otherwise have been allocated to the tubers. Flowering is also essential for breeding programs, where its timing and duration can dictate crosses that can be readily made (Kays and Kultur, 2005).

In the short-day cultivar illustrated in Figure 10.1e, flowering begins fairly late in the growing season, starting around the 23rd week after planting (latitude 33°57'N). Initially a flower is formed at the apex of the main stems, terminating vegetative growth. Flowering shoots are rapidly formed in the axils of the nodes along the stem, and within 1 to 2 weeks, a profusion of flowers has developed (e.g., >50 flowers per plant) (McLaurin et al., 1999). Flower number and dry weight peaked within 4 weeks of the onset and then declined thereafter. Swanton (1986), when contrasting six clones (three ecotypes), found that the number of flowers per plant ranged from 5.6 to 78; four clones assessed by Westley (1993) had an average of 67 flowers per plant.

The onset and duration of flowering vary widely among clones. When 190 clones were assessed, the onset of flowering ranged from 69 to 174 days after planting, and the time interval flowers were present on the plant from 21 to 126 days (Kays and Kultur, 2005). Thus, the timing, duration, and number of flowers per plant vary widely among clones and with planting time and production location and conditions.

The diameter of the head of the inflorescence ranges from 1.3 to 1.8 cm (six clones) and the mean number of seed per plant from 0.45 to 163 (Swanton, 1986). In wild clones, 9% of the biomass by the end of the season had been allocated to the flowers and fruit (Westley, 1993). If sexual reproduction was blocked, there was a substantial increase in biomass allocated to asexual means of reproduction in the form of more and larger tubers. Flowers in the late fall (November 1, Ontario, Canada) contained 2.46% N, 0.51% P, 2.02% K, 1.21% Ca^{2+}, and 0.68% Mg^{2+} (Swanton and Cavers, 1989).

FIGURE 10.5 Jerusalem artichoke flowers undergo a relatively consistent sequence of developmental events among bud formation, anthesis, and eventual senescence. Illustrated is the chronological sequence from the tight bud stage to flower senescence. The precise timing varies with clone and production conditions. Day 0 — tight bud stage, inner whorl of bracts still enclosing ligules (ray flower corollas); 2 — ligules green, exposed; 4 — ligules yellow-green, beginning to elongate; 6 — ligules yellow, elongating vertically; 7 — ligules beginning to unroll, still largely vertical in orientation, disk flower corollas closed; 8 — ligules open, first disk flowers on the outer whorl have their anthers emerging from the corolla; 9 — additional anthers and first stigmas emerging on outer whorls; 10 — about half of disk flowers open with stigmas emerged; 13 — all disk flowers open, outer whorl flowers displaying initial stigma senescence; 15 — ligule wilting and initial drying, disk flower stigmas and anthers largely withered, corollas intact; 17 — ligules further desiccated, disk flower corollas intact; 18 — ligules dried, starting to be shed, disk flower corollas intact; 19 — ligules shed, disk flower corollas beginning to wither.

10.1.4.3 Seed Development and Dormancy

Flowers are often sterile. When achenes are formed, generally there are few per flower (Russell, 1979; Swanton, 1986; Westley, 1993; Wyse and Wilfahrt, 1982). Typically the seeds are around 5 mm long × 2 mm wide, flattened, wedge shaped (obovate to linear-obovate), and smooth. Their external color is mottled black, gray, or brown with black spots (Alex and Switzer, 1976; Konvalinková, 2003). The seeds of wild and landrace accessions held in the U.S. Department of Agriculture (USDA) germplasm collection range from gray to tan to brown; size is predominantly 2 mm long and 1 mm wide (USDA, 2006).

Seed production varies with location (Balogh, 2001; Řehořek, 1997), clone, and year (Konvalinková, 2003). Wild clones had from 3 to 50 seeds per flower head (Wyse and Wilfahrt, 1982; Westley, 1993), while cultivars had 0.08 to 0.66 seed per flower head, or 0.4 to 24 seeds per plant. Weedy clones had 1.26 to 1.97 mature seeds per head, or 47 to 154 seeds per plant, while truly

wild clones had 4.93 to 5.36 mature seeds per head, or 79 to 163 seeds per plant (Swanton et al., 1992). Variation in the mean seed weight across clones was relatively small (i.e., 3.5 to 4.8 mg, mean of 4.5 mg), though individual seed weights ranged from 0.8 to 10.8 mg (Swanton, 1986).

Seed viability is generally low and clone dependent (Le Cochec, 1985; Swanton and Cavers, 1989). Wild populations tend to produce more flowers and have higher seed viability (i.e., up to 40%) than cultivated clones (Westley, 1993). For example, wild clones had a mean of 85 ovules per flower and produced an average of 21 mature achenes per flower for a fruit set of 23%. Each trait varied depending upon the location where the plants were grown, with ovules, mature achenes, and partially filled achenes per flower the most variable traits. The plants averaged 67 fruiting flowers or 1,025 achenes per plant. In contrast, cultivated clones grown in monoculture seldom produce seed in that, as an obligate outcrosser, there is very little potential for cross-pollination. With late-flowering clones, low seed production may also be due to the progressively cooler temperatures during the late fall and the shorter time interval for maturation.

The mature seeds contain 4.82% N, 0.90% P, 1.16% K, 0.12% Ca^{2+}, and 0.34% Mg^{2+} on a dry weight basis (Swanton and Cavers, 1989). The seeds of a representative cultivar had 45.5% oil, which was comprised of 5.7% palmitic, 5.8% stearic, 22.1% oleic, 64.6% linoleic, and 0.9% behenic acid. Seeds from wild clones were similar in composition but slightly higher in palmitic and lower in stearic acids (Seiler and Brothers, 1999). The percentage oil content of seed on a dry weight basis was, on average, 24.6% (range, 14 to 34%) for 36 accessions held in the USDA germplasm collection. For 22 accessions, a detailed oil analysis was conducted; the average composition was 63.4% linoleic acid (range, 44 to 80%), 18.8% oleic acid (range, 12 to 40%), 6.4% palmitic acid (range, 5 to 9%), and 3.4% stearic acid (range, 2 to 5%) (USDA, 2006).

At maturity the seeds display a strong dormancy (Toxopeus, 1991) that can be overcome with stratification (i.e., storage under cool (1.7°C), moist conditions) (Wyse and Wilfahrt, 1982). The percent germination after storage varies among studies, ranging from 4% after 6 months' storage (Swanton and Cavers, 1989) to 44% after 3 months' storage (Konvalinková, 2003).

Upon germination, the vigor of the seedlings is generally weak in contrast to *Helianthus* species that reproduce via seed production. In wild clones, only 44% of the seed produced germinated, and of the new plants formed, only 33% reproduced sexually during their first growing season (Westley, 1993). As a consequence, in breeding programs tuber yield evaluations should be made in the second season when the clone has been propagated using tubers.

10.1.5 Senescence

Senescence, an integral part of the normal developmental cycle of plants, can be viewed on a cellular, tissue, or organ level (Kays and Paull, 2004). The Jerusalem artichoke is an herbaceous perennial with monocarpic shoots. Thus, by the end of the normal developmental cycle, nearly all of the aboveground and much of the belowground plant is no longer living. After the first freezing temperatures in the fall, literally millions of cells that made up the plant die; exceptions would be the tubers and, when present, seeds. While in most instances freezing temperatures result in death of the plants, under controlled-temperature (20°C) short-day conditions, the plants also die, indicating the presence of a genetically programmed senescence mechanism. Prior to death, most of the somatic tissues undergo a controlled disassembly of their cells, allowing many of the carbohydrates, proteins, and phloem-mobile nutrient elements present to be reallocated to reproductive propagules. In addition to whole-plant senescence, a number of individual organs routinely senesce during the normal development of the plant.

In Jerusalem artichoke, organ senescence is a common occurrence, with individual leaves and, in some cases, branches dying during both the vegetative and reproductive phases. During growth, leaves and branches that are injured (e.g., herbivory, disease, mechanical damage) or in a poor light reception position within the canopy are routinely shed. The senescence of lower leaves during growth is generally caused by shading (Zubr, 1988a), a condition that is aggravated by high plant

population density (Hogetsu et al., 1960). The leaf area duration for plants was 792 $dm^2 \cdot day^{-1}$, with an average leaf longevity of 92 days (Nakano, 1975). The importance of leaf loss during the vegetative phase on yield is a function of the severity of the loss and its timing during the overall developmental cycle. Depending upon the cause of death, many of the mobile nutrients may be recycled out of the leaf. In contrast to the senescence of individual organs, whole-plant senescence is a process involving the onset of recycling in all of the leaves, in addition to other somatic tissue.

Reproduction triggers the onset of this latter form of senescence in many monocarpic species (Molisch, 1938), and removal of flowers and fruit often delays or prevents the onset of senescence; however, this is not always the case (for additional details, see Bleecker and Patterson, 1997; Hadfield and Bennett, 1997; Noodén, 1988; Noodén et al., 1997). For example, in Arabidopsis the development of reproductive structures stops the formation of new leaves needed for photosynthesis, leading to the plant's eventual death (Noodén and Penney, 2001). In this case, the developmental transition is controlled at the genomic level and instigated by endogenous mechanisms or external signals. For example, short days result in the transformation of apical tissue from vegetative to reproductive in pumpkin, triggering senescence (Wang et al., 2002). Jerusalem artichoke plants (short-day clones) grown in the greenhouse eventually die even though temperature conditions are optimal. The short day photoperiod in the late fall triggers the death of the plants whether they flower or not (buds removed). Similar plants exposed to a short days until mid-September (after the onset of tuber bulking) and subsequently moved to long day conditions (i.e., night interruption - short periods of low light during the middle of the dark cycle) initially resumed vigorous growth. If the flowers were removed, new lateral branches formed from most of the more apical nodes of individual branches; unpruned plants that flowered also grew vigorously, however, only at nodes of nonflowering branches (Kays, 2006). Eventually, however, both pruned and unpruned plants died even though exposed to long day conditions. Short days therefore appear to represent an environmental signal that triggers the eventual senescence and death of the plant.

The programmed nature of senescence allows recycling of resources from assimilate rich somatic tissues (e.g., leaves and stems) into generative tissues (tubers and seeds) facilitating reproduction. This scavenges material that would otherwise be lost, enhancing the reproductive effort, which has a direct impact on the harvest index. For example, Jerusalem artichoke plants that have allocated excessive resources into nonrecycleable structural components due to excess nitrogen or water have reduced tuber yields. The recycling processes involved are collectively called the senescence syndrome, which is a genetically programmed transition in the overall development of the plant (Bleecker and Patterson, 1997).

Senescence is highly regulated and requires the input of energy. The somatic tissues undergo complex cellular changes in ultrastructure and composition instigated by "senescence associated genes" (Becker and Apel, 1993). Specific genes are upregulated during this time, while others, such as those associated with photosynthesis, are downregulated. Upregulated genes include those for proteases, nucleases, transaminases, and other enzymes needed for recycling cellular components. In contrast, the expression of genes controlling C and N anabolism in the leaves (e.g., ADPglucose pyrophosphorylase and glutamine synthetase) is markedly reduced (Wiedemuth et al., 2005).

The developmentally programmed disassembly and senescence in the Jerusalem artichoke with the onset of reproduction is most graphically illustrated in the leaves (Figure 10.1b). Shortly after the onset of flowering, remobilization of nutrients from the canopy into the developing tubers begins. This process facilitates the eventual death of the leaves and increases their susceptibility to disease. The impact of recycling on the leaves is illustrated by the fact that detached leaves under appropriate conditions can survive longer than those attached to the plant (Edelman, 1963). Foliage death preceeding frost is ascribed to depletion of essential requisites (e.g., nitrogen), and late applications of nitrogen delay senescence, though without an increase in tuber yield (Morrenhof and Bus, 1990). Therefore, the number of leaves decline, with the foliage eventually killed by frost (Spitters, 1987; Tsvetoukhine, 1960). In early cultivars, most reserves are transferred before foliage death; in late cultivars, remobilization from the stems continues after death of the foliage (Barloy, 1984). At the

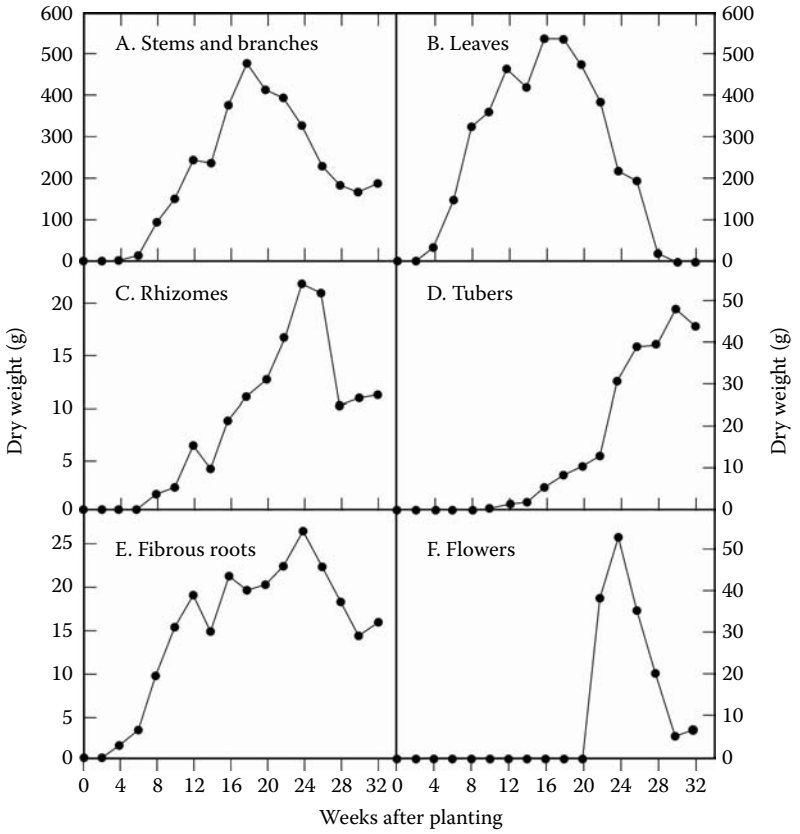


FIGURE 10.6 Changes in the dry weight of (a) stems and branches, (b) leaves, (c) rhizomes, (d) tubers, (e) roots, and (f) flowers per plant (cv. 'Sunchoke') during the growing season (30°57'N). (After McLaurin, W.J. et al., *J. Plant Nutr.*, 22, 1303–1313, 1999.)

end of recycling, virtually no sugars are left in the stems (Becquer, 1985; Barloy and Lemercier, 1991). Likewise, there is a decline in the dry weight of shoots, branches, rhizomes, fibrous roots, and flowers (Figure 10.6). Only the tubers continue to increase in dry weight (Figure 10.6d).

Organ and whole-plant senescence in the Jerusalem artichoke is a critical process that has a pronounced influence on the productivity of the species. Considering the importance of senescence, little is known about either its control or development at the cellular and molecular levels.

10.2 PHOTOSYNTHESIS

The Jerusalem artichoke is a C_3 species, fixing carbon via the reductive pentose phosphate pathway (Ehrgashev, 1976). It has a maximum photosynthetic rate that is higher than that for many C_3 species, comparable to or slightly exceeding that of cultivated and wild sunflowers (Lloyd and Canvin, 1977; Sharp and Boyer, 1986; Sobrado and Turner, 1986), and, in some instances, nearly comparable to that of certain C_4 species. There are relatively large differences (i.e., 29 to 40 μmol $CO_2 \cdot m^{-2} \cdot sec^{-1}$, or ~40%) among clones for maximum CO_2 assimilation rate (Table 10.2) (Soja and Haunold, 1991). The cultivar 'Waldspindel,' for example, consistently had one of the highest photosynthetic rates of the 10 clones tested but had a tuber yield that was only 35% of the highest-yielding clone. Hence, leaf photosynthetic rate is not a good indicator of yield potential. There is a close correlation, however, between both leaf nitrogen and chlorophyll contents and maximum photosynthetic rate, though tuber yield is not positively correlated with either (Soja and Haunold,

TABLE 10.2
Differences in Leaf Photosynthetic Rate Due to Clone and Stage of Development and Their Relationship to Final Tuber Yield

Clone	Leaf Photosynthetic Rate ($\mu M\ CO_2\ m^{-2}\ sec^{-1}$) Weeks after Emergence 4	8	14	Yield ($t\ ha^{-1}$)[a]
Nederösterreichische Landsorte	30 c[z]	40 a	31 d	10.8 a
K-8	31 bc	36 abcd	26 e	9.6 ab
Medius	31 bc	34 cd	33 bcd	8.6 bc
Rote Zonenkugel	30 c	35 cd	34 cd	8.6 bc
Violet de Rennes	30 c	29 e	26 e	8.1 bcd
Kärntner Landsorte	29 c	38 abc	33 cd	7.1 cde
Fuseau	33 b	36 abcd	24 e	6.8 de
Topianka	29 c	33 d	35 cd	6.6 de
Bianca	34 b	35 cd	37 b	5.5 c
Waldspindel	39 a	39 ab	44 a	3.8 f

[a] Final tuber yield at 27 weeks after emergence.
[b] Numbers in columns followed by different letters are significantly different at $p = 0.05$ by Duncan's test.

Source: Adapted from Soja, G. and Haunold, E., *Field Crop Res.*, 26, 241–252, 1991.

1991). The absence of a close correlation between maximum CO_2 assimilation rate and yield indicates that one or more additional factors are critical in determining yield, and while a high photosynthetic rate may be an important component of yield potential, it does not at this time represent a rate-limiting step.

10.2.1 Light

The light reactions of photosynthesis provide the energy required for the accumulation of carbon. As a consequence, the interception of photosynthetically active radiation is a critical component of biomass acquisition, such that there is a linear relationship between cumulative intercepted photosynthetically active radiation and biomass (Figure 10.7). The interception of light increases rapidly early in the growing season, when photosynthates are largely allocated to canopy establishment (Figure 10.8). With canopy closure the plants approach 100% light interception.

Young leaves saturate above 1700 $\mu E \cdot m^{-2} \cdot sec^{-1}$ (Soja and Haunold, 1991) and have a photosynthetic compensation point of ~55 to 60 $\mu mol \cdot m^{-2} \cdot sec^{-1}$. At the onset of flowering or tuber bulking, photosynthetic efficiency declines, as does leaf nitrogen content (Soja and Haunold, 1991). A number of plant and environmental factors interact, affecting the acquisition of carbon. Beer's law is commonly used at the canopy level to estimate light interception or absorption as a function of leaf area index. The light extinction coefficient for Jerusalem artichoke ranges from 0.78 to 1.01, varying with clone (Allirand et al., 1988; Spitters et al., 1988a). Leaf angle affects the amount of light striking the leaf. Typically the leaf angle distribution is between 0 and 55°, with the leaf azimuth distribution nearly random (Le Friant, 1983; Lemeur, 1973). Both leaf angle distribution and azimuthal distribution are used in calculating the extinction coefficient, which influences light penetration, interception, absorption, and sunlit leaf area index (Lemeur, 1973). When contrasted with the canopy of corn or soybean, Jerusalem artichoke absorbs more radiation in the top of the

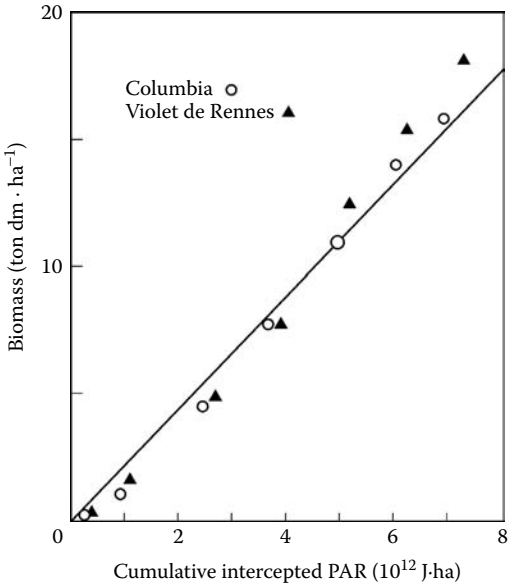


FIGURE 10.7 Relationship between total dry matter biomass production and the cumulative intercepted photosynthetically active radiation for 'Columbia' and 'Violet de Rennes' at 51°58'N. (After Spitters, C.J.T. et al., in *Topinambour (Jerusalem Artichoke)*, Report EUR 11855, Grassi, G. and Gosse, G., Eds., Commission of the European Communities, Luxembourg, 1988, pp. 37–43.)

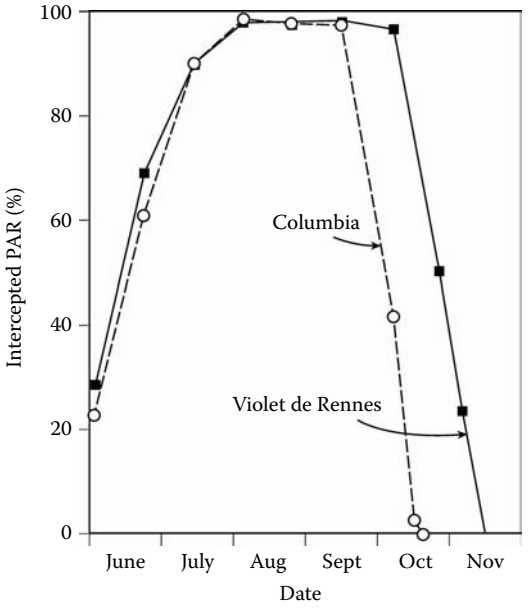


FIGURE 10.8 Changes in the percentage of photosynthetically active radiation intercepted by the foliage of 'Columbia' and 'Violet de Rennes' at 51°58'N. (After Spitters, C.J.T. et al., in *Topinambour (Jerusalem Artichoke)*, Report EUR 11855, Grassi, G. and Gosse, G., Eds., Commission of the European Communities, Luxembourg, 1988, pp. 37–43.)

canopy and less in the lower levels. The optical properties of the leaves are in keeping with most crop plants (Becquer, 1985; Le Friant, 1983), i.e., the albedo of the canopy is around 5% of the photosynthetically active radiation wavelengths. Due to differences in plant architecture, intercropping with potato (*Solanum tuberosum* L.) in alternate rows increased light interception by 42% (Paolini and DePace, 1997).

Leaf transpiration rates closely parallel photosynthetic rates over a range of light intensities (i.e., 400 to 1200 $\mu mol \cdot m^{-2} \cdot sec^{-1}$) (Soja and Haunold, 1991). Water use efficiency, therefore, remains rather stable relative to photosynthesis until the light intensity drops below 300 $\mu E \cdot m^{-2} \cdot sec^{-1}$. Here water use efficiency decreases sharply, with transpiration being higher relative to photosynthesis.

The chlorophyll concentration in the leaves varies among clones, with the sum of chlorophyll *a* and *b* ranging from 0.3 to 0.6 $g \cdot m^{-2}$ (Soja and Haunold, 1991). The ratio of chlorophyll *a* to *b* is similar across clones (i.e., 70 to 72% chlorophyll *a*, 28 to 30% chlorophyll *b*). Elevated chlorophyll content appears to be related to increased photosynthetic rate in some clones, as indicated by a positive correlation between photosynthetic rate and total chlorophyll content ($a + b$) ($r = 0.71$). Thus, clones with improved photosynthetic capacity could potentially be obtained by selecting for high chlorophyll.

10.2.2 Maximum Assimilation Rate

Maximum assimilation rate is correlated with leaf nitrogen and chlorophyll content (Soja and Haunold, 1991). Photosynthetic efficiency declines during tuber bulking, during which time nitrogen is translocated from the leaves into the developing tubers (Soja and Haunold, 1991; Somda et al., 1999). Ethylene has only a small inhibitory effect on the rate of photosynthesis (Pallas and Kays, 1982); however, photosynthetic capacity declines significantly with leaf age, especially while new leaves continue to be formed on the plant. Leaf position interacts with age in that older leaves tend to be at a progressively less desirable position in the light reception hierarchy. Thus, leaf position can strongly modulate the rate of carbon fixation. Leaves in more apical positions (e.g., the upper 0.5 m) on the plant tend to have at least double the gas exchange rate of more basipetal leaves (Table 10.3).

TABLE 10.3
Effect of Leaf Position on the Rate of Photosynthesis and Transpiration

Leaf Height from Base (cm)	Photosynthetic[a] Rate (%)	Transpiration[a] Rate (%)
300	100	100
280	91	94
250	84	82
225	47	45
215	37	23
195	7	9
165	5	9
120	27	30
95	21	23
70	20	19
50	5	5

[a] Percent of highest rate.

Source: Adapted from Soja, G. and Haunold, E., *Field Crop Res.*, 26, 241–252, 1991.

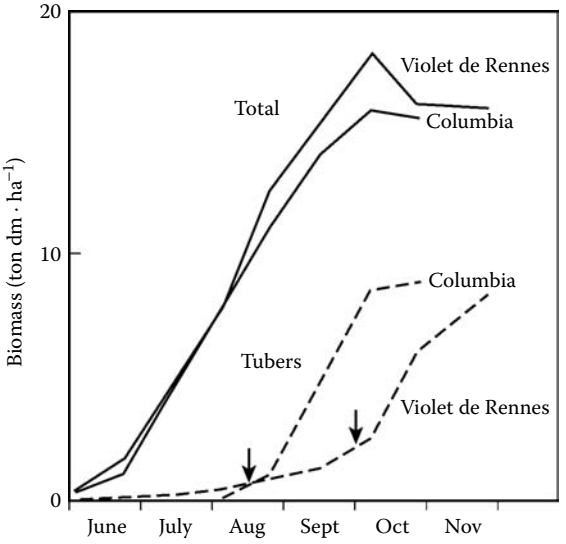


FIGURE 10.9 Seasonal pattern of dry matter allocation per plant and within the tubers for an early ('Columbia') and late ('Violet de Remmes') cultivar. (After Spitters, C.J.T. et al., in *Topinambour (Jerusalem Artichoke)*, Report EUR 11855, Grassi, G. and Gosse, G., Eds., Commission of the European Communities, Luxembourg, 1988, pp. 37–43.) Arrows indicate the timing of the onset of dry matter recycling from the stems into the tubers.

The effect of leaf position on the photosynthetic rate of Jerusalem artichoke (Soja and Haunold, 1991) is similar to that of the sunflower (English et al., 1979) in that leaf position becomes progressively more critical as the plant ages. When the plants reach their final height, only leaves in the upper 1/6 of the canopy display gas exchange rates greater than 50% of the most apical leaves (Table 10.3).

In addition to the degradation of chlorophyll in the oldest leaves at the base of the canopy, leaves midway on the stem, where branching has occurred, exhibit a loss in chlorophyll and a pronounced reduction in gas exchange. These changes begin with the onset of or just prior to rapid tuber development. As a consequence, only a relatively small portion of the canopy is involved in supplying photosynthates for tuber development during this period, with a majority of the dry matter recycled from aboveground storage sites (stems and leaves). During this period, the rate of increase in total dry matter within the plant declines markedly (Figure 10.9).

The canopy radiation use efficiency, the ratio of light absorbed to dry matter produced (Becquer, 1985; Gosse et al., 1986; Spitters, 1988; Spitters et al., 1988b), appears to improve during tuber bulking, possibly due to bypassing temporary storage in the stems or an increased capacity of the tubers to metabolize assimilates (Barloy, 1988; Schubert and Feuerle, 1997). The rate of carbon fixation, however, can be exacerbated by nutrition. When nitrogen uptake is restricted, premature leaf aging and a concurrent loss in photosynthetic capacity occur. Although it has not been tested in Jerusalem artichoke, extending the supply of available nitrogen later into the growing season of sunflowers maintains leaf photosynthesis and increases seed yield (Blanchet et al., 1986, 1987). Inadequate nitrogen is associated with declining photosynthetic rate in the Jerusalem artichoke and appears to have a greater impact on yield than insufficient phosphorus or potassium. Adequate phosphorus and potassium do influence whole-plant photosynthesis and assimilate translocation positively, but without enhancing single-leaf maximum photosynthetic rate (Soja and Haunold, 1991).

10.3 RESPIRATION

Respiration is a central metabolic process in plants that mediates the release of energy through the breakdown of carbon compounds and the formation of carbon skeletons necessary for maintenance and synthetic reactions. In contrast to the high degree of specialization among the various organs of a Jerusalem artichoke plant in the acquisition of energy, respiration occurs in all living cells and is essential for a diverse array of metabolic processes. The rate of respiration gives a very general indication of the overall rate of metabolism and can be used to calculate the percentage of the total fixed carbon that is subsequently loss.

10.3.1 Dark Respiration

Dark respiration of sugars involves a series of steps in three major interacting pathways: the glycolytic pathway, tricarboxylic acid pathway, and electron transport system. In glycolysis, sucrose translocated into the cells or fructose derived from inulin is broken down into pyruvic acid in the cytoplasm. Pyruvic acid is then translocated into the mitochondria, the location of the tricarboxylic acid cycle, where it is oxidized to carbon dioxide. Electrons released during oxidative steps in the glycolytic and tricarboxylic acid pathways enter the electron transport system, where they move through a series of complexes to the terminal acceptor, oxygen, yielding water. Energy is trapped chemically in the form of adenosine triphosphate (ATP), which is used throughout the cell for reactions requiring the input of energy. A fourth respiratory pathway, the pentose phosphate system, while not essential for the complete oxidation of sugars, functions by providing carbon skeletons, reduced nicotinamide adenine dinucleotide phosphate (NADP) required for certain synthetic reactions, and ribose-5-phosphate for nucleic acid synthesis.

10.3.2 Cyanide-Resistant Respiration

In addition to the normal electron transport system, Jerusalem artichoke tubers contain a second pathway called the cyanide-resistant or alternate pathway. A cross section of species (in some cases, only certain cells/tissues within a species) contains the alternate pathway, which is identified by its resistance to cyanide (e.g., hydrogen or potassium cyanide), a potent inhibitor of cytochrome oxidase, the enzyme that catalyzes the final step in the pathway. Cyanide-sensitive species have only the normal electron transport pathway. While cyanide does not actually function in the electron transport pathway, it is used to experimentally identify the presence of the alternate pathway. When only the normal pathway is present, cyanide inhibits respiration (measured as CO_2 emanation or O_2 uptake). In plants with the alternate pathway, cyanide stimulates respiration. The alternate pathway branches from the normal pathway at ubiquinone, with the electrons being transferred to an alternate cytochrome oxidase and subsequently to oxygen, forming water. When the alternate pathway is operative, the energy-trapping efficiency drops substantially, with only ~1 ATP, rather than 2.5, formed per reduced NAD. The remaining energy is lost as heat.

Jerusalem artichoke tubers are considered cyanide sensitive (i.e., the absence of a functioning alternate pathway); however, under appropriate conditions (e.g., exposure to 10 $ml \cdot l^{-1}$ ethylene in pure oxygen) the alternate pathway is activated, indicating that the alternative oxidase is either present or readily inducible (Theologis and Laties, 1982a, 1982b). Exposure of such tubers to cyanide results in the respiratory rate increasing over three-fold (i.e., from 14 ml $CO_2 \cdot g^{-1}$ fwt$\cdot h^{-1}$ in control tubers to 46 ml $CO_2 \cdot g^{-1}$ fwt$\cdot h^{-1}$).

The reason for the presence of the alternate pathway is not clear. One possible function is that when significantly increased levels of intermediates are needed during periods of high metabolic activity, their rate of synthesis is limited by the rate of the electron transport system. The alternate pathway may provide an unrestricted means of accelerating respiration and the production of the required intermediates. The alternative pathway's relationship to certain developmental processes supports this possibility. For example, cyanide inhibits the respiration of dormant tubers more than

it does nondormant tubers (Fol et al., 1989). Likewise, the alternate pathway does not appear to be a significant factor during tuber callus formation (i.e., 4% of O_2 uptake), but as adventitious roots begin to emerge from the callus, the alternate pathway is activated (Hase, 1987).

Jerusalem artichoke tubers have been used as a model system for studying various aspects of mitochondrial oxidation and the alternate pathway in a number of studies (e.g., Atlante et al., 2005; Rugolo et al., 1990; Rugolo and Zannoni, 1992). The mitochondria can be readily isolated and purified, facilitating a cross section of experiments (Liden and Moeller, 1988).

10.3.3 Respiratory Rate

Plant respiratory losses represent the composite of leaf, stem, flower, root, rhizome, and tuber losses, each of which varies in rate (Table 10.4). In general, young tissue (e.g., flowers; small, immature leaves) has higher rates of respiration than more mature tissue (e.g., stems). Leaves and rhizomes have higher respiratory rates than stems and branches. Tissues exhibiting relatively low respiratory rates (e.g., lower stem) tend to be more responsive to temperature, as indicated by a higher respiratory Q_{10}.* There are also significant differences in respiratory rate for specific plant parts among cultivars (e.g., 'Violet de Rennes' in general was lower than 'Medius' and 'Sunchoke').

The rate of respiration, and therefore dry matter loss, is modulated by temperature (Table 10.4), age of the respective organ, and, in some instances, plant population density. The respiratory rate of the leaves changes markedly with plant and organ age and location on the plant, but not with plant population density (Hogetsu et al., 1960). Respiration is higher in young apical leaves but decreases gradually as the individual leaf ages. For example, leaves very early in the season had rates of ~8.5 mg $CO_2 \cdot g^{-1}$ dwt$\cdot h^{-1}$ (May 17), which decreased to ~6 mg 71 days later (July 27) and to ~3.5 mg 35 days later (September 22). The respiration rate of mature and old leaves reached a fairly constant rate of 0.7 to 1.0 mg $CO_2 \cdot g^{-1}$ dwt$\cdot h^{-1}$. When respiration was expressed as a rate per unit of land area, leaves at a population density of 20 × 20 cm had the highest rate (~34 g dwt$\cdot m^{-2} \cdot day^{-1}$) in mid-July, declining thereafter. Stems respired at a rate of ~15 g dwt$\cdot m^{-2} \cdot day^{-1}$ (mid-July); the subterranean organs had the lowest rate (~4 g dwt$\cdot m^{-2} \cdot day^{-1}$). Plants at the widest spacing (lowest population density) had lower peak respiratory losses per unit area of land for each plant part.

The respiratory rate of Jerusalem artichoke is highly temperature dependent. The respiratory Q_{10} was calculated for the leaves, stems, subterranean organs (roots and rhizomes and tubers when present), and the whole plant. Jerusalem artichoke leaves had a Q_{10} of 2.0 (between 16 and 26°C); stems, 2.2 (9 and 22°C); subterranean organs, 2.3 (13 and 28°C); and the entire plant, 1.8 (16 and 26°C). For tubers stored at 0°C, the respiratory rate was approximately 10 mg $CO_2 \cdot kg^{-1}$ fwt$\cdot h^{-1}$ (Table 13.1), increasing to ~50 mg $CO_2 \cdot kg^{-1}$ fwt$\cdot h^{-1}$ at 20°C (Peiris et al., 1997). From 10 to 20°C the respiratory Q_{10} was 2.5. This translates into a dry matter loss of approximately 16 g·100 $kg^{-1} \cdot day^{-1}$ at 0°C, up to 80 g·100 $kg^{-1} \cdot day^{-1}$ at 20°C. In addition to giving off CO_2, respiration utilizes oxygen from the surrounding environment and releases heat (i.e., at 20°C approximately 80 J$\cdot kg^{-1} \cdot h^{-1}$), the latter of which must be dissipated to prevent the tubers from heating up during storage.

10.3.4 Respiratory Patterns

Plants and their individual parts display distinct patterns in their respiratory rate during development. One of the earliest studies on respiratory patterns was conducted on sunflower plants and component parts during an entire growing season (Kidd et al., 1921). In Jerusalem artichokes, total carbon respired from the leaves was calculated from the respiratory rate of different aged leaves × their weight (Hogetsu et al., 1960). The vertical distribution of leaf size (g dwt) and respiratory losses

* The Q_{10} indicates the effect of temperature on the rate of a reaction or process. It is the ratio of the rate (R) of a reaction at one temperature (T_1) vs. the rate at that temperature plus 10°C [$Q_{10} = (R \text{ @ } T_{1+10°C})/R \text{ @ } T_1$].

TABLE 10.4
Effect of Temperature on the Rate of Dark Respiration of Individual Plant Parts from Three Jerusalem Artichoke Cultivars

Plant Part	Temperature (°C)	Q_{10}[a]	Cultivar (mg $CO_2 \cdot kg^{-1}$ fwt$\cdot h^{-1}$)		
			Sunchoke	Medius	Violet de Rennes
Leaves (large)	20		152 a[b]	146 b	107 c
	30		280 b	313 a	261 c
		2.1			
Leaves (medium)	20		178 a	164 a	170 a
	30		465 a	346 c	419 b
		2.4			
Leaves (small)	20		253 a	202 c	245 b
	30		619 a	431 c	538 b
		2.3			
Flowers	20		637 a	409 b	310 b
	30		765 a	666 b	650 c
		1.5			
Flower stems	20		92 b	148 a	132 ab
	30		238 c	291 a	245 b
		20			
Rhizomes	20		174 b	223 a	114 c
	30		250 b	410 a	203 c
		1.7			
Stem (10–20)[c]	20		66 b	95 a	32 c
	30		180 b	231 a	105 c
		2.7			
Stem (30–45)	20		50 b	92 a	38 c
	30		164 b	272 a	110 c
		3.0			
Stem (70–80)	20		75 b	126 a	50 c
	30		216 b	295 a	176 c
		2.7			
Stem (90–105)	20		121 b	157 a	63 c
	30		260 b	351 a	182 c
		2.3			
Branches[d]	20		99 a	82 b	43 c
	30		159 b	172a	101 c
		1.9			

[a] Q_{10} for respiration.

[b] Cultivar means in horizontal rows followed by different letters are significantly different at the 5% level by Duncan's multiple-range test.

[c] Segment of the main stem in cm from the base of the plant.

[d] Lower 15 cm of side branches from near the base of the plant.

Source: Kays, S.J., unpublished data.

are presented in Figure 10.10 (Hogestsu et al., 1960). The maximum rate of respiratory losses occurred early in the season (e.g., June 19), with newly expanded leaves respiring at ~1.6 mg $CO_2 \cdot g^{-1}$ dwt. There was a progressive decline at later dates in the growing season.

Plant population density affected the amount of respiratory losses; at the highest density (10 × 10 cm), the total respiratory losses increased markedly in June. At the lower densities (20 × 20

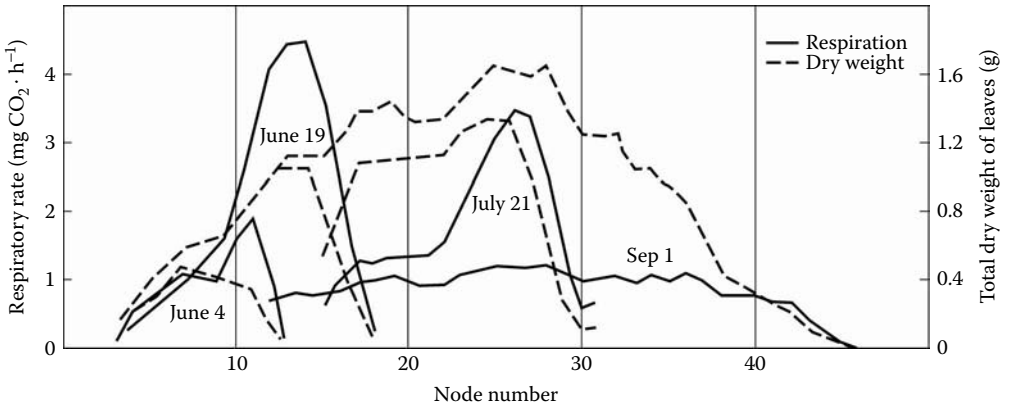


FIGURE 10.10 Vertical distribution by stem node of leaf respiratory losses and total leaf dry weight at four developmental stages during the growing season. (After Hogetsu, K. et al., *Jpn. J. Bot.*, 17, 278–305, 1960.)

and 30 × 30 cm), the increase was delayed until mid-July, coinciding with the maximum increase in dry weight of the plant (Figure 10.11) (Hogestsu et al., 1960). Individual plant parts differed in their contribution to respiratory losses, and the rate was affected by plant population density. The percentage of total dry matter acquisition that was lost via respiration was approximately 50% through mid-development, after which most of the photosynthetically fixed carbon was respired by the leaves. At higher plant population densities, earlier in the developmental sequence a net loss in carbon occurred. In the later stages, the losses in dry matter from leaves and stems via respiration, translocation, and shedding were not compensated for by new photosynthate, giving a net loss in weight.

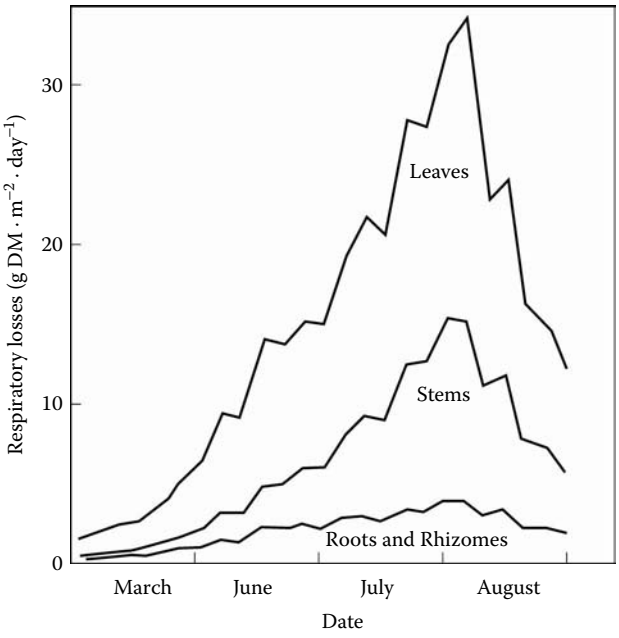


FIGURE 10.11 Change in daily respiratory losses for leaves, stems, and roots and rhizomes during the growing season. (After Hogetsu, K. et al., *Jpn. J. Bot.*, 17, 278–305, 1960.)

In general, young, rapidly metabolizing leaves had the highest respiratory rates. The high demand for energy and carbon compounds in actively growing cells results in a stimulation of respiration. As the age of the plant or individual organ increased, the respiratory rate decreased. The decline in whole-plant respiration could not be attributed simply to an increased percentage of nonrespiring structural cells since the initial respiratory rate of successive new leaves also decreased with the age of the plant. Hence, internal factors have a pronounced influence on respiration.

10.3.5 Photorespiration

The respiratory rate of chlorophyllous tissue as measured by the loss of CO_2 from the tissue proceeds at a higher rate in the light than in the dark. This light-stimulated loss of carbon, termed photorespiration, is a process that is in addition to or superimposed on the normal dark respiratory process in the plant. A significant portion of the carbon that is fixed in many species actually moves through the photorespiration pathway. In C_3 species such as Jerusalem artichoke, it is estimated that between 30 and 50% of the photosynthetically assimilated carbon in the leaves may be lost through the process of photorespiration.

10.4 ASSIMILATE ALLOCATION STRATEGY

The Jerusalem artichoke partitions photosynthates among growth, maintenance, and storage reactions, with allocation to growth predominating early in the season. This is illustrated by a biphasic growth pattern in the tubers that begins to be initiated relatively early in the growing season. Initial growth is slow as tuber storage capacity is formed, even though there is a surplus of assimilates available. During this time, excess photosynthate is stored in the stems, and even though tubers are present, bulking does not begin in earnest until late in the season for short-day clones (Denoroy, 1996; McLaurin et al., 1999; Spitters, 1990b; Spitters et al., 1988a) (Figure 10.9). The onset of the shift in allocation to tuber storage varies with cultivar and production conditions and appears to more or less coincide with flowering. During tuber bulking, carbon is derived from both new photosynthates and stored carbon recycled from the stem and, to a lesser extent, other organs. In early, day-neutral clones, the onset of tuber bulking is thought to be determined by a minimum temperature sum following emergence (van de Sande Bakhuyzen and Wittenrood, 1950; Zhou et al., 1984).

A key component in tuber bulking is the cessation of canopy growth and the onset of its dismantling (i.e., senescence syndrome), which appears to be regulated by exposure to short days. A similar cessation of growth in *Populus trichocarpa* Torr. & Gray* is controlled by the *CO*/*FT* genes, as is flowering in Arabidopsis (see Section 10.1.4). During short days in the fall, the growth of *P. trichocarpa* terminates and a significant portion of its leaf dry matter present is recycled into perennial components of the plant for growth the following season (Böhlenius et al., 2006). Photoperiodic control of this developmental change circumvents the potential risk of frost damage. The Jerusalem artichoke displays a similar developmental regulation by short days.

The biological rationale for the stem → tuber storage strategy may simply be a genetic holdover from one or both progenitors of Jerusalem artichoke. In seed-bearing species of *Helianthus*, the stem represents an essential storage site for carbon that is eventually repartitioned into the seed. The addition of tubers, superimposed upon the ancestral assimilate management strategy during the development of *H. tuberosus*, would not have necessarily eliminated the former. The existing system affords considerable reproductive flexibility to wild clones in that the relative allocation between sexual and asexual reproduction can be readily adjusted to prevailing conditions. Sexual

* Synonymous to *P. balsamifera* ssp. *trichocarpa* L. (Torr. & Gray ex Hook.) Brayshaw.

reproduction facilitates dispersal and genetic improvement but has a greater reproductive risk than asexual reproduction (Westley, 1993).

It has been estimated that from three to six ATPs per mole of sucrose, or 4 to 8% of the total biomass, is expended in the storage → recycling → restorage process (Meijer and Mathijssen, 1991). What, therefore, is the adaptive advantage of this reproductive strategy? It is possible that temporary storage allows delaying the decision as to the amount of resources to allocate between the primary reproductive options (i.e., sexual vs. asexual). In wild populations, when there is significant cross-pollination, and thus the potential for viable seed formation, stored resources can be so directed. It is also possible that transient storage is simply an evolutionary vestige from the species' non-tuber-bearing progenitors. In the sunflower, for example, stem storage allows amassing a reservoir of assimilates prior to the onset of flowering, thus maximizing the plant's reproductive potential.

Likewise, the efficiency of the system (total costs) can be further compromised by factors affecting the size of the temporary storage sites relative to actual needs. Insufficient or excess stem storage capacity affects the overall efficiency of the system and is known to be influenced by production factors. Conditions such as high nitrogen result in excessive top growth with a corresponding decrease in harvest index and tuber yield (Baillarge, 1942; Barloy, 1988a, 1988b). Thus, selecting for a more direct allocation of dry matter (i.e., directly to the tubers) might be advantageous if it is possible to genetically circumvent the stem as a temporary sink.

A second limitation of the existing dry matter acquisition/allocation strategy is that the rate of dry matter fixation declines substantially after the onset of the reallocation of dry matter from the aboveground plant parts to the tubers (Figure 10.9). This indicates the presence of a programmed shift to a senescence phase where the aboveground portion of the plant is progressively dismantled. There is a marked decline in the net input of dry matter into the system after the onset of the aerial senescence phase. The existence of a genetically controlled senescence mechanism is further evidenced by certain early-maturing lines/cultivars in which the aerial parts actually die prior to the end of the normal growing season. Selection of lines that maintain a high level of carbon fixation after the onset of tuberization, especially if coupled with earlier tuber development, could therefore potentially improve final yield.

Increased productivity in crop plants has arisen predominantly from altering the allocation of carbon and nutrient elements among vegetative and reproductive plant parts, rather than increases in photosynthetic efficiency. The ability of Jerusalem artichokes to produce optimum yields in a given environment is also strongly dependent upon the growth kinetics of individual plant parts, which are a function of the magnitude of carbon and nutrient element acquisition, transport, and allocation. During the early stages of growth, the vegetative tissue of Jerusalem artichoke* serves as a reservoir for carbon compounds and mineral nutrient element accumulation. During the shift from the vegetative to the reproductive phase, these organs assume an export function with mobilized dry matter accumulating in the developing reproductive storage sinks. The role of source–sink relations in the dry matter economy of a number of species has been reported (e.g., Drossopoulos et al., 1994; Garcia-Luis and Guardiola, 1995; Hocking, 1994; May et al., 1994; Picchioni et al., 1997). For example, in fruit and nut trees, carbon and nutrient element demand in the reproductive organs is partially met via redistribution from storage pools in perennial organs. Likewise, developing seeds of annual grains recycle labile nutrient element pools from senescing leaves.

In Jerusalem artichoke and other root and tuber crops, a significant portion of the total biomass at harvest is found in the underground storage organs (Kays, 1985; McLaurin et al., 1999; McLaurin and Kays, 1993; Meijer et al., 1993). The internal redistribution of carbon and nutrient elements that accumulate in the stems and leaves of Jerusalem artichoke plays an important role in the development of the tubers (McLaurin et al., 1999; Somda et al., 1999). Similar, but often more complex, accumulation and redistribution patterns occur for carbon and the mineral nutrient

* And a number of other species.

elements in individual plant parts. In addition to the impact of redistribution on yield, it is important to understand this accumulation and redistribution in developing appropriate fertilization strategies and in the selection of tissue sampling techniques for element analysis.

10.5 CARBON TRANSPORT

Leaves function in the acquisition of free energy captured in photosynthesis for the reductive fixation of carbon into carbohydrates. A major portion of fixed carbon is translocated out of the leaf during the day; however, when the transport capacity is exceeded, excess is converted to inulin, rather than starch,* for short-term storage within the leaf. Contrary to early reports (Thoday, 1933), inulin is synthesized in the leaves (Strepkov, 1959) and is thought to be converted back to sucrose during the dark period for translocation to the appropriate sinks (Ben Chekroun, 1990). The concentration of reserve carbon within the leaves varies widely during the day (Lemercier, 1987). Short-term leaf storage allows maximizing carbon acquisition when transport is the rate-limiting step in the process. In this manner, fixed carbon in the form of sucrose is translocated out of the leaf for distribution to other parts of the plant (Edelman and Popov, 1962; Dickerson and Edelman, 1966; Soja et al., 1989). It is estimated that as much as 80% of the carbon acquired in photosynthesis is transported in the plant's vascular system to import-dependent organs.

Transport occurs in the phloem and involves three general steps: phloem loading at the source, transport, and hydrolysis at the sink. After synthesis in leaf chlorenchyma cells, sucrose must traverse the plasma membrane of the cell and move into the apoplast. The molecules diffuse in the apoplastic solution to phloem cells, where they are transported across the plasma membrane against a concentration gradient via an energy-dependent process. The key initial step in the allocation of carbon is the loading of sucrose into the phloem, a process that creates the hydrostatic pressure required to drive its long-distance transport. Phloem loading is controlled by sucrose symporters in the plasma membrane of phloem cells. Symports represent a form of secondary active transport that are driven by coupling the passive flow of H^+ or Na^+ with the energetically uphill flow of the solute. The phloem plasma membrane sucrose symporter couples sucrose transport to the proton electrochemical potential difference across the membrane. The gene encoding the symporter has been cloned from a cross section of species, and its pivotal role demonstrated using antisense expression that results in reduced transport and subsequent plant growth (Kühn et al., 1996; Riesmeier et al., 1994). Sucrose also acts as a signaling molecule in the signal transduction pathway that regulates the symporter. For example, high levels of sucrose in the xylem result in a decline in sucrose symporter activity within 8 h (Chiou and Bush, 1998).

Sucrose transport can be acropetal or basepetal in direction with both the absolute flux and directional allocation important in determining yield. The directional flow of sucrose from individual leaves is controlled by the position of the leaf on the plant and the hierarchy of demand for photosynthates at any given moment. In the Jerusalem artichoke, basipetal translocation exceeds acropetal to immature leaves and stem, even in the early stages of growth when tubers were absent or very small (Soja et al., 1989). A critical step at the sink is the hydrolysis of sucrose, a process that is essential for the maintenance of the concentration gradient needed to drive diffusion in the phloem. Sucrose moves from the phloem into the cytoplasm of a sink cell, the route of which depends upon the presence or absence of continuity in the symplast. In the absence thereof, sucrose moves across the cell wall space, where it is hydrolyzed by a cell wall invertase forming fructose and glucose. If movement is symplastic (i.e., through the plasmodesmata), sucrose can be hydrolyzed by a cytoplasmic invertase (forming fructose and glucose), sucrose synthase (forming fructose and UDP-glucose), or vacuolar invertase (forming fructose and glucose) (Koch, 2004). The dominant invertase operative is thought to exert a critical influence on development. High vacuolar or cell wall invertase activity is believed to facilitate sink initiation and expansion, while high sucrose

* A small amount of carbon is stored as starch within the leaf (Ernst, 1991).

synthase activity facilitates storage and maturation of the cell. The monosaccharides formed appear to act as hexose sugar signals that upregulate a diverse array of early developmental genes.

Positional and temporal relationships relative to sucrose transport and allocation within the Jerusalem artichoke are not fully understood. The stem serves as a temporary storage site for carbon in the form of fructans prior to flowering; after flowering, sucrose is translocated directly to the tubers. The ability to synthesize fructans develops slowly in the stem, while young rhizomes have a high capacity for synthesis even before tuberization (Soja et al., 1989). Transport from an individual leaf is within a portion of the stem (~25% of the vascular bundles), reflecting the continuity of the phloem from an individual leaf to a sink and the absence of crossover into neighboring bundles. Distribution of sucrose initially occurs on the periphery of the stem with subsequent movement inward. The portion of the stem receiving sucrose is dictated by its vascular connections, and radial movement inward is restricted to cells interior to vascular bundles. Movement of sucrose into parenchyma storage sites within the stem occurs at a much slower rate than basipetal transport to the tubers. While the actual rate of transport within the stem has not been reported, transport is thought to decrease markedly as the plant becomes progressively older. The delay in incorporation of sucrose into the stem is thought to be similar to the time required for incorporation into fructans (Soja et al., 1989), suggesting that fructan synthesis may be a rate-limiting step. Sucrose is hydrolyzed and fructans begin to be synthesized, initially into lower molecular weight fructans (i.e., ~6 h); after 24 h, a higher-degree-of-polymerization fraction increases progressively from day 3 to 10. Lower, older sections of the stem have a higher percentage of sucrose converted into storage fructans than younger portions of the stem.

The stem is the primary sink until flowering, at which or slightly before storage capacity is lost. Unlike *Helianthus annuus*, in cultivated Jerusalem artichoke clones the flowers exerted very little sink activity. After flowering, the stems lose their ability to store assimilates. Existing polymers are degraded and transported to the tubers. Remobilization involves the hydrolysis of inulin into the component monosaccharide fructose, the synthesis of sucrose, sucrose loading in the phloem, transport, and unloading in the tubers followed by resynthesis of long-chain fructans. The vascular bundles supplying sucrose to the tubers are found in a ring-shaped area at the periphery, indicating a high degree of vascular continuity, similar to that of stem storage sites. Tubers receive sucrose in a narrow ring at their periphery, the percentage of the circumference depending upon vascular connections. Therefore, individual tubers in cross section may display ^{14}C-labeled photosynthates entirely around their perimeter, in only a portion, or not at all.

Late in the season, after the onset of the reallocation of carbon from aboveground storage sites to the tubers, sucrose translocated from the leaves bypasses storage in the stem and is moved directly to the tubers. Thus, toward the end of the growing season the tubers are supplied through phloem transport from two primary sources: recent photosynthates from the leaves and hydrolyzed fructans from the stems. During the last part of the growth cycle, the stem dry weight decreases by about 50% (Soja, 1983), accounting for the rapid growth of tubers late in the season, even though the photosynthetic capacity has diminished (Soja, 1988).

10.6 SINK STRENGTH IN RELATION TO ALLOCATION

Various centers of metabolic activity exhibit a high demand for photosynthates such that there is competition within the plant for available resources. Thus, during the development of the plant, at any moment in time, there exists a dominance hierarchy for photosynthates. In the Jerusalem artichoke, photosynthetically fixed carbon resources are allocated among maintenance reactions, production of additional structural components, and deposition within specialized storage sites within the plant. The allocation hierarchy shifts not only as the plant develops, but also in diurnal cycles. Therefore, photosynthate allocation depends upon both timing and assimilate availability.

Sink strength is a measure of the sink's ability to accrue photosynthates, and the rate of change in dry weight of a particular sink is considered indicative of its competitive ability within the plant.

During initial development, structural growth generally has a higher priority in the hierarchical scheme of photosynthate distribution than stem and tuber storage sites. The relative importance of structural development is illustrated by the fact that after severe defoliation, the stem and leaves have the highest priority for assimilates as the plant reestablishes its carbon fixation intrastructure (Swanton and Cavers, 1989).

It has been nearly a century and a half since Boussingault (1868) presented the hypothesis that "the accumulation of assimilates in an illuminated leaf may be responsible for a reduction in the net photosynthetic rate of that leaf." According to the Münch hypothesis for phloem transport, the greater the sink strength, the greater the depression in solute concentration in the phloem at the sink. This increases the concentration differential between the source and sink, creating the hydrostatic pressure head that drives the system.

There has been considerable debate on whether sink strength (fructan storage) or source availability is the rate-limiting factor controlling tuber yield. Arguments favoring sink strength as rate limiting include: (1) the differential in the decline in tuber yield vs. the decrease in leaf area when side branches are removed; (2) lack of variation in tuber sucrose level with the presence of side branches, apical dominance, and temperature; and (3) a decrease in apparent sink strength in unbranched plants (Schubert and Feuerle, 1997). Conversely, several lines of evidence indicate that tuber growth is to a large extent a function of assimilate availability (Denoroy, 1996). For example, if competing sinks for assimilates are suppressed (e.g., removal of buds/flowers/apices), tuberization is promoted (Couduroux, 1966; Westley, 1993). Likewise, factors that decrease the allocation of assimilates into canopy growth, such as the onset of flowering or the application of a growth inhibitor, increase tuberization (Meijer and Mathijssen, 1991; Morrenhof and Bus, 1990). Decreasing assimilate supply from the leaves through defoliation decreases tuber growth (Baillarge, 1942; Couduroux, 1966; Moule et al., 1967), or conversely, elevating the rate of carbon fixation through increased illumination increases tuber growth (Toxopeus, 1991). While it is possible that there are periods in which sink capacity is limited (e.g, early in the tuber storage phase), final yield appears to be dictated largely by assimilate supply.

The allocation of carbon accrued by the plant can be modulated by a number of factors. For example, environmental and cultural conditions, as well as differences among clones, can have a pronounced effect on allocation (Barloy, 1988b; Spitters, 1990b). Under conditions of high rainfall or excess nitrogen, the allocation pattern shifts in favor of vegetative growth. With moist conditions, top growth may reach 4 m in height and is generally accompanied by significantly reduced tuber yield. Under these conditions, aerial plant parts display a higher competitive ability for photosynthates.

Timing during the development cycle is also a critical factor. For example, during the first half of the developmental cycle, photosynthate is partitioned predominantly into stem storage sites (Incoll and Neales, 1970; McLaurin et al., 1999). However, with the onset of tuber bulking, allocation within the plant shifts dramatically. Now a major portion of new assimilate preferentially moves into the rapidly developing tubers, and assimilate previously stored in the stems begins to be recycled to the tubers.

In addition to differences in priority for assimilates among different types of sinks within a plant (e.g., stems vs. tubers), there exists competition for assimilates within a specific type of sink (e.g., tubers on the same plant). The factors controlling the flow of carbon to competitive sinks are not well understood, and a number of mechanisms can influence the preferential movement of carbon to one sink over another. Differences in the ability of a sink to deplete the supply of photosynthates in the phloem (unloading coefficient) alter the source $\rightarrow$ sink concentration gradient (i.e., driving force), increasing (or decreasing) the movement of carbon to that sink. Variation in the chronological order of inception of the sink is also a factor. Hence, large tubers have more cells that increase their potential to deplete the level of sucrose in the phloem. The position of the sink relative to the source of assimilate production can also be significant. Using mass flow models, sinks with identical unloading coefficients (strength), but at different distances from the source loading zone, can be shown to have differences in the absolute amount and percentage of the total

photosynthate unloaded into each; sinks close to the source have the advantage. Finally, vascular connections and lateral transport potential may also be important in the establishment of a hierarchy of carbon allocation between competitive storage sinks.

A dominance hierarchy also exists within individual sinks. When the level of photosynthate is high, lateral buds on the tubers begin to develop and act as competing sinks (Tsvetoukhine, 1960). Development of lateral buds results in tubers with a highly irregular form and reduced value for many uses.

10.7 ASSIMILATE ALLOCATION AND REDISTRIBUTION

Jerusalem artichokes temporarily store assimilates in several locations within the plant that are in excess to the amount needed for structural and maintenance purposes. Most of these reserves are reallocated to the tubers during bulking. While a cross section of assimilates is found in these sites, carbohydrates predominate, of which inulin is the primary storage form. In addition to mono- and disaccharides and small amounts of starch, a number of nutrients are found, many of which are phloem mobile and reallocated to the tubers during the latter part of the growing season.

Leaves, stems, branches, roots, and rhizomes function to varying degrees as sites for assimilate storage. During development of the aerial portion of the plant, it has been estimated that a maximum of only one third of the assimilates are allocated to the growing apices (Soja et al., 1989); the remainder are utilized for development of other structural components, energy and carbon skeletons for maintenance reactions, and storage. Various storage sites (e.g., stems vs. leaves) appear to differ in their general role in plant development and in the length of time the assimilates are stored. On a quantitative basis, the stems represent the most important of the temporary storage sites.

The leaves are known to temporarily store mono- and disaccharides, small amounts of starch, fructans, and nutrient elements (Schubert and Feuerle, 1992; Lemercier, 1987; Pollock, 1986; Soja et al., 1989; Somda et al., 1999). A portion represents short-term diurnal storage of carbon compounds during the light period (Lemercier, 1987) that are converted to sucrose and translocated out of the leaf during the night (Ben Chekroun, 1990). Temporary storage in the leaves is thought to arise when carbon acquisition is greater than the leaf's transport potential. In many species excess carbon is stored in the chloroplasts as starch; however, based upon the concentration of inulin vs. starch in Jerusalem artichoke leaves (9.47 vs. 0.45%), inulin appears to represent the primary form of carbon for short-term leaf storage (Schubert and Feuerle, 1992). In addition, fructans and a cross section of nutrient elements are stored until the onset of tuber bulking.

Roots and rhizomes also function as temporary storage sites and can synthesize and store fructans for a longer period of time than the stems (Soja et al., 1989). Up to 40% of the root dry weight may represent nonstructural carbohydrates (Hang and Gilliland, 1982). Root dry weight decreases during the final stages of tuber bulking (Figure 10.6) (McLaurin et al., 1999); however, if the tubers are removed, assimilate storage continues (Edelman, 1963). In wild clones, the rhizomes retain much of their assimilates and act as secondary propagules for the plant. In cultivated clones, however, the rhizomes generally recycle much of their assimilates and decompose in the soil fairly readily after death of the aboveground plant parts.

Stems and branches represent the primary sites for the temporary storage of assimilates with the percentage of reserves varying with cultivar, number of days after planting, geographic location, production conditions, and year (Kosaric et al., 1984). Estimates of the amount of reserve assimilates temporarily stored range from 25 to 70% of the stems' dry weight (Barloy and Lemercier, 1991; D'Egido et al., 1998; Hang and Gilliland, 1982; McLaurin et al., 1999; Spitters, 1987; Toxopeus, 1991) or 14 to 17% of their fresh weight (Ben Chekroun, 1990). Carbon is stored as mono- and disaccharides and fructans, with the latter comprising the greatest percentage (D'Egido et al., 1998). The average degree of polymerization of the fructans increases toward the base of the stem (Lemercier, 1987; Strepkov, 1960a, 1960b), with the medullar portion of the stem the primary site of deposition (Strepkov, 1960a, 1960b). The allocation of carbon into the stem occurs concurrently

with tuber growth until tuber bulking in short-day clones. In potato, 87% of the tuber dry weight is derived from current photosynthesis; however, in the Jerusalem artichoke, the decrease in stored reserve carbon in the plant is thought to account for nearly all of the tuber growth (Incoll and Neales, 1970).

Accumulation of fructans is enhanced by high light intensity and moderate temperatures. It is reduced by excess nitrogen or insufficient potassium (Soja and Haunold, 1991). Distribution of assimilates initially occurs on the periphery of the stem with subsequent movement inward. The portion of the stem receiving assimilates is dictated by its vascular connections. Radial movement inward is restricted to cells interior to vascular bundles.

The accumulation and redistribution of assimilates can be viewed as changes in dry matter, carbon, individual nutrient elements, or specific compounds (e.g., sucrose) or classes of compounds (e.g., inulins). In the following subsections, the quantitative and temporal accumulation and subsequent redistribution of dry matter, carbon, and nutrient elements in the various locations within the plant are described.

10.7.1 Dry Matter

The deposition of dry matter in the various structural components of the Jerusalem artichoke has been documented in a number of studies over a wide range of production conditions (Barloy, 1984; Lemercier, 1987; McLaurin et al., 1999; Meijer et al., 1993; Spitters et al., 1988a). The pattern of dry matter accumulation varies among clones due to differences in growth characteristics, photoperiodic requirements, time of planting, location, and other factors. Data from a study by McLaurin et al. (1999) (Figure 10.1 and Figure 10.6) illustrate the general temporal developmental pattern of a long-season (short-day) clone.

For long-season clones, the early vegetative stage involves a rapid increase in the number of aerial plant parts, with the exception of the flowers. The majority of assimilates are directed toward structural development such that on a numerical basis, much of the aboveground structure of the plant is formed (Figure 10.1). From an ecological standpoint, the expenditure of energy for rapid stem, branch, and leaf growth facilitates the plant's effective exploitation of aboveground resources. In the illustrated cultivar, the formation of shoots and branches plateaus by about the eighth week after planting, when approximately two thirds of the leaves have been formed (Figure 10.1a to c). At this time the rhizomes and tubers are just starting to develop.

During the dry matter accumulation stage, between the 8th and 18th weeks, there is a tremendous increase in dry weight of the aboveground plant parts (Figure 10.6), along with a progressive increase in rhizome and tuber number (Figure 10.1d and e). At their peak, stems and branches make up the largest percentage of the aboveground dry matter (i.e., 60 to 80%), with leaves comprising the majority of the remainder. The greatest distribution of stem dry matter is found in the lower nodes (Lemercier, 1987).

During the redistribution/tuber bulking stage, there is a rapid decline in the dry weight of the aboveground plant parts, with the exception of the flowers, and an increase in the dry weight of the tubers (Figure 10.6). Recycling of dry matter begins in earnest around the time of flowering in short-day clones. The precise timing of the onset differs among studies — flower initiation (Meijer and Mathijssen, 1991), bud formation (Morrenholf and Bus, 1990), flowering (Ben Chekroun, 1990; Barloy and Lemercier, 1991), or sometime after the onset of flowering (Spitters and Morrenhof, 1987). The reason for this variation is in part due to the fact that there is not a direct relationship between flowering and tuber bulking. In short-day flowering clones, both flowering and tuber bulking are modulated by day length; however, tuber formation will occur in the absence of the appropriate photoperiod (Soja and Dersch, 1993). With flowering, growth of the vegetative portion of the plant ceases and there is a developmentally regulated shift toward reproduction as the primary focus. New photosynthates are now allocated to the tubers (Fernandez et al., 1988, Soja et al.,

1989). Therefore, while flowering is not necessary for tuberization, it not only is temporally associated in short-day clones, but also indirectly influences tuber development.

The loss in stem and branch dry matter begins (i.e., ~18 weeks after planting) well before anthesis (>20 weeks after planting) in the short-day clone illustrated in Figure 10.6a. Assimilates at this point are no longer directed toward the stem apex (Fernandez et al., 1988, Soja et al., 1989). The maximum period of tuber growth (i.e., from 22 to 28 weeks after planting) (Figure 10.6d) corresponds to the period of the greatest weight loss from the stem and branches (Figure 10.6a) (McLaurin et al., 1999; Soja et al., 1989). The relative growth rate of the tubers at this time is approximately 35 $mg \cdot g^{-1} \cdot day^{-1}$ (Incoll and Neales, 1970), or ~36 g $dwt \cdot plant^{-1} \cdot week^{-1}$, between the 22nd and 30th weeks after planting (McLaurin et al., 1999). Rhizome and root dry matter increases until the 24th week after planting and then declines (Figure 10.6c and e). The degradation of the rhizomes after canopy death in the late fall, a common phenomenon among many of the cultivated clones, facilitates mechanical harvest.

Flower dry weight increases rapidly following the 20th week after planting (Figure 10.6f), reaching a peak the 24th week and then declining thereafter. At their maximum, the flowers represent only a very small percentage of the total dry matter in the plant (~1.5 to 2%), though this varies among clones (Barloy, 1984; McLaurin et al., 1999; Swanton, 1986).

Yield increases in many crops have come from altering the allocation of dry matter within the plant — e.g., winter wheat (*Triticum aestivum* L.) (Austin et al., 1989) — and, to a lesser extent, increasing total fixed dry matter — e.g., corn (*Zea mays* L. subsp. *mays*) (Russell, 1991). As more of the total assimilates are partitioned into the structure of interest, a smaller percentage is allocated to other components (e.g., stems, leaves) (Hay, 1995). Harvest index, a term first used by Donald (1962), is an indication of the "reproductive effort" (Harper, 1977), i.e., the ratio of the dry matter partitioned into the edible or useful portion of the crop to the total biomass. In grain crops, only the aboveground portion of the plant is considered; however, with root and tuber crops, the underground storage organs are the product of interest and are related to either aboveground dry matter or the aboveground and a portion of the belowground dry matter (e.g., rhizomes, large nonstorage roots), depending upon the study. The percentage of the dry matter partitioned into the Jerusalem artichoke tubers relative to the remainder of the plant reaches a maximum (approximately 70% of the total biomass of the cultivar illustrated) ~30 weeks after planting (Figure 10.6d). Therefore, approximately 7 $t \cdot ha^{-1}$ of biomass was allocated to nontuber components. The percentage of dry matter allocated to the tubers is comparable to sweetpotato (*Ipomoea batatas* (L.) Lam.), where 64 to 72% of the total dry matter is in the storage roots at harvest (McLaurin and Kays, 1993; Yoshida et al., 1970). In contrast, chicory (*Cichorium intybus* L.), which has virtually no stem, allocates approximately 77.5% of its dry matter into the storage root (Meijer et al., 1993).

10.7.2 Carbon

Carbon accumulation and redistribution parallels that of total dry matter, of which carbon comprises a major percentage. Alterations in the carbon content more accurately reflect changes in carbohydrates than total dry matter. During the early vegetative stage, the carbon content is low, with the concentration stabilizing around the 14th week after planting at 40% of the total dry matter (Figure 10.12) (Somda et al., 1999). The concentration in the various plant parts is relatively consistent even during the latter part of the growing season, when carbon is redistributed during tuber bulking.

The pattern of carbon accumulation differs among the various plant parts. The total carbon content of the aerial portion of the plant increases until a maximum is attained, ~20 weeks after planting, and then decreases progressively during tuber bulking (Somda et al., 1999). Aboveground plant structures have the highest carbon levels, with the content increasing more rapidly in the stems and branches than in the leaves. Both increase progressively until 18 to 20 weeks after planting. Initially leaves comprised more than half of the total plant carbon content; however, the net rate of carbon accumulation in the leaves declines to nearly zero during the latter part of the

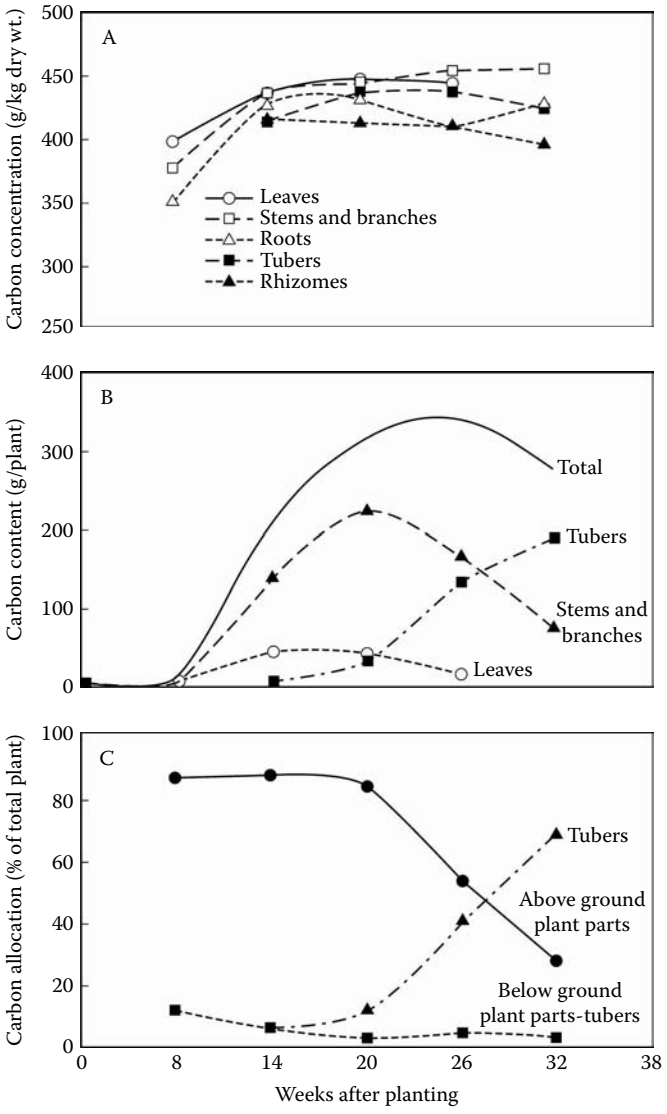


FIGURE 10.12 General distribution of carbon per plant during the growing season. Carbon concentration (A) and accumulation (B) in different plant parts, and carbon partitioned (C) into aboveground plant parts, belowground vegetative parts, and tubers and rhizomes grown at 30°57'N. (After Somda, Z.C. et al., *J. Plant Nutr.*, 22, 1315–1334, 1999.)

growing season (Somda et al., 1999). Toward the middle of the growing season, the stems and branches have the highest proportion of the plant's total carbon content, which subsequently decreases. Although the patterns of carbon accumulation were similar in both leaves and stems/branches, the leaves have a lower carbon content that begins to decline earlier (~6 weeks) than in the stems. In general, the allocation of carbon to aerial plant parts declines after mid-season, with the onset of tuber bulking, and there is a corresponding increase in allocation to the tubers and rhizomes.

Other belowground vegetative structures (i.e., roots and seed tuber) have only a relatively small proportion of the total carbon, though the root contribution is typically underestimated due to incomplete recovery during excavation. Thus, aboveground plant parts, in particular stems/branches,

TABLE 10.5
Elemental Concentration and Harvest Index of Jerusalem Artichoke Tubers

Element	Concentration	
	Fresh Weight	Dry Weight
	Macronutrient ($mg \cdot g^{-1}$)	
Carbon	93.26	437.80
Nitrogen	3.81	17.87
Phosphorus	0.73	3.41
Potassium	6.03	28.32
Calcium	2.28	10.70
Magnesium	0.17	0.80
Sulfur	0.27	1.28
	Micronutrient ($mg \cdot kg^{-1}$)	
Boron	2.43	11.41
Copper	1.02	4.78
Iron	14.80	69.47
Manganese	3.01	14.12
Zinc	3.16	14.85
Aluminum	39.69	186.32
Barium	3.34	15.70
Silicon	44.12	207.10
Sodium	17.83	83.72
Strontium	0.86	4.05
Chromium	nd	nd
Cobalt	nd	nd
Lead	nd	nd
Molybdenum	nd	nd
Nickel	nd	nd

Note: nd = not detectable (i.e., below the detection limits).

Source: Adapted from Somda, Z.C. et al., *J. Plant Nutr.*, 22, 1315–1334, 1999.

constitute the primary temporary sink for carbon, largely in the form of fructans that are remobilized later into the developing tubers and rhizomes.

Approximately 20 weeks after planting, tuber bulking accelerated, with stored carbon redistributed from other organs into the developing tubers (Somda et al., 1999). The tubers continued to accumulate carbon until the final harvest, at which time they contained 93.3 $mg \cdot g^{-1}$ dwt or 437.8 $mg \cdot g^{-1}$ fwt (Table 10.5). By the end of the developmental cycle the tubers accounted for approximately 68% of the total plant carbon content, compared to 28% for the stems and less than 2% for each of the other plant parts. Approximately 61.2, 65.3, and 42.7% of carbon in the leaves, stems/branches, and rhizomes, respectively, were redistributed to the tubers (or lost via respiratory or other processes). The stems/branches contributed the greatest percentage of carbon to the mature tubers (77.2%), followed by the leaves (14.7%) and rhizomes (1.7%).

Interestingly, during tuber bulking the concentration of carbon ($g \cdot kg^{-1}$ dwt) in the stems/branches and leaves remains relatively stable even though there is a pronounced decline in dry matter. This appears to be due to the other components of dry matter being redistributed at essentially the same

rate as carbon. Therefore, during export the remaining carbon maintains the same general ratio with the other components.

10.7.3 Nutrients

Like carbon, mineral nutrients are stored in the stems/branches, leaves, and other locations within the plant, many of which are redistributed to the tubers in the latter part of the developmental cycle. Somda et al. (1999) monitored changes in both the concentration and content of phloem-mobile macronutrients (N, P, K, S, Ca, and Mg) and micronutrients (Bo, Cu, Fe, Mn, and Zn) throughout the growing season. The complexity of the general patterns of nutrient element concentration and content in various plant parts during the season is in part related to the general phloem mobility of individual elements and their redistribution to reproductive organs during the latter part of the growth cycle.

The concentration of micronutrients in the various plant parts varies during the growing season. In general, the concentration of most decreases in aboveground parts during the vegetative growth period, and then increases or remains constant during tuber bulking (Somda et al., 1999). The concentration of P in the leaves and tubers remained four to eight times higher than those in other plant tissues regardless of harvest date. The leaves have the highest N, K, Ca, Mg, S, B, Cu, and Mn concentrations, while Fe and Na concentrate more in the roots. Zn levels are comparable in the roots and leaves; the tubers have the lowest levels of Fe, Mn, and Na.

While the stems/branches had lower concentrations of most nutrient elements, quantitatively they represented a major reservoir of nutrients. For example, 47.6% of the K and 36.5% of the P in the tubers at the end of the season are derived from the stem. The concentration of K decreased substantially between the 8th and 14th weeks after planting, and then remained fairly constant thereafter. Leaf N and K also declined as the plant developed.

The concentration of most nutrient elements remains fairly constant in the tubers throughout the growing season (Somda et al., 1999). Seiler (1990), likewise, found little change in the tuber concentration of Ca, P, K, Na, and Cu, though Mg, Mn, and Zn decreased. Soja and Liebhard (1984), however, found a decrease in P, K, Ca, Mg, Cu, Na, Zn, and Co in the latter part of the growing season.

P and, to some extent, N, K, and S are higher in the tubers, whereas Ca and Mn concentrations are much lower than in other plant parts, the selectivity of which is thought to be associated with the mobility of each element and its physiological function in the plant. Macronutrient harvest indices range from only 16% for Ca to 94% for P (Table 10.6). Among the micronutrients, only Cu, Fe, Na, and Zn harvest indices were above 50%. The concentration of the other mineral elements (Ba, Co, Cr, Mo, Ni, Pb, Si, and Sr) in the tubers is low.

Patterns of nutrient element accumulation in the plant, leaves, stems/branches, and tubers (Figure 10.13 and Figure 10.14) are similar to that of carbon. While the general patterns of each of the nutrient elements are similar, the amount accumulated varies with element and the plant part in question. The content in the entire plant, and that of the aboveground plant parts, increases to a maximum by mid-season, and then progressively decreases during tuber bulking the remainder of the growing season. The decline in the individual elements in the leaves and stems/branches is accompanied by their progressive increase in the tubers. By the end of the season, the stems contain as much as 77% of the less mobile total Ca and Mn in the plant, while the tubers contain more than 80% of the total N, P, K, S, and Cu. The stems, roots, and rhizomes had the smallest proportion (i.e., <5%) of most nutrient elements (Table 10.6).

Phloem-mobile nutrient elements, such as N, P, and K, are highest in the vegetative parts early in the season and decrease with maturity (Seiler, 1988; Somda et al., 1999) (Figure 10.15). Less mobile nutrient elements, such as Ca and Mn, generally increase during the latter part of the season (Figure 10.13 and Figure 10.16), reflecting in part dilution effects from growth and remobilization of carbohydrates to the tubers and other reproductive organs. The greater allocation of Ca and Mn in the aboveground plant parts compared to the belowground structures, including the tubers (Figure

TABLE 10.6
Percentage Distribution of Carbon and Nutrients in Jerusalem Artichoke Plant Parts at Harvest

	(% of Total Plant Content)				
Element	**Stems**	**Roots**	**Seed[a]**	**Rhizomes**	**Tubers**
Carbon	28.0	1.9	0.2	1.6	68.3
Nitrogen	10.5	0.8	0.1	0.9	87.7
Phosphorus	5.2	0.4	0.1	0.6	93.8
Potassium	14.3	0.4	0.1	1.5	83.6
Calcium	76.4	3.2	0.7	3.6	16.0
Magnesium	41.1	1.7	0.3	1.4	55.5
Sulfur	14.2	1.5	0.1	1.2	83.0
Boron	47.7	1.6	0.3	3.1	47.3
Copper	17.5	1.5	0.3	2.4	78.4
Iron	18.9	14.2	2.1	10.5	54.3
Manganese	77.0	3.2	0.7	4.1	15.0
Zinc	33.2	3.6	0.3	2.8	60.1

[a] Original propagation seed tuber.

Source: Adapted from Somda, Z.C. et al., *J. Plant Nutr.*, 22, 1315–1334, 1999.

10.15 and Figure 10.16), is consistent with the low mobility of Ca and Mg relative to N, P, and K (Picchioni et al., 1997; Somda et al., 1999; Swanton and Cavers, 1989). Among metabolic sinks, storage and reproductive organs appear to dominate carbon and nutrient element allocation in the plant. The allocation of phloem-mobile macronutrients (especially N, P, and K) is similarly controlled in most plant species (Hill, 1980).

The onset of tuber bulking results in major alterations in many of the nutrient element contents, changes that differ among the various parts of the plant (Somda et al., 1999). In general, nutrients in aerial plant parts decreased concurrently with increases in clonal reproductive structures (rhizomes and tubers). There is a dramatic redistribution from the leaf canopy (e.g., 72% reduction in K content; 61% in N, P, and Mg; 55% for Ca and S). Of the micronutrients, B and Fe were the most reduced; Mn the least (Figure 10.14). In general, there is considerable redistribution of N, P, K, and Cu, less of Mg, S, Fe, Zn, and B, and negligible Ca and Mn from the stems. The highest percentage of P (36.5%) and K (47.6%) in the tubers was reallocated from the stems, while much of the S and Bo was from the leaves (Table 10.7). At the termination of tuber bulking, little or no reserve assimilates remained in the stems (Barloy and Lemercier, 1991; Becquer, 1985), with the residual being largely structural and nonmobile components. After defoliation of the canopy at the end of the growing season, the tubers have the highest percentage of the total nutrient element contents — N (87.7), P (93.8), K (83.6), Mg (55.5), S (83.0), Bo (47.3), Cu (78.4), Fe (54.3), and Zn (60.1) — with the exception of Bo, which was comparable, and Ca and Mn, which were substantially higher in the stems. In general, elemental accumulation in the tubers occurs at the expense of the vegetative organs, and the patterns of accumulation are related to the mobility of the particular element in the phloem.

10.8 FRUCTAN METABOLISM

The general composition of the Jerusalem artichoke was established by a number of scientists (Belval, 1946, 1947a, 1947b; Colin, 1912, 1918; Conti, 1953a, 1953b; Dedonder, 1950a, 1950b,

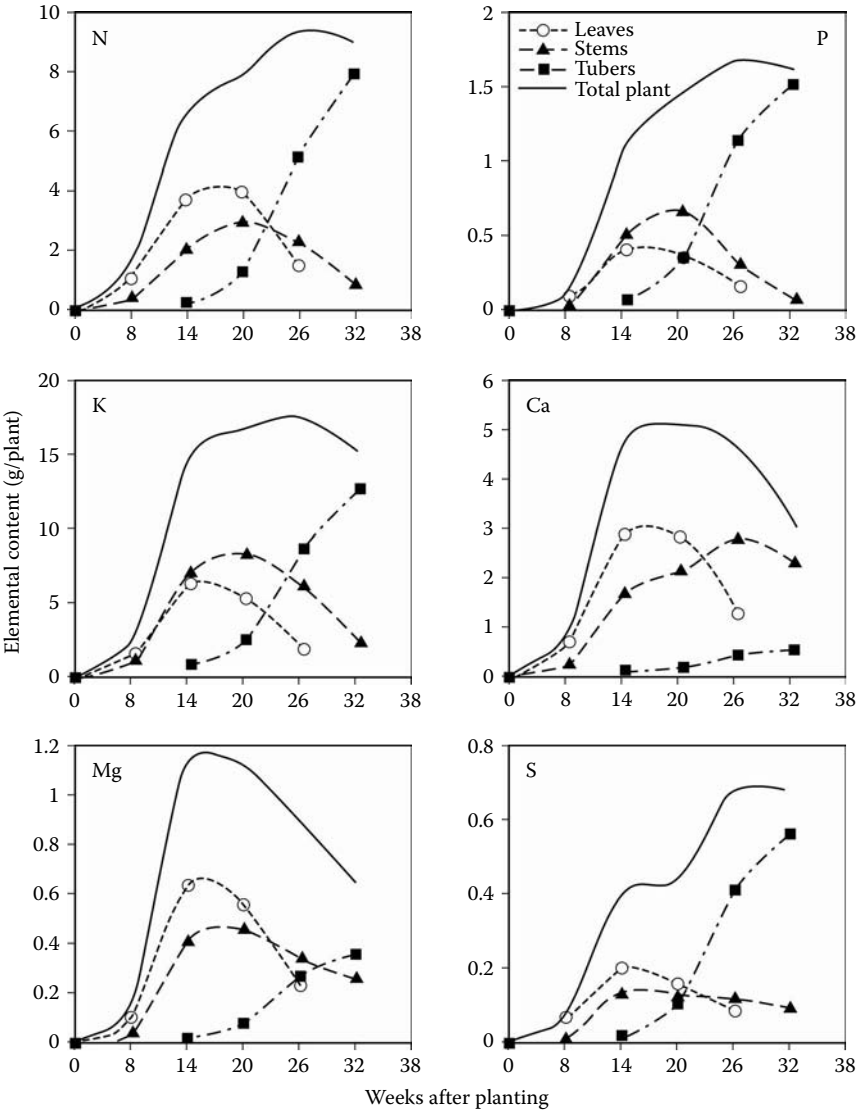


FIGURE 10.13 General distribution of macronutrients within the Jerusalem artichoke throughout the production cycle grown at 30°57'N. (After Somda, Z.C. et al., *J. Plant Nutr.*, 22, 1315–1334, 1999.)

1951a, 1951b; Schlubach and Knoop, 1932, 1933; Schlubach et al., 1952). Variation was found with tuber size, location within the tuber, and stage of development. For example, as tuber size increases, the concentration of reducing sugars increases from the center of the tuber to the periphery (Strepkov, 1961).

Most plants store carbon as polymers of glucose, of which starch is the predominant form. Approximately 10% of higher plants, however, store their carbohydrate reserves as polymers of fructose (Henry and Wallace, 1993). Fructose polymers (fructans) are synthesized in the vacuole, starting with sucrose. The degree of polymerization (number of monosaccharides present in the polymer) can range up to 250 fructosyl units with several basic structures. Typically the structures fall into one of four general categories: (1) (2→1)-linked β-D-fructans (inulins) such as those found in Jerusalem artichoke tubers and *Cichorium intybus* L. roots; (2) (2→6)-linked β-D-fructans (phleins) found in grasses such as *Phleum pratense* L. and *Festuca arundinacea* Schreber; (3)

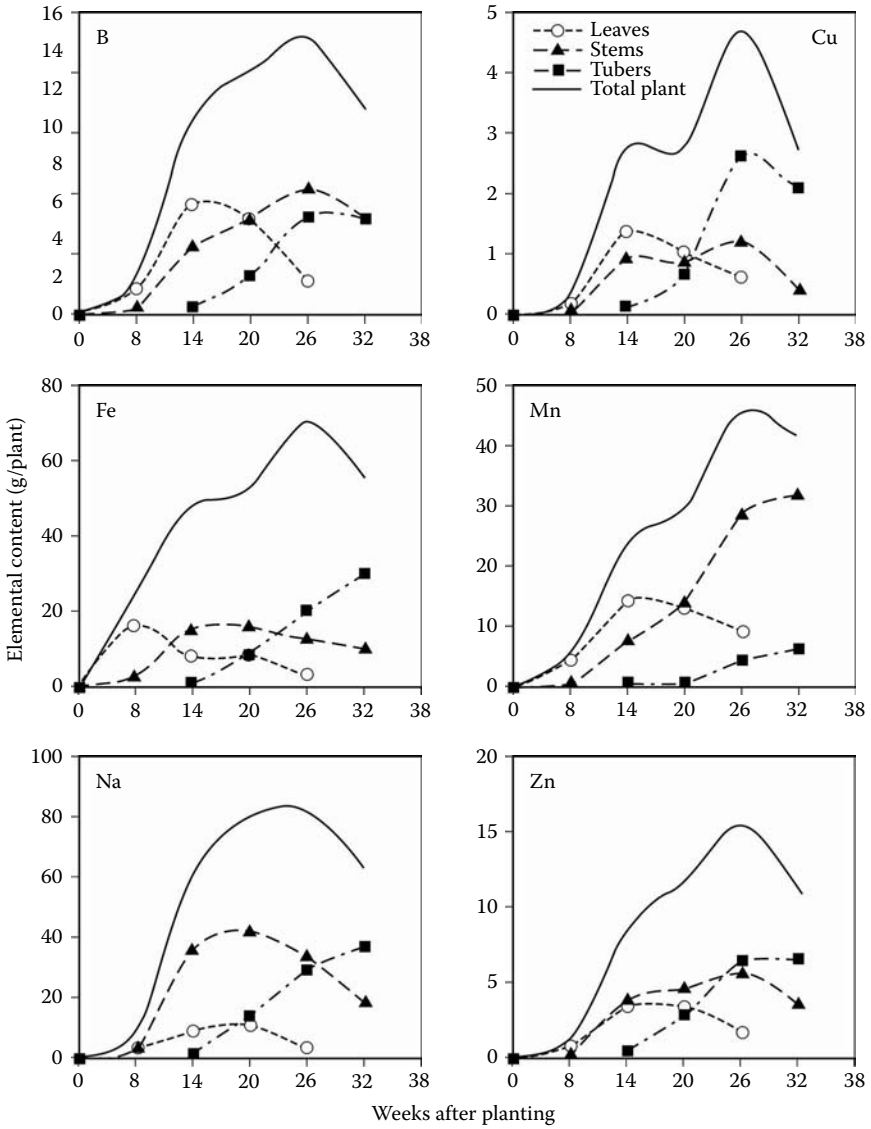


FIGURE 10.14 General distribution of micronutrients within the Jerusalem artichoke throughout the production cycle grown at 30°57'N. (After Somda, Z.C. et al., *J. Plant Nutr.*, 22, 1315–1334, 1999.)

highly branched (2→1) and (2→6)-mixed linkage β-D-fructans and fructan oligomers found in grasses such as *Triticum aestivum* L. and *Hordeum vulgare* L.; and (4) neokestose series of (2→1)-linked β-D-fructans found in *Asparagus* and *Allium* that elongate from both ends of the initial sucrose molecule (Carpita et al., 1989; Meier and Reid, 1982; Shiomi, 1989).

Fructans have several advantages as a storage form of carbon. Unlike starch, fructans are water soluble and contribute to the osmotic potential of the vacuole. Thus, polymerization and depolymerization reactions allow the cells to respond rapidly to changing environmental conditions by shifting the average chain length of the polymer pool (Pavlides, 1988). For example, cellular sap pressed from tubers in the autumn contained 282 $mg \cdot ml^{-1}$ of total fructan with an osmolarity of 446 $mOsmol \cdot kg^{-1}$. After cold storage, the fructan content declined by 50% (141 $mg \cdot ml^{-1}$), while the osmolarity changed only approximately 22% (Frehner et al., 1984). Thus, accumulation of fructans is often correlated with the acquisition of frost hardiness and drought tolerance (Pontis

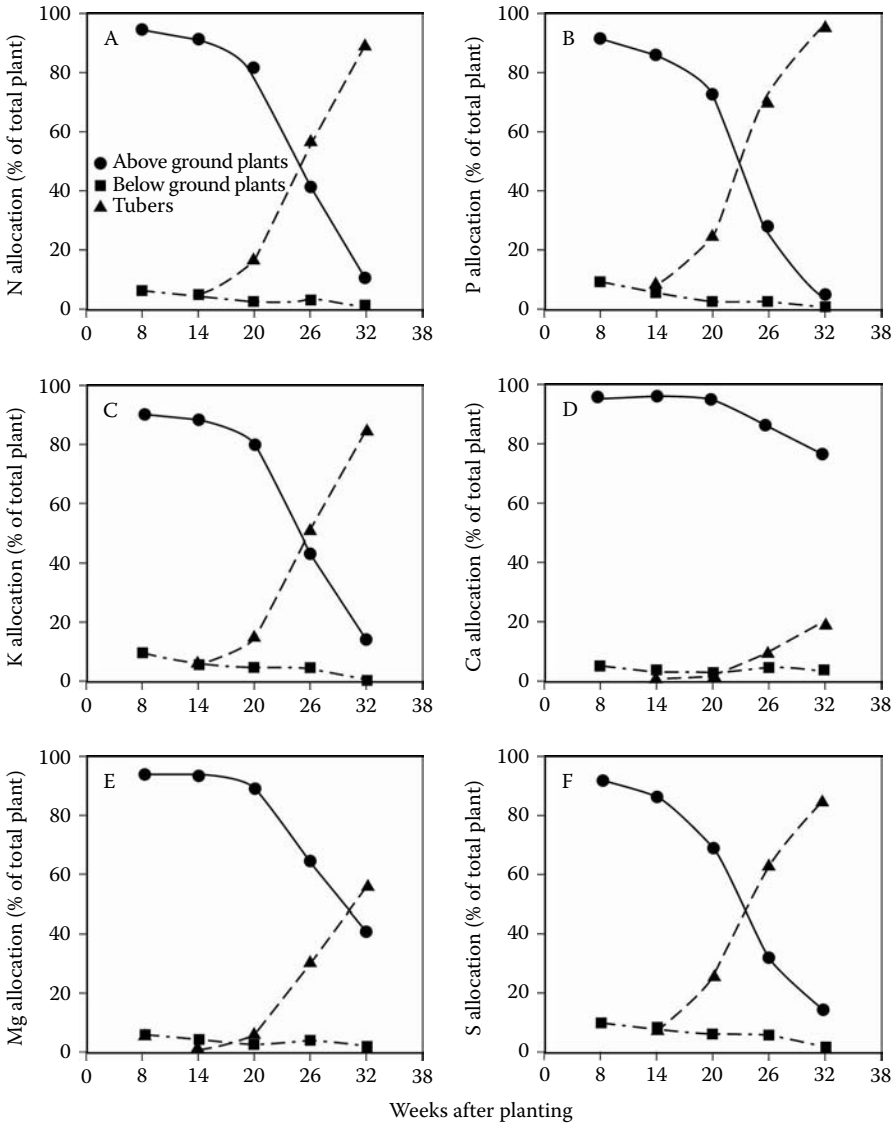


FIGURE 10.15 General allocation of macronutrients within the Jerusalem artichoke throughout the production cycle in the aboveground vegetative structures, belowground vegetative structures, and tubers and rhizomes (grown at 30°57'N). (After Somda, Z.C. et al., *J. Plant Nutr.*, 22, 1315–1334, 1999.)

and Campillo, 1985). An additional advantage is that the pathways for synthesis and degradation are tolerant of low temperatures (Koops and Jonker, 1994; Pollock, 1986). For example, the rate of the initial polymerization enzyme decreases only slowly between 28 and 8ºC (i.e., 2×) (Wagner and Wiemken, 1986).

In Jerusalem artichoke, starch is absent or present at very low levels in the leaves (Pollock, 1986; Strepkov, 1960a, 1960b), stems (Lemercier, 1987), and tubers, while fructans predominate. The fructans are a homologous, straight-chain series of β-1,2-linked fructose polymers connected to a terminal sucrosyl moiety. They represent an extension of sucrose by sucrose-derived fructosyl units (Wiemken et al., 1995). The degree of polymerization in the tubers ranges from 3 to approximately 50, though typically the 30 to 35 range represents the upper limit from a quantitative standpoint for Jerusalem artichoke. The actual range in polymer lengths varies depending upon the

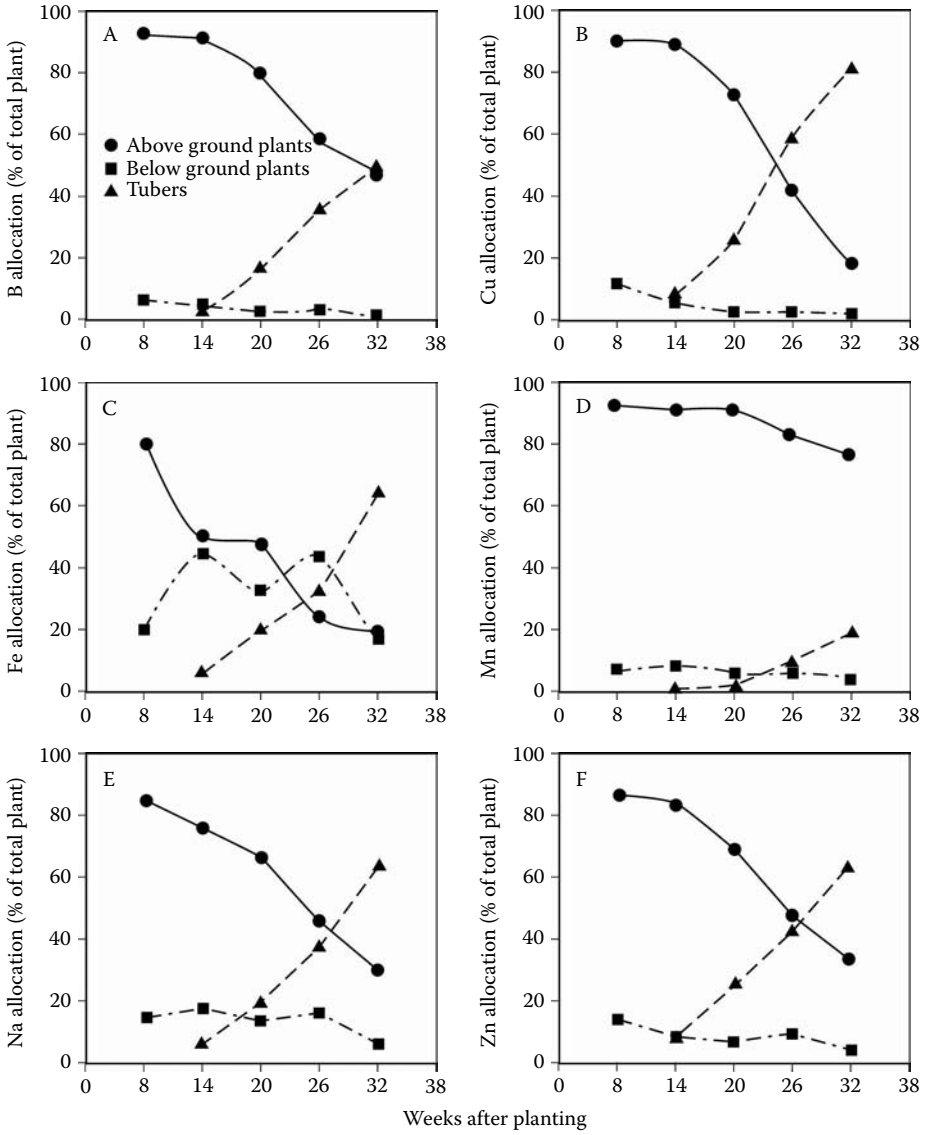


FIGURE 10.16 General allocation of micronutrients within the Jerusalem artichoke throughout the production cycle in the aboveground vegetative structures, belowground vegetative structures, and tubers and rhizomes (grown at 30°57'N). (After Somda, Z.C. et al., *J. Plant Nutr.*, 22, 1315–1334, 1999.)

developmental stage of the organ in which they are present and the conditions to which the organ has been exposed. In the fall, as the tubers mature, long-chain-length polymers predominate; however, during dormancy and with sprouting, the mean chain length shortens dramatically (Figure 10.17).

Inulin synthesis in the tubers occurs in the vacuoles of storage parenchyma cells. Kaeser (1983) proposed a model for the transport of sucrose into the central vacuole that involves the formation of vesicles within the cytoplasm that contain sucrose and inulin synthesis enzymes. The vesicles transfer their contents into the vacuole via two possible mechanisms: (1) the cytoplasmic vesicle fuses with the tonoplast and through pinocytosis releases its contents into the vacuole, or (2) vesicles originating from plasmalemma invaginations are tied off into the vacuole, resulting in

TABLE 10.7
Percentage Apparent Redistribution of Carbon and Nutrients from Aboveground Parts of the Jerusalem Artichoke

	Percentage Redistribution from[a]			Percentage Contribution of Amounts in Mature Tubers[b]		
Element	**Leaves[c]**	**Stems**	**Rhizomes**	**Leaves**	**Stems**	**Rhizomes**
Carbon	61.2	65.3	42.7	14.7	77.2	1.7
Nitrogen	59.4	68.5	36.6	28.1	26.0	0.1
Phosphorus	60.8	87.7	64.3	16.5	36.5	1.2
Potassium	71.7	73.5	31.0	34.8	47.6	0.1
Calcium	56.7	17.2	—	3.4	4.0	—
Magnesium	63.3	42.1	—	11.5	53.9	—
Sulfur	54.3	30.2	27.3	19.1	7.4	0.5
Boron	68.9	24.2	—	78.4	32.2	—
Copper	51.9	62.2	—	34.1	36.7	—
Iron	58.3	35.5	—	16.2	19.2	—
Manganese	34.9	—	—	79.5	—	—
Zinc	50.5	36.7	—	25.6	32.0	—

[a] Percentage redistribution was calculated as [(maximum amount in organ – amount at final harvest)/maximum amount] × 100.
[b] Percentage contribution of net amount was calculated as [(maximum amount in organ – amount at final harvest)/final amount in tubers] × 100.
[c] Final harvest for leaves was at 26 weeks after planting, prior to total leaf shedding.

Source: Adapted from Somda, Z.C. et al., *J. Plant Nutr.*, 22, 1315–1334, 1999.

a double-membrane vesicle within. With time, they increase in volume, the intravesicular membranes disintegrate, and the interior of the vesicle becomes fibrous.

10.8.1 Fructan Polymerization/Depolymerization Reactions

Fructans in the Jerusalem artichoke are synthesized by the concerted action of two fructosyl transferases that were derived from invertase genes (Van Laere and Van den Ende, 2002). In the initial step (Figure 10.18), the trisaccharide 1-kestose (G-F-F) is synthesized from two sucrose molecules (G-F) in a reaction catalyzed by the enzyme sucrose:sucrose fructosyl transferase (SST; EC 2.4.1.99). The reaction products are 1-kestose and glucose, and the reaction is essentially irreversible due to the high free energy of hydrolysis ($\Delta G = 27.6$ kJ·mol^{-1}) (Lewis, 1984).

$$\underset{\text{sucrose}}{\text{G-F}} + \underset{\text{sucrose}}{\text{G-F}} \xrightarrow[\text{1-SST}]{} \underset{\text{1-kestose}}{\text{G-F-F}} + \underset{\text{glucose}}{\text{G}}$$

Kestose synthesis by 1-SST is limited by the availability of sucrose in the 0 to 100 mol·m^{-3} range (Cairns and Ashton, 1991; Van den Ende and Van Laere, 1993). Therefore, high sucrose concentrations favor the rate of the first polymerization step and indirectly the synthesis of longer-chain-length polymers due to an elevation in 1-kestose concentration, which acts as a fructosyl donor. Glucose is converted to sucrose by sucrose synthase in the cytosol (Pollock, 1986; Wiemken et al., 1986) (Figure 10.18).

A second enzyme, fructan:fructan 1-fructosyl transferase (1-FFT; EC 2.4.1.100) is responsible for chain elongation with 1-kestose and fructans with a degree of polymerization of >3 acting as

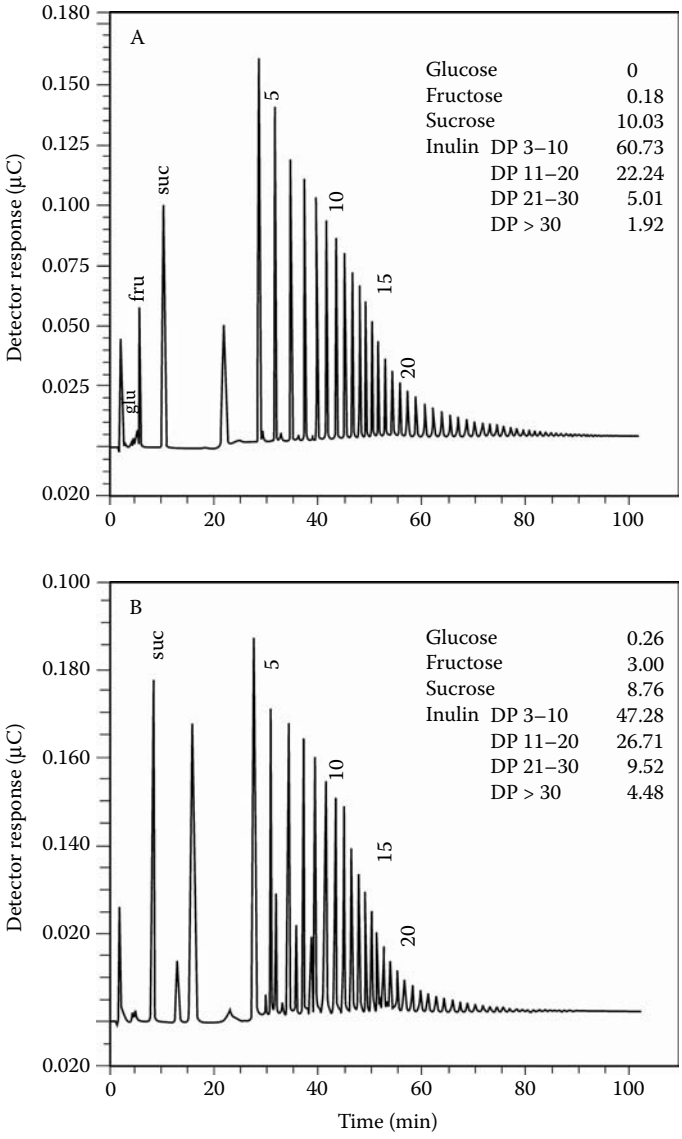


FIGURE 10.17 Fructan polymer distribution in Jerusalem artichoke tubers as illustrated by HPAEC-PAD chromatograms at 20 weeks after planting (A) and after 8 weeks storage at 5°C (B). The sugar and inulin composition is given for each date. Individual peak numbers indicate the degree of polymerization (DP); numbers indicated as 3′, 4′, etc., represent inulo-*n*-ose fractions (i.e., lacking a terminal glucose) of varying degrees of polymerization. (After Saengthongpinit, W. and Sajjaanantakul, T., *Postharvest Biol. Technol.*, 37, 93–100, 2005.)

donors of the fructosyl residues. Sucrose and fructans of high degrees of polymerization (i.e., >20) are preferential acceptors of the fructosyl unit over shorter-chain-length fructans (Edelman and Jefford, 1968).

$$\underset{\text{acceptor}}{\text{G-F-F}_n} + \underset{\text{donor}}{\text{G-F-F}_m} \quad \underset{\text{1-FFT}}{\leftrightarrow} \quad \underset{\text{acceptor}}{\text{G-F-F}_{n+1}} + \underset{\text{donor}}{\text{G-F-F}_{m-1}}$$

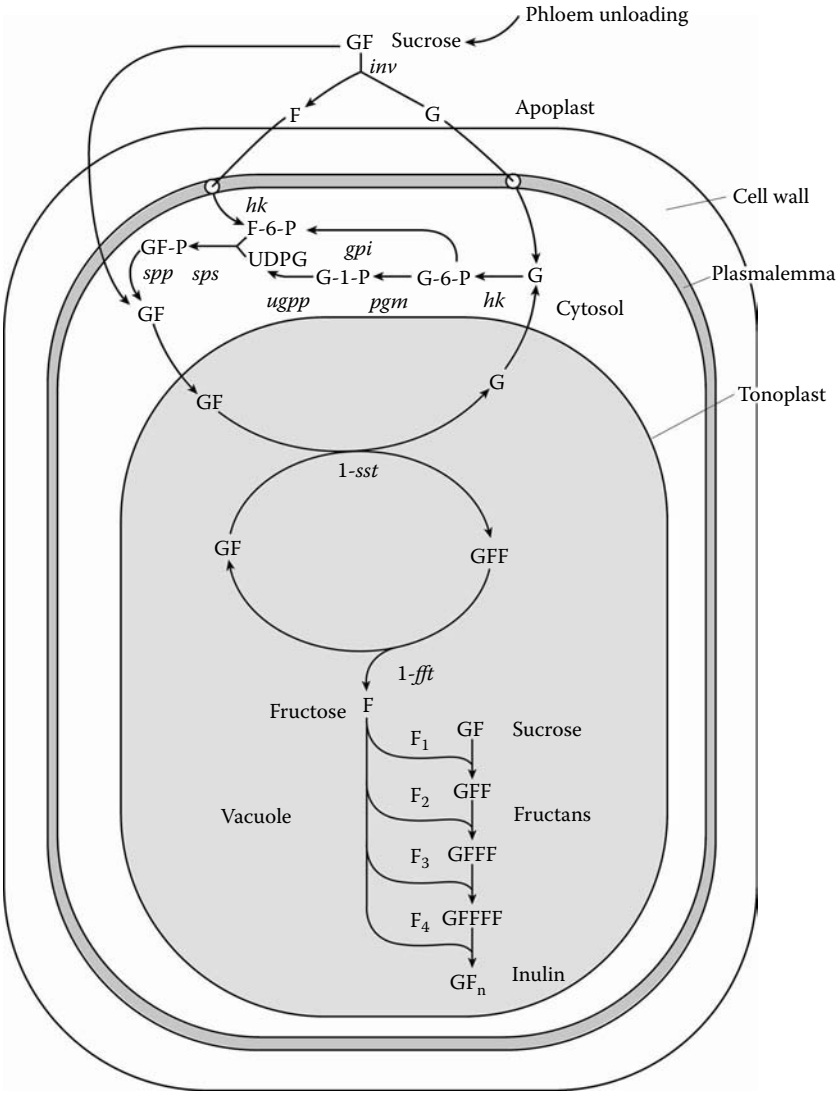


FIGURE 10.18 Biosynthesis of fructans in the vacuole. Sucrose within the cytosol moves into the vacuole, where fructose is removed by *1-sst* and attached to a second sucrose molecule forming 1-ketose. The fructose is then removed by *1-fft* and attached to the growing fructan chain. Through repeat cycles, individual fructose molecules are progressively added, with the final length of the chain (degree of polymerization) determined by the characteristics of the *1-fft* enzyme and other enzymes and conditions operative at that time. Key enzymes in the synthesis of inulin are sucrose:sucrose 1-fructosyltransferase (*1-sst*) and fructan:fructan 1-fructosyltransferase (*1-fft*). (After Van Laere, A. and Van den Ende, W., *Plant Cell Environ.*, 25, 803–813, 2002.) Abbreviations: *inv* = invertase; *hk* = hexokinase; *sps* = sucrose phosphate synthase; *spp* = sucrose phosphate phosphatase; *pgi* = phosphoglucose isomerase; *gk* = glucose kinase; *pgm* = phosphoglucomutase; *pgpp* = UDP-glucose phosphorylase; GF = sucrose; G = glucose; F = fructose; GFF = 1-kestose; G-1-P = glucose-1-phosphate; G-6-P = glucose-6-phosphate; F-6-P = fructose-6-phosphate; GF-P = sucrose phosphate; UDP-G = uridine diphosphate glucose.

In the fall, the tuber sucrose concentration tends to be low; thus, longer-chain-length molecules act as acceptors of the fructosyl group, resulting in the formation of longer-chain-length fructans (Edelman and Jefford, 1968). Increased kestose concentration is essential for chain lengthening since kestose, followed by short-chain fructans, are the best fructosyl donors (Edelman and

Dickerson, 1966; Wiemken et al., 1986). Therefore, low sucrose content is essential during fructan synthesis; otherwise, 1-FFT merely transfers the fructosyl unit from 1-kestose to sucrose, forming the same products as the reactants (i.e., 1-kestose and sucrose). Both enzymes (1-SST and 1-FFT) are localized in the vacuole (Carpita et al., 1991; Darwen and John, 1989; Frehner et al., 1984).

Inulin degradation is catalyzed by both 1-FFT and 1-fructan-β-fructosidase (1-FEH; EC 3.2.1.80), an exohydrolase also derived from invertase (Van den Ende et al., 2000a, 2000b). The reaction catalyzed by 1-FFT, critical in the synthesis of longer-chain-length polymers, is reversible and participates in depolymerization. Thus, fructosyl units from longer-chain-length fructans can be transferred to those of low molecular mass. In contrast, 1-FEH hydrolyzes fructan molecules at the terminal, nonreducing fructosyl residue (exolytic attack), releasing fructose.

$$\text{G-F-F}_{m} \quad \rightarrow \quad \text{G-F-F}_{m-1} \quad + \quad \text{F}$$

$$\text{donor} \quad \text{1-FEH} \quad \text{donor}_{m-1} \quad \text{fructose}$$

Two different 1-FEH enzymes (A and B) are thought to be present in the tubers (Edelman and Jefford, 1964). 1-FEH will not hydrolyze sucrose and is noncompetitively inhibited by the molecule (Incoll and Neales, 1970; Wiemken et al., 1986). In dormant tubers, only 1-FFT and 1-FEH are active (Wiemken et al., 1986), with 1-FEH producing fructose during sprouting (Edelman and Jefford, 1968). Fructose released from the vacuole is converted in the cytoplasm to glucose, and subsequently to sucrose, via sucrose synthase for transport to the growing sprouts.

10.8.2 Enzymes

Three enzymes, sucrose:sucrose 1-fructosyl transferase (1-SST), fructan:fructan 1-fructosyl transferase (1-FFT), and 1-fructan-β-fructosidase (1-FEH), appear to control fructan polymerization and depolymerization in the Jerusalem artichoke. Each is sequestered in the vacuole of the cells in which they are expressed and has a pH optimum in the acid range (pH 5.0 to 5.5), in keeping with a vacuolar origin (Frehner et al., 1984).

10.8.2.1 Sucrose:Sucrose 1-Fructosyl Transferase

Sucrose:sucrose 1-fructosyl transferase appears to be a glycoprotein with a pH optimum of 5.0 and a molecular weight of 65 to 70 kDa (Scott, 1968). It has a lower temperature optimum than many plant enzymes and a relatively low Q_{10}, allowing it to function effectively at lower temperatures. For example, the enzyme's activity decreases slowly (i.e., by only a factor of 2) between 28 and 8ºC (Wagner and Wiemken, 1986).

The complete cDNA for 1-sst has been isolated and the peptide sequence for *1-SST* determined (Figure 10.19) (van der Meer et al., 1998). The gene for SST appears to encode for a single copy, yielding two polypeptides of approximately 27 and 55 kDa, which are encoded by a single mRNA of 630 codons. Based upon the predicted structure, the initial 100 amino acids are thought to represent a targeting signal sequence, potentially conferring directional control over movement of the protein into the vacuole. The deduced amino acid sequence is very similar to 1-FFH (i.e., 61% homology) and to vascular plant invertases. The similarity between 1-SST and invertase is not surprising since both catalyze similar enzymatic reactions involving cleavage of the G-F bond of sucrose. They differ, however, in that 1-SST transfers the fructosyl unit to a sucrose acceptor molecule rather than simply releasing the molecule into an aqueous medium, as in the case of invertase.

The gene for 1-SST is expressed in organs undergoing fructan synthesis, such as tubers and stems. The highest expression occurs in the tubers during development (van der Meer et al., 1998). A surprisingly high level of SST mRNA is also found in the flowers, where fructans may serve as a carbohydrate source for seed development. The gene is not, however, expressed in mature or sprouting tubers.

Fructan:fructan fructosyl transferase (FFT)

MQTPEPFTDLEHEPHTPLLDHHHNPPPQTTTKPLFTRVVSGVTFVLFFFGFAIVFIVLNQQNSSVRIVTNSEKSFIRYSQTDRLSWERTAF**HFQP**A
KNFIY**DPDG**QLFFTF**HMGWYH**MF**YQYNP**YAPV**WGN**MS**WGHSVSKDMINW**YE**LP**V**AMVP**TE**WYDIEGV**LS**GS**TTVLPNGQI**FA**LY**T**GN**
AN**DFSQ**L**QC**K**A**VP**VN**LS**DPLLIEW**V**KYE**D**NPI**LYT**PPG**I**G**L**KD**Y**RDPST**V**WT**PDG**KH**RMI**MG**TKRGNTMVLVYY**TT**DY**T**NY**EL**LD**EP**LH**S
VPN**T**D**MWECVD**F**YPVS**LTNDSA**LDM**AAY**GS**GIKH**V**IKE**S**WEGHGM**DWYSIGTYD**AI**NDKW**T**PD**N**PE**L**DVGIGLRC**D**Y**GR**F**FASK**SL**YD**PL
KKRRIT**WGYVGE**S**D**SADQ**DLS**R**GWA**TVY**N**VGR**TIVLD**RK**T**G**T**H**LLH**WPV**EE**V**ES**LR**YNGQ**EFK**EIK**LE**PG**SIIPLD**IGTATQLDIVATFE**V
DQAA**L**NA**T**SET**D**DIYG**CTTS**L**G**AAQ**R**GS**LGPFG**LA**VLAD**GTL**SE**LT**PVYFYIAK**KA**DG**GVS**TH**FC**TD**KL**RSS**L**D**YDGERV**VYG**GT**VPV**LDD
EELT**MRLLVDHSIVEGFAQ**G**GRTV**ITSRA**YPTKAIY**EQ**AK**L**FLFNNATGTSVKASLKIW**QM**ASAPIHQYPF

Sucrose:sucrose 1-fructosyltransferase (SST)

MMASSTTTTPLILHDDPENLPELTGSPTTRRLSIAKVLSGILVSVLVIGALVALINNQTYESPSATTFVTQLPNIDLKRVPGKLDSSAEVEWQRSTY
HFQPD**KNFIS**D**PDG**PMY**HMGWYH**LE**YQYNP**QSAI**WGN**IT**WGHSVSKDMINW**FH**LP**F**AMVP**DH**WYDIEGV**MT**GS**A**TVLPNGQI**IM**LY**S**G**
NAYDL**SQ**V**QC**L**A**YA**VN**S**SDPLLIEW**K**KYE**G**NP**V**LL**PPG**V**GY**K**D**F**RDPST**L**WS**GPDG**EY**RM**V**MG**SKHNETI**G**CALIYH**TT**NF**T**HF**EL**KE**E**V
LHAVPHT**G**M**WECVD**L**YPVS**TVHTNG**LDM**VDN**G**PNVKY**V**LKQ**S**GDEDRH**DWY**AI**GSYD**IV**NDKW**Y**PD**D**PE**N**DVGIGLR**Y**D**F**G**K**F**Y**ASK**T
F**YD**QH**KKRR**VL**WGYVGE**T**D**PQKY**DLS**K**GWA**NILN**I**PR**TVVLD**LE**T**K**T**N**LIQ**WP**I**EE**T**E**N**LR**SKKYD**EFK**DVE**L**R**PG**ALVPLE**IGTATQLDI**
VATFEI**DQ**KM**L**EST**LEA**D**VLFN**CTTSE**G**SVA**RSV**LGPFG**VV**VLAD**AQR**SE**QL**PVYFYIAK**DI**DG**TSRT**YFCADET**RSS**K**D**VSVGKW**VYG**SS
VPVLPG**E**KYN**MRLLVDHSIVEGFAQ**N**GRTV**VVTSRV**YPTKAIY**NA**AK**V**FLFNNATGISVKASIKIW**K**M**GEAELNPFPLPGWTFEL

FIGURE 10.19 Deduced amino acid sequence for fructan:fructan transferase (FFT) and sucrose:sucrose 1-fructosyltransferase (SST). (From van der Meer, I.M. et al., *Plant J.*, 15, 489–500, 1998.) Amino acids in bold represent homology between FFT and SST. Symbols: A = alanine; C = cysteine; D = aspartate; E = glutamate; F = phenylalanine; G = glycine; H = histidine; I = isoleucine; K = lysine; L = leucine; M = methionine; N = asparagine; P = proline; Q = glutamine; R = arginine; S = serine; T = threonine; V = valine; W = tryptophan; and Y = tyrosine.

10.8.2.2 Fructan:Fructan 1-Fructosyl Transferase

Fructan:fructan fructosyl transferase has a molecular weight of approximately 70 kDa and can be separated into five species with pH values between 4.5 and 5.0. The enzyme has a pH optimum for fructosyl transfer activity between 5.5 and 7.0 and a temperature optimum in the 25 to 35ºC range. Like 1-SST, 1-FFT has a low Q_{10} (i.e., 1.14 between 25 and 5ºC), indicative of its ability to function at relatively low temperatures (Koops and Jonker, 1994). The rate of transfer of fructosyl groups increases with substrate concentration up to 100 mol·m^{-3}.

The cDNA encoding *1-fft* has been isolated and the peptide sequence of *1-FFT* identified (van der Meer et al., 1998). Like 1-SST, it has an initial targeting signal sequence of 100 amino acids, which appears to control movement into the vacuole. The deduced amino acid sequences of the cDNAs for 1-FFT and 1-SST are highly similar. Based upon Southern blot hybridization, both enzymes appear to encode for single-copy genes. Both genes have been introduced into petunia, conferring the ability to synthesize high molecular weight fructans (van der Meer et al., 1998). Thus, 1-SST and 1-FFT appear to comprise the entire fructan biosynthesis pathway (Figure 10.18).

10.8.2.3 Fructan 1-Exohydrolase

Fructan 1-exohydrolase (FEH) is an exo-fructosidase that depolymerizes fructans. It utilizes a multichain attack; i.e., a single-terminal glycosidic linkage of a substrate molecule is hydrolyzed before the next substrate molecule is randomly chosen (in contrast to moving down the chain one residue at a time) (Marx et al., 1997). The enzyme has an apparent molecular mass of 75 to 79 kDa (Marx et al., 1997), slightly larger than those of chicory (Classens et al., 1990) and oat fructan 1-exohydrolase (Henson and Livingston, 1996), and a pH optimum of 5.2. Fructan 1-exohydrolase is inactive on sucrose and noncompetitively inhibited by sucrose (Incoll and Neales, 1970; Wiemken et al., 1986). The enzyme hydrolyzes terminal β-(2-1)-fructosyl-fructose linkages in a linear manner. Branched oligomers with β-(2-6)-linkages are little hydrolyzed. Two hydrolases are thought to be present in Jerusalem artichoke and appear to be glycoproteins based upon their binding to Con A.

10.8.3 Regulation

The fact that the enzymes for both fructan polymerization and depolymerization are found in the vacuole (Frehner et al., 1984) indicates that relatively precise control over gene expression and enzyme activity must be operative. Early work by Edelman and Jefford (1968) established a distinct temporal control over gene expression that was further substantiated by van der Meer et al. (1998). During tuber growth, 1-SST and 1-FFT are present (Edelman and Jefford, 1968; Wiemken et al., 1986) and catalyze the synthesis reactions (Figure 10.18). 1-SST has a rapid turnover and is thought to control the overall rate of fructan synthesis in *Hordeum vulgare* (Nagaraj et al., 2004). 1-FEH, in contrast, is essentially absent during periods of fructan synthesis (Edelman and Jefford, 1968), and while 1-SST is expressed during periods of synthesis, it is not present during dormancy and sprouting. The rate of synthesis by 1-SST is limited by sucrose concentration in the 0 to 100 mol·m^{-3} range (Cairns and Ashton, 1991; Van den Ende and Van Laere, 1993).

In contrast, 1-FFT is present during both inulin synthesis and depolymerization, though its activity decreases during tuber storage (Edelman and Jefford, 1968). During synthetic conditions, 1-FFT catalyzes chain elongation; however, during depolymerization, when sucrose is not present, 1-FFT moves fructosyls from the longer-chain-length polymers to shorter polymers (Lüscher et al., 1993). In dormant and sprouting tubers, only 1-FFT and 1-FEH are active (Figure 10.20). The hydrolysis rate of 1-FEH depends upon the degree of polymerization of the substrate (increasing up to 8), is inhibited (noncompetitively) by sucrose (Incoll and Neales, 1970; Wiemken et al., 1986), but is not affected by fructose content (Edelman and Jefford, 1968). 1-FEH is inhibited by 10 n*M* sucrose (Marx et al., 1997), well within the concentration in dormant tubers. Thus, feedback inhibition by sucrose allows the rate of depolymerization to be adjusted to the rate of sucrose export from the storage tissue.

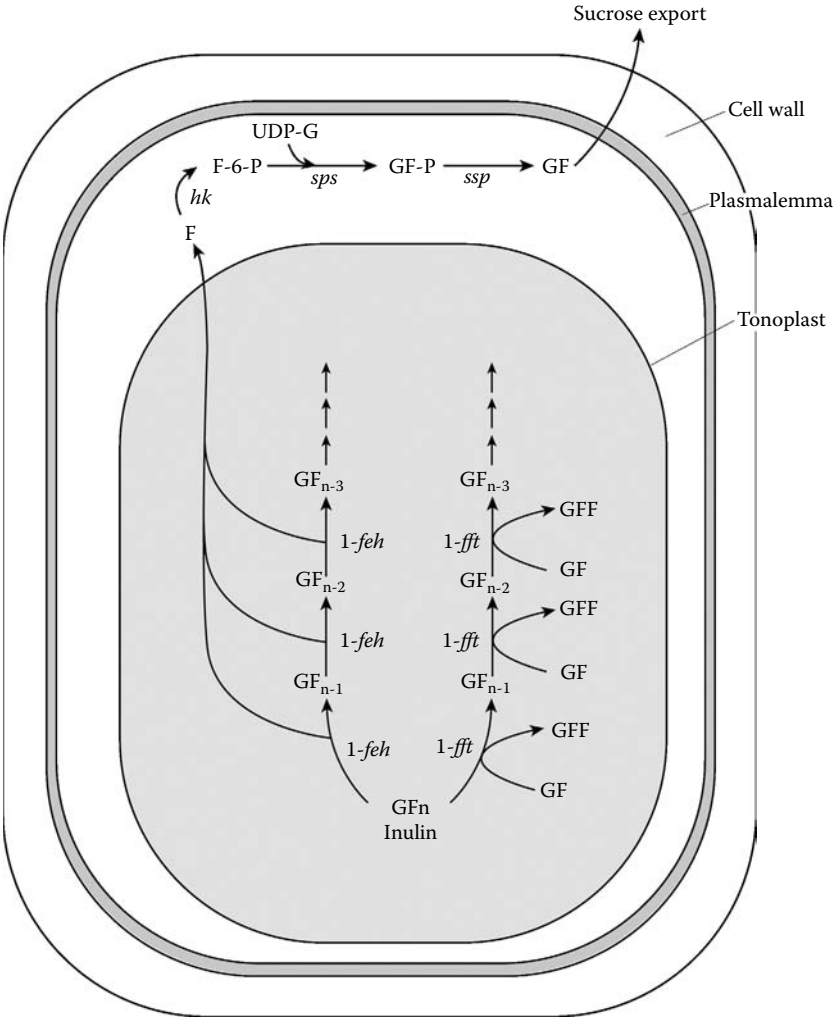


FIGURE 10.20 The action of fructan 1-exohydrolase and fructan:fructan 1-fructosyltransferase in dormant and sprouting tubers on inulin depolymerization. Abbreviations: 1-*feh* = fructan 1-exohydrolase; *1-fft* = fructan:fructan 1-fructosyltransferase; *hk* = hexokinase; *spp* = sucrose phosphate phosphatase; *sps* = sucrose phosphate synthase; GF = sucrose; G = glucose; F = fructose; GFF = 1-ketose; GF-P = sucrose phosphate; UDP-G = uridine diphosphate glucose; F-6-P = fructose-6-phosphate.

Therefore, during growth, fructan synthesis is regulated by 1-SST and the availability of sucrose. In dormant and sprouting tubers, regulation of depolymerization is controlled by 1-FEH. While control of fructan metabolism in the Jerusalem artichoke has been elucidated using tubers, it is reasonable to assume similar control mechanisms are operative in the stems, even though accumulation of high-degree-of-polymerization fructans tends to be faster in the former than the latter (Soja et al., 1989).

10.8.4 Changes in Polymerization during Development

Fructans are found within the vacuole, and catabolic and anabolic enzymes and alterations occur therein (Carpita et al., 1991; Wiemken et al., 1986). Alterations in the fructans require the input of energy, most of which is thought to be associated with the recycling of glucose to fructose in the cytoplasm. It has been estimated that the cost is between 4 and 8% of the total mass of assimilates (Edelman, 1963; Meijer and Mathijssen, 1991).

The *1-FFT* gene present is a critical factor in the degree of polymerization achieved in that it is responsible for elongation. The amino acid sequence varies slightly, as do the properties of the enzyme among species. The 1-FFT found in the Jerusalem artichoke gives a fairly short chain length distribution. In contrast, *Echinops ritro* L. (Vergauwen et al., 2003), *Cynara scolymus* L. (Hellwege et al., 2000), and *Viguiera discolor* Baker (Itaya et al., 1997) have substantially higher degrees of polymerization. Their 1-FFTs preferentially select longer inulin chains as acceptors, while Jerusalem artichoke has a higher affinity for short substrates, hence the shorter mean degree of polymerization of its fructan polymers (Edelman and Jefford, 1968; Koops and Jonker, 1994; Shaw et al., 1993).

A relatively small amount of reducing inulo-*n*-oses, fructans without a terminal glucose (Ernst et al., 1996), are formed from fructosyl transfer from inulin to free fructose by 1-FFT. In chicory, they are thought to appear when fructose accumulates during fructan breakdown and 1-FFT activity is still high (Van den Ende and Van Laere, 1996). A similar mechanism is probably operative in Jerusalem artichoke and responsible for the small amounts of inulo-*n*-oses formed (Saengthongpinit and Sajjaanantakul, 2005).

During rapid growth of the tubers, the degree of polymerization increases leading up to the fall, while the reducing sugar content declines (Strepkov, 1961). There can be temporal fluctuations in the mean chain length depending upon sucrose availability and the resulting concentration of G-F-F (Incoll and Neales, 1970; Lemercier, 1987). The degree of polymerization peaks prior to the tubers reaching their maximum dry weight, and subsequently declines due to the action of 1-FEH and 1-FFT (Ben Chekroun, 1990; Zubr and Pedersen, 1993), dropping from a mean of 8–10 to 4–6. Both enzymes are active prior to and during storage (Wiemken et al., 1986). 1-FFT, which is normally responsible for increasing the length of the fructan chains, removes fructose in the absence of sucrose late in the season. 1-FEH, in contrast, is upregulated during the late fall and is responsible for depolymerization. Fructose moves from the vacuole into the cytoplasm for use as substrate for energy and carbon skeletons for synthetic reactions or where, in the spring, it combines with glucose to form sucrose for transport to the developing sprouts (Edelman and Jefford, 1968). The hydrolysis rate of 1-FEH is dependent upon the degree of polymerization of the substrate, increasing up to 8, and is not impeded by fructose concentration (Edelman and Jefford, 1964).

10.8.5 Effect of Depolymerization on Potential Uses of Inulin

Some uses of inulin are dependent upon the degree of polymerization. For example, when inulin is hydrolyzed to produce high-fructose syrup, the lower the initial degree of polymerization, the greater the contamination with glucose from the terminal sucrose molecule. Likewise, the physical and chemical properties of inulin in food products vary with chain length, and as a consequence, the degree of polymerization can dictate potential uses and markets. When inulin is used for alcohol production, however, shorter degrees of polymerization are more effectively converted.

The fact that composite inulin extracts can be fractionated on a commercial scale into reasonably discrete chain length classes allows tailoring of the product to intended market uses. Hence, the chain length condition of the raw product is important in that it is relatively easy to depolymerize inulin to give shorter-chain-length fractions; however, current *in vivo* attempts to create longer-chain-length polymers on an economically viable scale have not been optimistic.

10.9 ADDITIONAL METABOLIC PATHWAYS

A diverse cross section of enzymes has been studied in Jerusalem artichoke (Table 10.8), some simply because the tuber provides a convenient source that can be easily stored. In other instances, especially where there are relatively unique properties involved, the focus has been on the role of the enzyme system in the species. The following describes several such enzymes.

TABLE 10.8
Enzymes Studied in Jerusalem Artichoke

Enzyme Name	EC Number[a]	References
Arginase	3.5.3.1	Lambert and Duranton 1970; Wright et al., 1981
Arginine decarboxylase	4.1.1.19	Bagni et al., 1983
AMP aminohydrolase	3.5.4.6	Le Floch and Lafleuriel, 1983
ATPase	3.6.3.1	Chaubron et al., 1994; Petel and Gendraud, 1986, 1988
Ascorbate free radical reductase	1.6.5.4	Arrigoni et al., 1981
Cinnamate 4-hydroxylase	1.14.13.11	Batard et al., 1997, 1998, 2002; Benveniste and Durst, 1974; Benveniste et al., 1977, 1982, 1986, 1989; Cabello-Hurtado et al., 1998; Didierjean et al., 2002; Fonne-Pfister et al., 1988; Gabriac et al., 1985, 1991; Kochs et al., 1992; Lesot et al., 1990; Ponnamperuma and Croteau, 1996; Reichhart et al., 1982; Salaun et al., 1978, 1981, 1982, 1989, 1993; Schalk et al., 1997, 1997; Schoch et al., 2003; Teutsch et al., 1993; Tijet et al., 1999; Werck-Reichhart et al., 1988, 1990, 1993
Cinnamic acid hydroxylase	1.14.13.11	Durst, 1976
Cyclic AMP phosphodiesterase	3.1.4.16	Giannattasio et al., 1974
Diamine oxidase	1.4.3.6	Torrigiani et al., 1989
Fructan:fructan 1-fructosyltransferase	2.4.1.100	Darwen and John, 1989; Frehner et al., 1984; Hellwege et al., 1998; Koops and Jonker, 1994; Leuscher et al., 1996; Van den Ende et al., 2006; van der Meer et al., 1998; Van Tunen et al., 1996
Fructan exohydrolase	3.2.1.80	Van den Ende et al., 2000
Fructan β-fructosidase	3.2.1.80	Jhon and Kim, 1988; Kupin et al., 2002; Xie and Xiang, 1997
Fructotransferase	4.2.2.17	Kobayashi et al., 1989
Glucose-6-phosphate dehydrogenase	1.1.1.49	Aitchison and Yeoman, 1973
Inulinase — see fructan β-fructosidase	—	—
Invertase	3.2.1.26	Goupil et al., 1988; Little and Edelman, 1973; Venuat et al., 1993
Nucleosidase, adenosine	3.2.2.7	Le Floc'h and Lafleuriel, 1981
Nucleosidase, inosine	3.2.2.2	Le Floc'h and Lafleuriel, 1981
Pectin methylesterase	3.1.1.11	Macey, 1965
Peroxidase	1.11.1.1	Bastin, 1968; Hirsch, 1975
Phenolase/polyphenol oxidase	1.14.18.1	Park et al., 1991; Zawistowski et al., 1988a, 1988b, 1987a, 1987b
Phenylalanine-ammonia lyase	4.3.1.5	Ambartsumian et al., 2000; Durst and Duranton, 1970; Hirsch, 1975
Phosphatase I and II	3.1.3.16	Larondelle et al., 1989; Van Schaftingen and Hers, 1983
Phosphofructokinase	2.7.1.11	Black and Wedding, 1968
Phosphatase	3.1.3.2	Hirsch, 1975; Palmer, 1970
Phosphoenol pyruvate carboxylase	4.1.1.31	Dubost and Gendraud, 1987
Quinone reductase	1.6.5.5	Spitsberg and Coscia, 1982
Succinyl CoA synthetase	6.2.1.4	Palmer and Wedding, 1966; Wedding et al., 1966
Sucrose synthase	2.4.1.13	Keller et al., 1988; Pontis et al., 1972; Noel and Pontis, 2000; Pontis and Wolosiuk, 1972; Sakalo and Lukashova, 1993; Salerno et al., 1979; Wolosiuk and Pontis, 1974
Sucrose:sucrose 1-fructosyltransferase	2.4.1.99	Darwen and John, 1989; Dickerson and Edelman, 1966; Edelman and Dickerson, 1966; Frehner et al., 1986; Koops and Jonker, 1996; Praznik et al., 1990; Scott et al., 1966; Van den Ende et al., 2000; Van Tunen et al., 1996

TABLE 10.8 (CONTINUED)
Enzymes Studied in Jerusalem Artichoke

Enzyme Name	EC Number[a]	References
Transglutaminase	2.3.2.13	Del Duca et al., 1993, 1994; Della Mea et al., 2004; Falcone et al., 1993; Villalobos et al., 2001
Urease	3.5.1.5	Lambert and Duranton, 1970
UDP-glucose pyrophosphorylase	2.7.7.9	Lambert and Duranton 1970
UDP-D-glucuronate decarboxylase	4.1.1.35	D'Alessandro and Northcote, 1977
UDP-D-xylose-4-epimerase	5.1.3.5	D'Alessandro and Northcote, 1977

[a] Enzyme Commission numbers are a numerical classification scheme for enzymes, based on the chemical reactions they catalyze.

Cytochrome represents a superfamily of enzymes that are involved in secondary metabolism, such as the phenylpropanoid and terpenoid biosynthesis pathways (Donaldson and Luster, 1991; Hallahan et al., 1993; Nelson et al., 1993; Schuler and Werck-Reichhart, 2003). There are 272 P450-encoding genes in the Arabidopsis genome and 458 in rice (Schuler and Werck-Reichhart, 2003). P450s play dominant roles in the synthesis of lignin, UV protectants (flavonoids, coumarins, sinapoyl), pigments (anthocyanins), defense compounds (isoflavonoids, hydroxamic acids, glucosinolates, cyanogenic glucosides, terpenes), hormones (gibberellins, brassinosteroids, auxin), and oxygenated fatty acids (see reviews by Morant et al., 2003; Schuler and Werck-Reichhart, 2003). Werck-Reichhart's laboratory (Institut de Biologie Moleculaire des Plantes, Strasbourg, France) has studied CYP73s found in Jerusalem artichoke (Teutsch et al., 1993), which catalyze the second step in the phenylpropanoid pathway (see Table 10.8 for additional references). *Trans*-cinnamate 4-hydroxylase (EC 1.14.13.11) catalyzes the 4-hydroxlation of cinnamic acid, the first oxidative step in the synthesis of lignin, flavonoids, coumarins, and other phenylpropanoids, and therefore may be a potential transgenic manipulation target for altering lignification, defense-related reactions, or metabolism of xenobiotics. The coding sequence for the enzyme has been identified (Teutsch et al., 1993) and expressed in yeast (Urban et al., 1994). Wounding results in an upregulation of the pathway primarily mediated through gene activation and an increase in *CYP73A1* mRNA (Batard et al., 1997).

Plants can accumulate, transform, and store exogenous chemicals via conjugation, compartmentalization, or binding, reducing or eliminating their toxic effects. The cytochrome P450 oxidases are involved in the metabolism of exogenous pollutants, herbicides, and other compounds (Durst and Nelson, 1995; Werck-Reichhart, 1995). The enzyme 7-ethoxycoumarin *O*-de-ethylase catalyzes the *O*-dealkylation of 7-ethoxycoumarin in Jerusalem artichoke and is strongly induced in response to exogenous chemicals (Werck-Reichhart et al., 1990). The gene has been cloned into yeast and, while highly xenobiotic inducible, is not responsive to mechanical stress (Batard et al., 1998).

The downstream synthesis of two coumarins, ayapin (6,7-methylenedioxy-coumarin) and scopoletin (6-methoxy-7-hydroxy-coumarin), is of biological interest due to their apparent roles as phytoalexins. Their accumulation has been correlated with resistance to pathogens in *Helianthus* (Tal and Robeson, 1986a, 1986b) and as feeding deterrents (Olson and Roseland, 1991). Both compounds are found in Jerusalem artichoke tubers (Cabello-Hurtado et al., 1998), and their synthesis via the phenylpropanoid pathway involves the first three steps leading to the activation of 4-coumaroyl CoA (Werck-Reichhart, 1995). Several routes have been postulated; ayapin does not appear to be derived from scopoletin (Cabello-Hurtado et al., 1998).

10.10 MOLECULAR GENETICS

One of the earliest reports on the molecular biology of the Jerusalem artichoke genome was an estimate of the haploid DNA sequence length (0.23×10^{12} Da) (Nze-Ekekang et al., 1974). Heyraud et al. (1987) subsequently compared differences in BamH restriction fragments of chloroplast DNA between *H. annuus* and *H. tuberosus*. Knowing the entire nucleotide sequence of the plant would be highly advantageous in that it would provide a map of where individual genes were located and a wealth of information, facilitating the development of superior new cultivars via both conventional plant breeding and transgenic methods. It would also promote understanding of how, when, and where individual genes are expressed.

The size of a species genome and the extent of its noncoding region are critical factors in that as each increases, the complexity and expense of sequencing increase. Plants vary widely in the size of their genomes, from very small (Arabidopsis) to exceptionally large (lily). The genome for *Arabidopsis thaliana* (L.) Heynh. is 0.16 Gb in length (Bennett et al., 2003); sunflower, 3.5 Gb (Price et al., 2000); and Jerusalem artichoke, ~10 Gb.* While the entire genome of Arabidopis has been sequenced, and detailed genetic maps have been developed with over 2000 single sequence repeats (SSRs), sequence tagged sites (STSs), and expressed sequence tag (EST) markers in *H. annuus* (Burke et al., 2002, 2004; Pashley et al., 2006; Rieseberg et al., 2003; Tang et al., 2003; Tang and Knapp 2003), very little is known about *H. tuberosus*. Based on the crop's current economic status coupled with the daunting task of sequencing a genome of the size of *H. tuberosus*, the lack of information is not all that surprising. As of January 6, 2006, GenBank listed only 119 entries with DNA sequence information and 83 entries with protein sequences (GenBank, 2006). Therefore, partial or complete gene sequences encoding for only a relatively small cross section of polypeptides are available. For example, the amino acid sequence has been ascertained from the nucleotide sequence for sucrose:sucrose 1-fructosyl transferase (Figure 10.10). The following lists the primary proteins that have been studied:

- Agglutinin/trypsin inhibitor (Chang et al., 2003a, 2003b, 2006; Liu et al., 2002; Zhu and Chang, 2002)
- *Leafy Cotylenon-Like* gene (Fambrini et al., 2006)
- Class I knox gene HtKNOT1 (Chiappetta et al., 2006)
- Plastidic ATP/ADP transporter HtAATP (Meng et al., 2005)
- Metallothionein-like gene htMT2 (Chang et al., 2002a, 2002b, 2004)
- Dehydrin (Giordani et al., 2003)
- Cyclin and cyclin-dependent kinase genes Heltu CYCD1,1, CYCD3,1, CDKA,1, CDKB1,1 (Freeman et al., 2003)
- Cytochrome P450 CYP76B1 (Didierjean et al., 2002)
- Cytochrome P450 CYP81B1 (Cabello-Hurtado et al., 1998; Werck-Reichhart, 1998)
- Levanase — inserted into *H. tuberosus* (Arzumanyan et al., 2001)
- Sucrose:sucrose 1-fructosyl transferase (Koops et al., 1999; van der Meer et al., 1998; Sevenier et al., 1998)
- Fructan:fructan 1-fructosyl transferase (Van den Ende et al., 2006a, 2006b; van der Meer et al., 1998; Hellwege et al., 1998)
- 7-Ethoxycoumarin *O*-de-ethylase CYP76B1 (Batard et al., 1998, 2002)
- Calnexin (Hasenfratz et al., 1997)
- Cinnamate 4-hydroxylase CYP73A1 (Batard et al., 1997; Teutsch et al., 1993)
- Napaline synthase (NOS)–neomycin phosphotransferase (NPT-II) (Pugliesi et al., 1993)
- Invertase (Venuat et al., 1993)
- Lectin (van Damme et al., 1999)

* Ten Gb is only a rough estimate of the length.

- Na^+/H^+ antiporter (Yan, Y. et al., unpublished data)
- Helianthinin (Anisimova et al., 2004)

Much of the genome is comprised of noncoding regions (introns), areas that do not contain the genetic information for a gene. If, instead of sequencing the entire genome, individual genes could be located, isolated, and sequenced, the speed would be greatly increased and the cost reduced. *H. tuberosus* has been included as one of the 17 species in the Compositae Genome Project, the objective of which is to develop resources for functional, comparative, and evolutionary genomics of the genus. The initial objective is to identify ESTs, small segments of either the 5′ or 3′ end of expressed genes. Using these tags, it is possible to select only the regions of DNA that encode for proteins, ignoring noncoding introns that make up a relative high percentage of the genome. To date (January 6, 2006), 19,176 ESTs have been described for *H. tuberosus* (Compositae Genome Project Data Base, 2006).

10.11 YIELD

The yield of Jerusalem artichoke and products derived therefrom is strongly modulated by the geographical location of production, cultivar grown, and growing conditions. Location is critical in that it affects the length of the growing season and the photoperiodic conditions to which the plant is exposed. As the latitude increases toward the North (or South) Pole, the length of the growing season becomes progressively shorter and the change in the photoperiod over the growing season progressively greater. Since the crop requires a relatively long season for maximum productivity and the reproductive phase of most clones is sensitive to short days, geographical location is critical. The impact of location can be seen in the increasing tuber yield in Western Europe, when the production was assessed in 19 locations from Stockholm to southern Italy (i.e., 55 to 60ºN, 6.5 $t \cdot ha^{-1}$; 50 to 55ºN, 7.1 $t \cdot ha^{-1}$; 45 to 50ºN, 10 $t \cdot ha^{-1}$; 40 to 45ºN, 15 $t \cdot ha^{-1}$) (Barloy and Fernandez, 1991). In very northern locations, the growing season is sufficiently short that tubers may not be formed, though the aboveground portion of the crop could be harvested. Total fresh weight displayed a similar but less extreme geographical response.

Jerusalem artichoke breeders have developed cultivars/clones that range in their photoperiodic response for flowering from day neutral to short day. Long-season (short-day) clones often do not set tubers when grown at high latitudes. As a consequence, the clone–geographical location interaction is critical to maximizing productivity. Yield data vary widely depending upon the cultivar and the conditions under which the crop was grown. Inappropriate cultivar selection for the climate in a production location invariably results in substandard yields (Morrenhof and Bus, 1990; Zubr and Pedersen, 1993).

10.12 GROWTH ANALYSIS AND MODELING

A number of models have been constructed to better understand the development physiology of Jerusalem artichoke. These models quantify the amount of solar radiation intercepted, the efficiency with which light is converted into dry matter, and the distribution of dry matter around the plant over time. Assimilated dry matter is used for structural growth or as storage reserves in different plant parts.

Jerusalem artichoke models, representing growth under optimal (nonlimiting) conditions, have been refined in the light of data from field experiments. Growth analysis and modeling provide knowledge that can be applied when utilizing the crop for different applications, for example, to increase the productivity of a particular plant part (usually the tubers) or to predict potential yield and quality under different growing conditions. Models also help to identify new research directions,

to explain situations where yields do not meet expectations, and to point to improvements in agricultural practices.

10.12.1 Distribution of Growth and Reallocation of Compounds

A portion of the sunlight intercepted by the green leaves of a plant is converted into chemical form and assimilated as dry matter. The degree to which this occurs defines the efficiency of the photosynthetic system. The assimilated compounds are translocated throughout the plant for structural growth, maintenance reactions, and storage reserves. Dry matter allocated to the formation of new leaves increases the light interception area, and therefore the assimilation rate. A plant loses resources through respiration and dry matter loss, for example, through leaf abscission. Ultimately, at the end of a growing season, dry matter will be distributed to reproductive structures and storage tissues.

The developmental stages of Jerusalem artichoke are generally recognized as emergence and canopy development, rhizome formation, flowering, tuberization, and senescence. Key development stages are accompanied by changes in the pattern of dry matter partitioning. This involves a decline in dry matter in the foliage and an increase in dry matter in storage organs or reproductive plant parts.

The upper leaves store assimilates on a daily basis, as they are produced by photosynthetic processes. Assimilates, mainly fructose and sucrose but also some fructans and starch, increase in the leaves during the day and are translocated to the stems and branches at night (Denoroy, 1996; Strepkov, 1960a). Initially, structural growth has priority in the stem (the main aboveground shoot), but later in the growing season assimilates are stored in the stems. A characteristic feature of Jerusalem artichoke is the temporary storage of large amounts of assimilates in the stems prior to tuber bulking (Incoll and Neales, 1970; Spitters, 1988). The proportion of sugars and the average degree of polymerization of inulin increase toward the bottom of the stem. The stem storage reserves are eventually reallocated to the tubers, starting with the reserves in the lowest part of the stem.

A number of models have described assimilation efficiency in Jerusalem artichoke (e.g., Allirand et al., 1988; Becquer, 1985; Denoroy, 1993; Denoroy et al., 1990; Spitters, 1988). The LINTUL sink-limited model, for instance, incorporated a temperature–sum time axis, starting at plant emergence; a light interception component, based on leaf area index; and a light utilization efficiency component, based on an assimilate production coefficient and a conversion to dry matter coefficient. The LINTUL model assigned first priority to aerial structural growth and second priority to tuber growth, and had different parameters for early- and late-maturing cultivars (Denoroy, 1993). Parameters, for example, reflected the particular importance of temperature regimes for early-maturing cultivars and the critical role of photoperiod in the development of late-maturing cultivars (Meijer and Mathijssen, 1991; Nitsch, 1965).

In a simulation model for growth and yield formation, daily growth rate was calculated from simulations of radiation intercepted by the crop canopy and average light use efficiency using data from periodic harvests (Spitters, 1988, 1990a, 1990b; Spitters et al., 1988b). The model predicted the allocation of assimilated dry matter to the various sink–sources (e.g., stems and tubers) at different points during the growing season. When two versions of the model were assessed using field data, they confirmed that the onset and rate of tuber filling and foliage senescence were critical processes in the modeling of tuber yield formation.

Modeling studies have highlighted the two distinct stages of tuber growth (e.g., Barloy, 1988b). The first phase involves rhizome elongation and the initiation of tuberization, followed by a period of relatively slow tuber growth. The second phase is one of rapid tuber growth, in which dry matter (predominantly carbohydrates) temporarily stored in the stem is translocated to the tubers (Incoll and Neales, 1970). The dry matter biomass of the tubers is thought to originate from three main sources: (1) photosynthetic assimilates from the leaves during the first phase of tuber growth, (2) the transfer of stem reserves to the tubers, and (3) photosynthetic processes during the second phase of tuber growth (Barloy, 1988b). The relative importance of these sources depends on a complex interaction among cultivar, time of planting, geographic location, and climatic conditions. The

transfer of reserves from the stem to tubers begins when the tubers have already attained around 35% of their final dry weight, although the relative importance of the dry matter sources can vary considerably after this. For instance, the final tuber biomass of an early-maturing cultivar ('D19') was derived 38% by growth phase 1 photosynthesis, 15 to 25% by stem-to-tuber transfer. and 37 to 47% by growth phase 2 photosynthesis, while the corresponding values for a late-maturing cultivar ('Violet de Rennes') were 36%, 38 to 50%, and 14 to 26% (Barloy, 1987).

The total biomass production of a late-maturing cultivar ('Violet de Rennes') was higher than for an early-maturing cultivar ('Blanc précoce') in field experiments in France (Barloy, 1987, 1988b). Modeling showed that this was due to the longer persistence of optimal leaf area, which enabled a greater assimilation of dry matter. However, the tuber yields of the two cultivars were not different, because the growth of the late cultivar was interrupted by unfavorable climatic conditions. The reallocation of inulin from stem reserves to the tubers was interrupted by frosts that killed the aerial plant parts. Although remobilization of assimilates goes on after the death of foliage, translocation stops at air temperatures below –0.3ºC (Gendraud, 1975). In late-maturing cultivars, up to 50 to 60% of the carbohydrates reallocated to the tubers come from temporary stem storage. In contrast, early-maturing cultivars generally can complete the translocation of inulin into their tubers before senescence. Early-maturing cultivars are more likely to have earlier transfer of assimilates into the tubers soon after tuberization, and are less dependent on the transfer of storage reserves from the stem (Barloy, 1987).

The temporary storage of carbohydrates in the stem can therefore be unfavorable in terms of tuber yield and inulin productivity. Significant amounts of inulin are translocated to the tubers of late-maturing cultivars very late in the growth cycle. Early frosts can disrupt the reallocation of this inulin to the tubers (Denoroy, 1996; Zubr, 1988a). Temporary stem storage is also costly, in terms of the metabolic costs of relocation and of the formation and maintenance of extra storage tissue (Denoroy, 1996). The ratio between structural matter and temporarily stored inulin in the stems varies considerably among cultivars. Therefore, plant breeding programs (see Chapter 8) focusing on maximizing tuber yields and inulin productivity should include genotypes that store most of their inulin in the tubers from the start of tuberization onward (Meijer et al., 1993; McLaurin et al., 1993).

A model of crop growth, development, and yield formation was used to compare Jerusalem artichoke and chicory — the two main agricultural sources of inulin (Meijer et al., 1993). The pattern of assimilation in the two crops was very different. Chicory is a biennial, with only vegetative growth in the first season and dry matter distributed to the storage roots during the second season. A greater fraction of total production is diverted to structural stem matter in Jerusalem artichoke. Most dry matter is allocated to the stem until the reproductive phase of Jerusalem artichoke, mainly in the form of structural stem material, but also as stored carbohydrates.

The discrepancy between the simulations of the models and experimental data from Jerusalem artichoke grown in the field is often large, in the case of early versions of the LINTUL model, for example, due to over- or underestimation of leaf area extension, ontogenetic development, and the distribution of assimilates with time (Denoroy, 1993). The models have been improved over time, however, in the light of experimental evidence. Collectively they have provided useful insights into the development physiology and biochemistry of Jerusalem artichoke.

10.12.2 Leaf Area

The acquisition of carbon is strongly modulated by the surface area of photosynthesizing leaves; hence, understanding leaf area development is germane to efforts to increase yield. In many crops, biomass is linearly related to the amount of light intercepted (Monteith, 1977). This is certainly the case for Jerusalem artichoke, where total productivity is strongly correlated with the amount of solar radiation intercepted (Denoroy, 1996; Meijer et al., 1993). Leaf area, leaf duration, and photosynthetic efficiency of the crop canopy determine how much light is intercepted and subsequently utilized (Table 10.9).

TABLE 10.9
Biological Parameters, Their Descriptions, and Values for Jerusalem Artichoke

Parameter	Description	Value	Reference
Azimuthal distribution of leaves	Horizontal direction of a celestial point from a terrestrial point, expressed as the angular distance from a reference direction; azimuthal distribution found to be nearly random (so the variation of k over time was ignored)	Random	Lemeur, 1973; Monti et al., 2005
Biological yield	Total biomass of the crop	15–30 t DM·ha^{-1}	Denoroy, 1996; Meijer et al., 1993
Canopy light extinction coefficient (k)	Calculated using the function LI = 1 – exp$^{(-k*\text{LAI})}$, where LI is the fraction of light intercepted by the canopy and LAI is leaf area index (m^2 leaf·m^{-2} land)	Varies[a]	
Crop growth rate (CGR)	(Weight$_2$ – weight$_1$)/(time$_2$ – time$_1$)	Varies[a]	
Growing degree days	Cumulative total of mean daytime temperature in °C above a baseline temperature (for Jerusalem artichoke typically 0°C). The value increases throughout the growing season with final values depending upon location and length of the growing season	~3000°C (Italy)	Monti et al., 2005
Harvest index (HI)	(Mass of the plant part of interest/plant mass) × 100	~64–78%	McLaurin et al., 1999; Schittenhelm, 1996; Baldini et al., 2003
Leaf angle (La)	Angle of the leaf from horizontal in degrees	0–55º	Lemeur, 1973
Leaf area (LA)	Leaf area/plant (cm^2·plant^{-1})	Varies[a]	
Leaf area index (LAI)	Leaf area/unit area of land; varies during the season; the following is the maximum reported (m^2 leaf·m^{-2} land)	9.8	Hay and Offer, 1992
Leaf area duration (LAD)	Leaf area integrated over time, i.e., LAD = $^1/_2\Sigma(\text{LAI}_n + \text{LAI}_{n+1})/(\text{time}_{n+1} + \text{time}_n)$	~790 dm^2·day^{-1}	Nakano, 1975
Leaf azimuth angle	Leaf direction relative to north (360°)	Varies	
Leaf chlorophyll content	Sum of chlorophyll a + b	~0.3–0.6 g·m^{-2}	Soja and Haunold, 1991
Leaf chlorophyll a-to-b ratio	Ratio of the amount of chlorophyll a to b	2.5:1; 2.4:1	Soja and Haunold, 1991
Leaf longevity (average)	Average number of days a leaf remains on the plant	92 d	Nakano, 1975
Leaf maximum photosynthesis rate	Single leaf maximum photosynthetic rate	29–40 µmol CO_2 m^{-2}·sec^{-1}	Soja and Haunold, 1991
Leaf nitrogen concentration (N_{leaf})	g N·kg^{-1} leaf dm	35 g N·kg^{-1}dm	Somda et al., 1999
Leaf temperature (T_{leaf})	Temperature in °C at the leaf surface	27–37, varies[a]	Monti et al., 2005
Leaf zenith angle	Angular distance between the leaf and the sun	Varies	
Light extinction coefficient (k)	Extinction coefficient for a particular substance is a measure of how well it absorbs electromagnetic radiation at particular wavelengths	0.78–1.01	Allirand et al., 1988
Maximum photosynthetic rate (P_{max})	Leaf photosynthesis under saturated light conditions	11–30 µmol CO_2·m^{-2}·sec^{-1}; 29–40 µmol CO_2·m^{-2}·sec^{-1}	Baldini et al., 2004; Soja and Haunold, 1991

TABLE 10.9 (CONTINUED)
Biological Parameters, Their Descriptions, and Values for Jerusalem Artichoke

Parameter	Description	Value	Reference
Net assimilation rate (NAR)	$(w_2 - w_1)(\ln LA_2 - \ln LA_1)/(t_2 - t_1)(L_2 - L_1)$	Varies	
Nutrient contribution to tubers (%)	[(Maximum amount in organ – amount at final harvest)/final amount in tubers] × 100	Varies[b]	Somda et al., 1999
Nutrient redistribution to tubers	[(Maximum amount in organ – amount at final harvest)/maximum amount in tubers] × 100	Varies[b]	Somda et al., 1999
Photosynthetic compensation point	Where the rate of photosynthesis is equal to respiratory losses	-55 to 60 $\mu mol \cdot m^{-2} \cdot sec^{-1}$	Soja and Haunold, 1991
Photosynthetic light saturation intensity	Light intensity at which maximum photosynthesis is attained	~1700 $\mu E \cdot m^{-2} \cdot sec^{-1}$	Soja and Haunold, 1991
Photosynthetically active radiation (PARi)	Electromagnetic energy in the 400–700 nm wavelength range. Measured as the photosynthetic photon flux (PPF) in mole of $quanta \cdot sec^{-1} \cdot m^{-2}$	Varies	
Radiation use efficiency (RUE)	Determined as the slope of the regression of total dry biomass and cumulated intercepted PARi	~2.9 $g \cdot MJ^{-1}$	Becquer, 1985; Gosse et al., 1986; Spitters, 1988
Relative growth rate (RGR)	$(\ln weight_2 - \ln weight_1)/(time_2 - time_1)$	Varies	
Specific leaf area (SLA)	Leaf area/leaf dry mass ($m^2 \cdot g^{-1}$)	Varies[a]	
Specific leaf nitrogen (SLN)	$N_{leaf} \times SLA$	Varies	
Stomatal conductance (g_s)	Numerical measure of the rate of passage of carbon dioxide through the stomata ($mmol \cdot m^{-2} \cdot sec^{-1}$)	400–1400, varies[c]	Monti et al., 2005
Tuber density	$kg \cdot m^{-3}$	511	Kays, unpublished data
Tuber respiratory rate	mg $CO_2 \cdot kg^{-1} \cdot hr^{-1}$ @ 0°C	10.2	Peiris et al., 1997
Tuber respiratory heat	$J \cdot kg^{-1} \cdot hr^{-1}$ @ 0°C	111	Peiris et al., 1997
Water use efficiency	g $DM \cdot l^{-1}$ water transpired	1.1–1.9	Conde et al., 1991

[a] Varies with the stage of growth, cultural conditions, and other factors.
[b] Varies with nutrient, organ of interest, stage of development, and other factors.
[c] Varies with temperature, moisture status, and other factors.

Absolute measurements of leaf area alone give an imprecise indication of the capture of solar radiation because of the way leaves are arranged within the plant's canopy. Leaf area index (LAI) is a measure of the extent of the plant's canopy. It is the surface area of leaves (one side) relative to a given unit of land area (typically $m^2 \cdot m^{-2}$), and for most terrestrial plants, the leaf area index ranges from 2 to 15. The index represents the number of complete layers of leaf material. Therefore, a plant having 1 m^2 of leaf surface covering 1 m^2 of ground would have a leaf area index of 1.0. For many plants, the leaf area index increases with age until reaching a maximum between 2.0 and 5.0 or higher. The optimum leaf area index in Jerusalem artichoke is 4 to 6, which is lower than for crops like rice (6 to 12) (Yoshida and Parao, 1976) and pineapple (9 to 10) (Bartholomew and Kadzimin, 1977) with more vertical leaves.

Various methods of measuring leaf area index are in common use, including destructive harvesting and direct leaf measurement, and indirect nondestructive methods involving optical instrumentation. In addition to plant age, the leaf area index is partially determined by genotype,

environmental factors, and crop management practices. The leaf area index influences photosynthetic efficiency and plant growth rate. In the closely related cultivated sunflower (*H. annuus* L.), it is known to vary substantially with plant growth stage and fertilizer treatment. In Cordoba, Spain, the leaf area index ranged from 0.7 to 3.0 (Gimenez et al., 1994); in California, from 0.2 to 2.2 (Joel et al., 1997); and in Buenos Aires, Argentina, from 3.5 to 5.8 (Scurlock et al., 2001; Trapani et al., 1992).

In Jerusalem artichoke, light interception efficiency is related to its leaf area index (Barloy, 1987) and varies with cultivar (Barloy, 1988a, 1988b). The leaf area index of early-maturing and late-maturing cultivars ('Columbia' and 'Violet de Rennes') peaked at around 5.0 and 6.0, respectively, in the Netherlands. The cumulated light interception for 1 year was 712 and 821 $MJ \cdot m^{-2}$ for the early and late cultivars, respectively. The foliage of early-maturing cultivars can sometimes deteriorate prematurely in warmer years, thereby wasting a substantial part of the solar radiation (Meijer et al., 1993). Leaf area index peaked at 9.8 in Scotland, enabling a very high efficiency of radiation interception (Hay and Offer, 1992).

The early growth of leaves is limited by temperature (Meijer et al., 1993), with early leaf area index expansion fitting models with accumulated degree days (Becquer, 1985; Denoroy, 1996; Jouis, 1985). In fact, the rate of increase of leaf area correlates better with temperature than with time (Allirand et al., 1988; Becquer, 1985). After canopy closure, the leaf area index increases almost linearly with degree days, with dry matter accumulation a linear function of intercepted radiation (Allirand et al., 1988). Total dry matter production is closely correlated with the sum of intercepted radiation, when calculated with actual leaf area index data. A trend was reported toward lower efficiencies under arid conditions, probably due to a near light saturation rate of leaves and a higher respiration rate, giving a lower rate of dry matter assimilation to intercepted radiation (Denoroy, 1993).

Several models that quantify the amount of light intercepted by Jerusalem artichoke crops during the growing season (e.g., Allirand et al., 1988; Lemeur, 1973) build upon existing models, and in particular upon a model developed by Monteith (1977). The total production of dry matter in barley, potatoes, sugar beet, and apples was strongly correlated with intercepted radiation in this model, with the efficiency of use of intercepted light to form carbohydrates being around 2.4% (1.4 $g \cdot MJ^{-1}$ solar energy) (Monteith, 1977). The light response curves of photosynthesis and the biochemical pathway of Jerusalem artichoke are typical of carbohydrate-storing C_3 plants, facilitating the adoption of existing models (Denoroy, 1996).

Canopy architecture affects the leaf area index and determines the degree of shading of lower leaves. The canopy architecture differs among cultivars, which vary in stem and leaf number and leaf size. The initial development of the canopy and leaf area index is in part a function of stem number, which is in part dependent upon seed tuber size, shape, condition, and cultivar. Large, healthy seed tubers tend to produce more stems, which accelerate early canopy development (Barloy, 1988; Jouis, 1985). For example, 'Blanc précoce' plants had, on average, 3 to 5 stems and 800 to 1000 small leaves, compared to 1 or 2 stems and 350 to 450 large leaves for 'Violet de Rennes' (Barloy, 1988b). These variables are included in models that quantify light interception. An increase in the number of stems does not necessarily affect the total number of tubers; however, because stems act as a temporary storage of dry matter, stem number can affect tuber number and dry weight, especially in late-maturing cultivars (Baillairgé, 1942; Barloy, 1987; Becquer, 1985).

Jerusalem artichoke has a planophile canopy (horizontal leaves), as opposed to an erectophile canopy (erect leaves). Models show that erectophile canopies are generally more efficient in their light-intercepting capacity (Chen et al., 1994; Lemeur, 1973). Jerusalem artichoke cultivars vary in the amount of branching and in leaf orientation from top to bottom of the canopy. In a typical canopy, planophile leaf angle distribution is almost uniform between 0 and 55º, while leaf azimuth distribution is nearly perfectly random when leaf area is large (Lemeur, 1973). The canopy architecture of Jerusalem artichoke and three other crops was incorporated into a model to assess how well each intercepted solar radiation for several solar elevations. Jerusalem artichoke and sunflower

(planophile canopies), and maize and soybean (erectophile canopies) intercepted direct light to a similar extent over a daily period, although maize and soybean had a better distribution of light absorption in the lower canopy layers (Lemeur, 1973). Incoming light is intercepted efficiently by the upper leaves of Jerusalem artichoke due to their angle. The leaves in the top layer (top quarter) of the canopy intercept half of the absorbed daily radiation, with leaves on the bottom layer (lowest quarter) intercepting less than 5%, the difference being most pronounced at lower solar elevations (Lemeur, 1973).

A relatively low leaf area index during the spring is a limiting factor in exploiting early-season solar radiation. The leaf area index of 11 cultivars grown in Denmark, for instance, was less than 1.0 up to the end of May, indicating a relatively low exploitation of available radiation during the spring. The index increased rapidly from mid-June, in all cases, with the exception of a dwarf clone, reaching a maximum of 4.2 in early-maturing cultivars and 6.2 in late-maturing cultivars (Zubr and Pedersen, 1993). The light interception coefficient (k) at canopy level in Jerusalem artichoke models varies from 0.78 to 1.01, when fitted to experimental data, and is dependent on cultivar, with higher values recorded for late-maturing cultivars (Allirand et al., 1988; Denoroy, 1996; Spitters et al., 1988b). Once a full leaf canopy is established, Jerusalem artichoke has a high potential productivity due to a high efficiency for intercepting and converting light energy to dry matter (Barloy, 1987; Varlet Grancher et al., 1982).

Leaf area duration [$LAD = {}^1/_2\Sigma\ (LAI_n + LAI_{n+1})(time_{n+1} - time_n)$] provides a measure of the longevity (generally in weeks) of the canopy, which is related to potential for carbon fixation (Table 10.9). Leaf area duration is depicted graphically as the area beneath the curve when the leaf area index is plotted against time. In opposition to the development of progressively greater leaf areas are a number of factors (e.g., foliar diseases, nutritional deficiencies). The presence of rust (*Puccinia helianthi* Schw.), which is generally more prevalent on older leaves, can have a significant effect on leaf area. Likewise, with the onset of flowering, apical growth and increases in leaf area terminate and the onset of leaf senescence begins to decrease the plant's leaf area. Shedding of healthy leaves is strongly enhanced by shading (Zubr, 1988a) and high temperatures (Meijer, 1993). Leaves shed from the plant are typically the oldest, which are found toward the base of the canopy, and hence in a poor light reception position. As a consequence, production practices that increase shading (e.g., high plant densities) accelerate shedding. In contrast, application of nitrogen during this period impedes leaf loss, though without a positive effect on eventual tuber yield (Morrenhof and Bus, 1990).

Light use efficiency (the efficiency of light energy conversion) is usually expressed in models as the slope of regression of the gross amount of dry matter produced upon the cumulative amount of intercepted light. Light use efficiency depends on canopy architecture, the chemical nature of dry matter produced, and other factors.

In addition to light interception, the acquisition of minerals (e.g., nitrogen, phosphorous, and sulfur) from the environment is vital for photosynthetic processes to proceed efficiently. Chemical composition is one component of dynamic simulation modeling (Denoroy, 1996).

10.12.3 Biological Yield and Harvest Index

Biological yield is a measure of the total biomass of a crop. It is of particular relevance where Jerusalem artichoke is grown as an energy crop. Total dry weight or total biomass of Jerusalem artichoke ranges from 6 to 9 $t{\cdot}ha^{-1}$ when grown under poor conditions to 20 to 30 $t{\cdot}ha^{-1}$ under particularly favorable conditions (Denoroy, 1996). The total biomass in the Netherlands, for example, was 16.4 to 16.8 $t{\cdot}ha^{-1}$ for an early-maturing cultivar ('Columbia') and 15.7 to 19.3 $t{\cdot}ha^{-1}$ for a late-maturing cultivar ('Violet de Rennes') in field trials over 2 years (Meijer et al., 1993).

The harvest index is the ratio between economic yield and biological yield. It is usually determined by the weight of the economic component in relation to the total plant weight, and therefore gives an indication of the relative distribution of assimilates between the tubers and the

remainder of the plant. It is a useful index when working to increase the productivity of a particular plant part. In Jerusalem artichoke, the harvest index is usually related to tuber yield, although for biomass and other applications other components may be quantified.

The Jerusalem artichoke has a relatively high harvest index for the tubers, due to a significant extent to the reallocation of dry matter from the aboveground plant parts to the tubers during the latter part of the season. The harvest index (the fraction of the total biomass allocated to the tubers) increased in an approximately linear manner with time (expressed in day-degrees) during tuber bulking, in a model based on field data (Spitters, 1988), to a maximum value of 0.60. The growth rate of tubers is initially constant and relatively slow. After flower initiation, a faster constant growth rate occurs. The xylem expands considerably on tuber initiation, but growth is thereafter due to parenchyma cells accumulating carbohydrates (Zubr and Pedersen, 1993).

The harvest index varies between early- and late-maturing cultivars. A higher harvest index in more northern latitudes generally occurs in early cultivars (0.60 to 0.78) than in late cultivars (0.50 to 0.55), despite a similar total productivity per unit of time (Barloy, 1988b; Denoroy, 1996). Jerusalem artichoke tubers were found to have a higher harvest index than sugar beet or root chicory storage organs (Schittenhelm, 1999). The harvest index for Jerusalem artichoke (~0.70) is superior to most seed crops — e.g., wheat, 0.43 to 0.54 (McLaren, 1981); barley (*Hordeum vulgare* L.), 0.55 to 0.63 (Ellis and Russell, 1984); rice (*Oryza sativa* L.), 0.55 to 0.62 (Anon., 1978); corn, 0.47 to 0.57 (Place and Brown, 1987); and cowpea (*Vigna unguiculata* (L.) Walp. subsp. *unguiculata*), 0.44 to 0.64 (Fernandez and Miller, 1985) — in which carbon storage within the seed is reduced to a relatively narrow period. Most root and tuber crops, in contrast, allocate dry matter to their storage organs over a much greater portion of the growing season.

In the cultivar 'Sunchoke,' grown in southeastern U.S., the harvest index reached 0.70 by the end of the growing season, with a tuber yield of 14.6 $t \cdot ha^{-1}$. High harvest indexes and tuber yields are dependent on the efficient reallocation of dry matter from aboveground into subterranean plant parts. The 'Sunchoke' study suggested that yield could potentially be improved through earlier tuber induction and development (McLaurin et al., 1999).

The harvest index for tubers generally increases under conditions that are inhibitory to vegetative growth and flowering, such as shading, low temperatures, and short day lengths (Denoroy, 1996). Relatively high planting densities (e.g., 5 to 8 plants$\cdot m^{-2}$) favor maximum tuber yields, and therefore give higher harvest indexes (Barloy and Le Pierres, 1988). However, very high planting densities (e.g., 11 plants$\cdot m^{-2}$) result in increased aerial plant growth, at the expense of rhizome and tuber growth, and a decreased harvest index (Denoroy, 1996; Hay and Offer, 1992).

Average dry weight yields of Jerusalem artichoke tubers range from 4 to 6 $t \cdot ha^{-1}$ to 10 to 15 $t \cdot ha^{-1}$, and vary between 12 and 26% of fresh weight (Denoroy, 1996). Dwarf cultivars tend to have higher dry weight than fresh weight (i.e., 25 to 26% dwt) (Zubr and Pederson, 1993) due to the lower water content of the tubers, which is known to vary with soil moisture and other factors.

10.12.4 Crop Growth and Assimilation Rates

A number of factors determine the rate and extent of plant growth, in particular the daily amount of light energy intercepted, light use efficiency, partitioning of dry matter between different plant parts, dry matter losses, and the duration of growth (Charles-Edwards et al., 1986). Dry matter losses occur chiefly through leaf abscission, which increases in times of water stress and other adverse environmental conditions. However, leaves are generally lost from the bottom of plant canopies, often to be replaced by new leaves at the top of canopies that have better light interception capability.

Crop growth rate is calculated in models from the daily incoming photosynthetically active radiation, the fraction intercepted by the foliage, and the average efficiency of light use (Spitters, 1988). Photosynthetically active radiation (wavelength, 400 to 700 nm) amounts to 50% of the total incoming solar radiation. In Jerusalem artichoke, light use efficiency was found to increase

slightly with the development of the crop, being 2.2 g dwt·MJ^{-1} of photosynthetically active radiation before August 15, compared to 2.5 g dwt·MJ^{-1} after August 15 (Spitters et al., 1988b).

Relative growth rate is a measure of growth divided by weight, or the rate of growth per unit weight (usually in terms of dry weight). The relative growth rate allows for more equitable comparisons of data than using absolute growth rate. Relative growth rate is constant in the case of exponential growth. However, in the real world the relative growth rate of plants slows as they become larger, up to the point where a plant reaches its maximum weight or size.

The net assimilation rate is a measure of a plant's growth with respect to its leaf area, or the amount of dry matter produced by the plant per unit of leaf area. It relates to the amount of light energy intercepted by the plant. In younger plants, the amount of light intercepted is proportional to leaf area, but as a plant grows, its leaves shade one another and light intercepted per unit leaf area decreases. This contributes to the trend of declining relative growth rate with increasing plant dry weight (Charles-Edwards et al., 1986). The relationship between growth rate and leaf area can be complicated, however, because changes in leaf thickness over time can increase leaf weight even though leaf surface area remains the same.

The conversion rate of intercepted radiation at the canopy level to dry matter (i.e., radiation use efficiency) has been estimated in a number of models for Jerusalem artichoke (Becquer, 1985; Denoroy, 1996; Gosse et al., 1986; Spitters, 1988). A greater conversion rate at tuber filling has been recorded, probably due to lower energy costs of chemical synthesis, fewer losses when temporary storage in the stem is bypassed, or the stimulation of photosynthesis when the storage processes in the tubers become more effective (Barloy, 1988b; Denoroy, 1996).

10.13 ENVIRONMENTAL FACTORS AFFECTING YIELD

Jerusalem artichoke thrives under a wide range of growing conditions. However, yields can be greatly affected by environmental factors, including solar radiation, temperature, length of the growing season, and rainfall.

10.13.1 Radiation

Sunlight drives photosynthesis, a process that enables plants, in basic terms, to convert carbon dioxide and water into carbohydrates and oxygen. Chlorophyll molecules, primarily in the leaves, trap radiant energy of particular wavelengths (400 to 700 nm) for conversion into chemical energy. Therefore, light intensity and quality, along with the development, structure, and arrangement of leaves, are key factors affecting photosynthetic efficiency.

The interception of solar radiation is a function of leaf area. However, the mutual shading of leaves, or shade from other plants or objects, reduces a plant's ability to utilize available solar radiation. Jerusalem artichokes can grow in the shade, but with reduced growth parameters (Schubert and Feuerle, 1992); direct and full sunlight is essential for optimal yields. Full radiation is also needed for flowering, and shaded parts of a canopy produce fewer flowers. Jerusalem artichoke has a rapid growth rate, with stems reaching 2.5 to 3 m in height, allowing it to rise above other plant species. In open field situations, therefore, plant stand structure will chiefly determine the amount of solar radiation reaching an individual plant's leaves.

The canopy architecture of Jerusalem artichoke was incorporated in a model looking at how efficiently four different crops intercepted solar radiation. Leaf angle and azimuthal distribution of light were determined, and the light-trapping function for each crop canopy calculated for several solar elevations. Jerusalem artichoke, sunflower, maize, and soybean intercepted direct light to a similar extent over a daily period, although maize and soybean had a better distribution of light absorption in the lower canopy layers. The leaves on the top layer (top quarter) of Jerusalem artichoke canopies intercepted half of the absorbed daily radiation, with leaves on the bottom layer

(lowest quarter) intercepting less than 5%, with the difference most pronounced at lower solar elevations (Lemeur, 1973).

A relatively low leaf area index during the spring is a limiting factor in exploiting early-season solar radiation. The leaf area index of 11 Jerusalem artichoke cultivars grown in Denmark, for instance, was less than 1 up to the end of May, indicating a relatively low exploitation of potentially available radiation during the spring. The leaf area index increased rapidly from mid-June, in all cases barring a dwarf cultivar, reaching a maximum of 4.2 in early-maturing cultivars and 6.2 in late-maturing cultivars (Zubr and Pedersen, 1993). Once a full leaf canopy has established, Jerusalem artichoke is a crop that efficiently captures solar radiation.

In a modeling study of Jerusalem artichoke productivity, foliage dry matter content was found to be a linear function of annual intercepted radiation (Allirand et al., 1988). Yearly productivity variations in France, in terms of biomass, were also explained in great measure by differences in the absorption of solar radiation (Barloy, 1988b).

10.13.2 Temperature

Temperature is directly related to the rate of vegetative plant growth, with the rate of all biochemical processes in plants being temperature dependent. Within a species-specific range, usually from a few degrees above 0ºC up to a maximum peak around 20 to 35ºC, increasing temperatures accelerate chemical processes in the leaves. Increased rates of photosynthesis and chemical metabolism within a species' physiological range of temperatures result in increased vegetative growth (Meyer et al., 1973). The leaf area index of Jerusalem artichoke, for instance, is in proportion to the temperature experienced during the growing season (Allirand et al., 1988).

Most Jerusalem artichoke cultivars require average annual temperatures of between 6 and 26ºC, within a growing season of at least 125 frost-free days (CAB International, 2001; Cosgrove et al., 2000; Duke, 1983). Jerusalem artichoke is more tolerant of frost than maize and many other crops, and can therefore be grown in more northerly latitudes in North America, where it has agronomic requirements similar to those of sugar beet (Fleming and GrootWassink, 1979).

Soil temperatures of at least 6.7ºC are usually required before planted tubers start to sprout and develop (Cosgrove et al., 2000), although tubers can initiate sprouts and roots below 5ºC (Kosaric et al., 1984). Cold temperatures (5ºC or lower) are required to break dormancy. Jerusalem artichoke tubers are frost resistant, and crops can be grown in areas as cold as Alaska, if planting starts as soon as the soil is workable. Tubers can withstand months of freezing while in the ground, as long as soil temperatures do not drop much below 0ºC. Jerusalem artichoke tubers freeze at temperatures below –2.2ºC (Whiteman, 1957). Freezing damage causes a rapid deterioration in the physiological condition of tubers below –7ºC, with tissue breakdown and, in particular, pith decomposition (Steinbauer, 1939).

In contrast to the tubers, the stems and leaves of Jerusalem artichoke are readily killed by frost. Therefore, if the tops are required for fodder or other uses, they must be cut prior to the first frost. The tubers are harvested after the tops have been killed by frost, to ensure that sufficient nutrients have been translocated to the tubers. Frost also enhances the sweetness of the tubers, raising sugar yields for certain industrial applications and improving their flavor for culinary usage.

Jerusalem artichoke tolerates hot summer temperatures, especially in regions that also experience cold temperatures. The optimal leaf area to capture solar radiation is reached earlier in warmer climates. In warmer climates, in places where temperatures and day lengths differ little between the seasons, the cooler periods and shorter day lengths favored by the early and late growth stages are absent. Jerusalem artichoke can grow under tropical conditions, but yields are often suboptimal. Crop failures have been noted in the tropics, for example, the Philippines (Piper, 1911; Steinbauer, 1939). These failures may be due to an extended resting period (e.g., over 7 months) in tubers not exposed to sufficiently low winter temperatures (Steinbauer, 1933). Low-temperature storage shortens the resting period of Jerusalem artichoke tubers (Haber, 1934; Steinbauer, 1939). In experiments,

tubers stored at 0 and 2.2ºC had a prompt and vigorous sprouting response when planted, but the sprouting response was poor for tubers held at 10ºC (Steinbauer, 1939). Without experiencing a period of near-freezing temperatures, the tubers do not readily initiate sprouting.

Nevertheless, Jerusalem artichoke has been successfully cultivated in many tropical regions. Plants are much smaller and mature earlier, yielding smaller and fewer tubers than in temperate regions. However, because growth rates are faster near the equator, two consecutive crops can potentially be produced. In the tropics, Jerusalem artichoke is preferably grown at altitudes of around 300 to 750 m, although in India it is cultivated up to altitudes of 3,600 m (CAB International, 2001).

10.13.3 Photoperiod

Marked seasonal variations in the relative length of day (light) and night (dark) occur in all parts of the world, except for the tropics. Plant species can be affected in different ways by changes in day length or photoperiod, being day neutral, long day, or short day responsive. Jerusalem artichoke is a photoperiod-sensitive short-day plant that requires long light periods followed by shorter light periods to trigger the shift to the reproductive stage of development. Flowering and tuberization are both modulated by photoperiod in Jerusalem artichoke. Different critical lengths of the dark period initiate flowering, and then tuber formation in the fall.

Jerusalem artichoke was a model in some of the early research on plant photoperiodism (e.g., Garner and Allard, 1923). Subsequent studies have established critical day lengths for Jerusalem artichoke, although a wide variation has been observed between different clones (Kays and Kultur, 2005). The critical day length for a range of clones was found to be between 13 and 13.5 h (Allard and Garner, 1940; Hamner and Long, 1939; Zhou et al., 1984). With longer day length, vegetative growth is favored, with flower and tuber formation impeded.

Tubers form readily when plants are exposed to a 9-h photoperiod, but not when exposed to an 18-h photoperiod. Exposure of any one leaf, but not the terminal bud, to a 9-h photoperiod was found to induce tuber formation, even though the rest of the plant experienced an 18-h photoperiod. The leaves are therefore the site of the photoperiodic reaction, the effects of which are communicated to the rhizomes and tubers via chemical signals (Hamner and Long, 1939; Meyer et al., 1973).

Jerusalem artichoke does not perform well in the tropics or other areas where day length varies little during the season. In the photoperiodic conditions encountered in the tropics, vegetative growth stops earlier, and tuber initiation starts sooner, than in more northerly latitudes, resulting in shorter plants and smaller tubers (CAB International, 2001).

The synchronization of flowering is essential for genetic crossing in plant breeding programs. Flowering in most Jerusalem artichoke clones is controlled by photoperiod, with day lengths of 10 to 12 h initiating flowering (Hackbarth, 1937; Zhou et al., 1984). However, substantial genetic variation is found in the date and duration of flowering in Jerusalem artichoke clones. In a comparison of 190 clones, the onset of flowering ranged from 69 to 174 days after planting, while the duration of flowering ranged from 21 to 126 days (Kays and Kultur, 2005). Early-flowering clones may represent day-neutral types in which flowering is controlled by the stage of development rather than photoperiod (Denoroy, 1996), or they may represent clones that when planted early enough achieve sufficient size to receive the short-day photoperiodic stimulus before the day length becomes too long.

In lower latitudes, within the typical range of Jerusalem artichoke, the choice of planting date is the best way to synchronize flowering, using data for days to flowering after planting at a particular location (Kays and Kultur, 2005). However, at higher latitudes, such as in Northern Europe, flowering can occur too late for the production of seed, even with early planting dates. In this case, for desirable genetic crosses, growth under controlled photoperiodic conditions may be necessary, in order to advance the onset of flowering for plant breeding purposes. In a Germany study, artificially shortening day length for up to 12 weeks brought forward flowering in certain cultivars

(Löhrke, 1956). Earlier flowering may also be induced, in regions with long late-season day lengths, by shading plants or forcing plants in a glasshouse (Góral, 1998; Sawicka and Wadysaw, 2005).

10.13.4 Precipitation

Precipitation affects plant physiology indirectly, via the soil water content, soil aeration, atmospheric humidity, and other means. Although precipitation encompasses all liquid and solid forms of water deposited from the atmosphere, including rain, drizzle, dew, hail, hoar frost, and snow, rainfall is the most important type affecting the growth of plants. Jerusalem artichoke tolerates annual precipitation in the range of 31 to 282 cm (Duke, 1983). However, an evenly distributed rainfall of up to 125 cm is preferred for optimal growth (CAB International, 2001). The crop is tolerant of drought and survives short periods of flooding. Its water use efficiency is estimated to be between 1.1 and 1.9 g $dm \cdot l^{-1}$ of water transpired (Conde et al., 1991).

High levels of rainfall in the autumn and winter can encourage disease and hinder harvesting, while insufficient rainfall in summer may necessitate irrigation. Tuber yields in nonirrigated plots were more severely affected by summer drought conditions than sugar beet and root chicory yields, in a 3-year German study. The authors suggested that the longer taproots of sugar beet and chicory were more capable of exploiting water from lower soil levels than the comparatively shallow-rooted Jerusalem artichoke, in times of water stress. However, in a year when water stress became particularly severe, yield depression in the three crops was similar (Schittenhelm, 1999).

Different irrigation treatments were used to produce different levels of water stress, at three different growth stages, under semiarid conditions in central Spain. It was found that a certain degree of drought stress during the first growing stage had no effect on tuber yield, and might even be beneficial. However, if plants were stressed during the final late-season growth stage, tuber yield was dramatically reduced. Drought-stressed plants had a decreased leaf area index, an acclimation strategy that reduces water loss from the plant (Conde et al., 1988, 1991).

Under very arid conditions, Jerusalem artichokes survive without watering, but only reach a limited height (1 to 1.5 m) and yield relatively few small-sized tubers (Fernandez et al., 1988). Due to the thin epidermal layer of the tuber, the crop is prone to lose water in dry soils. Irrigation can double the yield of tubers in arid climates.

Adequate soil moisture is important to ensure vigorous growth during the earlier vegetative stages (Stauffer et al., 1981). Leaves are indicators of soil moisture: wilting occurs with moderate to low soil water, and senescence occurs under extremely restricted water conditions (Kosaric et al., 1984). Tubers are especially sensitive to drought in the late season, when water shortages can impact tuber bulking (Jouis, 1985).

Under hot and dry Mediterranean conditions, Jerusalem artichoke needs adequate rainfall or irrigation for acceptable yields in terms of inulin and sugar production. However, heavy rainfall in the spring or late in the season may have adverse effects on the sugar yield from Jerusalem artichoke tubers (De Mastro et al., 2004).

10.13.5 Wind

The tall growth of Jerusalem artichokes makes them potentially vulnerable to wind damage. Plants can grow up to 1.5 to 2.5 m tall and have a relatively shallow rooting system for their size. Although plants can tolerate moderate winds due to their thick rigid stems, in exposed and windy sites plants can be blown over. Lodging results in compression of the three-dimensional canopy into a much smaller area that invariably leads to shading and significant leaf shedding. Falling plants can also damage surrounding plants, and other vegetables in smallholding situations. This is an acknowledged problem in windy coastal sites in England, such as Cornwall (Smit and McMillan Browse, 2000). Late growth is especially vulnerable to eddying gusts that can bend over or break the stems.

Zubr (1988a) reported breaking and lodging of tall stems during storms in Denmark, while Le Cochec and de Barreda (1990) recorded losses due to wind and hail in French field trials.

With small plots in exposed sites, lodging can be prevented using strong poles, staked at 1.5-m (5-ft) intervals along Jerusalem artichoke rows. Wires run between the stakes at heights up to 1.5 m, to which the stems are secured with string, prevent plants from blowing over (Smit and McMillan Browse, 2000; Wood, 1979). Dwarf varieties are better able to withstand strong winds.

Earthing up the stems in hills enables plants to be more stable and better able to withstand strong winds. Mounding up the soil when plants are around 90 to 120 cm tall also encourages additional root development, which also improves anchorage. Uprooting is more likely in light or medium soils (Wood, 1979).

The tops of Jerusalem artichoke can also be cut off at 1.5 m to reduce the likelihood of wind damage (Wood, 1979), which in this instance prevented the plants from flowering. Wind also affects leaf temperature and the rates of photosynthesis and transpiration, with resulting but minor effects on growth rate (Meyer et al., 1973).

10.14 PRODUCTION FACTORS AFFECTING YIELD

Jerusalem artichoke does not require much management to produce acceptable tuber yields. Shoemaker (1927) concluded, for instance, that it was "the most easily cultivated tuber or root crop to be found in the Temperate Zone". However, a number of production practices can significantly boost Jerusalem artichoke productivity and enhance the quality of products derived from the plant. These include soil treatment, irrigation, planting density, choice of cultivar, time from planting to harvest, weed control, and the use of growth regulators. Tight soils also tend to impede rhizome development, causing the tubers to be formed adjacent to the stem. This is an undesirable condition in that the tubers are distorted, reducing their value for fresh market, and their separation from the stem is more difficult when used for industrial purposes.

10.14.1 Soil Type and Treatment

Jerusalem artichoke grows better on relatively infertile land and in nutritionally depleted soils than most crops (Baillarge, 1942; Pätzold, 1957). Tubers are produced under soil conditions, for instance, that are too poor to support potatoes or sugar beet (Shoemaker, 1927; Boinot, 1942). Jerusalem artichoke is therefore a desirable crop on marginal land, particularly in dry regions with poor soils. In addition, its fibrous root system also helps to break up uncultivated land. However, not all marginal land is suitable for obtaining satisfactory tuber yields (Kosaric et al., 1984). Low yields were reported for peat and poorly drained soils and those low in fertility (Hergert, 1991; Lim and Lee, 1983; Pejin et al., 1993).

Although Jerusalem artichoke can grow on poor soils, tuber size tends to be small and yields are low. Jerusalem artichoke prefers fertile soils, which are necessary for high yields. The highest tuber yields are typically obtained in light, sandy soils of good fertility. Jerusalem artichoke is adapted to rich sandy loams and well-drained alluvial soils (Huxley, 1992).

Under certain circumstances, high yields can be produced in heavy soils, which generally have better water retention properties than other soil types. In fact, under conditions of low rainfall and no irrigation, yields may be higher on heavy loams (Kosaric et al., 1984). In New Jersey, in a year (1930) with particularly low rainfall (9.9 cm instead of the normal 20.1 cm between mid-August and mid-October), tuber yields were 10.4 $t \cdot ha^{-1}$ on heavy loam soil compared to 4.7 $t \cdot ha^{-1}$ on light sandy loam soil. The corresponding sugar yields were 2.0 metric tonnes on heavy loam compared to 0.91 $t \cdot ha^{-1}$ on light sandy loam soil. The heavy loam soil retained twice the moisture of the light sandy soil (22.6% cf. 13.8% water content in soil). In years of heavy rainfall, however, superior tuber and sugar yields occurred on sandy loam soils. Heavier soils may therefore give a greater certainty of yield than light-textured soils in drier regions (Sprague et al., 1935).

Problems due to waterlogging and difficulties with harvesting make heavier soils unsuitable for tuber production in many regions (e.g., Pilnik and Vervelde, 1976). This is especially the case on clay soils. In wet seasons or with irrigation, with around 10 to 13 cm (4 to 5 in.) of water between August and October, yields are generally higher on lighter soils, while tubers are also easier to lift from the ground than from heavier soils. In sandy soils, little soil adheres to the roots on harvest, whereas in heavy clay soils up to 40% of the harvest weight can be accounted for by adhering soil (Shoemaker, 1927). Furthermore, very wet soils can result in thin tubers of low weight, which develop at greater distances from the stalk (Kosaric et al., 1984). In experiments with four different soil types (sandy, clay, "field soil," and humus) in Korea, the highest yields were obtained in humus (63 $t \cdot ha^{-1}$), while the lowest (23 $t \cdot ha^{-1}$) were in clay soil (Lee et al., 1985).

Jerusalem artichoke thrives in a wide range of soil types and pH levels, but production is favored by slightly alkaline soils. Clay soils that are prone to waterlogging, for instance, may become too acid for optimum tuber growth. Optimal pH is in the range of 4.5 to 8.6 (Duke, 1983; Kosaric et al., 1984). In acid soils, plants benefit from the addition of lime to the soil (Simons, 1977). Liming the soil with calcium-based fertilizers can significantly raise yields; this effect is primarily due to the change in soil pH (Lee et al., 1985). In a study in the U.S., the addition of lime alone increased tuber yields on sandy loams of low pH (5.9) by up to 6.8% (Sprague et al., 1935).

In soils of low fertility, fertilization with high-phosphate fertilizer, especially early in the growing season, is recommended to increase yields (Yamaguchi, 1983). A range of fertilization treatments have been recommended for Jerusalem artichoke, although the addition of excessive nitrogen favors top growth at the expense of tuber development.

After planting, the soil can be ridged up around plants, either along rows or around individual plants as hills. This can also be done when plants are around 30 cm tall, as part of mechanical weeding operations. Earthing up the soil around the base of young stalks favors tuber formation, because it increases the amount of buried stem from which the tubers can develop. It also improves the stability of mature plants and makes harvesting easier, as tubers are less deeply buried in the soil. Mulching when plants are around 30 cm tall has a similar effect, helping to ridge up plants while suppressing weeds and conserving soil moisture (Wood, 1979). In wet soils, ridging may reduce rotting by helping to dry out the soil immediately around developing seedlings (Shoemaker, 1927).

10.14.2 Irrigation

The application of supplemental water can have a pronounced impact on yield. Both emergence and bulking stages are particularly sensitive to water deficit stress, with the vegetative stage being less susceptible (Conde et al., 1991). Final tuber growth can be significantly limited by insufficient water (Ben Chekroun, 1990; Milord, 1987; Mezencev, 1985). Judicious application of water increases water use efficiency and harvest index (Conde et al., 1988, 1991), although excess irrigation can result in excessive top growth, reduced yield, and a lower harvest index.

The timing and amount of irrigation depend upon rainfall, plant population density, fertilization rate, soil type, and other factors. Generally, some supplemental irrigation is needed for the crop; the drier the production conditions, the greater the number of applications needed. In Germany, eight applications were made during the season for a total of 147.5 $l \cdot m^{-2}$ (Schittenhelm, 1991). Irrigation increased dry matter yield of early clones and tuber weight by 28.2% without altering the number of tubers. When contrasting nonirrigated and two irrigation rates (a total of 1,500 and 2,500 $m^3 \cdot ha^{-1}$ over five applications), Mimiola (1988) found that the fresh weight yield increased from 29.3 to 40.7 and 57.9 $t \cdot ha^{-1}$, respectively. Application of water is generally achieved using overhead sprinklers and low pressure; low-volume irrigation is recommended for tighter soils (see also Section 12.5).

10.14.3 Plant Population Density

The population density of Jerusalem artichoke plants affects growth parameters and yield. As the plant population increases, the number, fresh weight, and yield of tubers per plant decreases (Berenji and Kisgeci, 1988). Tubers are typically planted at three or four plants per square meter and generally at row spacing of around 1 m (CAB International, 2001). However, planting distances chosen vary for cultivar, region, and available water resources, and can influence the final height and spread that the plants are likely to attain. Shoemaker (1927) noted, for example, that Jerusalem artichoke in Michigan, which grows moderately tall and does not flower, can be grown closer together than the taller and spreading, flowering plants obtained in the more southerly latitudes of Washington, DC.

Typically recommended planting guidelines, for instance, 50 to 60 cm spacing within rows 0.7 to 1 m apart, are designed to give optimal yields, without reducing average tuber size as a result of crowding. Greater distances between rows or hills increase individual plant yield, but overall yield per unit area is reduced (Boswell, 1959; Kosaric et al., 1984).

In trials in the U.S., planting distances of between 30.5 cm (12 in.) and 91 cm (36 in.) were examined within rows that were 1.5 m (5 ft) apart. Closer plant spacing within rows increased yields per unit area, with 61 cm (2 ft) recommended as optimal. Increasing plant spacing from 30.5 to 61 cm increased mean tuber size, but spacings over 61 cm had no further effect on tuber size. Larger tops and increased number of tubers occurred at spacings of 61 cm and over (Boswell et al., 1936).

In the same trials, the distance between rows was varied from 0.61 m (2 ft) to 1.83 m (6 ft), keeping plant spacing within rows constant (61 cm). The mean tuber size was larger at a row separation of 0.91 m (3 ft) than 0.61 m, but beyond 0.91 m no further change in mean tuber size occurred. Row separation distances of 0.91 m were recommended in all states but Oregon, where rows 1.52 to 1.83 m (4 to 6 ft) apart were favored due to the more extensive top growth of plants. Wider plant spacings within rows, 121.9 cm (48 in.), were also recommended in Oregon (Boswell et al., 1936).

Different plant population densities, obtained using rows that radiated from a central point, resulted in differences in both tuber weight and tuber number in an experiment in the former Yugoslavia. Tuber yield for 'Violet Commun' cultivar decreased from 2.2 kg to 0.3-0.4 kg per plant with increasing plant density. The effect of plant density was especially notable up to four to six plants per square meter, but the decline in yield for individual plants was compensated by a greater number of plants per unit area, leading to an upward trend in yield per unit area. At densities higher than four to six plants per square meter, however, the depression in yield for individual plants could not be compensated by additional plants (Berenji and Kisgeci, 1988).

Researchers in Spain found that the optimum density for highest tuber yield was between 30,000 and 40,000 plants·ha^{-1}, with rows separated by about 80 cm and a plant spacing of around 36 cm, when irrigation and fertilization were deployed. At higher plant densities (50,000 plants·ha^{-1}), fertilization significantly increased yield, although at lower plant densities fertilization only had a marginal or no effect on yield (Fernandez et al., 1988).

In experiments in Korea, using row widths from 30 to 90 cm and within-row planting distances from 5 to 75 cm, it was found that highest tuber yields were obtained with 50 to 70 cm between rows and 15 to 30 cm between individual plants in each row. It was concluded that the best spacing for Jerusalem artichoke was 70 by 30 cm — equivalent to 47,620 plants per hectare (Lee et al., 1985).

The incidence of irregular-shaped tubers was greater in the outer rows of plantings than in central rows, according to Shoemaker (1927), who suggested that this was because growth was unrestrained by competition. However, more recent studies have shown that closer planting densities increase the incidence of irregular-shaped tubers. Planting density was one of the variables manipulated in experiments, conducted in Denmark, aimed at finding optimum cultivation parameters for obtaining the maximum number of grade 1 Jerusalem artichoke tubers (smooth, rounded, and

healthy tubers; over 20 g per tuber). Raising plant density from two to eight plants per square meter almost doubled the yield of grade 1 tubers. The average tuber weight decreased by 20% at the closer spacing, although the average weight of grade 1 tubers only decreased by 10% (Klug-Anderson, 1992).

Cultivars differ in their response to plant density; some cultivars can be planted close together without growth or tuber yield being detrimentally affected, while other cultivars are more sensitive to crowding. Dwarf cultivars may be particularly amenable to close spacing. A short-stemmed dwarf clone was specially bred in the Netherlands to test whether reduced tops might favor tuber development. However, no yield benefit was observed compared to established cultivars ('Précoce Commun' and 'Eigen Nabouw'). The short-stemmed dwarf clone produced suboptimal yields at the standard planting density, due to incomplete canopy cover. This enables weeds to establish and represents an inefficient collection of solar radiation. When planting density was increased three-fold in conjunction with additional nitrogen (140 $kg \cdot ha^{-1}$), however, a relatively high tuber yield was obtained. The dwarf cultivar yielded up to 11,100 $kg \cdot ha^{-1}$ dry matter in the tubers, in sandy soils with adequate rainfall, which was comparable with the late cultivar 'Eigen Nabouw,' but still lower than the early cultivar 'Précoce Commun' (Pilnik and Vervelde, 1976).

Intercropping rarely works with Jerusalem artichoke because of its vigorous and tall growth. The closed foliage canopy suppresses intercrops as effectively as competing weeds. The exception is maize (*Zea mays* L.), a tall crop that benefits from soil and climatic conditions similar to those of Jerusalem artichoke (Riotte, 1978). However, this intercrop combination is rarely utilized.

10.14.4 Length of Growing Season

Jerusalem artichoke has a long growing season, for instance, longer than for wheat, maize/corn, and most other crops. The length of the growing season is a key factor in Jerusalem artichoke production. A growing season of at least 4 to 5 months, with at least 125 frost-free days, is typically required for tuber development, although this varies with cultivar. Cultivars are chosen for planting in a particular area partly on the basis of their early- or late-season maturation. Early-maturing cultivars have been developed for shorter growing seasons, while late-maturing cultivars perform best when the growing season is long.

Cultivars bred for early-season production are generally shorter in height than cultivars bred for late-season production (Kiehn and Chubey, 1993). They potentially yield less, but are often more productive in areas where the length of the growing season is short than late-season cultivars that require a longer growing season before tuber bulking. In Northern Europe, the shorter growing season favors cultivars that set tubers earlier in the season. Early-season cultivars produced higher yields than late-season cultivars, for example, in the Netherlands (46 $t \cdot ha^{-1}$ cf. 38 $t \cdot ha^{-1}$), because the growing season was insufficiently long for the optimal growth of late cultivars. The growth pattern among cultivars was closely related to flowering time. At flowering, leaf production terminates and photosynthetic efficiency declines. Many late cultivars did not flower in this Dutch study (Spitters et al., 1988a).

In a French study, late cultivars (e.g., 'Violet de Rennes') produced more total biomass than early cultivars (e.g., 'Blanc précoce'), but tuber yields were the same. The superior leaf area index of late cultivars could not be translated into superior tuber yields due to constraints on the life cycle as a result of unfavorable fall climatic conditions (Barloy, 1988b). Planting early in the spring ensures a longer growing season. In Southern Europe, this equates to February and not later than March. Later plantings result in reduced yields.

A long growing season is desirable for the production of maximum yields of tubers. However, a longer growing season also results in a reduction in the ratio of fructose to glucose in the tubers. A declining level of fructose (as a percentage of total reducing sugar) with delayed harvest has been shown in experiments in Canada, Britain, and the Netherlands (Dorrell and Chubey, 1977; Chubey and Dorrell, 1974a; Bacon and Edelman, 1951; Pilnik and Vervelde, 1976). In general,

September harvesting gave fructose concentrations of 82 to 91%, while November harvesting yielded fructose concentrations of 73 to 79%. However, due to increased tuber yield at later harvest, the total fructose yield is higher with later harvest, and this usually more than compensates for the decrease in fructose concentration (Fleming and GrootWassink, 1979). The manipulation of the duration of the growing season will therefore depend on the intended usage of the crop. Selected data for a range of geographical locations is given in Table 10.10.

10.14.5 Weeds

The rapid growth and tall size of Jerusalem artichoke, with a leaf canopy that shades the ground, prevent weeds from being a significant problem for production over most of the growing season. However, Jerusalem artichoke needs to establish, and it takes around 2 months for shade from the canopy to cover the ground. Within this time, weeds can potentially be a problem for the crop. Therefore, for optimal growth some form of weed control may be necessary during the establishing phase in fields prone to weed infestation. This can, for instance, take the form of mechanical hoeing or pre- or postemergence chemical control (see Section 12.3.1).

After the leaf canopy has established, Jerusalem artichoke outcompetes practically all plants (Kosaric et al., 1984; Schittenhelm, 1996). Yield losses due to weeds are therefore lower than for most other crops. Storage organ yield losses attributed to weed competition under irrigation, for instance, averaged 8% in Jerusalem artichoke over 3 years, compared to 70 and 47% in sugar beet and chicory, respectively (Schittenhelm, 1999). These results were obtained in field experiments in Germany that compared the agronomic performance of the three crops, in fields with complete weed control and no weed control. Significant tuber yield reductions only occurred in one of the 3 years for Jerusalem artichoke, when particularly high weed levels were recorded. The predominant weeds in the fields were field pansy (*Viola arvensis* Murr.), annual bluegrass (*Poa annua* L.), common groundsel (*Senecio vulgaris* L.), low cudweed (*Gnaphilium uliginosum* L.), and small-flower galinsoga (*Galinsoga parviflora* Cav.) (Schittenhelm, 1999). Other common early-season weeds described in Jerusalem artichoke fields include quack or couch grass (*Elytrigia repens* (L.) Nevski = *Agropyron repens*) (Pilnik and Vervelde, 1976).

Due to its ability to outcompete weeds, Jerusalem artichoke was once advocated as a form of weed control in soils given no other form of cultivation. Two years of Jerusalem artichoke cultivation, for example, appeared to clear soil of quack grass (Shoemaker, 1927). However, Jerusalem artichoke is more commonly known as a weed itself, especially in cereals in the U.S. The tubers are difficult to harvest completely and volunteers result. If Jerusalem artichoke is cultivated on the same piece of ground for a number of years, volunteer plants developing among newly planted tubers pose little problem. If the following crop in a rotation is maize/corn, Jerusalem artichoke can become a significant weed problem. Chemical, mechanical, and control approaches are used to control Jerusalem artichoke as a weed (see Section 12.3.2).

10.14.6 Growth Regulators

Endogenous plant growth regulators are thought to play a role in the allocation of dry matter within Jerusalem artichoke plants. For example, the balance between abscisic acid and gibberellin, under the influence of day length, has been proposed to influence tuberization (Denoroy, 1996), with elevated gibberellins acting to inhibit tuberization. However, the assumptions that must be made when extracting phytohormones from plant tissue and potential pharmacological effects of exogenously applied treatments make drawing conclusions as to their endogenous roles tenuous at best. Resource allocation within the plant, however, has been manipulated by the application of exogenous growth regulators or influencing endogenous growth regulators. For example, the treatment of plants with growth inhibitors, such as triazoles, which inhibit gibberellic acid synthesis, decreases stem length, increases tuber number, and increases the sugar content of tubers (Denoroy, 1996).

TABLE 10.10
Selected Yield Data for Jerusalem Artichokes and Products Derived Therefrom for a Cross Section of Geographical Locations

Yield Indices	Latitude	Location	Reference
Total Biomass (t DM·ha^{-1})[a]			
20–30	—	Europe	Barloy and Fernandez, 1991
23	37°34'	Korea (Seoul)	Lyu and Song, 1986
Tubers: Fresh Weight (t·ha^{-1})			
13–62	55°40'	Denmark (Copenhagen)	Klug-Anderson, 1992; Zubr, 1991
54	52°22'	Germany (Güterfelde)	Honermeier et al., 1996
42–46	51°58'	Netherlands (Wageningen)	Pilnik and Vervelde, 1976; Spitters et al., 1969
40	48°13'	Austria (Seibersdorf)	Soja and Liebhard, 1984
66	48°5'	France (Rennes)	Gabini, 1988
40–126	46°28'	Ukraine (Odessa)	Varlamova and Prikhodko, 1996
45–56	46°12'	Washington (Prosser)	Hang and Gilliland, 1982
47–70	45°15'	Serbia and Montenegro (Novi Sad)	Pejin et al., 1993
6.4–46	45°6'	Canada (Morden)	Stauffer et al., 1975
4.4–77	45°6'	Canada (Morden)	Chubey and Dorrell, 1974a, 1982; Dorrell and Chubey, 1977; Kiehn and Chubey, 1985, 1993
90	43°36'	France (Montpellier)	Chabbert et al., 1985a
50–60	42°59'	Italy (Avezzano)	Gabini and Corronca, 1991
53–58	41°54'	Italy (Rome)	Mimiola, 1988
46–70	41°40'	Spain (Soria)	Fernández and Curt, 2005; Fernandez et al., 1988
41–80	41°8'	Italy (Bari)	De Mastro, 1988
74	40°30'	Spain (Madrid)	Conde et al., 1988
36	37°34'	Korea, Seoul	Lim and Lee, 1983
Tubers: Dry Weight (t·ha^{-1})			
7–12	57°15'	Denmark (Frederiksberg)	Zubr and Pedersen, 1993
6–8	55°40'	Denmark (Copenhagen)	Zubr, 1993
10	52°22'	Germany (Güterfelde)	Honermeier et al., 1996
4–15	51°58'	Netherlands (Wageningen)	Meijer and Mathijssen, 1991; Pilnik and Vervelde, 1976; Spitters, 1987; Spitters et al., 1988
4–11	48°13'	Austria (Seibersdorf)	Soja and Liebhard, 1984; Soja et al., 1993
11–12	45°15'	Serbia and Montenegro (Novi Sad)	Pejin et al., 1993
2–13	45°6'	Canada (Morden)	Kiehn and Chubey, 1993
11	41°40'	Spain (Soria)	Fernandez et al., 1988
10–17	41°8'	Italy (Bari)	De Mastro, 1991; Losavio et al., 1996
Tops: Dry Weight (t·ha^{-1})			
4–9	55°40'	Denmark (Copenhagen)	Zubr, 1993
5–30	55°27'	Scotland (Ayr)	Hay and Offer, 1992

14	47°19'	Korea (Seoul)	Lim and Lee, 1983

TABLE 10.10 (CONTINUED)
Selected Yield Data for Jerusalem Artichokes and Products Derived Therefrom for a Cross Section of Geographical Locations

Yield Indices	Latitude	Location	Reference
4.9	46°52'	North Dakota (Fargo)	Seiler, 1993
16	46°12'	Washington (Prosser)	Hang and Gilliland, 1982
4–24	45°15'	Serbia and Montenegro (Novi Sad)	Pejin et al., 1993
8–15	41°54'	Italy (Rome)	D'Egido et al., 1998
6–14	41°40'	Spain (Soria)	Fernández and Curt, 2005
Inulin (t·ha^{-1})			
10–13 (tubers)	46°28'	Ukraine (Odessa)	Varlamova and Prikhodko, 1996
13.7(tubers)	46°4'	Italy (Udine)	Baldini et al., 2003
6.8 (tops)	41°54'	Italy (Rome)	D'Egido et al., 1998
Total Sugar (t·ha^{-1})			
9	52°16'	Germany (Braunschweig)	Schittenhelm, 1996
8	48°13'	Austria (Seibersdorf)	Soja and Liebhard, 1984
6–9	45°6'	Canada (Morden)	Stauffer et al., 1975
3–9	43°36'	France (Montpellier)	Chabbert et al., 1985a
7–10	42°59'	Italy (Avezzano)	Gabini and Corronca, 1991
4.5–9.8	41°54'	Italy (Rome)	Caserta and Cervigni, 1991
8–15	41°8'	Italy (Bari)	De Mastro, 1991
Fructose (t·ha^{-1})			
13.3	46°4'	Italy, Udine	Baldini et al., 2003
Fructose/Glucose Ratio			
5.3–2.45:1 (tubers)	45°37'	France (Montpellier)	Ben Chekroun et al., 1996
5.7–1	45°6'	Canada (Morden)	Chubey and Dorrell, 1974a
5.6:1 (tops)	41°54'	Italy (Rome)	D'Egido et al., 1998
Ethanol (l·ha^{-1})			
3,060 (tubers)	55°40	Denmark (Copenhagen)	Zubr, 1988
3,970–7,448 (tubers)	52°16'	Germany (Braunschweig)	Schittenhelm, 1987
5000 (tubers)	48°13'	Austria (Seibersdorf)	Soja and Liebhard, 1984
2,500–7,500 (tubers)	43°36'	France (Montpellier)	Chabbert et al., 1983; Guiraud et al., 1982
3,840–5,850 (tubers)	~48°	Germany (southwest)	Kahnt and Leible, 1985
3,900–4,500 (tubers)	42°59'	Canada (London)	Duvnjak et al., 1981
11,000 (tubers)	43°43'	Italy (Pisa)	Ercoli et al., 1992
5,600 (tubers)	38°32'	California (Davis)	Williams and Ziobro, 1982
11,230 (tops)	–43°32'	New Zealand (Christchurch)	Judd, 2003
1,920–4,580 (tops + tubers)	45°6'	Canada (Morden)	Stauffer et al., 1975
Protein			
From leaves: 20–24% of leaf DM	44°4'	U.S. (Waseca, MN)	Rawate and Hill, 1985
From yeast grown on extract: 2 t·ha^{-1}	43°36'	France (Montpellier)	Apaire et al., 1983
Gross Energy (GJ·ha^{-1})			
140–280	55°27'	Scotland (Ayr)	Hay and Offer, 1992

[a] DM = dry mass.

Growth retardants have been applied to crops to test whether artificially reducing top growth leads to increased tuber yields. In the Netherlands, retardants were applied to the cultivars 'Précoce Commun' and 'Eigen Nabouw' with disappointing results. The compound B-9 or SADH (succinic acid 2,2-dimethylhydrazide) was applied on two occasions at the rate of 0.6 kg·ha^{-1}. Its retardant effect was only of short duration, and it did not affect the ultimate height of plants or the amount of foliage produced. Hadacine (N-formylhydroxy-aminoacetic acid) was applied on three different dates at a rate of 1.5 kg·ha^{-1}. It had little effect on growth, but caused some foliage damage and slightly reduced tuber yield (Pilnik and Vervelde, 1976).

Some herbicides have also been applied to the foliage of mature Jerusalem artichoke, to reduce vegetative growth with the aim of encouraging tuber filling and thereby increasing tuber yields. This causes biochemical changes in the tubers, but it is unclear whether yields are beneficially affected. Spraying Jerusalem artichoke foliage with 2,4-D in September, for example, increased water uptake and reduced sugar content in the tubers (Conti, 1957). Maleic hydrazide also increased water uptake, while accelerating fructose conversion to glucose during tuber storage (Kosaric et al., 1984).

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11 Pollinators, Pests, and Diseases

A range of organisms (e.g., microorganisms, invertebrates, and vertebrates) interact with Jerusalem artichoke in the wild and in cultivation. Pollination is primarily by insects, and although propagation is usually through tubers, seed set is important in plant breeding programs. Many pest and disease organisms have been reported on Jerusalem artichoke. Relative to other crops, Jerusalem artichoke has few serious pest and disease problems. However, high yield losses can occur, especially when fungal or bacterial infestations affect the tubers.

11.1 INSECT POLLINATORS

Pollination of *Helianthus* species is predominantly by honeybees and bumblebees (Cockerell, 1914), although other insects may be active. *Helianthus* are "all-day flowers," presenting a continuous pollen and nectar resource for bees and other insects. Jerusalem artichoke, like nearly all *Helianthus* species, is largely self-incompatible, and as a consequence, cross-pollination is essential for the production of viable seed, with self-pollination being a rare event.

Hurd et al. (1980) conducted surveys and a literature search to compile a list of bees known to visit species of *Helianthus*, including *H. tuberosus* (Table 11.1). Male bees visiting *Helianthus* get covered with pollen and may be as effective at pollination as females (Cockerell, 1914); therefore, visits of both male and female bees were included in the list. Bee species in six families visited Jerusalem artichoke flowers, including bumblebees (Apidae), miner bees (Andrenidae), sweat bees (Halictidae), and leafcutting bees (Megachilidae), although the European honeybee (*Apis mellifera* L.) was not a recorded visitor (Hurd et al., 1980; Hilty, 2005). Honeybees also rarely visit certain varieties of cultivated sunflowers, although they are attractive to bumblebees. Hurd et al. (1980) speculated that this difference might be due to variations in corolla tube length, making nectar inaccessible to honeybees. Wasps, flies, beetles, and butterflies have also been reported on Jerusalem artichoke flowers; some of these may play a minor role in pollination.

In sunflowers (*Helianthus annuus*) the seed is the article of commerce and adequate pollination is essential. Therefore, much of the pollination literature has focused primarily upon cultivated sunflowers (Hurd et al., 1980; McGregor, 1976). Although similar in appearance and growth habit to sunflower, Jerusalem artichoke is different in a number of important respects. Sunflowers are grown as annuals and are propagated by seed, whereas Jerusalem artichokes are perennial and usually propagated from tubers or tuber pieces. In contrast to sunflower, the seeds of Jerusalem artichoke are not edible and are not used as a source of oil or for any other commercial application. Jerusalem artichoke does not produce much seed, and may not produce any in northerly latitudes. Therefore, insect pollination is crucial in sunflowers, but of less importance in the cultivation of Jerusalem artichoke. Nevertheless, insect cross-pollination is vital for the production of seed in plant breeding programs, while viable seed is an important factor in the dispersal of wild *Helianthus tuberosus*.

11.2 INSECT PESTS

Helianthus is native to North America, where many insects have coevolved with the genus. In North America, over 150 phytophagous insects have been reported on the sunflower (Hilgendorf and Goeden, 1981; Rajamokan, 1976; Rogers, 1988), while over 240 insect species have been recorded on sunflower in Central and Eastern Europe (Maric et al., 1988). With this exceptionally wide cross

TABLE 11.1
Bees Recorded Visiting Jerusalem Artichoke Flowers

Family Name	Species Name
Andrenidae	*Andrena accepta*
	Andrena aliceae
	Andrena chromotricha
	Andrena helianthi
	Andrena simplex
	Pseudopanurgas rugosus
	Pterosarus innuptus
	Pterosarus labrosiformis labrosiformis
	Pterosarus labrosus
	Pterosarus piercei piercei
	Pterosarus solidaginis
Anthoporidae	*Epeolus autumnalis*
	Svastra oblique
Apidae	*Bombus griseocollis*
	Bombus nevadensis
	Bombus pennsylvanicus pennsylvanicus
	Bombus vagans vagans
	Triepeolus concavus
	Triepeolus lunatus
Colletidae	*Colletes compactus*
Halictidae	*Augochlorella striata*
	Dufourea marginatus
	Dialictus imitatus
	Dialictus pilosus pilosus
	Dialictus zephyrus
	Evylaeus pectinatus
	Evylaeus pectoralis
	Halictus ligatus
	Lasioglossum coriaceum
	Nomada vincta vincta
Megachilidae	*Megachile albitarsis*
	Megachile brevis
	Megachile inimica
	Megachile latimanus
	Megachile pugnata pugnata
	Megachile boltoniae
	Megachile coloradensis
	Megachile coreopsis
	Megachile rustica
	Megachile trinodis
	Megachile vernoniae

Source: Compiled from lists in Hurd, P.D. et al., *Smithsonian Contributions to Zoology* 310, Smithsonian Institute Press, Washington, DC, 1980.

section of insects, some of which cause substantial damage to the sunflower (Charlet et al., 1997; Schulz, 1978), it is surprising that there are virtually no reports of serious insect pests on Jerusalem artichoke.

Table 11.2 lists the relatively small number of species that have been reported to feed on the crop. However, damage is typically so slight that no pesticides are recommended, much less cleared for use. No data for yield loss related to insects have been reported in the literature. The lack of serious insect pests reflects to some degree significant levels of resistance and tolerance (Rogers and Thompson, 1978). Meanwhile, vigorous growth ensures that aphids and leaf feeders only minimally affect Jerusalem artichoke (Kosaric et al., 1984). The fact that Jerusalem artichokes are not extensively grown in monoculture has contributed to the lack of crossover of insect pests from *H. annuus* and other species.

The following is a brief overview of the biology of several of the more important insect species, based largely on data gathered from infestations of *H. annuus*, that have been reported to feed on *H. tuberosus*.

11.2.1 Sunflower Beetle

The sunflower beetle (*Zygogramma exclamationis* Fab.) is a leaf feeding species that is considered an important pest of cultivated sunflowers in North America, as evidenced by periodic outbreaks necessitating chemical control (Westdal, 1975). The insect also feeds on Jerusalem artichokes, although Kosaric et al. (1984) reported that plants were avoided even when beetle populations were high. The principal damage to sunflower is caused by the adults after they emerge from hibernation in the spring. Feeding on the leaves of young plants causes serious damage and defoliation. Subsequent damage is caused by the larvae feeding at night, producing holes in the leaves. The larval stage, approximately 6 weeks in duration, is followed by the pupal stage, which occurs in the soil and lasts for 10 to 14 days. Adults emerge in the latter part of the growing season and feed on apical leaves prior to overwintering in the soil. In the northern U.S. and Manitoba, there is typically only one generation per year.

The eggs are cigar shaped, yellow to orange in color, 1.5 to 2 mm in length, and found on the stems and abaxial leaf surfaces (Criddle, 1922; Westdal, 1975). The larvae are a dull yellow-green color, humpbacked, and about 10 mm in length at maturity. Pupae are yellowish and found in the soil. The adults are 6 to 8 mm long by 4 to 5 mm wide with a dark brown head and thorax. Elytra display alternating light and dark brown stripes, with the lateral dark stripe like an exclamation point.

Predators and parasites often provide sufficient control. However, in some years chemical control is required, typically when the population exceeds one beetle for every two plants (Westdal, 1975). Pesticide applications should be made early in the season when the adults are emerging and, if needed, after the eggs have hatched.

11.2.2 Sunflower Budworm

The sunflower budworm or bud moth (*Suleima helianthana* Riley), considered a minor pest of the sunflower in which damage is sporadic, also feeds on the Jerusalem artichoke (Pedraza-Martinez, 1990; Rogers, 1979). In North America, the insect is found from Maryland to California and south to Mexico. Damage is caused by larval feeding, typically on the apical bud or axils of upper leaves, producing distorted, misshapen plants. Young larvae act as leaf miners or enter a leaf rib, while older larvae enter and feed on buds, leaf axils, stems, and bracts.

Eggs are ovoid (0.6 to 0.4 mm in diameter) and translucent-white with a wrinkled appearance (Ehart, 1974). They are normally laid singly on the growing point, apical leaves (more so on the abaxial side), and at the base of flower heads. Larvae are smooth, have cream-colored bodies with a yellow-brown head, and are about 15 mm in length. Larvae progress through five instars, each requiring 4 to 6 days. Pupae are oblong (1.3 to 5 mm or longer) and typically found in the

TABLE 11.2
Insects Known to Feed on Jerusalem Artichoke

Common Name	Latin Binomial
Aphids	[Homoptera: Aphididae]
	Aphis debilicornus Gillette & Palmer
	Aphis fabae Scopoli
	Aphis gossypii Glover
	Aphis helianthi Monell
	Aphis ranunculi Kaltenbach
	Macrosiphum euphorbiae Thomas
	Protrama penecaeca Stroyan
	Trama rara Mordvilko
	Trama troglodytes von Heyden
	Uroleucon compositae Theobald
	Uroleucon gobonis Matsumura
	Uroleucon helianthicola Olive
Banded sunflower moth	[Lepidoptera: Tortricidae]
	Cochylis hospes Walsingham
Checkerspot butterflies	[Lepidoptera: Nymphalidae]
	Chlosyne spp.
Cotton leafworm	[Lepidoptera: Noctuidae]
	Spodoptera littoralis Boisduval
Leafworm	[Lepidoptera: Noctuidae]
	Gortyna xanthemes Germar
Cutworm	[Lepidoptera: Noctuidae]
	Agrotis segetum Denis & Schiffermüller
Grasshoppers	[Orthoptera: Locustidae]
	Locusta spp.
Grasshoppers	[Orthoptera: Acrididae]
	Melanoplus spp.
Green looper moth	[Lepidoptera: Noctuidae]
	Chrysodeixis eriosome Doubleday
Flea beetle	[Coleoptera: Chrysomelidae]
	Chaetocnema confinis Crotch
Stem borers	[Lepidoptera: Noctuidae]
	Papaipema spp.
Sunflower beetle	[Coleoptera: Chrysomelidae]
	Zygogramma exclamationis Fab.
Sunflower budworm	[Lepidoptera: Olethreutidae]
	Suleima helianthana Riley
Sunflower maggot	[Diptera: Tephritidae]
	Strauzia longipennis Wied.
Sunflower moth	[Lepidoptera: Pyrlidae]
	Homoeosoma electellum Hulst
Sunflower seed maggot	[Diptera: Tephritidae]
	Neotephritis finalis Loew.
Sunflower seed weevil	[Coleoptera: Curculionidae]
	Smicronyx fulvus LeConte
Sunflower stem weevil	[Coleoptera: Curculionidae]
	Cylindrocopturus adspersus LeConte
Tiger moth	[Lepidoptera: Arctiidae]
	Pyrrharctia isabella J.E. Smith

TABLE 11.2 (CONTINUED)
Insects Known to Feed on Jerusalem Artichoke

Common Name	Latin Binomial
Tortoise beetles	[Coleoptera: Chrysomelidae]
	Cassida spp.
Wireworm	[Coleoptera: Elateridae]
	Agriotes lineatus L.
Weevil	[Coleoptera: Curculionidae]
	Hypera zoilus Fab.

Source: Data compiled from Barker, 1990; Beregovoy and Riemann, 1987; Blackman and Eastop, 2000; CAB International, 2001; Charlet, 1983; Charlet et al., 1992; Criddle, 1922; Foote, 1960; Foote and Blanc, 1963; Gillette and Palmer, 1932; Goeden et al., 1987; Hill, 1987; Hilty, 2005; Laberge and Sackston, 1987; Mordvilko, 1931; Patch, 1938; Rogers, 1979; Rogers et al., 1978; Satterthwait, 1946; Satterthwait and Swain, 1946; Theobald, 1927; Westdal, 1975; Westdal and Barrett, 1960.

stem-feeding tunnels near the entrance hole (Ehart, 1974). Adult moths have gray to brown forewings, marked with two dark bands and a light patch on the back half of the wing tips (Riley, 1881). The head and thorax are pale gray. In North Dakota and Minnesota, two generations are possible within a growing season. While damage may be readily visible in sunflower (e.g., plant deformity and stalk breakage), losses are not sufficient to warrant chemical means of control.

11.2.3 Sunflower Stem Weevil

Stem weevils (*Cylindrocopturus adspersus* LeConte), a significant economic pest of sunflowers in the Great Plains of the U.S., also feed on the Jerusalem artichoke, although feeding activity is substantially lower (Barker, 1990; Charlet, 1983; Charlet et al., 1992). Trichome density, which is significantly higher in *H. tuberosus* than in cultivated lines of *H. annuus*, did not appear to be the reason for the higher level of resistance (Barker, 1990). Though the adults feed on the stem and leaves, the primary damage is due to the larval stage tunneling within the lower stem. Feeding by the first two instars is not substantial, although the last instars destroy the pith and weaken the stem. Under appropriate conditions, the weakened stems lodge, breaking over about 10 cm above the ground.

Adults overwinter in the stalks and root crowns and in the spring deposit eggs under the epidermis at the base of the stem (Rogers and Serda, 1982). The eggs are glossy white but turn pale brown with maturity and have a dark spot at one end. Larvae emerge in 1 to 2 weeks. The fourth instar is creamy brown in color with a brown head. Adults are brown with dark brown and white spots on the elytra. Females are larger (3.5 to 6 mm) than the males (2.8 to 4.5 mm). One generation is produced per year (Charlet, 1987).

In sunflowers, insecticides have been an effective means of control, though the larvae population within the stalk must be quite high (above 80) before a significant effect on yield is realized (Rogers and Jones, 1979). At present, stem weevil does not pose a production problem for Jerusalem artichokes.

11.2.4 Sunflower Maggot

The sunflower maggot (*Strauzia longipennis* Wied.) is considered a minor pest of sunflower even though it is widely distributed in North America, and fields with 100% of the plants infested have been reported (Schulz and Lipp, 1969). The insect also attacks the Jerusalem artichoke (Charlet et al., 1992; Laberge and Sackston, 1987; Westdal and Barrett, 1960). Maggot larvae tunnel within the pith of the stem, where damage ranges from slight to the complete destruction of the pith (Westdal and Barrett, 1960). Even with severe infestation, the plants remain healthy with no visible external symptoms. Internal damage does not have an adverse effect on yield (Westdal and Barrett, 1962).

Sunflower maggots overwinter as pupae in the soil, emerging in the spring to oviposit when the plants are about 30 cm high. The eggs are white, smooth, oval (1.0 to 0.35 mm), and laid singly beneath the epidermis near the apical meristem. Larvae emerge in 7 to 8 days and tunnel into the pith, where they move either acropetally or basipetally. They are pale yellow (9 by 2.5 mm) and proceed through three instars over approximately a 6-week period. A pupa is enclosed within a pale yellow puparium (6 by 2.25 mm) found in the soil. The adult is a showy, yellow fly with wings displaying dark bands of variable pattern. The females are slightly larger than the males (8 vs. 7 mm long).

The insect can be controlled with insecticides applied after oviposition. However, the absence of an economic effect mitigates against their use. There have been no reports of significant damage to Jerusalem artichokes.

11.2.5 Banded Sunflower Moth

The banded sunflower moth (*Cochylis hospes* Wlshm.; also cited as *Phalonia hospes* Wlshm. (Schulz, 1978)) is a relatively minor pest of sunflower that attacks the flower heads and causes seed destruction. However, damage has increased in North Dakota in recent years (Charlet et al., 1995). While the insect is also found on Jerusalem artichoke (Beregovoy and Riemann, 1987), its activity is of no economic consequence. The banded sunflower moth is found from the East Coast of the U.S. to the Dakotas, and south into Kansas, Arkansas, and Texas, as well as in Saskatchewan and Manitoba in Canada (Westdal, 1949).

11.2.6 Sunflower Moth

The sunflower moth (*Homoeosoma electellum* Hulst) is a serious pest of sunflower and has been reported on Jerusalem artichoke (Satterthwait and Swain, 1946). The damage, however, is almost exclusively to the seed head and, as a consequence, of no importance to Jerusalem artichoke production.

11.2.7 Sunflower Seed Maggot

The sunflower seed maggot (*Neotephritis finalis* Loew.) is found in northern Mexico and throughout North America (Foote and Blanc, 1963). While the Jerusalem artichoke can serve as a host (Charlet et al., 1992; Goeden et al., 1987), like the sunflower moth, damage is largely on the seed and other flower parts, and as a consequence, the maggot is not a significant pest of the crop.

11.2.8 Grasshoppers

A variety of grasshoppers (Orthoptera: Locustidae and Acrididae), which are generalists, will feed on Jerusalem artichokes when their populations are sufficiently large. Damage is to the foliage, but is seldom of sufficient magnitude to impact productivity.

11.2.9 Leafworms and Cutworms

Leafworms (Lepidoptera: Noctuidae) are generalist feeders that have been recorded on Jerusalem artichoke leaves, occasionally in large numbers. The most significant species in this respect is *Spodoptera littoralis* Boisduval, which feeds on at least 87 plant species of economic importance in around 40 families. It lays spherical eggs, white yellowish (0.6 mm), on younger leaves. Larvae proceed through six instars, reaching up to 45 mm in length, feeding mainly at night (CAB International, 2001).

Cutworms (Lepidoptera: Noctuidae) are generalists whose large caterpillars (50 mm long) attack plant stems at ground level and tubers in the soil, especially near the soil surface. The cutworm *Agrotis segetum* Denis & Schiff. has been recorded feeding on Jerusalem artichoke (CAB International, 2001).

11.2.10 Aphids

Blackman and Eastop (2000) listed six aphid species from Jerusalem artichoke (compared to 21 species from sunflower): *Macrosiphum euphorbiae* Thomas, *Protrama penecaeca* Stroyan, *Trama troglodytes* von Heyden, *Uroleucon compositae* Theobald, *Uroleucon gobonis* Matsumura, and *Uroleucon helianthicola* Olive. They do not cause serious damage to either the above- or below-ground plant parts.

The potato aphid *M. euphorbiae* has been recorded feeding on a large number of crop plants, including the leaves of Jerusalem artichoke. Its primary or winter host is *Rosa* spp.; it is highly polyphagous on secondary or summer hosts, being found on over 200 plant species in 20 families. *M. euphorbiae* is a medium-sized (1.7 to 3.6 mm), spindle- or pear-shaped aphid, which is usually green in color, although sometimes yellow or pink. It is North American in origin, but is now found worldwide, with a relatively recent spread into Eastern Asia (Blackman and Eastop, 2000).

P. penecaeca is a very large aphid (3.8 to 5.0 mm), dirty grayish white in color, which has been recorded on the roots of *H. tuberosus* in northern India (Blackman and Eastop, 2000; Verma, 1969).

T. troglodytes is a large, plump white aphid found on the roots of Jerusalem artichoke and other *Helianthus* spp.; it is invariably attended by ants. This species occurs in Europe, western Siberia, Central Asia, and Japan (Blackman and Eastop, 2000; Eastop, 1953).

U. compositae is a medium- to large-sized aphid (1.9 to 4.1 mm), broadly spindle shaped and shiny dark red to almost black in color. It colonizes the flower stems and leaf mid-ribs of plants in the family Compositae, including Jerusalem artichoke. It is widely distributed in Africa and on the Indian subcontinent and has also been found in South America (Brazil, Surinam), several Pacific Islands, Taiwan, and Sicily. No sexual forms have been recorded. Taxonomically, it is difficult to separate from the East Asian species *U. gobonis*, and it may represent an anholocyclic race of that species (Blackman and Eastop, 2000; Eastop, 1958).

U. gobonis is similar in size and appearance to *U. compositae*, dark greenish to black in color, and found on flower stems and the underside of leaves of Compositae in the Far East (Korea, Mongolia, China, Japan, and Taiwan). Holocyclic (annual sexual phase) and anholocyclic (entirely parthenogenic) life cycles have been recorded (Blackman and Eastop, 2000; Takahashi, 1923).

U. helianthicola is a large- to medium-sized, broadly spindle-shaped, red to reddish brown aphid that feeds exclusively on the leaves of species of *Helianthus*, including Jerusalem artichoke. *U. helianthicola* is widespread in the U.S. Sexual morphs have not been recorded (Blackman and Eastop, 2000; Olive, 1963).

Two aphid species were listed by Hills (1987) as minor pests *(Aphis fabae* Scopoli and *Aphis gossypii* Glover). A number of other aphid species (e.g., *Aphis debilicornus* Gillette & Palmer, *Aphis helianthi* Monell, *Aphis ranunculi* Kaltenbach, and *Trama rara* Mordvilko) have also been

recorded on Jerusalem artichokes (Gillette and Palmer, 1932; Mordvilko, 1931; Patch, 1938; Rogers and Thompson, 1978; Theobald, 1927). They appear to cause little damage.

11.3 MOLLUSKS, NEMATODES, AND OTHER PESTS

Mollusks of the class Gastropoda (slugs and snails) can inflict severe damage on Jerusalem artichokes. Young plants, in particular, are highly attractive to slugs and can be destroyed. Mulches, for example, of leaves or bark, can be used to help protect young plants from slug damage in the spring and early summer months.

Slugs also attack the tubers in the autumn and those left in the ground during the winter. Tubers tend to be hollowed out by slugs. They may be controlled by setting traps, using aluminum sulfate or other slug pellets, or, in small holdings, picking off manually (Biggs at al., 1993). In areas prone to slug damage, it is advisable to harvest tubers in late autumn and store them under slug-free conditions over winter.

In cultivated sunflowers in Europe, damage from gastropods tends to be minor in drier regions, such as Spain, but can be serious in wetter regions, such as western and central France; for instance, 75% of the French sunflower crop was treated with molluskicide in 1997. The main damage arises in the spring, soon after seedlings emerge, when plants can be defoliated or completely severed. Humid conditions and low temperatures, which slow plant development and extend the period of vulnerability, are associated with higher crop losses from gastropods (Hommay, 2002). Mollusk damage to Jerusalem artichoke is therefore also likely to be most severe under these conditions.

Giant land snails (Achatinidae) have spread from their native Africa to many parts of the world, where they have caused significant economic and ecological impacts. During the 1980s, they started to become crop pests in the West Indies. The giant land snail species *Limicolaria aurora* Jay, for instance, has caused serious damage to crops, including Jerusalem artichoke, in Martinique (Mead and Paley, 1992; Raut and Barker, 2002).

Results from field experiments suggest that Jerusalem artichoke tubers can be left in nematode-infested soils, without yield being adversely affected. The tubers appear to be resistant to the nematodes that inflict damage on other root vegetables. Cultivation of nematode-neutral Jerusalem artichoke caused a 45% reduction in the potato-eating nematode population in infested fields in one study (Goffart, 1955). Therefore, Jerusalem artichoke is useful as a rotational substitute for sugar beet or potato in nematode-infested fields (Conti, 1953; Kosaric et al., 1984).

Jerusalem artichoke seeds are consumed by a range of songbirds and game birds (Hilty, 2005). Birds can be a particular problem in crops grown for seed as part of plant breeding programs (Le Cochec and de Barreda, 1990). Deer, rabbit, and other browsing herbivores eat seedlings, leaves, and flowers of Jerusalem artichoke. This may be a problem in fields next to woodland or other uncultivated areas populated by mammals. In gardens and small holdings in Europe, Jerusalem artichoke is said to be rarely troubled by browsing deer or rabbits (Thomas, 1990), although deer browse aerial plant parts in larger plantings near woodland. In an investigation of fallow deer (*Cervus dama dama* L.) feeding preferences on Jerusalem artichoke in a research preserve, a connection was found between feeding preference and the mineral content of different varieties, although there was no evidence that Jerusalem artichoke is used as a food source for specifically acquiring minerals. Total phenol content of different Jerusalem artichoke varieties also influenced feeding preference (Gleich et al., 1998). Occasionally, the stems of wild Jerusalem artichoke are used by muskrats and beavers for their dens and dams, respectively, in the U.S. (Hilty, 2005).

11.4 FUNGAL, BACTERIAL, AND VIRAL DISEASES

A wide range of microorganisms (fungi, bacteria, viruses, and mycoplasms) mediate substantial losses to crop plants during both the production phase and postharvest period. While Jerusalem

TABLE 11.3
Diseases of Jerusalem Artichoke

Organism	Common Name	Plant Part Affected	
		Tubers	Tops
Botrytis cinerea Pers.	Gray mold rot	+	
Coleosporium helianthi (Schwein) Arth.	Yellow rust		+
Erwinia carotovora spp. *carotovora* (Jones) Bergey et al.	Bacterial soft rot	+	
Erysiphe cichoracearum DC.	Powdery mildew		+
Fusarium acuminatum Ell. & Everh.		+	
Fusarium oxysporum Schlecht.	Fusarium wilt rot	+	+
Fusarium pallidoroseum (Cooke) Sacc.	Fusarium rot	+	
Fusarium roseum (Lk.) Snyd. & Hans.	Fusarium rot	+	
Fusarium roseum var. *arthrosporioides* (Sherb.) Messiaen, Cassini	Fusarium rot	+	
Fusarium solani var. *coeraleum* (Sacc.) Booth		+	
Fusarium roseum var. *culmorum* (Swabe) S.N. & M.	Fusarium rot	+	
Penicillium cyclopium Westl.	Blue mold rot	+	
Penicillium palitaus Westl.	Blue mold rot	+	
Phoma exigua Desm. var. *exigua* Prill. & Delacre		+	
Plasmopara helianthi Novot.	Downy mildew		+
Pseudomonas fluorescens Migula		+	
Pseudomonas marginalis (Brown) Stevens		+	
Pseudomonas syringae pv. *tagetis* (Hellmers) Young, Dye and Wilkie	Apical chlorosis		+
Puccinia helianthi Schwein	Rust		+
Rhizoctonia solani Kühn	Rhizoctonia rot	+	
Rhizopus stolonifer (Ehrenb.: Fr.) Vuill.	Rhizopus rot	+	
Rhizopus tritici Saito		+	
Sclerotinia minor Jagger	Sclerotinia wilt		+
	Watery soft rot	+	
Sclerotinia sclerotiorum (Lib.) de Bary	Sclerotinia wilt		+
	Watery soft rot	+	
Sclerotium rolfsii Sacc.	Southern wilt/rot	+	+

Source: Data compiled from Baillarge, 1942; Barloy, 1988; Cassells et al., 1988; Cunningham, 1972; Dounine et al., 1935; Gaudineau and Lafon, 1958; Gregoire, 1984; Johnson, 1931; Kozhevnikova and Onufriev, 1960; Laberge and Sackston, 1986; Laberge and Sackston, 1987; Lhoutellier, 1984; McCarter and Kays, 1984; Shah and Zakaullah, 1989; Shane and Baumer, 1984; Ravault, 1952; Snowdon, 1992; Thompson, 1928.

artichoke is widely touted as relatively disease-free, a number of microorganisms (Table 11.3) represent significant production or storage problems. Many of the foliar diseases affect a wide range of species in the *Helianthus* genus, including cultivated sunflowers (Gulya et al., 1997; Zimmer and Hoes, 1978). There appears to be no disease that can be said to be specific to Jerusalem artichoke. Fungal pathogens are especially a problem in cool and moist climatic conditions, for example, in Northern Europe (Cassells et al., 1988). However, in the U.S., no fungicides are registered for use on the crop (Cosgrove et al., 2000). Pest and disease problems may increase for crops grown as perennials in the same field.

At present, the number of diseases that represent significant problems for the Jerusalem artichoke are only a fraction of that for sunflower (Gulya and Masirevic, 1991). This is no doubt due in part to the fact that the Jerusalem artichoke is currently a very minor crop in North America. As the acreage in production increases, in all probability, the litany of pathogens causing significant production or postharvest problems will increase. The following critiques some of the more serious diseases of Jerusalem artichoke.

11.4.1 Rust

Puccinia helianthi Schw., a basidiomycete, causes serious losses in Jerusalem artichoke (McCarter and Kays, 1984) and sunflower (Zimmer and Zimmerman, 1972). The organism is found only on the genus *Helianthus*, though more than 35 species are affected (Arthur, 1905; Arthur and Cummins, 1962; Hennessy and Sackston, 1972; Zimmer and Rehder, 1976). Jerusalem artichoke genotypes vary in their level of susceptibility, and lines with high levels of resistance have been used to incorporate resistance genes into the sunflower through interspecific hybridization (Pustoviot, 1960; Pustoviot et al., 1976).

P. helianthi has three stages (telial, pucnial, and uredial), which occur on a single host. Both the uredial stage in the summer and the telial stage, which overwinters, are clearly visible. The uredial stage is seen as small, circular, powdery, orange to black pustules, most notably on the leaves, but also found on virtually all aerial vegetative surfaces. The uredial stage is the most damaging and begins on the older leaves at the base of the plant and progresses upward during the season. The disease can be lethal to highly susceptible genotypes. The severity of the infestation varies with the level of resistance of the host, age of the plant, and environmental conditions. Though always present, some years are much more conducive for development of the organism (McCarter and Kays, 1984).

In the State of Georgia, the first uredia were detected when the plants were about 1 m tall and developed rapidly thereafter, with numerous pustules appearing on the foliage (McCarter and Kays, 1984). The organism was especially prevalent on the abaxial surfaces of the leaves but can also be found on the stems. If the young foliage becomes infected, further development can be inhibited. Symptoms start on the older leaves at the base of the plant and progress upward toward the growing point. The pustules can became so abundant that the foliage appears blighted. With severe rust infections, most of the foliage is killed by the end of the growing season. Toward late fall the uredial stage is converted to the black telial stage.

There are three primary means of controlling *P. helianthi,* although only one method is currently a viable commercial option:

- Sanitation/rotation. In more northern regions, teliospores are the typical overwintering structure, while in the south, urediospores can survive. In warm areas, the organism may also overwinter as mycelia on wild *Helianthus* species, providing a ready inoculum when the Jerusalem artichokes emerge in the spring. Thus, elimination of native species in the vicinity helps to reduce the risk of a severe infestation. Crop rotation is also recommended because the telial spores are present on residual plant material from the previous season.
- Chemical control. Under field test conditions, rust could be controlled using mancozeb (2.24 $kg \cdot ha^{-1}$) sprays applied to runoff at 7- to 10-day intervals starting when the plants were about 40 cm high and continuing until 2 weeks before harvest (McCarter and Kays, 1984). Rust control resulted in a 29% (13 $t \cdot ha^{-1}$) increase in tuber yield. Unfortunately, mancozeb is not approved for use on Jerusalem artichokes in the U.S., nor are 8 to 11 or more spray applications realistic from an economic standpoint. The results do, however, underscore the need for the incorporation of resistance into commercial cultivars.
- Resistance. Control of the organism would be best facilitated through the introduction of resistant cultivars. Two genes for resistance (R_1 and R_2) have been identified and incorporated into sunflower (Sackston, 1962). Unfortunately, there are few breeding programs for Jerusalem artichokes, and as a consequence, rust-resistant commercial cultivars are not currently available.

11.4.2 Southern Wilt/Blight/Collar Rot

Sclerotium rolfsii Sacc. can result in serious losses, especially when grown on land previously planted with Jerusalem artichokes (McCarter and Kays, 1984) or other susceptible crops. The organism has a host range of over 500 species encompassing both monocots and dicots (Aycock, 1966; Farr et al., 1989). Susceptible crops include alfalfa, beans, corn, pea, potato, okra, eggplant, tomato, pepper, sugar beet, and numerous other vegetable crops.

The disease is prevalent in the southern parts of the northern temperate zone and in subtropical and tropical regions of the world. In the U.S., southern wilt is found widely in the southeastern states (e.g., Georgia, Florida, Mississippi, North Carolina, South Carolina) (Farr et al., 1989) and represents a primary obstacle to commercial production in these areas (McCarter and Kays, 1984). The disease has also been reported on Jerusalem artichokes in Ghana and Malaysia (Thompson, 1928).

S. rolfsii is a soilborne fungus that overwinters as light tan to dark brown spherical sclerotia, 0.5 to 2 mm in diameter. Warm temperatures (27 to 30°C) are optimum for mycelial growth and sclerotial formation (Punji, 1985). Germination of the sclerotia is inhibited at pH values above 7 and low temperatures, though the organism can grow in a temperature range of 8 to 40°C. The organism produces a water-soaked, round to elliptical lesion at the base of the stem, which becomes brown with age. The lesion eventually girdles the stem, causing extensive rotting of the pith tissue, which subsequently mediates wilting of the aerial portion of the plant. White mycelium, under appropriate moisture conditions, may cover the stem lesions and the soil surface at the base of the plant along with numerous white to brown sclerotia.

Small, residual tubers in the soil that are not collected by mechanical or hand harvest appear to serve as a food base for the organism during the subsequent cropping season (McCarter and Kays, 1984). In addition, mechanical harvesting appears to spread the sclerotia in the field, increasing the distribution of the disease.

Control in the field centers on cultural practices, although chemical means have been tested. Cultural manipulations to facilitate control, such as land selection (where *S. rolfsii* susceptible species have not been grown) and crop rotation, have met with only marginal success due to the extensive host range, the large quantities of sclerotia produced, and their ability to persist for years in the soil (Punji, 1985). Rotation with nonsusceptible crops (e.g., cereals) and control of weeds that are susceptible are recommended for fields with a history of southern wilt. Soil fumigation with methyl bromide greatly reduced Jerusalem artichoke plant losses over untreated areas (15 vs. 60% of the plants) and increased yield (2.5 times) (McCarter and Kays, 1984). Other soil treatments, metam-sodium and pentachloronitrobenzene (PCN), were substantially less effective. However, due to the differential between the cost for soil chemical treatment and raw product value, chemical control does not appear to be a commercially viable option. At present, the best approach for circumventing the disease is to grow Jerusalem artichokes outside of climatic regions in which the organism thrives.

S. rolfsii also causes storage rots in tubers that appear sound at harvest (Thompson, 1928). The fungus produces a silky white mold on which numerous spherical sclerotia appear (Snowdon, 1992). Postharvest losses can be controlled by low-temperature storage or, in the absence of refrigeration, through the use of prestorage fungicide dips (Thompson, 1928).

11.4.3 Powdery Mildew

An obligate ascomycetes, *Erysiphe cichoracearum* DC., powdery mildew, can be moderately severe on some Jerusalem artichoke lines in the southern U.S., while others remain essentially disease-free (McCarter, 1993). *E. cichoracearum* infects a wide range of species, especially so in the Compositae family. It is found worldwide and is especially critical in the hot, humid tropics and subtropics. Damage in temperate regions tends to be limited. The disease appears as white to gray areas on the leaves and occasionally on the stems, which is caused by superficial mycelium. With

time, the mycelium spreads such that the infected areas enlarge and coalesce, covering the entire leaf. Typically, first symptoms are on the upper surfaces of older leaves, and the infected leaves eventually turn yellow and abscise. The white surface coloration is due to the conidia, which give a powdery appearance. Conidia are born in long chains that are elliptical to barrel shaped.

Powdery mildew form cleistothecia, the overwintering structures of the organism. Cleistothecia are 90 to 135 μm in diameter and have numerous unbranched appendages. Development of cleistothecia is stimulated by cool weather, and they are seen as black, pinhead-sized dots scattered over the surface of the leaves. Cleistothecia are found on infested stubble, which acts as an inoculum, providing conidia or ascospores that infect new plants the following season.

Control is possible through the development of resistant cultivars, the use of foliar fungicides, and cultural practices. There is considerable genetic variation in the Jerusalem artichoke gene pool for resistance. For example, McCarter (1993) found 3 of 36 lines displaying high levels of resistance. However, in temperate regions, powdery mildew tends to occur only late in the season, if present, and does not result in significant losses (McCarter and Kays, 1984). As a consequence, little emphasis has been placed on breeding for resistance. Turning the stubble under in the fall helps decomposition and represses the amount of inoculum.

11.4.4 Sclerotinia Wilt/Rot

Sclerotinia sclerotiorum (Lib.) de Bary, an ascomycete, is a widespread pathogen that infects the stems, roots, and tubers of Jerusalem artichoke (Bisby, 1924). It is prevalent in temperate, subtropical, and tropical regions of the world. The organism attacks a wide range of hosts (i.e., over 360 species, including rape, lettuce, potato, tobacco, and many legumes) (Farr et al., 1989; Prudy, 1979) and, based upon losses, is considered the most important sunflower disease in North America (Gulya, 1996). Infestation causes early wilt, stalk rot, and degradation of the tubers (sclerotinia wilt, white mold, or cottony soft rot). *S. sclerotiorum* is the most common fungal pathogen and the most significant disease of Jerusalem artichoke globally in economic terms. Nevertheless, epidemics are rare, with single plants or small patches affected.

S. minor Jagger also causes similar symptoms of root and tuber rot and wilt. Both species produce sclerotia as the overwintering stage and are distinguished by the size and shape of the sclerotia (i.e., *S. minor* — uniformly round, 0.5 to 2 mm in diameter; *S. sclerotiorum* — irregular in shape, 1 cm or more in diameter). There is no apparent physiological specialization, so isolates from one crop can infect another, although the degree of virulence varies. For example, isolates of *S. sclerotiorum* from hop (*Humulus lupulus* L.) and swede (*Brassica napus* L.) and *S. minor* were lethal to Jerusalem artichoke (Keay, 1939).

Sclerotinia wilt is due to the infection of the roots by mycelia derived from germinating sclerotia in the soil. Germination is stimulated by root exudates with the mycelium extending 5 to 30 mm outward. Infection is dependent upon the actively growing roots coming in contact with the mycelia and can occur anytime during the plant's development. Light brown, water-soaked lesions develop at the root–stem interface at the soil surface. Soil moisture and temperature (20 to 25°C) conditions that are conducive to plant growth are also favorable for germination and infection. The organism can spread to adjacent plants, a condition that appears to be favored by high plant densities. Under humid conditions, white mycelium develops and eventually sclerotia. Sclerotia begin as soft, white masses but become hard and dark brown to black.

In continuous culture, the inoculum progressively builds up in the soil, leading to greater losses each year (e.g., 1% loss in year 1, 19% in year 2, and 22% in year 3 for the cultivar 'Nahodka') (Cassells and Walsh, 1995). Control, therefore, is best mediated through rotation with nonhost crops. Since the sclerotia can survive in the soil for up to 7 years, a 3- to 5-year rotation is recommended. Jerusalem artichoke can be rotated with small grains or maize, but not dry edible beans, sunflowers, safflower, mustard, or soybeans — all crops susceptible to sclerotinia wilt. Effective control of weeds, which may act as hosts, and volunteer Jerusalem artichokes is also

essential. Breeding for resistance is complicated by the general difficulty in breeding Jerusalem artichokes and the fact that there is a general lack of resistance throughout all species affected by the organism. However, in a relatively small collection of Jerusalem artichoke germplasm (34 genotypes), several lines displayed field resistance (Cassells and Walsh, 1995). The potential for increasing the level of resistance via somaclonal variation and initial screening under laboratory conditions has been reported. Nodes were cultured on a modified Murashige and Skoog medium and regenerated on a second medium. Adventitious shoots 1 cm in height were excised and placed back on the nodal culture medium for further development. Somaclones selected for their ability to grow on a calcium-free medium correlated with resistance to artificial inoculation and field resistance to sclerotinia wilt. Whether the resistance holds up through subsequent generations remains to be established.

11.4.5 Apical Chlorosis

A bacterial foliage disease caused by *Pseudomonas syringae* (Ps) pv. *tagetis* (Hellmers) Young, Dye, and Wilkie results in significant Jerusalem artichoke losses (Shane and Baumer, 1984), primarily in the northern U.S. and Canada. In Minnesota in 1983, approximately 15% of 25,000 ha of Jerusalem artichokes was affected. Infected plants display extreme apical chlorosis, small dark necrotic leaf spots (1 to 2 mm in diameter) with faint chlorotic halos, and large chlorotic spots, sometimes with small gray necrotic centers. The effect of the disease on stand establishment is pronounced. Sprouts emerging from the soil can be nearly or completely chlorotic and often do not survive. Stand reductions in Minnesota were as high as 50%, with some fields plowed under. In Canada, however, mortality was limited (Laberge and Sackston, 1986). Apical chlorosis can be observed at all stages of plant development, and the leaves are uniformly chlorotic, including the veins. Some plants recover, with subsequent leaves being normal in coloration, though the original chlorotic leaves remain yellow.

In addition to Jerusalem artichoke, the disease has been reported on marigold (*Tagetis* spp.), sunflower (*Helianthus annuus* L.), ragweed (*Ambrosia* spp.), dandelion (*Taraxacum officinale* Weber), and compass plant (*Silphium prefoliatum* L.). The bacteria are soil- and tuber-borne and are further disseminated via rain and wind. When not already present in the tubers, the organism enters the plant through stomates and surface wounds. High temperatures (e.g., 28 to 30°C) and relative humidity favor the development of the pathogen (Stapp, 1961).

When conditions are favorable, control of the disease is difficult in that ragweed and dandelion, which are widespread weeds, provide inoculum. A critical production factor is to guard against the use of infected tubers. Since seed tubers typically display no apparent symptoms (Laberge and Sackston, 1986), inspections of source fields prior to flowering should be made. Stored tubers (5°C for 6 months) displayed a substantially greater incidence of chlorosis upon sprouting than tubers sprouted prior to storage (i.e., 83 vs. 10%) (Laberge and Sackston, 1986), indicating that storage may predispose the propagules for the successful development of the pathogen. Interestingly, tubers collected from chlorotic plants do not always produce infected plants. The timing of infection relative to tuberization or other factors may therefore be critical.

11.4.6 Tuber Rots

Harvested plant parts undergo substantial losses due to the stress imposed by invading microorganisms. While production pathogens are widely focused upon, 50% or more of the final retail value of most agricultural plant products is accrued after harvest (Kays, 1997). As a consequence, storage and marketing losses in quality and quantity are extremely important. Losses of Jerusalem artichoke tubers due to storage pathogens vary widely in magnitude and are frequently significant (Barloy, 1988; Cassells et al., 1988; Dounine et al., 1935; Johnson, 1931; McCarter and Kays, 1984;

Snowdon, 1992). Approximately 20 organisms have been shown to cause tuber rots (Table 11.3), although losses for many can be circumvented through proper storage conditions.

1. Bacterial soft rot, caused by *Erwinia carotovora* ssp. *carotovora*, results in tubers that are soft and slimy in appearance (listed as *Bacillus carotovorus* and *Bacillus aroideae* by Johnson (1931)). The organism gains entry through surface wounds. Secondary bacterial invaders such as *Pseudomonas fluorescens* and *Pseudomonas marginalis* follow fungal invasion (Johnson, 1931; McCarter and Kays, 1984) and cause rots over a temperature range of 5 to 25°C. Bacterial rots can be substantially reduced with storage at low temperatures (e.g., 0 to 2°C).
2. Blue mold rot, caused by *Penicillium*, results in decay only at relatively high temperatures (e.g., 20°C). The organism is only weakly virulent and gains access through wounds or lesions made by other fungi.
3. Fusarium rot is caused by several *Fusarium* species and is frequently isolated from diseased tubers (McCarter and Kays, 1984). Rots were most severe at 25 to 30°C and can be prevented with temperatures below 5°C.
4. Gray mold rot is caused by *Botrytis cinerea*, which results in a pale brown discoloration and sunken lesions on the tuber surface. At high relative humidities, the surface becomes covered with white mycelium and subsequently with gray-brown spores (Johnson, 1931). The interior of the tubers discolors and softens. The organism can cause serious storage losses even at low temperatures.
5. Rhizoctonia rot results in a brown discoloration of the tubers, caused by *Rhizoctonia solanii*. While occasionally isolated from diseased tubers, it is not a serious postharvest pathogen of Jerusalem artichoke.
6. Rhizopus rot caused by *Rhizopus stolonifer* (= *R. nigricans* Ehrenb.) and *R. tritici* results in a dark brown discoloration and tuber softening. At high humidities, mold growth can be extensive. Of the two organisms, *R. stolonifer* is a more serious storage problem in that it is active at temperatures between 6 and 20°C. Refrigeration prevents *R. tritici*, which is active at temperatures above 20°C. While storage at 2°C represses the development of both organisms, *R. stolonifer* remains one of the most critical low-temperature pathogens of Jerusalem artichoke (Johnson, 1931).
7. Sclerotium rot is a serious tuber rot in the field and storage (McCarter and Kays, 1984), caused by *S. rolfsii*. The tubers display robust white to light brown mycelium with numerous spherical sclerotia. Postharvest losses can be largely prevented with low-temperature storage (Johnson, 1931; Thompson, 1928).
8. Watery soft rot caused by *S. sclerotiorum* and *S. minor* often develops on tubers that appear sound at harvest but subsequently succumb in storage (Gaudineau and Lafon, 1958). The tubers become covered with a dense white mycelium and irregular sclerotia, which progress from white to dark brown or black. Though storage at low temperatures repressed development, *S. sclerotiorum* can cause serious losses at low temperature (Johnson, 1931).

Prevention of storage pathogens centers on the use of proper handling practices and storage conditions. Tubers from fields with high incidence of disease should not be stored, and inoculum (e.g., tubers with even small amounts of rot) should be removed prior to storage. The plant material should be handled in such a manner as to minimize wounding and stored at 0 to 2°C and a high relative humidity (~95%). Care should be taken to prevent condensation from forming on the surface of the tubers during storage. Condensation is caused by fluctuations in temperature and by the use of sealed polyethylene bags. While prestorage fungicide dips have been shown to be effective in reducing certain storage rots, no chemicals are currently cleared for commercial use in the U.S.

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12 Agronomic Practices

Jerusalem artichoke can grow in nutritionally poor soils with minimal cultivation. However, good agronomic practices considerably increase crop productivity. Practices that raise tuber and biomass yields include choice of cultivar, planting date, effective weed control, fertilization, irrigation, and good harvesting procedures.

12.1 PLANTING DATE

Jerusalem artichoke is normally propagated vegetatively, from tubers or tuber pieces. The optimal planting date for Jerusalem artichoke tubers varies with region, climatic conditions, and the cultivar used. When grown as a perennial, the crop regenerates from tubers left in the ground in the fall. For an annual crop, or to start a perennial planting, tubers can be planted in the fall or during the winter, but planting usually occurs in the spring (e.g., February to mid-April in the northern hemisphere) when the soil is workable (Kosaric et al., 1984; Mimiola, 1988; Shoemaker, 1927; Sprague et al., 1935). Harvest typically occurs around 130 days later.

The early sowing of tubers enables plants to optimize photosynthesis in response to the longest day lengths, strongest light intensity, and maximum temperatures during the growing season. In Northern Europe, planting of early-maturing cultivars in February ensures that the crop canopy is well established by the summer, although weather conditions often make later plantings more practical. Planting is more usual from mid-March to mid-April in Europe, for example, in Scotland (e.g., April 3; Hay and Offer, 1992), France (e.g., mid-April; Ben Chekroun et al., 1996), Germany (e.g., April 9–12; Schittenhelm, 1999), and Denmark (e.g., March 24; Zubr and Pedersen, 1993). In France, planting date and choice of cultivar were significant factors in terms of biomass production, because they optimized leaf area index and the duration of interception of solar radiation (Barloy, 1988). Cultivars selected for early maturity tended to produce higher and less variable yields in Denmark than late-maturing cultivars, because the translocation of photosynthetic products from the aerial plant parts to the tubers is often disrupted by frost late in the growing season (Zubr and Pedersen, 1993). Therefore, delayed planting in the spring can lead to significant decreases in yield and the size of harvested tubers.

Planting typically occurs from February to April, and no later than mid-May, in North America. In the U.S. (Washington, D.C.) in the 1930s, tuber yields were reduced on average by 28% over 2 years when planting was delayed by nearly 2 months (from April 5 to June 1, and March 30 to May 26, respectively), with yield reductions of up to 50%. Tuber size at harvest also decreased with delayed planting. It was therefore recommended that tubers be sown early in the spring, as soon as the soil becomes workable (Boswell et al., 1936). In Georgia, U.S., tubers of numerous cultivars were planted on March 24 in a study on flowering dates (Kays and Kultur, 2005).

Planting dates were March 17–24 for experimental studies in Egypt (Ragab et al., 2003) and early to mid-March in Turkey (Killi et al., 2005). In South Korea, differences in spring planting dates affected vegetative growth and tuber yield, with earlier plantings resulting in better growth and yield, providing the soil was sufficiently warm early in the season (Lee et al., 1985).

In the southern hemisphere, planting dates run counter to those in the northern hemisphere. In southern Australia, for instance, planting occurs in September and October, with tubers harvested in March or June the following year (Parameswaran, 1994).

12.2 PLANTING

In gardens or allotments, tubers obtained from the grocery store could be used for planting (unlike potatoes), because Jerusalem artichoke is relatively pest- and disease-free. Tubers can also be carefully harvested and saved, stored indoors (e.g., in the dark at 0°C and 90 to 95% relative humidity), for replanting in the spring.

Jerusalem artichoke is propagated from whole tubers or cut tuber pieces. Larger tubers can be cut into several smaller pieces, but each piece must include at least one "eye" or bud, from which a new stem develops. Two or three eyes are usually recommended to ensure good crop establishment (e.g., Wood, 1979). Larger tubers with numerous buds will produce more stems. This will result in more leaf growth to capture solar radiation more efficiently early in the season, but may be detrimental, for example, in terms of variable planting density and tuber size (Denoroy, 1996). It has been reported that whole tubers produce better plants (Kosaric et al., 1984), although this is not always the case. Tubers or tuber pieces, between 45 and 60 g, are generally recommended for planting, with pieces smaller than this tending to give lower yields (Boswell, 1959; Kovac et al., 1982).

In trials in the U.S., with "seed tuber" pieces of $^1/_4$ oz (7.1 g), $^1/_2$ oz (14.2 g), 1 oz (28.4 g), and 2 oz (56.7 g) fresh weight, a larger net yield of tubers was obtained with each successively larger tuber piece. With each hill planted with a single seed tuber piece, increasing the size of the planted pieces also increased the number of stalks (stems) per hill. Little difference in tuber yield was observed with pieces of 2 oz (56.7 g), 3 oz (85.1 g), and 4 oz (113.4 g). Plants from 113.4-g pieces tended to be a few inches taller than plants from smaller tuber pieces, while their tubers tended to be greater in number and smaller in size, with no difference in yield. However, for all tuber pieces below 113.4 g, size did not affect the mean size of harvested tubers. In most cases, there was no difference in yield for tuber pieces compared to whole seed tubers. In some cases, however, whole tubers were superior to cut pieces, and this was attributed to the prevailing arid conditions drying out the cut pieces to a greater extent than the whole tubers. The authors recommended using high-yielding, disease-free tubers of around 56.7 g, preferably whole tubers, but cut if necessary (Boswell et al., 1936). In a more recent Danish study, the size of seed tubers planted (25 to 200 g) had only a small effect on plant characteristics and no effect on tuber yield (Klug-Andersen, 1992).

Presprouting can have a positive effect on emergence, by increasing early growth rate (which is limited by low temperatures in the spring). However, sprouting tubers must be handled carefully during planting to avoid damage, because if damage occurs, then any advantage may be lost (Denoroy, 1996).

Seedbed preparation is similar to that for potato (*Solanum tuberosum* L.). Immediately prior to planting the soil is plowed, an operation that is faster and cheaper on lighter (e.g., sandy) soils. Mechanical potato planters (sometimes modified) are used to plant Jerusalem artichoke tubers, with satisfactory results. Jerusalem artichoke is planted at a rate of around 20% lower than that for potato, for example, 1,675 kg·ha^{-1} for Jerusalem artichoke cf. 2,100 kg·ha^{-1} for potato (Frappier et al., 1990). Seed tubers are planted in rows, on the level, in individual small hills or in ridges. A distance of 50 to 60 cm between seed tubers (plants) within rows, and 70 to 130 cm between rows, is usually recommended, giving a planting density for maximum yield per area that does not depress average tuber size through crowding. It was estimated that approximately 30,000 seed pieces were required per hectare, or 1,400 to 1,800 kg·ha^{-1} of tubers (Kosaric et al., 1984).

Planting depths of around 10 to 15 cm are usually recommended (e.g., Biggs et al., 2003). Deeper planting results in deeper tubers and more difficult harvesting operations. However, optimal planting depth will be dependent on climatic conditions. Planted tubers should be covered with earth carefully to avoid damage. Trials in the 1930s in the U.S. looked at tuber yields with planting depths of 3, 4, 5, and 6 in. (7.6, 10.2, 12.7, and 15.2 cm, respectively), for three Jerusalem artichoke cultivars ('Blanc Ameliore,' 'Chicago,' and 'Waterer'). Two years' data in Oregon showed that a

planting depth of 10.2 cm produced optimal yields, with larger tubers harvested than with other planting depths. Planting depths of less than 10.2 cm produced inferior yields compared to 10.2- and 12.7-cm depths, probably due to tubers drying out through insufficient moisture. Planting depths of 15.2 cm or more are too deep, with consistently inferior yields and harvesting becoming more difficult. A planting depth of 10.2 cm was recommended, except in semiarid regions and at high altitudes, where the surface soil frequently dries out, where a planting depth of 12.7 cm was recommended (Boswell et al., 1936).

Emergence for Jerusalem artichoke is generally high, in the order of 90 to 100% (Hay and Offer, 1992). However, emergence declines in drier and warmer climates, where tubers dry out, especially when small tuber pieces are used (Mezencev, 1985). The time of emergence after planting differs between cultivars and is mainly determined by soil temperature. It can be as early as 2 weeks after planting, but is usually 3 to 5 weeks. Earthing up around the stems, when plants are around 0.3 m tall, benefits productivity by helping with moisture retention and concentrating tubers for ease of harvest (Cosgrove et al., 2000).

12.3 WEED CONTROL

Weed control in Jerusalem artichoke can be separated into two categories: (1) control of weeds in Jerusalem artichoke grown as a crop plant and (2) control of volunteer Jerusalem artichoke in subsequent crops. The latter category has received considerably more attention in that the species is a highly competitive weed in most agricultural crops. Even with thorough hand harvest, a sufficient number of small tubers and rhizome (stolon)* pieces remain in the soil to give a solid stand of artichokes the following year. In addition, a small percentage of the tubers/tuber pieces can remain dormant in the soil during the subsequent cropping season and, depending upon location and cultivar, not sprout until the following year. It is therefore possible to have a stand of soybeans following Jerusalem artichokes in which the aboveground volunteer population is eliminated using herbicides, only to have a significant stand emerge during the third season. Hence, controlling weed Jerusalem artichoke is a more daunting task than controlling weeds in Jerusalem artichoke grown as a crop.

12.3.1 Control of Weeds in Jerusalem Artichokes

Prolific weed growth may adversely affect the establishment and early growth of Jerusalem artichoke, necessitating weed control. Since mature plants reach 2 to 3 m in height, however, once the canopy of the crop is established it generally shades out all competition. Short-stemmed Jerusalem artichoke cultivars may be more susceptible to weed competition, because a longer time elapses before canopy closure. The importance of the height of competing plants can be seen in the difference in competitive ability of corn (maize) compared to soybean with Jerusalem artichokes. The yield of soybean, with its lower growth habit, is much more repressed than corn (Wyse et al., 1986; Wyse and Young, 1979). Weed species that are successful once the stand is established are typically climbing plants such as morning glories. However, there is no indication that these species result in a reduction in Jerusalem artichoke yield. Early-season weed control can be achieved in weedy crops by mechanical or chemical means.

Mechanical weed control methods include hoeing, harrowing, and earthing the soil up around the plants. Hand hoeing may be beneficial on allotments and small holdings, but is impractical over large areas. Interrow cultivation until plants reach around 0.5 m in height (e.g., two separate cultivations) controls weeds until the leaf canopy is sufficient to outcompete weeds (Stauffer, 1979). However, care should be taken when harrowing, to avoid damaging the developing rhizomes

* The rhizomes are often incorrectly identified as "stolons" in Jerusalem artichoke literature. For additional details, see Section 10.1.2.

TABLE 12.1
Herbicides Tested for Weed Control in Jerusalem Artichoke

Herbicide	Application	Tolerance
Chloramben	Preplant incorporation	Good
EPTC	Preplant incorporation	Good
Ethalfluralin	Preplant incorporation	Good
Metribuzin	Preplant incorporation	Good
Pendimethalin	Preplant incorporation	Good
Trifluralin	Preplant incorporation	Good

Source: Adapted from Wall, D.A. et al., *Can. J. Plant Sci.*, 67, 835–837, 1987.

(stolons) and the shallow rooting system; harrowing not more than 4 to 5 cm into the soil has been recommended (Kosaric et al., 1984).

Currently no herbicides are cleared for use in the U.S. to control weeds in Jerusalem artichokes. Preliminary tests with several herbicides have been reported (Table 12.1). For example, the cultivar 'Columbia' displayed satisfactory tolerance to preplant incorporated treatments of chloramben, S-ethyl dipropylthiocarbamate (EPTC), ethalfluralin, pendimethalin, and trifluralin, although metribuzin resulted in considerable damage, manifested as chlorosis and necrosis of leaf margins, and reduced plant height. Tuber yield, however, was not increased by weed control, whether via herbicides or hand weeding, when compared to weedy control treatments (Wall et al., 1987).

Chemical control reduces weed populations, but this rarely results in increases in tuber yields. Treflan (0.88 $kg \cdot ha^{-1}$), for example, controlled weeds and increased tuber yields in one study (Stauffer, 1975). Herbicides more often have no effect on tuber yield or cause yield to be decreased (Kosaric et al., 1984). When the selective preemergence herbicide promethryn was tested on a new short-stemmed dwarf cultivar and two established cultivars ('Précoce Commun' and 'Eigen Nabouw'), it was found to depress tuber yields by 5%, compared to mechanical weeding controls, despite being effective at controlling weeds (Pilnik and Vervelde, 1976). Similar yield-depressing effects have been noted with trifluralin (Kosaric et al., 1984). In Poland, weed control by herbicides (linurex, afalon, azogard, and cyanazine) did not increase the quality of tubers, compared to mechanical tillage without herbicide. The highest contents of dry matter, fructose, protein, and ash were found in tubers from the control without herbicides (Sawicka, 2004).

Jerusalem artichoke therefore has a high tolerance of weed competition, especially when weed populations are low and comprised of relatively low growing species or those that do not develop early in the spring. Under these conditions, Jerusalem artichokes generally can be grown without the use of herbicides.

12.3.2 Control of Jerusalem Artichoke in Subsequent Crops

The Jerusalem artichoke is a highly competitive weed, capable of maintaining itself in areas once established and invading new areas via tubers, rhizomes, and, to a lesser extent, under appropriate ecological conditions, seed (Alex and Switzer, 1976; Konvalinkova, 2003). Seed production, however, is generally limited due to high levels of self-incompatibility (Mayfield, 1974). It has been shown to range from 3 to as many as 50 seeds per inflorescence (Russell, 1979; Wyse and Wilfahrt, 1982), the latter being the exception rather than the rule. Swanton (1986) found two cultivated biotypes that produced 8 and 66 seeds per 100 inflorescences, two wild biotypes that produced 126 and 197 seeds per 100 inflorescence, and two riverbank biotypes that produced 493 and 536 seeds per 100 inflorescences. On a per-plant basis, this gave 0.4 to 24 seeds per plant for the cultivated

biotypes, 47 to 154 seeds per plant for the wild biotypes, and 79 to 163 seeds per plant for the riverbank biotypes. When seeds are present, they may play a key role in the spread of the species to new habitats. Once established, the rapid increase in plant numbers appears to be due to the regenerative capacity of the tubers and rhizomes.

As a weed, the Jerusalem artichoke tends to present the greatest problem as a volunteer after production as a crop (Wall and Friesen, 1989) and, to a lesser extent, due to invasion from border areas of the field. The rhizomes facilitate dispersal in that they may reach lengths of up to 100 cm outward from the parent plant (Swanton, 1986), with rhizome length varying with genotype, soil type, and production conditions. Tubers are produced at the ends of the rhizomes, and as many as 75 or more can be produced by a single plant. Most undisturbed tubers and rhizomes in the upper 10 to 15 cm of soil produce new shoots the following season (Russell, 1979). Successful shoot development, however, decreases at greater tuber depths; for example, at 25 cm only 25% of the tubers produced shoots within 58 days. It is the underground tubers and rhizomes that make eliminating Jerusalem artichokes by cultural means or herbicides difficult, in that both types of propagules can overwinter as far north as the southern third of Canada and produce new plants the following year (Vanstone and Chubey, 1978).

The Jerusalem artichoke has prolific shoot growth, and if the population is sufficiently high, it forms a dense canopy suppressing crop growth, especially so for crop species of relatively short stature such as soybean. As a weed in these crops, Jerusalem artichoke can have an extremely serious impact on yield. For example, as few as four plants per meter of row can reduce the yield of soybeans by 71% and corn by 25% (Wyse and Wilfahrt, 1982; Wyse and Young, 1979). Lower densities in soybean also have a significant effect on yield (i.e., 1 and 2 tubers·m^{-1} of row gave 31 and 59% reductions) (Wyse et al., 1986). Soybean leaf area and relative growth rates are repressed at 2 and 4 tubers·m^{-1} of row and net assimilation rate by 4 tubers·m^{-1}. Likewise, competing Jerusalem artichokes decrease the height, number of branches, and total seed weight of soybeans (Wyse et al., 1986).

There are three general approaches to controlling Jerusalem artichokes as a weed: chemical, mechanical, and crop rotation. The method selected depends upon a number of factors, such as the necessity for continuous cropping, suitable rotational crops, costs, geographical area, equipment availability, weed density, and other factors.

12.3.2.1 Chemical Control

Rotation to a monocotyledonous crop following Jerusalem artichoke greatly broadens the number of herbicides available and potential cropping options. With monocots such as corn (maize), barley, oats, or wheat, control is more readily attainable in that a number of broadleaf herbicides are available that provide relatively good control of Jerusalem artichoke. Herbicides that have been tested for Jerusalem artichoke control in these crops are listed in Table 12.2. The availability of a number of postemergence herbicides facilitates control that ranges from good to poor. Preemergence application of glyphosate or paraquat generally initially reduces weed pressure; however, unless the crop is planted late enough to allow all of the Jerusalem artichokes to emerge, control is typically inadequate.

When the following crop is a dicotyledon, however, the options are more restricted. Preemergence herbicides such as glyphosate or paraquat generally give poor results in soybeans, where control is dependent upon the Jerusalem artichoke population completely emerging prior to application. The timing of tuber/rhizome sprouting is a function of the depth of the propagation material in the soil and genotype (Swanton and Hamill, 1983; Swanton and Cavers, 1988). The deeper the tubers, the greater the time required for emergence (Russell and Stroube, 1979; Swanton and Cavers, 1988), and hence the greater the potential for only partial control. Tubers sprouting after emergence of the crop plant are not controlled with these herbicides. Other factors that influence the timing of Jerusalem artichoke emergence are the size of the tuber/rhizome pieces, soil type, maturity of

TABLE 12.2
Herbicides Tested for the Control of Volunteer Jerusalem Artichoke

Crop	Herbicide	Application	Control	Source
Barley	Chlorsulfuron	Post[a]	Poor	i
Barley	Clopyralid	Post	Very good	bi
Barley	Clopyralid + 2,4-D	Post	Good	hi
Barley	Dicamba + 2,4-D	Post	Good	hi
Barley	Dicamba + mecoprop + 2,4-D	Post	Good to very good	gk
Barley	Glyphosate	Pre[b]	Poor to good	hi
Barley	Glyphosate + dicamba + 2,4-D	Pre/post	Good	i
Barley	Glyphosate + paraquat	Pre	Poor	g
Barley	MCPA	Post	Poor	gi
Barley	Paraquat	Pre	Poor	gh
Barley	Picloram + 2,4-D	Post	Poor	i
Barley	2,4-D	Post	Good	efghik
Corn/maize	Atrazine	Pre/post	Good	k
Corn/maize	Clopyralid	Post	Good	j
Corn/maize	Dicamba	Post	Fair to good	j
Corn/maize	Dicamba + 2,4-D	Post	Fair to good	j
Corn/maize	Glyphosate	Pre	?	c
Corn/maize	Hornet?	Post	Good	j
Corn/maize	2,4-D	Post	Fair	cj
Corn/maize	Sulfonylurea	Post	Fair to good	j
Oats	Dicamba	Post	Good	k
Oats	Dicamba + mecoprop + 2,4-D	Post	Good	g
Oats	2,4-D	Post	Good	k
Wheat	Dicamba	Post	Good	k
Wheat	Dicamba + mecoprop + 2,4-D	Post	Good	g
Wheat	2,4-D	Post	Good	k
Soybean	Acifluorfen	Pre	Poor	k
Soybean	Bentazon	Pre	Poor	k
Soybean	Chlorimuron-ethyl	Post	Good	j
Soybean	Chlorimuron-ethyl + thifensulfuron-methyl	Post	Good	j
Soybean	Glyphosate	Pre	—	a
Soybean	Glyphosate	Post rope-wick	—	j
Soybean	Imazethmpyr	Post	Good	j
Various	Atrizine	Pre/post	—	c
Various	Glyphosate	Spot treatment at bud stage	Poor to very good	ajk
Various	Glyphosate	Bud to bloom	Fair to good	j
Various	Dicamba	Bud to bloom	Fair to good	j
Various	2,4-D	Bud to bloom	Poor to good	aj

Note: Data taken from: a = Coultas and Wyse, 1981; b = Hamill, 1981; c = Russell and Stroube, 1979; d = Swanton, 1986; e = Swanton and Brown, 1980, f = Swanton and Brown, 1981; g = Vanstone and Chubey, 1978; h = Wall and Friesen, 1989; i = Wall et al., 1986; j = Salzman et al., 1997; k = Wyse and Wilfahrt, 1982.

[a] Herbicide application after seedling emergence.

[b] Herbicide application before seedling emergence.

the material when severed from the parent plant, soil temperature, and planting time. Tubers/tuber pieces present a greater control problem than rhizomes/rhizome pieces in that they are more highly adapted reproductive propagules (Swanton and Cavers, 1986). Several postemergence herbicides

(e.g., chlormuron-ethyl, chlormuron-ethyl + thifensulfuron-methyl, and imazethmpyr) also give good control (Salzman et al., 1992).

An alternative approach has been to use Round-up Ready soybeans, a transgenic cultivar that is tolerant of glyphosate. Two applications of glyphosate give complete control of all tubers/rhizomes that have sprouted. Dormant tubers, however, are not controlled and can germinate the following year in more southern locations, such as southeastern Missouri (Kays, unpublished data). As a consequence, a 3-year rotation is needed to adequately control volunteer Jerusalem artichokes. Under Canadian conditions, tuber and rhizome fragments that did not emerge the year following formation apparently decomposed by the end of the season (Swanton and Cavers, 1988; Swanton et al., 1992). The longevity of propagation material in the soil appears to be a function of the genotype, size of the pieces, and climatic conditions.

Round-up Ready cotton is another possible rotation option following Jerusalem artichoke; however, the existing cultivars lose their resistance to glyphosate as the plant develops. Due to the timing of cotton vs. Jerusalem artichoke emergence, only a small percentage of the weed population can be controlled prior to the cotton plants becoming susceptible to the herbicide. Hence, it is not possible to achieve adequate control. If the cotton is planted late, after relatively complete sprouting of the volunteer Jerusalem artichokes, adequate control may be achieved.

Another variation in herbicide control of volunteer Jerusalem artichokes in soybeans is through the use of roller, pipewick, or bobar wick applicators (Coultas and Wyse, 1981) with glyphosate or 2,4-D amine, the former being more effective. At least two applications approximately 2 weeks apart are recommended, and the weeds should be at least 15 cm taller than the soybeans before treatment. Variable results appear to be due to the lack of uniformity in height of the Jerusalem artichokes. At this time, selective application techniques have not proven to be sufficiently effective.

12.3.2.2 Mechanical Control

Jerusalem artichokes can be controlled by leaving the ground fallow the following season and eliminating the volunteer plants via mowing or cultivation (discing or rototilling). Both approaches require multiple treatments. The object of mechanical control is to deplete the carbon storage reserves in the underground tubers/rhizomes without allowing the plant to develop new tubers. As a consequence, timing mowing or tillage to coincide with all of the plants having emerged is important, and mowing close to the soil surface is desirable. The first mowing (or tillage) should be done prior to the plants producing rhizomes (Wyse and Wilfahrt, 1982), and especially before rapid bud and flower production of genotypes in which flowering precedes tuber formation (Swanton and Carvers, 1988).

Mechanical control generally requires two to three timely mowing or tillage operations during the fallow season to control the plant. In areas with mild winters where dormant tubers may survive, additional spot control may be essential the following year.

12.3.2.3 Crop Rotation

Rotation to a forage or small grain crop can also help to repress volunteer Jerusalem artichokes (Wyse and Wilfahrt, 1982). Volunteer Jerusalem artichokes in hard red spring wheat fields in Minnesota had their tuber numbers greatly repressed (i.e., 1 or 2 tubers/plant) in contrast to when competing with soybeans or corn (i.e., 50 to 60 tubers/plant). The effect appears to be a function of timing rather than allopathy. The Jerusalem artichokes emerge substantially later than the wheat, and therefore are at an initial competitive disadvantage. In addition, the wheat is harvested in mid-summer, prior to tuber formation, again repressing the reproductive development of the plant. Other possible rotational crops are forages that have rapid regrowth after cutting, especially those that require multiple cuttings during the summer. While crop rotation alone generally will not completely

eliminate weed Jerusalem artichokes, if used in conjunction with spot herbicide treatments, the plant can be effectively eliminated.

Four-year rotations established in France in the 1920s alternated Jerusalem artichoke in the first year with oats in the second, clover in the third, and wheat in the fourth. By the time the wheat was grown, no Jerusalem artichoke remained in the fields. The mid-summer harvesting of oats and clover helps to destroy developing Jerusalem artichoke volunteers. This type of rotation effectively clears the ground of Jerusalem artichoke (Shoemaker, 1927).

12.3.2.4 Novel Control Techniques

The bacteria *Pseudomonas syringae* pv. *tagetis*, which is pathogenic to Jerusalem artichoke (Shane and Baumer, 1984), can apparently be used to repress weed populations. Spray applications of the organism (5×10^8 cells·ml^{-1}) in aqueous buffer with a non-ionic organosilicone surfactant (e.g., Silwet L-77 or Silwet 408), the latter being essential for infection, are said to produce severe disease symptoms, although no data were shown (Johnson et al., 1996).

12.4 FERTILIZATION

The Jerusalem artichoke has long been touted as an extremely efficient crop relative to its nutritional requirements. Reports of it following another row crop such as corn (maize) or soybeans and achieving high yields without supplemental fertilization are not uncommon. The fact that there is sufficient residual fertilizer present in the soil after a previous crop, and that the Jerusalem artichoke is a relatively efficient user of available nutrients, should not lead one to believe that the crop can be consistently grown without supplemental fertilization. The objective in agriculture generally is to maximize the monetary return per hectare, rather than to attain the maximum theoretical yield potential. The nutrients removed per hectare are a significant component in the equation; otherwise, replacement costs are passed along to the subsequent crop, confounding the accurate assessment of the true cost/hectare of the product. Hence, substantially higher yields can be achieved with the appropriate level of available nutrients. Unfortunately, research studies on the fertility requirements of the crop are extremely limited, and those detailing the initial residual level of fertilizer along with supplemental rates are virtually nonexistent. As a consequence, a better understanding of the actual fertilization requirements is needed.

Jerusalem artichoke is responsive to supplemental fertilizer, and the response is significantly modulated by soil type (Lim and Lee, 1983). Soils with high organic matter gave substantially higher tuber yields (Table 12.3) at a given base fertilization level (100 kg each of N, P, and K per ha). The effect of organic matter was no doubt in part due to the higher level of nutrients available in the soil at the onset and throughout the growing season. Tuber yields in the high-organic-matter plots were double or greater than those of the other treatments. Likewise, in the high-organic-matter soil, there was a substantial shift in the size distribution of the tubers. Larger, faster-growing plants produced substantially larger tubers (Table 12.3). A typical Jerusalem artichoke fertilizer requirement has been given as N, 70 to 100 units; P, 80 to 100 units; and K, 150 to 250 units (Fernandez et al., 1988b; Barloy, 1988).

Leaf mineral content (Somda et al., 1999) was found to be, in general, within the sufficiency range found for other root and tuber crops (Table 12.4a and b), although Ca and B were substantially higher, and to a lesser extent K. In contrast, nitrogen tended to be lower than in cassava and potato. The concentrations of Mn, Na, Zn, and Cu tended to be lower in Jerusalem artichokes grown in Poland, though cultivar differences may in part account for the variation (Brokowska et al., 1996). When sewage sludge was used as a fertilizer supplement, the leaf concentration of Mn, Cd, and Co increased substantially over control plants (Brokowska et al., 1996). Copper, Ni, and Zn also increased, though to a much lesser extent. Spraying plants with inorganic forms of selenium can

TABLE 12.3
Effect of Soil Type on the Yield and Tuber Size Distribution of Jerusalem Artichoke

Soil Type	Organic Matter (%)	Tops mt·ha^{-1}	Tubers mt·ha^{-1}	% in Various Tuber Size Categories[a]		
				Large	Medium	Small
Loamy sand	0.52	14 b[b]	36 b	4	27	72
Silty clay	0.61	16 b	25 c	3	38	61
Loam	1.21	12 b	23 c	4	41	58
High OM[c]	25.04	35 a	64 a	20	42	51

[a] Average sizes of categories: large, 68 to 70 g; medium, 33 g; small, 12 g.
[b] Different letters denote statistically significant differences.
[c] Loam soil with high organic matter.

Source: Adapted from Lim, K.B. and Lee, H.J., *Seoul Natl. Univ. Coll. Agric. Bull.*, 8, 91–101, 1983.

TABLE 12.4A
Comparison of Jerusalem Artichoke Leaf Elemental Content (%) with Ranges in Other Root and Tuber Crops

Crop	Element (%)					
	N	P	K	Ca	Mg	S
Jerusalem artichoke[a]	3.37	0.38	5.36	2.67	0.54	0.16
Cassava[b]	5.0–6.0	0.3–0.5	1.2–2.0	0.6–1.5	0.3–0.5	0.3–0.4
Potato[c]	4.0–6.0	0.2–0.5	4.0–11.5	0.6–1.0	0.5–1.5	0.2–0.4
Sweet potato[d]	3.3–4.5	0.2–0.5	3.1–4.5	0.7–1.2	0.35–1.0	—

[a] Mean of all leaves at mid-season.
[b] Mature leaves from new growth.
[c] Most recent fully developed leaves; tuber half-grown.
[d] Most recent fully developed leaves; mid-season.

Source: Adapted from Mills, H.A. and Jones, J.B., Jr., *Plant Analysis Handbook II*, 2nd ed., Micromacro Publ., Athens, GA, 1996; Somda, Z.C. et al., *J. Plant Nutr.*, 22, 1315–1334, 1999.

raise selenium levels, potentially enhancing the crop's value in animal and human nutrition (Nyberg, 1991).

The crop is responsive to nitrogen nutrition with typical rates of application ranging from 60 to 120 kg N·ha^{-1}. In a fairly extensive study in Germany (3 years, 27 genotypes), yield increases between the 60 and 120 kg N·ha^{-1} rates were not significant (Honermeier et al., 1996). With increasing nitrogen nutrition, there is not necessarily a correlation between content and tuber yield (Soja et al., 1993).

Jerusalem artichoke tuber production is reduced if excessive nitrate is added to the soil. High nitrate levels change the relationship between aerial and subterranean parts of the plant, in favor of vegetative growth (Leible and Kahnt, 1988). Excessive nitrates also encourage the concentration of certain minerals, which may result in increasing tissue fragility (Barloy, 1988). In a Korean study, single applications of Ca, P, and K increased tuber yields by 43, 14, and 18%, respectively,

TABLE 12.4B
Comparison of Jerusalem Artichoke Leaf Elemental Content (ppm) with Other Root and Tuber Crops

	Element (ppm)									
Crop	Al	B	Ba	Cu	Fe	Mn	Na	Si	Sr	Zn
Jerusalem artichoke	81.79	49.28	54.26	10.63	90.89	130.25	117.0	1947	66.60	34.99
Cassava	—	15–20	—	7.0–15	60–200	50–250	—	—	—	40–100
Potato	—	25–50	—	7.0–20	50–150	30–450	—	—	—	20–250
Sweet potato	—	25–75	—	4.0–10	40–100	40–250	—	—	—	20–50

Source: Adapted from Mills, H.A. and Jones, J.B., Jr., *Plant Analysis Handbook II*, 2nd ed., Micromacro Publ., Athens, GA, 1996; Somda, Z.C. et al., *J. Plant Nutr.*, 22, 1315–1334, 1999.
Evapotranspiration was calculated as W = R + I – ET, where W = variation in soil water content between two consecutive measures, R = rainfall, I = irrigation, and ET = evapotranspiration.

compared to an unfertilized control, but the addition of nitrogen reduced tuber yields by 94% (Lee et al., 1985). Moderate nitrogen fertilization is most beneficial at higher plant densities.

Phosphorus rates have ranged between 14 and 100 $kg \cdot ha^{-1}$, and potassium between 52 and 100 $kg \cdot ha^{-1}$. Phosphorus fertilization can have a significant effect on tuber sugar content, although the requirements depend heavily on soil type and other agronomic factors (Bachmann, 1964; Kosaric et al., 1984).

The addition of lime or calcium-based fertilizers to soil can have a beneficial effect on tuber yield, through adjusting the soil pH to the optimal range (4.5 to 8.6) for Jerusalem artichoke (Lee et al., 1985).

12.5 IRRIGATION

The Jerusalem artichoke is considered a species with a relatively high tolerance to water stress, even though its native habitat is not arid. It has been reported by some to be more responsive to high moisture than water deficit conditions (Dolganova and Ismagulova, 1973; Kaskar and Prokhorov, 1970; Markarov, 1984; Nazartevsky, 1936). However, its tolerance to water stress is evident from the fact that it can be readily grown without irrigation, even in semiarid production regions. For example, in central Italy, where the rainfall between June and September is only about 12.5 cm, approximately 10 $t \cdot ha^{-1}$ of tuber dry matter can be produced without supplemental irrigation (Mecella et al., 1996). The crop also displays a relatively high water use efficiency (Belhak, 1983; Filimonov and Mamin, 1983). The water use efficiency of Jerusalem artichokes grown for forage was 14.17 mm $H_2O \cdot t^{-1} \cdot ha^{-1}$, for instance, comparable to sudangrass (*Sorghum H drummondii* (Nees ex Steud.) Millsp. & Chase) (14.23 mm) and superior to maize (*Zea mays* L.) (17.29 mm) and grain sorghum (*Sorghum bicolor* (L.) Moench) (19.70 mm) (Tóth and Lazányi, 1988). While Jerusalem artichoke will grow under moisture deficit stress conditions, a better understanding of the actual water requirements is essential to maximize productivity; for instance, what level of stress can the plant withstand, and when during its developmental cycle is it most susceptible?

Water deficit stress has a much more pronounced effect on the aerial plant parts than on the tubers (Mecella et al., 1996). Aerial biomass accumulation in a low irrigation treatment (27.5 cm H_2O) was 36% greater than the unirrigated control, while the high irrigation rate (37.6 cm) was 98% greater than in control plots. Only small differences (i.e., 1.5 $t\ dm \cdot ha^{-1}$) were found in tuber yield between two levels of irrigation (27.5 and 37.5 cm) under semiarid conditions. When the crop was allowed to regrow from tubers remaining in the soil (thinned to 3 $plants \cdot m^2$) the second

year as a forage crop, the difference between the high and low irrigation treatments on aerial biomass accumulation was extremely small (Scandella et al., 1996). Whether this was due to a higher plant density in the second year or the timing of water stress periods is not clear. Low-input irrigation over a 2-year period was beneficial for cultivar 'Violet de Rennes,' with biomass and sugar yields from the aerial plant parts higher than for unirrigated plants, although no differences were observed for tuber parameters (Neri et al., 2002).

To determine which developmental stage is the most susceptible to water deficit stress, Conde et al. (1991) grew Jerusalem artichokes under three irrigation regimes, which were based upon the amount of water removed from the soil: nonstressed (100% replacement of water lost due to evapotranspiration (ET)*), 50% of the water lost due to ET replaced, and 25% replacement. The water deficit stress was imposed at different developmental stages (i.e., throughout the growing season or at the initial, middle, or final third of the season).** The severity of the water stress imposed and its timing each had a significant effect on productivity. The greater the water stress, the more pronounced the impact on yield. Nonstressed plants yielded 15.7 t tuber dm·ha^{-1} vs. 12.7 t·ha^{-1} for the intermediate level of stress (50% replacement) and 6.2 t·ha^{-1} for the severe stress, when the water stresses were imposed over the entire growing season. Timing of the stress was also critical relative to final yield. Water stress early in the season (first third) did not have a significant effect on final tuber yield, whereas stress during the middle developmental period had a pronounced effect on final yield. The middle third of the growing season is the period during which the most rapid accumulation of dry matter occurs. Hence, it stands to reason that restriction of dry matter accumulation during this period would impact final yield. Stress during the latter third of the growing season tended to be less severe than stress occurring during the middle third. During the latter third of the season, the focus is more on the recycling of existing dry matter stored in aerial parts to the tubers, a process that appears to be less sensitive to water stress conditions.

The Jerusalem artichoke appears to adjust to the water deficit conditions, as indicated by the intermediate level of yield reduction obtained with moderate stress imposed throughout the growing season (Conde et al., 1987, 1991). Moderate water stress in the first developmental stage may even have a beneficial effect on yield in some cases, with Jerusalem artichoke plants decreasing their leaf area index and increasing specific leaf weight as an acclimation strategy to water stress (Conde et al., 1988). While water stress can have a significant impact on final yield, it does not appear to alter the maturation time of the crop (Mecella et al., 1996). The latter is largely controlled by photoperiod (see Section 10.14.3).

The irrigation method utilized for Jerusalem artichoke depends on a number of factors (e.g., soil type, degree of slope, equipment available, personal preference). When appropriate, furrow irrigation is highly cost effective. Sprinkler irrigation systems are constrained because they need to deal with the height of Jerusalem artichoke plants (up to 4 m) (Fernandez et al., 1988b), although center-pivot systems can generally be used.

Irrigation is necessary to produce economic yields of tubers and biomass in the very hot and arid conditions encountered in central Spain. Yields can be doubled in extreme cases; for example, irrigation raised yields from 20 to 30 t·ha^{-1} to 60 to 80 t·ha^{-1}, with a corresponding increase in plant height from 1 to 1.5 m to 2 to 3.5 m. Irrigation was provided along furrows, at a rate of 500 to 700 m^3·ha^{-1} per watering, with eight or nine waterings per season (Fernandez et al., 1988b). Efficient water use by Jerusalem artichoke (cv. 'Violet de Rennes') under low-soil-moisture conditions was demonstrated in the Madrid region. Plant growth under three hydric regimes was tested: 100 to 80%, 100 to 60%, and 100 to 40% soil water content (on available soil water basis). The crop was most efficient in its water use in the 100 to 40% hydric regime, although lower productivity

* Evapotranspiration was calculated as W = R + I - ET where W = variation in soil water content between two consecutive measures, R = rainfall, I = irrigation, and ET = evaporation.

** Developmental stages: I. From planting until approximately 70% canopy closure (approx. 75 days); II. From the end of stage I until approximately 50% flower opening (approx. 70 days); III. From the end of stage II until leaf senescence (approx. 60 days).

occurred than in the 100 to 80% regime. Water consumption by the crop was in the order of 550 to 850 $l \cdot kg^{-1}$ of total biomass (dry matter), with the amount of evapotranspiration depending on the frequency of water supply. It was concluded that under the test conditions the number of days between consecutive waterings should not exceed six in the absence of rainfall, to prevent the soil water content from falling below 40% of available water (Fernandez et al., 1988a). Similarly, in trials in Italy, Jerusalem artichoke tuber yields were 18% higher in irrigated treatments (100 and 25% reestablishment of evapotranspiration) than in unirrigated controls (De Mastro, 1995; De Mastro et al., 2004). Irrigation can also be beneficial in other, less arid, areas of Europe. For instance, additional watering (around 620 $l \cdot m^2$) raised tuber and sugar yields in rain-fed crops in Germany (Stolzenberg, 2005).

However, supplemental irrigation in some locations and for some crop uses may be counterproductive. Irrigation lowered the reducing sugar concentration of tubers compared to those grown without irrigation (16.5% cf. 17.6%), for example, in a Canadian study where management practices were manipulated (Dorrell and Chubey, 1977). This effect may, in part, be due to enhanced vegetative growth under irrigation, which delays the formation of belowground carbohydrate reserves. Similarly, in an Italian study, it was concluded that irrigation was not necessary when Jerusalem artichoke was grown for its tuber fructan content (Monti et al., 2005). This accords with observations of lower tuber sugar yields in years with wet springs in Europe (De Mastro et al., 2004). Plants under irrigation may also flower later than those that are not irrigated (Kosaric et al., 1984). In addition, excessive watering may increase the incidence of fungal and bacterial disease and can make harvesting more difficult due to waterlogging.

As Jerusalem artichoke is relatively tolerant of salt stress, it may be possible to irrigate with diluted seawater or water from other saline sources to ease pressure on freshwater resources in regions where these are scarce. Field experiments to this end have been conducted in a coastal semiarid area of Shangdong Province, China, with four treatment regimes (nonirrigated and 25, 50, and 75% seawater irrigation). Total dissolved salts (TDSs) accumulated in the soil in the nonirrigated treatment. For the 25 and 50% seawater irrigation treatments, although TDS also accumulated significantly, a trend toward desalinization was observed over time, with TDS decreasing by 34.9 and 40.1%, respectively, over 3 years. Tuber yields in the 25 and 50% seawater irrigation treatments were higher than in the unirrigated and 75% seawater irrigation treatments. This study suggested that using 25 and 50% seawater to irrigate Jerusalem artichoke was feasible in terms of soil properties and crop yield (Zhao et al., 2005). The physiology of plants irrigated with a range of seawater in freshwater dilutions (seawater:freshwater, 0:1, 1:9, 1:4, and 1:3) was also studied in China. After 60 days of irrigation, the highest leaf area index (LAI) was achieved by plants irrigated with freshwater, while the lowest LAI was in the most saline (1:3) treatment. The photosynthetic rate was lower in the most saline irrigation treatment, but yields of tubers were not significantly reduced (Pu et al., 2005).

Jerusalem artichoke was found to be moderately tolerant in terms of soil salinity in greenhouse and field trials in Australia (Newton et al., 1991), based on the categories of Maas and Hoffmann (1977). This has implications for growing the crop for biomass on marginal land. Around 45% of the Shepparton irrigation region in southeastern Australia, for example, has moderately saline soils and has potential for growing Jerusalem artichoke for biomass (Newton et al., 1991). Groundwater is used for irrigation, affecting some control over salinity. The salinity of irrigated water was varied in greenhouse (0.7 to 12 $dS \cdot m^{-1}$) and field experiments (0.3 to 10 $dS \cdot m^{-1}$). The chlorine concentration in the leaves was found to increase linearly with increasing soil salinity. Leaf sodium levels remained low, except at the very highest salinity, although stem sodium levels rose considerably, suggesting that a mechanism was operating to restrict levels of leaf sodium. Tuber yield was more salt sensitive than aboveground biomass yield, with tuber yield decreasing dramatically (e.g., 50%) when salinity reached 7.5 $dS \cdot m^{-1}$ and higher (Newton et al., 1991).

Irrigation recommendations are dependent upon the portion of the plant to be harvested (tops, tubers, or both) and the relative cost of irrigation. Soil type also affects irrigation decisions, for

example, with sandy soils holding water less readily than clay soils. Irrigation, where it is deployed, can be a large proportion of total production costs, and yield increases must result to justify the expense (see Chapter 14).

12.6 HARVESTING AND HANDLING

The harvesting method used depends upon whether the crop has been grown primarily for tubers or for aerial plant parts that are to be harvested prior to tuber bulking (Baldini et al., 2003). Highest yields are typically obtained with the formation of tubers. However, there are instances when harvest of the aerial plant parts is distinctly superior, for example, when grown in soils that inhibit tuber formation due to high mechanical impedance or other factors. Permanent or semipermanent meadow plantings for aerial part harvesting may also be a viable option on land of insufficient quality for row crop production.

12.6.1 Harvest of Tubers

Tuber harvesting involves five basic operations:

- Top removal
- Lifting tubers and separating them from soil, stones, stems, and other debris
- Hand sorting
- Consolidation into bulk transport containers
- Transport to the site of utilization or storage

The method utilized will depend upon the number of hectares to be harvested, harvesting equipment available, value of the raw product, soil conditions, personal preference, and other considerations. The level of harvest technology varies with location, ranging from hand harvest of small plots to the use of modified multirow potato harvesters.

The first step is removal of the tops, which should not be undertaken until the stems have dried completely because plants will generally continue to translocate stored carbohydrates and minerals into the tubers after the leaves have been killed by frost. With mechanical harvesting of large fields, the dried tops are chopped and deposited away from the unharvested rows. The tops should be cut as close to the soil surface as possible to reduce any residue that would have to be subsequently discarded. A wide assortment of mechanical harvesters is available. The tubers are lifted by undercutting and placed on a vibrating apron generally made of rods placed perpendicular to the flow of tubers to remove loose soil. Mechanical separation allows the loose soil to pass through the rods on the apron and onto the ground. A number of different sifting action machines are available (e.g., rotating drums, oscillating bar grids).

Potato harvesters are typically modified by using either larger-diameter rods or rubber sleeves on the existing rods to decrease the width of the opening, to accommodate the smaller size of the Jerusalem artichoke tubers. Air blast, vacuum, and other methods are available for stone and clod removal, as used for potatoes, although the smaller size of Jerusalem artichoke tubers makes some hand sorting inevitable. The simplest harvesters drop the tubers back on the surface of the soil in a window, where they are picked up by hand. Due to the small size of the tubers, this is very labor intensive. Therefore, modified potato harvesters (one to six rows) are the preferred method for large areas, as mechanical harvest and bulk handling can substantially reduce harvesting costs. Efficiency of recovery depends upon the soil conditions, operational speed, and tuber size and position relative to the stem. Tuber shape and size vary among cultivars (Gutmanski and Pikulik, 1994), and cultivars with uniform large tubers are desirable for mechanical harvest.

Inspection allows for the removal of clods, stones, stems, and other debris not separated on the apron. The closer rods on the apron make this an essential step in that substantially fewer stones

and clods are removed during mechanical separation. At this stage, manual separation of tubers that are tightly compressed to the stem can also occur. As the tubers exit the back of the harvester they are deposited in trucks with large hoppers or tractor-drawn trailers moving in tandem with the harvester. When harvested into pallet boxes, they are either dropped in the field when full or off-loaded onto flatbed trailers. To minimize the damage to the tubers, it is essential that drop distances are not greater than 10 to 15 cm. Harvested product should be moved as quickly as possible into protected areas out of direct sunlight, and subsequently transported to storage or processing facilities.

12.6.2 Harvest of the Aboveground Plant Parts

Timing is crucial when the crop is harvested for the tops. The optimum time is when tuber bulking is just beginning. This ensures that there will be sufficient propagation material left in the ground to form the next season's crop, but the majority of the fructans still remain in the aerial plant parts for harvest. Timing, therefore, varies widely with cultivar and production conditions.

Harvest involves cutting the aboveground portion of the plant near the soil line with a sickle bar mower or similar cutter. The tops are left lying on the ground to dry in the sun. Drying is essential if there is to be a time interval between harvesting and processing. The requirement for field drying necessitates that weather conditions be favorable for a sufficient number of days to dry the tops to a desirable moisture content. When adequately dry, the tops are generally compressed into large-volume round or rectangular bales. Automatic stacking and loading devices can be used to minimize handling. Once on trailers or trucks, the product is moved to the processing site (e.g., extraction or fermentation) or placed under shelter to prevent rewetting due to rain and rot formation.

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13 Storage

Storage serves to lengthen the time interval during which a product can be marketed and is an essential part of the production–marketing–utilization chain for most agricultural products (Kays and Paull, 2004). This is especially true when production is substantially greater than can be utilized during the harvest season. Conservation of surplus product through storage enables the processor or consumer to obtain the product over a longer period. Likewise, storage gives the producer a chance to market additional product, increasing monetary returns. Thus, some form of storage is an integral part of the overall production of Jerusalem artichokes, whether for fresh market, propagation material, or industrial use.

Agricultural material that represents a feedstock for industrial processing should ideally be available throughout the year, allowing the facility to operate year-round. However, this is seldom the case in that most crops, including the Jerusalem artichoke, mature during a relatively narrow period. As a consequence, it is economically desirable to store the crop, spreading its availability over as long of an interval as needed (e.g., 4 to 9 months). For Jerusalem artichokes that are to be processed to inulin, storage significantly reduces the size of the processing facility required. A smaller facility decreases capital investment and the number of workers required and allows employing them over a longer interval. Collectively, this translates into a significantly lower final product cost. The economics of scale, therefore, have a pronounced effect on inulin production costs. In many locations, however, the entire crop must be harvested in the early fall, prior to the soil freezing or becoming too wet. When this occurs, the tubers, regardless of their intended use, must be stored in some manner.

13.1 STORAGE OPTIONS

The three primary storage options for Jerusalem artichokes are refrigerated storage, common storage (cooling is obtained from the natural low temperatures of the outdoor air or soil; examples of common stores are root cellars, champs, and pits (Shoemaker, 1927)), and *in situ* field storage (Ballerini et al., 1988; Cormany, 1928; Sibley, 1924). In the first two options (refrigerated and common storage), the tubers are harvested in the fall and placed in storage. With field storage, however, the tubers are left in the ground and harvested as needed.

Cold storage is highly effective; however, its use significantly increases the cost of the raw product. Regardless, refrigerated storage is routinely used for seed and fresh-market tubers, especially in locations where field storage is not a viable alternative. Root cellars, champs, and pits are used when the tubers must be harvested in the fall, prior to the ground freezing or other adverse conditions occurring, and refrigeration is not available or its expense prohibits utilization. In a French study, Ballerini et al. (1988) evaluated three methods of bulk common storage where 4 to 5 tons of tubers were covered with earth that was periodically sprinkled with water, or covered with plastic. The tubers were held for 120 to 150 days under ambient conditions between February and May. Dry matter decreased from 22 to 17% over 100 days, and there was approximately a 2% loss of sugar per week. Storage in aboveground silos did not reduce losses.

The selection of *in situ* field storage is dependent upon several factors. Location is the primary determinant in the potential success of *in situ* field storage. Field storage is a viable option in production locations in the northern hemisphere that are at sufficiently high latitudes as to ensure cold soil temperatures throughout the winter, and far enough south to avoid the surface of the soil freezing solid and preventing harvest. Also essential are relatively sandy, well-drained soils that

allow the use of harvest machinery throughout the winter. Therefore, locations that have a maximum number of potential harvest days are preferable in that they increase harvest flexibility and reduce the risk of extended periods in which the processing facility must be shut down. Locations that do not meet these criteria generally require the use of refrigerated or some form of common storage.

13.2 STORAGE CONDITIONS

Jerusalem artichoke tubers can be successfully stored for up to 6 to 12 months, if held at temperatures between 0 and 2°C and a high relative humidity. Success is highly cultivar dependent, with some cultivars being much more susceptible to storage losses (Steinbauer, 1932). With low humidity, the tubers shrivel readily and are more likely to decay than if kept in a moist atmosphere. While stored tubers have relatively low respiratory rates when held at low temperature (Table 13.1) (Peiris et al., 1997), there is a slow but progressive loss in dry matter due to respiration (e.g., 16.2 g·100 kg^{-1}·day^{-1} at 0°C). Likewise, the tubers produce heat (vital or respiratory heat, e.g., 111 J·kg^{-1}·h^{-1} at 0°C), which must be removed if the product temperature is to be maintained at the desired level.

13.3 STORAGE LOSSES

Storage losses are due primarily to desiccation, rotting, sprouting, freezing, and inulin depolymerization. While desiccation losses can be relatively easily circumvented with proper storage conditions, desiccation still remains a significant storage problem. The tubers lack a corky surface layer of cells with a high water diffusion resistance such as that found on potatoes (Decaisne, 1880). In addition, the surface cells can be readily injured, facilitating desiccation (Traub et al., 1929a). Due to the thin periderm, the tubers lose moisture when a vapor pressure deficit exists between the tubers and their surrounding atmosphere: the greater the deficit, the faster the loss of moisture. As a consequence, storage in a high relative humidity (RH) environment (e.g., 90 to 95% RH) is essential (Steinbauer, 1932; Johnson, 1931; Shoemaker, 1927; Traub et al., 1929a).

Storage rots are also a serious problem (Barloy, 1988; Cassells et al., 1988; Johnson, 1931; McCarter and Kays, 1984), and their propensity for development is in most cases highly temperature dependent (i.e., higher storage temperatures result in greater losses). Approximately 20 organisms causing storage rots have been isolated from Jerusalem artichoke tubers (see Table 11.3). The most frequent diseases isolated were *Botrytis cinerea* Pers. and *Rhizopus stolonifer* (Ehrenb.: Fr.) Vuill., though *R. stolonifer* and *Sclerotinia sclerotiorum* (Lib.) de Bary are the most serious organisms causing rots at low storage temperatures (Johnson, 1931). *Sclerotium rolfsii* Sacc. and *Erwinia carotovora* spp. *carotovora* (Jones) Bergey et al., in contrast, are not significant pathogens at temperatures below 20°C. Control of postharvest rot organisms is facilitated by storage at low

TABLE 13.1
Respiratory Rate and Vital Heat of Jerusalem Artichoke Tubers at Various Storage Temperatures

	Storage Temperature (°C)			
	0	**5**	**10**	**20**
Respiratory rate (mg CO_2·kg^{-1}·h^{-1})	10.2	12.3	19.4	49.5
Vital heat (J·kg^{-1}·h^{-1})	111	134	211	537
Rate of dry matter loss (g·100 kg^{-1}·day^{-1})	16.2	20.1	31.7	80.1

Source: Peiris, K.J.S. et al., *HortTechnology*, 7, 46–48, 1997.

temperatures (i.e., 0 to 2°C), removal of tubers displaying disease prior to storage, minimization of mechanical damage to the tubers, and proper humidity control. For additional details, see Chapter 11.

The potential duration of tuber storage is determined to a significant extent by the length of the dormant period. Once the tubers begin to sprout, respiratory, dry matter, and moisture losses increase markedly, resulting in a rapid decline in quality and marketability. The tubers possess a dormancy mechanism that prevents sprouting immediately after harvesting, which is fulfilled by exposure to low temperatures (Steinbauer, 1939). Low storage temperature (i.e., 0 to 2°C), while removing the inhibition of sprouting, prevents the sprouts from developing. Therefore, the best method for preventing sprouting is storage at low temperatures (i.e., 0 to 2°C).

Jerusalem artichoke tubers freeze at temperatures below –2.2°C (Whiteman, 1957), and temperatures around –10°C, whether in the field or storage, result in rapid deterioration. Significant chemical and physical alterations occur in the plasma membrane, most notably losses of sterols and phosphatidylethanolamine (Uemura and Yoshida, 1986) with a concurrent decline in membrane function. Nonlethal freezing temperatures (≥ –5°C), however, result in little damage. As with most fleshy plant products, the temperature at which freezing damage occurs and the extent of the damage vary with cultivar, season, preconditioning, rate of freezing, and other factors (Kays and Paull, 2004).

13.4 ALTERATIONS IN COMPOSITION DURING STORAGE

During storage the tubers undergo significant alterations in carbohydrate chemistry, which, depending upon the intended use, can have a pronounced effect on quality. It is important to be cognizant of the fact that inulin is not one compound but a series of molecules of varying chain length (Tanret, 1893) that begin to depolymerize during storage (Bacon and Loxley, 1952; Ben Chekroun et al., 1994; Colin, 1919; Dubrunfaut, 1867; Jefford and Edelman, 1960, 1963; Modler et al., 1993a, 1993b; Rutherford and Weston, 1968; Schorr-Galindo and Guiraud, 1997; Thaysen et al., 1929; Traub et al., 1929b), whether harvested or left *in situ*. The degree of polymerization is critical for uses such as fat replacement or high-fructose syrups. With the former, as the chain length decreases, the ability of inulin to mimic a lipid diminishes. Likewise, with progressive depolymerization, the ratio of fructose to glucose decreases and upon hydrolysis yields progressively less pure fructose syrup. For example, during winter storage the ratio of fructose to glucose decreased appreciably (Cabezas et al., 2002; Dorrell and Chubey, 1977; Kakhana and Arasimovich, 1973; Soja et al., 1990: Stauffer et al., 1981). The ratio of fructose to glucose declined from 11–12 to 3 (Chabbert et al., 1985; Schorr-Galindo and Guiraud, 1997), with variation depending upon the cultivar; thus, syrups derived from stored tubers would contain substantially more glucose. Decreased polymerization, however, improves the conversion to alcohol in the absence of a supplemental hydrolysis step (Chabbert et al., 1985).

In nature tubers are the primary reproductive propagule for the species and depolymerization provides low molecular weight carbon compounds for respiration and sets the stage for the rapid recycling of stored carbon during sprouting in the spring (Edelman and Jefford, 1968). Depolymerization occurs via the action of two enzymes, fructan-exohydrolase (FEH) and fructan-fructan-fructosyl transferase (FFT), which are active in the tubers (Edelman and Jefford, 1968; Wiemken et al., 1986). Fructan-exohydrolase removes a single terminal fructose molecule at a time (Edelman and Jefford, 1964; Pollock, 1986) and is noncompetitively inhibited by sucrose (Wiemken et al., 1986). It is associated with the tonoplast membrane of the vacuole, facilitating the release of fructose into the cytosol, where it is converted to sucrose by sucrose synthase for transport out of the cell. FFT, in contrast, catalyzes the transfer of fructosyl units from inulin to sucrose (GF), giving a net shortening of the mean chain length, which appears to facilitate the subsequent remobilization of stored carbon during sprouting (Edelman and Jefford, 1964; Jefford and Edelman, 1960) (see

TABLE 13.2
Relative Percentage of Sugars and Inulin in Tubers Stored for 10 Weeks at Different Temperatures

Component (relative %)	Storage Temperature (°C)[a]			
	Fresh	–18	2	5
Monosaccharides	3.26 a	1.26 b	2.51 ab	1.05 b
Sucrose	8.76 b	4.33 c	8.22 b	10.23 a
Inulin DP 3-10	47.28 b	40.82 c	46.33 b	57.06 a
DP 11-20	26.71 b	31.67 a	27.48 b	23.64 c
DP 21-30	9.52 c	15.29 a	11.93 b	6.77 d
DP >30	4.48 b	6.65 a	3.54 b	1.27 c

[a] Means within rows with different letters are significantly different at $p < 0.05$ according to Duncan's multiple range test.

Source: Saengthongpinit, W. and Sajjaanantakul, T., *Postharvest Biol. Technol.*, 37, 93–100, 2005.

Section 10.8.1). Both enzymes function at low temperatures, even though there is relatively little utilization of the carbon while in cold storage (Pollock 1986).

A number of factors affect the rate of depolymerization. The rate of hydrolysis, for example, varies with the degree of polymerization of the substrate molecules, increasing in rate as the length increases to a degree of polymerization of 8. Rate, however, does not appear to be directly modulated by fructose concentration (Edelman and Jefford, 1964). Storage temperature also modulates the rate of depolymerization with storage at 2°C impeding hydrolysis relative to 5°C (Table 13.2) (Kang et al., 1993; Modler et al., 1993a; Saengthongpinit and Sajjaanantakul, 2005). When *in situ* storage (7 months) in Canada was compared with cold storage (1°C), the total reducing sugar content was significantly lower in the spring harvested tubers (Kiehn and Chubey, 1982). The fructose concentration, however, was not significantly different. In contrast, *in situ* storage in central Washington resulted in insignificant losses in dry matter (Hang and Gilliland, 1982).

13.5 CONTROLLED ATMOSPHERE STORAGE

Controlled atmosphere storage has been shown to impede depolymerization, apparently through an effect on enzyme activity. Storage of the tubers in 22.5% CO_2 (20%O_2) significantly retarded the rate of inulin degradation (Denny et al., 1944). Cultivar, likewise, affects the degree of depolymerization during storage. Inulin in the cultivar 'Columbia' was substantially more degraded than inulin in 'Fusil,' 'Sunroot,' or 'Challenger' (Modler et al., 1993a), indicating the potential for selecting cultivars with reduced depolymerization via plant breeding.

13.6 IRRADIATION

Irradiation has been used to facilitate the storage potential of a relatively small number of fleshy fruits and vegetables, the benefit being through reduced insect, pathogen, and sprouting losses (Kays and Paull, 2004). Exposure to x-rays at 8,000 or 16,000 rad inhibited sprouting during storage (Pätzold and Kolb, 1957); however, exposure to 4,000 rad had no effect. In contrast, gamma irradiation of Jerusalem artichoke tubers, depending upon exposure, caused softening, disintegration, and discoloration and greatly accelerated depolymerization (Salunkhe, 1959).

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14 Economics

Economic data for the production and utilization of Jerusalem artichoke are relatively scarce, because the crop is not currently grown on a large commercial scale. However, there are some economic analyses for crop production and the use of Jerusalem artichoke for bioethanol and inulin production that highlight its potential. Bioethanol is in demand as a gasoline additive and biofuel, while inulin is increasingly used as a food ingredient. The tops and tubers of Jerusalem artichoke also have many other potential applications.

14.1 CROP PRODUCTION AND STORAGE

A detailed analysis of the annual costs of producing Jerusalem artichoke tubers and tops was made by Frappier et al. (1990) for three regions of Canada: Quebec, western Canada, and eastern Canada. The figures for Quebec are summarized here, for tops in large bales (small bales were also considered) and for a land cost of Canadian \$2,500·ha^{-1}, which is equivalent to the typical cost of maize (corn; *Zea mays* L.) land in Quebec (Table 14.1). For tubers, total variable and fixed costs were Canadian \$1,718.64 and \$1,028.58, respectively, with total annual production costs (including additional transportation and storage) being \$3,798.95. For tops in large bales, total variable and fixed costs were \$503.07 and \$791.56, respectively, and total annual costs were \$1,492.14 (cf. \$1,587.63 for tops in small bales).

When Jerusalem artichoke is grown for tuber production, the crop is cultivated as an annual and costs apply every year, except for the cost of spraying Dicamba herbicide, which is spread over 2 years. Treflan (1.5 l·ha^{-1}) is used as an herbicide to control weeds in Jerusalem artichoke, while Dicamba is used to eradicate Jerusalem artichoke before the next crop (e.g., maize) is grown on the same site. The crop is cultivated as a perennial, however, when grown for top production (tops harvested each year), and therefore a number of variable costs are spread over several years. The same initial quantity of seed tubers (1,675 kg·ha^{-1}) is purchased for both tuber and top production, for instance, but the annual cost for tuber production (\$492.45) is spread over 5 years for top production (\$98.49). The costs of planting, eradication with Dicamba, fertilizer application (0.26 t·ha^{-1} N and 0.25 t·ha^{-1} mixed P and K fertilizer), and plowing are also spread over 5 years for top production. The cultivar 'Columbia' was considered for tuber production (an average yield of 41.4 t·ha^{-1} from several Canadian studies), while 'Oregon White' was assessed for top production (average yield 40.5 t·ha^{-1}). The tops are assumed to be baled as hay at 14% moisture (having been cut at 25% moisture), with hay yield being 11.9 t·ha^{-1}. In Quebec, Jerusalem artichoke is likely to be grown as a break crop in rotation with maize (Frappier et al., 1990).

As land price decreases, variable costs are unaffected but several fixed costs are reduced (e.g., management, interest and taxes on land). For tuber production, total annual costs fell from \$3,798.95 (land price of \$2,500·ha^{-1}) to \$3,676.70, \$3,570.75, and \$3,501.48 for land prices of \$1,750·ha^{-1}, \$1,100·ha^{-1}, and \$675·ha^{-1}, respectively. For the production of tops in large bales, annual costs fell from \$1,492.14 (land price of \$2,500·ha^{-1}) to \$1,369.89, \$1,276.14, and \$1,194.67 for land prices of \$1,750·ha^{-1}, \$1,100·ha^{-1}, and \$675·ha^{-1}, respectively. Land prices tend to be cheaper in western Canada and other areas of eastern Canada. For instance, at 1990 prices, land in the less fertile eastern townships was around \$1,000·ha^{-1}, while marginal land in the eastern townships was around \$675·ha^{-1}. Total annual costs for the production of tuber and tops in large bales in western Canada, where Jerusalem artichoke is likely to be grown in rotation with cereals, were \$3,879.03 and \$1,577.66, respectively, for a land price of \$1,000·ha^{-1}. In eastern Canada, the total annual

TABLE 14.1
Annual Cost of Producing Jerusalem Artichoke Tubers and Tops in Large Bales, Given a Land Value of Canadian $2500·ha^{-1}, in Quebec (1990 Costs)

Item	Tubers Cost ($·ha^{-1})	Tops in Large Bales Cost ($·ha^{-1})
Variable costs:		
Seed tubers (1675 kg·ha^{-1})	492.45	98.49
Fertilizer	139.33	139.33
Herbicide (Treflan)	16.29	16.29
Herbicide (Dicamba)	14.12	5.65
Fungicide	54.47	10.89
Insecticide	0.00	0.00
Baler twine	—	11.00
Plowing and vibroshank	15.22	3.05
Spraying operations	4.16	2.90
Planting and hilling	27.13	—
Planting, fertilizing, mowing, and tossing	—	13.30
Cutting tops and harvesting	59.46	—
Raking and round baling	—	6.98
Transport to farm	89.16	5.70
Labor	466.73	103.20
Crop insurance	109.48	18.78
Interest on operating capital (15.5%)	230.64	67.51
Total variable costs	1,718.64	503.07
Fixed costs:		
Management	149.05	120.68
Tractor and machinery	544.61	335.96
Interest on land (13%)	325.00	325.00
Taxes on land (0.3%)	7.50	7.50
Other insurance	2.42	2.42
Total fixed costs	1,028.58	791.56
Transportation	231.65	67.24
Storage	820.08	130.27
Total costs	3,798.95	1492.14

Source: Adapted from Frappier, Y. et al., Baker, L., *Farm Level Costs of Production for Jerusalem Artichoke: Tubers and Tops*, Working Paper 90-2, Macdonald College of Agricultural Economics, Quebec, Canada, 1990.

production cost for tubers was $5,301.78 for a land price of $1,000·ha^{-1}, while the annual cost for the production of tops in large bales was $2,696.26 (Frappier et al., 1990). However, when the crop is grown for bioethanol production, land price turns out to be a minor factor in comparison to crop yield and conversion factor (liters of ethanol per tuber weight) (see below).

Tractor and machinery costs are higher for "seed tuber" production than for top production. For tuber production, machinery is needed for seed preparation (e.g., slicer, seed powderer), seedbed preparation (e.g., plow, vibroshank), planting (e.g., two-row potato planter), spraying, fertilizer application, the pulling of sprayers and other devices (i.e., three tractors: 112, 60, and 40 kW), hilling (e.g., six-row cultivator), cutting tops, and harvesting (e.g., potato harvester, wagon, boxes).

For top production, machinery is required for seed preparation, seedbed preparation, planting, spraying, fertilizer application, the pulling of sprayers and other devices (i.e., two tractors: 60 and 40 kW), harvesting (e.g., mower conditioner, round baler), and handling (e.g., wagon, fork). A storeroom is required for tuber storage, and a shelter for baled tops, with total storage costs much higher for tubers than for tops (Table 14.1). Storage costs for tubers were based on the total operating costs for a refrigeration storeroom for bulk potatoes having a capacity of 1,014 tonnes, and included depreciation, insurance, electricity, and building maintenance (Frappier et al., 1990).

Storage cost estimates for tubers in Georgia in 1998 were made by Kays (unpublished data), assuming a refrigerated space of 40 × 80 × 200 ft (640,000 ft^3), which holds 925 MT of tubers. The tubers would generate heat of 111 $J \cdot kg^{-1} \cdot h^{-1}$ and have a respiration rate of 10.2 mg $CO_2 \cdot kg^{-1} \cdot h^{-1}$ at 0°C. The energy required to cool this space, if full of tubers, is 1 $kW \cdot ft^{-3} \cdot year^{-1}$, or 320,000 kW for 6 months (the approximate storage time required for processing). Using electrical costs based upon GA Power figures for 1998 — $16.75 base charge per month and over 200,000 kWh usage at $0.06667 kWh — total energy costs will be $21,344 for 6 months. The building cost, based on construction costs provided by John Avilies (CS Integrated), for the store size of 40 × 80 × 200, at $65·$ft^{-2}$, will be $1,040,000, depreciating at 4.5% per year over 35 years, or $46,800 per year. Therefore, the total cost for storing 925 MT of tubers for 6 months is $68,144, or $75·$MT^{-1}$ of tubers ($0.034 per pound). If the raw product is around $0.03 per pound, storage effectively doubles the raw product cost. Locations where *in situ* storage is possible would have a distinct advantage.

A framework for assessing the profitability of alternative (energy) crops, in comparison to traditional (food) crops, was developed by Caserta et al. (1995). The model assumes that a farmer will only choose an energy crop (e.g., Jerusalem artichoke) if its gross margin (GM_e) is equal to or higher than that of the traditional crop (GM_f). The gross margin is given by the difference between the income received from the saleable product and by-products (taking into account any subsidies and financial incentives) and the variable costs of its production. A threshold price (TP) is thereby established, which is the minimum price the alternative energy crop can be sold for in order to obtain a gross margin equal to that of the traditional crop. If the threshold price for the alternative crop is higher, then it becomes economically convenient for the farmer to grow it.

This economic framework was used to compare six energy crops, including three potential feedstocks for bioethanol production in Europe (Jerusalem artichoke, sugar beet, and sweet sorghum), with the data of particular relevance to several Italian provinces. In Europe, a key subsidy relates to set-aside land, on which energy but not food crops can be grown. The estimated subsidy for Jerusalem artichoke on set-aside land in the mid-1990s was 270 ECU·ha^{-1} (Caserta et al., 1995). The total cultivation cost for Jerusalem artichoke was, on average, estimated as 2,147 ECU·ha^{-1}, although considerable variation may occur. This cost was lower than for sugar beet (2,356 ECU·ha^{-1}), but higher than for sweet sorghum (1,606 ECU·ha^{-1}). Yields of Jerusalem artichoke were, on average, 49 t·ha^{-1}, higher than for sugar beet (32 t·ha^{-1}) and slightly lower than for sweet sorghum (52 t·ha^{-1}). The threshold prices for the primary energy products of Jerusalem artichoke ranged from 16 to 37 ECU·ha^{-1} on productive land and 10 to 30 ECU·ha^{-1} on set-aside land, enabling a lower selling price to be economically convenient on set-aside land. The threshold price decreases as crop yield increases, and there is scope through research and development to raise Jerusalem artichoke productivity. The cost of the agricultural phase in relation to the bioethanol product was, on average, 267 ECU·1,000 l $ethanol^{-1}$ on productive land and 194 ECU·1,000 l $ethanol^{-1}$ on set-aside land for Jerusalem artichoke. The agricultural phase costs in this analysis were lower than the equivalent gasoline price (Caserta et al., 1995).

An optimal production plan for Jerusalem artichoke within Dutch agriculture was developed by Koster and Schneider (1989), using a decision scheme and a linear programming model (Linea), taking into account four phases: production, primary processing, industrial processing, and marketing. The estimated production cost was 2,382 Dutchflorins (Dfl) ·ha^{-1} (seed tubers, 640 Dfl·ha^{-1}; fertilizer, 287 Dfl·ha^{-1}; pest control, 128 Dfl·ha^{-1}; capital costs, 250 Dfl·ha^{-1}; planting and harvesting, 990 Dfl·ha^{-1}; plus insurance, farmers' union tax, and tare contribution). Labor and land costs were

not included. In a cropping plan for 55 ha in northeast Netherlands, the gross margin for Jerusalem artichoke was estimated as 2,500 Dfl·ha^{-1}, which equates to the minimum financial yield required before the crop can be put into the cropping plan. In comparison, gross margins for winter wheat, fodder maize, and sugarbeet were 2,250, 1817, and 3,935 Dfl·ha^{-1}, respectively. The cropping plan was determined not only by gross margins, but also by rotation requirements and labor availability. Tuber yields were assumed to be averaging 45 t·ha^{-1}. A total financial yield of around Dfl 4,882 was needed to obtain a gross margin of 2,500 Dfl·ha^{-1}, requiring a minimum or threshold price of 108 Dfl·t^{-1} of tubers. Harvesting both the tubers and tops enhances the financial return on Jerusalem artichoke, and the value gained through a variety of by-products could ultimately determine whether Jerusalem artichoke features as a significant industrial crop within European cropping systems.

14.2 BIOFUEL PRODUCTION

Jerusalem artichoke has good potential as a biomass feedstock for the production of bioethanol (see Chapter 7). However, estimating the economic viability of bioethanol production from energy crops can be problematic. The cost of producing bioethanol from energy crops can vary, for instance, due to site-specific costs of land, feedstock, and processing, while economic viability is primarily dependent on the cost of competing fossil fuels, and this relationship may shift suddenly and unpredictably. In general, key factors determining economic viability are capital costs, feedstock costs, the value of by-products, levels of subsidy, the presence of tax incentives, and bioethanol yield (Baker et al., 1990; von Sivers and Zacchi, 1996).

Production costs depend on crop yields and include the costs of cultivation, harvesting, and transport to biorefineries. Jerusalem artichoke has relatively low cultivation costs compared to other energy crops, as it generally requires low inputs in terms of irrigation, fertilization, and pesticides. The distance between crop and biorefinery can be an important factor, as found for maize, where transport distances of around 15 miles are considered the upper limit in terms of an overall cost-effective energy balance (RFA, 2006). Ranged against this is the size of the biorefinery facility, with low capacities being less economically viable than larger capacities.

Economic evaluations of the farm-scale production of ethanol from Jerusalem artichoke (tops and tubers) in Canada have been conducted, for different processing plant sizes, in Quebec, western Canada, and eastern Canada (Baker et al., 1990; Frappier et al., 1990; Kosaric et al., 1982; Kosaric and Vardar-Sukan, 2001). The cost of ethanol production varied by land price and region. The total cost of tuber production per hectare varied from a high of Canadian $4,432 to a low of $3,502, while the total cost of producing tops (in large bales) per hectare varied from a high of $1,493 to a low of $1,195. For both tubers and tops, the cost of production per area decreased as land value decreased, with costs lowest on the least expensive land in parts of Quebec. However, higher yields in western Canada compared to Quebec (53 cf. 41 t·ha^{-1} for tubers and 100 cf. 41 t·ha^{-1} for tops) accounted for a relatively low cost per ton, which more than compensated for land price. Operator returns, for instance, given a comparable land value of 1,100 $·ha^{-1}, were 107 and 160 $·ha^{-1} for tubers in Quebec and western Canada, respectively (Kosaric and Vardar-Sukan, 2001). Ethanol feedstock costs, given upper and lower values for Jerusalem artichoke yield ranges, for two land prices in western Canada and Quebec are summarized in Table 14.2. The data show that feedstock costs decrease considerably with increased yield, whereas land price has a relatively minor effect. As the conversion factor of biomass to ethanol increased, feedstock costs were further reduced (Table 14.3). For instance, in Quebec (land price, 2,500 $·ha^{-1}), given a high tuber yield (76 t·ha^{-1}), feedstock costs for ethanol production dropped from 0.50 l·t^{-1} (conversion factor, 100 l·t^{-1}) to 0.42 and 0.33 $·l^{-1}, with conversion factors of 120 and 150 l·t^{-1}, respectively (Kosaric and Vardar-Sukan, 2001). In regional terms, yields of tubers and tops are the decisive factor. Ethanol production from tubers is most economical at the farm level in Quebec, while western Canada is advantageous in economic terms for ethanol production from tops (Frappier et al., 1990). Above-average Jerusalem artichoke yields needed to be achieved in Quebec and western Canada (given 1990 prices), however,

TABLE 14.2
Ethanol Feedstock Costs (Canadian $·l), for Upper and Lower Values of Jerusalem Artichoke Tuber and Tops Yield Ranges, for Different Land Prices in Western Canada and Quebec, Given a Conversion Factor of Biomass to Ethanol of 100 l·t^{-1}

Region	Western Canada		Quebec	
Land price ($·ha^{-1})	1,100	500	2,500	675
Crop yield (t·ha^{-1}):				
Tubers (30)	1.29	1.27	1.27	1.17
Tubers (76)	0.51	0.50	0.50	0.46
Tops (30)	0.26	0.25	0.50	0.40
Tops (100)	0.12	0.11	0.15	0.12

Source: Adapted from Kosaric, N. et al., Ethanol from Jerusalem Artichoke Tubers, paper presented at Bioenergy R&D Seminar, Winnipeg, Canada, March 20–31, 1982; Kosaric, N. and Vardar-Sukan, F., in *The Biotechnology of Ethanol: Classical and Future Applications*, Roehr, M., Ed., Wiley-VCH, New York, 2001, pp. 90–226.

TABLE 14.3
Ethanol Feedstock Costs (Canadian $·l) for Lower, Middle, and Upper Values of Tuber Yield Range, and Increasing Ethanol Conversion Factors (l·t^{-1} tubers), Given a Land Price of $2,500·ha^{-1} in Quebec

Conversion factor (l·t^{-1})	Tuber Yield (t·ha^{-1})		
	30	50	76
80	1.58	0.95	0.62
100	1.27	0.76	0.50
120	1.06	0.63	0.42
140	0.90	0.54	0.36
150	0.84	0.51	0.33

Source: Adapted from Frappier, Y. et al., Baker, L., *Farm Level Costs of Production for Jerusalem Artichoke: Tubers and Tops*, Working Paper 90-2, Macdonald College of Agricultural Economics, Quebec, Canada, 1990; Kosaric, N. and Vardar-Sukan, F., in *The Biotechnology of Ethanol: Classical and Future Applications*, Roehr, M., Ed., Wiley-VCH, New York, 2001, pp. 90–226.

TABLE 14.4
Cost Breakdown and Comparison (Canadian $) for the Production of Ethanol from Jerusalem Artichoke, for Three Farm-Scale Processing Plant Sizes

	Processing Plant Size		
Costs/Credits	**$3.0 \cdot 10^5$ kg**	**$3.6 \cdot 10^6$ kg**	**$4.0 \cdot 10^6$ kg**
Fixed operating costs	0.75	0.63	0.30
Direct operating costs	0.20	0.20	0.29
Raw material	0.17	0.17	0.17
By-product credits	0.55	0.55	0.55
Net cost of ethanol ($·l)	0.55	0.43	0.21

Source: Adapted from Kosaric, N. et al., Ethanol from Jerusalem Artichoke Tubers, paper presented at Bioenergy R&D Seminar, Winnipeg, Canada, March 20–31, 1982; Kosaric, N. and Vardar-Sukan, F., in *The Biotechnology of Ethanol: Classical and Future Applications*, Roehr, M., Ed., Wiley-VCH, New York, 2001, pp. 90–226.

for the bioethanol produced to be competitive (e.g., with bioethanol produced from maize/corn) as a transportation fuel (Baker et al., 1990).

The cost of on-farm ethanol production decreased as processing plant size increased, from a net ethanol cost of 0.55 $\$\cdot l^{-1}$ with a plant capacity of 3×10^5 kg feedstock to 0.21 $\$\cdot l^{-1}$ for a plant capacity of 4×10^6 kg feedstock (Kosaric et al., 1982). Raw material (Jerusalem artichoke tops and tubers) and by-product credits, from the sale of protein-rich pulp and stillage, remained constant, while fixed operating costs (e.g., depreciation, maintenance, labor, and taxes) were considerably reduced for a larger plant size (Table 14.4). For a plant with a capacity of 4×10^6 kg, ethanol cost was estimated to be about 40% of the price of gasoline in Canada in 1995 (Kosaric and Vardar-Sukan, 2001).

In an analysis of feedstock requirements and output for a 100×10^6 liter processing plant with Jerusalem artichoke tubers, it was shown that the overall ethanol production cost was sensitive to both input feedstock cost and the value of the feed by-product obtained. Each change in feedstock cost of $4 per ton resulted in a change of about 5 cents per liter in the cost of production, while each change of $20 per ton in soymeal price (on which by-product credit is based) translates into a change of 1.4 cents per liter in the cost of production (Kosaric and Vardar-Sukan, 2001). Favorable energy balances obtained for maize in the U.S. also partly rely on energy credits arising from animal feed by-products (Hill et al., 2006). The energy input costs of cultivating Jerusalem artichoke are likely to be lower, although the sale of by-products, such as tuber pulp, protein concentrate, and animal feed, will similarly be key to the economic feasibility of using it as an energy crop.

The total annual variable production costs for Jerusalem artichoke grown as a potential feedstock for ethanol production in Australia were estimated as (Australian dollars) $\$1{,}606 \cdot ha^{-1}$ and $\$1{,}126 \cdot ha^{-1}$ for tubers and tops (as an annual), respectively, by Parameswaran (1995). The additional costs of harvesting and cleaning the tubers ($\$480 \cdot ha^{-1}$) mainly accounted for the difference (as tops are cut and removed anyway for tuber harvest). Irrigation is a significant production cost in Australia, estimated at $\$256 \cdot ha^{-1}$ annually (including water and labor). The other major costs, which were effectively the same for tubers and tops, were for seed tubers ($\$90 \cdot ha^{-1}$), fertilizers ($\$235 \cdot ha^{-1}$), and labor for planting and cultivation ($\$190 \cdot ha^{-1}$). Total variable production costs were higher than for maize ($\$880 \cdot ha^{-1}$), the established feedstock for ethanol production, especially when maize was compared to Jerusalem artichoke tubers. However, the production costs of ethanol from Jerusalem artichoke tubers and maize were estimated as 46 to 65 cents$\cdot l^{-1}$ and 49 to 61 cents$\cdot l^{-1}$ ethanol,

respectively, assuming 440 l·t^{-1} and 350 l·t^{-1} fermentable material (based on higher yields per hectare of fermentable sugars for Jerusalem artichoke). It was concluded from this analysis that Jerusalem artichoke tubers could be a competitive feedstock for ethanol production if tuber yields of about 70 to 80 t·ha^{-1}, yielding 15 to 16 t·ha^{-1} of fermentable sugar, were obtained. It was further noted that energy crops should ideally not compete for land with high-quality food or fiber crops. Jerusalem artichoke grown on marginal agricultural land therefore is seen as having good potential as a bioethanol feedstock in Australia (Parameswaran, 1994, 1995).

In Spain, it has been concluded that Jerusalem artichoke is a potentially viable economic alternative to sugar beet and maize as a feedstock for bioethanol. Furthermore, it was suggested that biomass from all these crops could be used to profitably substitute for gasoline, provided that taxes on hydrocarbons were completely removed from bioethanol fuels (Fernandez, 1998). The main production costs for Jerusalem artichoke in Spain are sowing, fertilization, irrigation, harvesting, and transport (Table 14.5), with fertilization, sowing, harvesting, and transport accounting for the highest energy inputs, and irrigation the most man-hours of labor (Fernandez et al., 1988). Crop production costs on irrigated land were given as 1,098 ECU·ha^{-1}, including harvesting and transport (Fernandez, 1998). Tuber pulp was sold as a by-product, with 0.5 kg of tuber pulp obtained per liter of ethanol produced, while dry stems were used as a local fuel (e.g., in the biorefinery). Given an annual tuber yield of 68,000 kg·ha^{-1}, and with 12 kg of tubers producing 1 l of bioethanol, production costs were 0.192 ECU·l^{-1} of bioethanol. The size of the biorefinery or distillery affected ethanol production cost, as expected from previous studies. The fixed and variable distillery costs, in a plant producing 40 million l of ethanol per year, were around 0.09 ECU·l^{-1}, with the dry stems used as a fuel (0.147 ECU·l^{-1} otherwise). Gross production costs were therefore 0.282 ECU·l^{-1}.

TABLE 14.5
Estimated Energy Inputs and Relative Production Costs (% of Total) per Hectare for Jerusalem Artichoke Grown in the Duero Basin, Spain

Item	Energy Input (Mcal·ha^{-1})	Manpower (6 Mcal·h^{-1})	% of Total Production Costs
Stubble plowing	250	15	3.71
Cultivating	100	6	1.48
Basic fertilization	124	3	12.54
Harrowing	100	5	1.18
Tuber preparation	—	—	1.10
Sowing	1,460	120	12.02
Herbicide treatment	100	3	2.73
Surface fertilization	951	3	4.21
Cultivating	150	9	2.22
Furrow irrigation	—	240	11.65
Stem harvesting	300	18	5.78
Tuber harvesting	600	36	16.90
Stem transport[a]	240	14	3.42
Tuber transport[a]	1,320[b]	108[b]	21.06

[a] Local transport only (average distance 10 km).

[b] Includes tuber loading.

Source: Adapted from Fernandez, J., in *Topinambour (Jerusalem Artichoke)*, Report EUR 11855, Grassi, G. and Gosse, G., Eds., Commission of the European Communities (CEC), Luxembourg, 1988, pp. 153–157.

TABLE 14.6
Production Costs of Jerusalem Artichoke for Bioethanol Production in Denmark in 1987

Item	Cost (ECU·ha^{-1})	% of Production Cost
Soil preparation	95.09	8.48
Fertilization	241.28	21.52
Seed tubers	284.01	25.33
Planting and cultivation	145.43	12.97
Harvesting (tops and tubers)	166.73	14.87
Transport	112.59	10.04
Miscellaneous	76.07	6.79
Production costs	1,121.20	100

Source: Adapted from Zubr, J., in *Topinambour (Jerusalem Artichoke)*, Grassi, G. and Gosse G., Eds., Report EUR 11855, Commission of the European Communities (CEC), Luxembourg, 1988, pp. 165–175.

Given an ethanol purchase price of 0.544 ECU·l^{-1}, gross profit per hectare was calculated to be 1505 ECU·ha^{-1}, or more if tuber pulp sales are included (Fernandez, 1998).

In Denmark, the costs of producing ethanol from Jerusalem artichoke were calculated in 1987 by Zubr (1988b). Total production costs were calculated as 1,387 ECU·ha^{-1}, after 266 ECU in land charges compensation was added to production expenses of 1,121 ECU·ha^{-1} (Table 14.6). The costs of seed tubers and fertilization were the major production costs. Raw material costs from Jerusalem artichoke for bioethanol production were calculated from total production expenses after subtracting the value of by-products. Given fresh weight tuber yields of 39 t·ha^{-1}, the cost of producing tubers was estimated as 31.62 ECU·t^{-1} (176.11 ECU·t^{-1} volatile solids). The cost of producing tops, assuming yields of 32 t·ha^{-1} and taking into account transport expenses and the value of macronutrients, was 4.83 ECU·t^{-1} (22.71 ECU·t^{-1} volatile solids). To estimate production costs of bioethanol, the cost of raw materials was expressed per unit of fuel, taking into account the efficiency of alcoholic fermentation, capital depreciation, and processing expenses. The production cost of alcohol from Jerusalem artichoke tubers was estimated to be 0.55 ECU·l^{-1}, of which 46.9% represented raw material costs. At 1987 prices, ethanol produced from Jerusalem artichoke was not competitive with fossil fuels. However, by-products make Jerusalem artichoke more cost-effective. In addition to ethanol, tuber residues left after alcoholic fermentation, along with fresh and ensiled tops, were used for methane (biogas) production in the Danish analysis. The cost of producing methane was calculated as 0.15 ECU·m^3, 0.12 ECU·m^3, and 0.10 ECU·m^3, for tuber residue, tops, and ensiled tops, respectively (Zubr, 1988b).

Higher yields of biogas can be obtained if the crop is grown predominantly for top production. An economic analysis for the aerial parts of Jerusalem artichoke as a feedstock for biogas production in Sweden was conducted by Gunnarson et al. (1985). It was assumed that biogas production, by combined hydrolysis and methanogenic digestion, was 210 m^3 EO (m^3 equivalent of oil = 10 MWh), corresponding to the aboveground yield from 75 ha (i.e., equivalent to six to eight farms). The energy content in this aboveground biomass is sufficient to heat, for example, a small factory in Sweden. The total costs of producing and using Jerusalem artichoke for fodder, food, and energy purposes were calculated as 13,680 Swedish crowns (SEK) per hectare in 1984 (when U.S.$1 = 8.24 SEK). Costs incurred were related to cultivation, harvesting, conservation, digestion, and the combustion of biogas (Table 14.7). Planting the tubers was the main cultivation cost (3,530 SEK·ha^{-1}), with soil preparation (110 SEK·ha^{-1}) and weeding (430 SEK·ha^{-1}) incurring lower costs.

TABLE 14.7
Costs of Producing and Using Jerusalem Artichoke, and Revenues Needed from Fodder, Methane (Biogas), and Tubers to Break Even, in Sweden in 1984

Item	Swedish Crowns·ha^{-1}
Cost:	
Cultivation	4,070
Harvesting	4,840
Conservation	2,390
Digestion	1,150
Combustion	1,230
Total costs	13,680
Revenue:	
Fodder product	920
Methane (biogas)	8,960
Tubers	3,800

Source: Adapted from Gunnarson, S. et al., *Biomass*, 7, 85–97, 1985.

Machinery used for potatoes needed to be adjusted for the planting and harvesting of Jerusalem artichoke, because of the small and irregular tubers. Harvesting the tubers was more expensive (3,400 SEK·ha^{-1}) than harvesting aboveground parts (1,440 SEK·ha^{-1}). Green material was stored in horizontal silos for conservation (2,390 SEK·ha^{-1}). It was assumed that three different products could be obtained in the Swedish study: biogas; a fodder product from the residues of the digestion process; and the tubers for use as a table vegetable, fructose source, or seed for future plantings. With the crop grown primarily for tops (which are harvested at their peak in September and October), tuber yields were assumed to be half normal yields. To break even, the annual revenues were estimated as 8,960 SEK·ha^{-1} for the biogas, 920 SEK·ha^{-1} for the fodder product, and 3800 SEK·ha^{-1} for the tubers. The analysis showed that it would be possible, under the circumstances of the study, to obtain an economically feasible system, providing that the minimum marketing price of tubers did not fall below 0.34 SEK·kg^{-1} (Gunnarson et al., 1985).

Bioethanol can be processed into fuel additives, especially ethyl tert-butyl ether (ETBE), and this adds value because the market price for ETBE is significantly higher than for pure ethanol. In a European study in the early 1990s, ethanol production from Jerusalem artichoke and other biomass crops could not compete with gasoline in the absence of subsidies for bioethanol production. However, the economics were much more favorable when bioethanol was converted to ETBE and other additives, because ethanol can then command a higher selling price (Spelman, 1993). In North America, bioethanol is similarly more profitable when sold in the form of an octane enhancer, or in blends with gasoline, than when sold as pure bioethanol (gasohol). In 1989, for instance, the ethanol price, when used as an octane enhancer, was as high as Canadian \$0.37·l^{-1} in a methanol/ethanol blend (M5E3), but as low as \$0.25·l^{-1} for gasohol (Heath, 1989; Baker et al., 1990). Therefore, Jerusalem artichoke is most likely to be competitive as an energy crop if the ethanol produced from it is used for ETBE and other gasoline additives rather than as a petroleum replacement. However, bioethanol is increasingly competitive with gasoline, due to increases in gasoline prices and financial incentives that favor non-fossil fuels. The increase in biorefineries seen in the U.S. in 2006, for instance, was market driven.

14.3 INULIN

The two crop plants that accumulate inulin in sufficient quantities for its commercial extraction are chicory (*Cichorium intybus* L.) and Jerusalem artichoke. Chicory is currently the predominant source of plant-derived inulin, with relatively little extracted from Jerusalem artichoke. The predominance of chicory for inulin extraction is largely due to it replacing sugar beet (*Beta vulgaris* L.), with sugar beet extraction machinery suitable for the processing of chicory. Therefore, Jerusalem artichoke must be seen to have financial or other advantages over chicory for it to gain in importance as a feedstock for inulin and fructooligosaccharide production.

The three largest European inulin producers all use chicory as a feedstock:

- Orafti, based in Belgium, was regarded as the market leader in 2006. It operates in 75 countries and sells inulin under the Beneo™ brand. Products include the Synergy® inulin range, Raftiline® inulin, Raftilose® oligofructose, and Raftisweet® fructose syrups.*
- Cosucra (Cosucra Group Warcoing) is also based in Belgium and produces inulin ingredients under the Oliggo-Fiber® brand name.** Cargill Health and Food Technologies hold exclusive marketing rights in North America.
- Sensus is based in the Netherlands and produces inulin and inulin-derived products under the Frutafit® and Frutalose® brand names.*** Calleva has marketing rights in the U.K.

In addition, Beghin Meiji produces synthetic fructooligosaccharides, which are not plant derived.

The three producers (Orafti, Cosucra, and Sensus) supply inulin to major food manufacturers, including Danone, Heinz, Kellogg, Müller Dairy, Nestlé, and Unilever. Inulin has been predominantly used in dairy products, such as yogurts, but is being added to an ever-increasing range of foods for its prebiotic effects and other properties (see Chapter 6), which can raise the food's market value. In recent years, there has been a rapidly growing market for functional foods, and therefore for inulin and fructoligosaccharides (oligofructose).

The increasing global demand for inulin has resulted in an expansion in chicory production. Chicory is grown as an annual crop, so producers have to predict increasing demand a year in advance. The greater area of chicory under cultivation each year has mainly been processed through the ongoing conversion of sugar beet processing facilities (as demand for sucrose falls), although purpose-built facilities have also been constructed. Orafti has converted a number of sugar beet processing facilities, including one in Oreye, Belgium, in 1999, which in 2006 remained the largest chicory extraction unit in the world (400,000 tonnes of roots annually). Orafti invested 165 million euros to build a second chicory extraction plant in Chile, which was operating by 2006. Southern hemisphere production, acting as a useful counterseason to European production, helps to meet predicted global demand for inulin. The Warcoing group has processed sugar beet since the mid-1800s, but as Coscura, in 2003, it completely switched to concentrate on inulin and health foods. Cosucra converted a former sugar beet factory in northern France to significantly raise annual production in 2006. The prebiotic market is likely to continue growing, with the global growth consultants Frost & Sullivan predicting annual growth of 9.7% up to 2010, making the European fructan (inulin and oligofructose) market worth around £180 million by 2010 (Anon., 2004; Orafti, 2006).

The price of inulin has been around 2.5 to 3.0 euros per kilo in recent years (2006) and has remained relatively stable because the producers have been successful in predicting the year-on-year increase in demand for inulin. Price rises for inulin products occurred in 2004 due to rising oil prices, which increased on-farm and processing production costs. Orafti raised the prices of its

* Registered trademarks of Orafti, Tienen, Belgium.
** Registered trademark of Cosucra, Warcoing, Belgium.
*** Registered trademark of Sensus, RG Roosendaal, The Netherlands.

Raftiline inulin and Raftilose oligofructose, for example, by around 4% in January 2005 (Anon., 2004).

Chicory production is likely to continue increasing to meet demand for inulin. However, additional sources of inulin are also under investigation. Jerusalem artichoke tubers are a rich source of inulin, and the crop can offer some advantages over chicory. In particular, it can grow in areas where chicory root yields are poor, increasing the overall area on which inulin-producing crops can be grown. The agronomic performances of chicory and Jerusalem artichoke were compared in Germany, with Jerusalem artichoke storage organ yield losses through weed competition, under irrigation, and with no weed control being much lower than for chicory (8% cf. 47%). The ability to grow Jerusalem artichoke with no or minimal weed control is a distinct commercial advantage, although in the German study savings on herbicide costs did not compensate for the lower sugar yields obtained from Jerusalem artichoke. Severe water stress caused similar yield loss in both crops (Schittenhelm, 1999). In other studies, comparing agronomic performance of Jerusalem artichoke with those of chicory and sugar beet, yields of Jerusalem artichoke were generally lower (Meijer et al., 1993; Sah et al., 1987; Thome and Kühbauch, 1987; Zubr, 1988a), although sugar yields were superior to chicory yields in a U.S. study (Haber et al., 1941). An advantage of chicory over Jerusalem artichoke is that its inulin profile is richer in molecules with higher chain lengths (degree of polymerization). Chicory has around 71% of its inulin having a degree of polymerization over 9 and over, for instance, while the equivalent figure for Jerusalem artichoke is 48% (Bornet, 2001). Inulin with a higher average degree of polymerization can command higher prices, as it is preferred for many high-value food and nonfood applications.

One of the major inulin producers probably needs to become involved in the processing of Jerusalem artichoke before it can start to become established as a significant industrial crop in Europe. To become a viable alternative to chicory as a source of inulin, Jerusalem artichoke needs to match chicory's gross margins and profitability. In the Netherlands, chicory was grown on 4,250 ha in 1998, with an average productivity of 35,000 to 50,000 $kg \cdot ha^{-1}$. Production costs and gross margin per hectare (1998) were 2,484 and 1,481 euros, respectively. Sensus is the single processor of chicory roots in the Netherlands (where the crop is combined with that produced in Belgium). Jerusalem artichoke has good potential as an industrial crop for the Netherlands, however, because it is adapted to light soils, has a large gene pool to facilitate genetic improvement, and can be utilized to produce a wide range of food and nonfood by-products (Stutterheim and Struik, 1998). The types of by-product exploited, in addition to inulin, may be key to Jerusalem artichoke's future success as a European crop.

In addition to pure inulin and fructooligosaccharides, Jerusalem artichoke is processed in a number of different ways for the health food market. Jerusalem artichoke flour is used in a wide range of foods, such as pasta for diabetic diets, for example, while extracts are sold in pill form for their health-promoting properties.

14.4 FUTURE PROSPECTS FOR UTILIZING JERUSALEM ARTICHOKE

Jerusalem artichoke provides the raw material for a wide range of products (Table 14.8). For example, it can be used as a vegetable, as animal feed, as a source of inulin, and as a bioethanol feedstock. It is therefore a very versatile crop. Jerusalem artichoke can be grown as an annual or a perennial, depending on its end use, while all parts of the plant can be utilized, for food, feed, industrial, or energy applications. By-products will be important in determining the economic feasibility of using Jerusalem artichoke in preference to other crops or feedstocks. While using the tubers as a source of inulin, for instance, the tops can be used for fodder, energy production, or the manufacture of low-quality paper or fiberboard.

The demand for two products obtainable from Jerusalem artichoke — inulin and bioethanol — dramatically increased at the start of the 21st century, as they help address key health, energy and environmental challenges faced by society. Inulin ingredients in foods help combat obesity and

TABLE 14.8
Main Products and By-products Obtainable from Jerusalem Artichoke

Product	Plant Part
Inulin	Tubers
Vegetable	Tubers
Fodder	Tops and tubers
Seed tubers	Tuber
Oligofructose	Tubers
Fructose	Tubers
Flour	Tubers
Juice	Tubers
Extract (in health products)	Tubers
Ethanol	Tops and tubers
Gasoline additive (EMBE)	Tops and tubers
Biogas (methane)	Tops
Animal feed pellets	Tops and tubers
Pulp for animal feed	Tops and tubers
Protein concentrate	Leaves
Pulp for paper/fiberboard	Stalks
Furfural	Stalks

diabetic epidemics, while bioethanol helps to decrease our dependency on nonrenewable oil resources and improves air quality.

Inulin is predominantly produced from chicory, with Jerusalem artichoke the main alternative crop source. There is a growing market for inulin in the food industry, as a prebiotic ingredient, a low-calorie sweetener and fat replacement, and a thickener and bulking agent. In addition, inulin can be converted to a wide range of chemicals with numerous food and nonfood industry applications (Table 14.9). The different chain length profiles of inulin, oligofructose, and fructose are suited to different food industry applications, while purified inulin and some of its derivatives also have medicinal and diagnostic uses. Industrial products obtained from the chemical processing of inulin include alcohol, polymers, epoxides, and resins. They have many industrial uses, for example, as plasticizers, surfactants, binders, and emulsions (Table 14.9).

The potential applications of Jerusalem artichoke are continuing to increase as technologies advance. Meanwhile, global climate change will alter agricultural landscapes during the 21st century. The area of land suitable for Jerusalem artichoke production will massively increase in Canada, Alaska, and northern Europe (from Scotland to Siberia), by 2070 (Canadian Forestry Service, 2006; Tuck et al., 2006).

A wide range of cultivars and clones have been described for Jerusalem artichoke, although there has been little in the way of systematic breeding compared to other crops. Nevertheless, there is a considerable gene pool available for genetic improvement, in wild populations and via hybridization with other *Helianthus* species. For Jerusalem artichoke to achieve its potential, there is a need for improved cultivars, bred for either high-quality or high-quantity production of a particular plant part or component (e.g., tuber size or inulin content), or bred for high productivity as a multipurpose crop (e.g., energy and by-product). In the short term, field trials can identify existing clones that have the most promise for particular situations and applications. Jerusalem artichoke may then start to be fully exploited as a valuable resource.

TABLE 14.9
Potential Uses of Inulin from Jerusalem Artichoke[a]

Chemical	Applications
Inulin prebiotic	Ingredient in numerous foods
Inulin dietary fiber	Low-calorie fiber/bulking agent and thickener
Inulin ingredient	Fat replacement in low-calorie foods
Inulin ingredient	Sweetener/low-calorie sugar replacement
Oligofructose prebiotic	Ingredient in numerous foods
Fructose (crystallized)	Numerous food industry uses
Fructose (syrups)	Numerous food industry uses
High-fructose syrups	Numerous food industry uses
Highly purified inulin	Medicinal/diagnostic uses
Fructooligosaccharides	Numerous food industry uses
Cyclic inulooligosaccharides	Many potential industrial uses
Fructose dianhydrides	Low-calorie sweeteners
Furfural	Solvent, used in oil refining and in resins
Hydroxymethylfurfural	Numerous industrial uses
Mannitol	Numerous industrial uses
Glycerol	Numerous food and nonfood industry uses
1,2-Propanediol	Food, nonfood, and medicinal uses
Ethylene glycol	Antifreeze
Acetone	Numerous industrial uses
Butanol	Numerous industrial uses
2,3-Butenediol	Fuel additive and use in plastics
Succinic acid	Numerous industrial uses
Lactic acid	Numerous food and nonfood industrial uses
Inulin esters	Plasticizers, surfactants, and binders
O-Succinoylated inulin	Drug carrier
Methylated inulin	Precursor for additional products
Inulin carbonates	Insolubilizaton of biologically active molecules
O-(Carboxymethyl)inulin	Detergent binder
Inulin ethers	Immunological assays
Dialdehyde inulin	Precursor for additional products
Inulin carbamates	Emulsions and suspensions
Inulin-amino acids	Medicinal usage
O-(Cyanoethyl)inulin	Paper industry usage
O-(3-Amino-3-oxopropyl)inulin	Emulsifier and surfactant
O-(Carboxyethyl)inulin	Inhibits precipitation of calcium carbonate
O-(3-Hydroxyimino-3-aminopropyl)inulin	Chemical industry uses
O-(Aminopropyl)inulin	Used in detergents
O-(Aminopropyl)inulin derivatives	Range of industrial uses, including cosmetics
Stearoyl amide	Surfactant and emulsifier, used in detergents
N-Carboxymethylaminopropylated inulin	Sequestering agent for detergents
Cycloinulohexaose derivatives	Used in cosmetics
Alkoxylated inulin	Stabilizing properties
Inulin phosphates	Thermally reversible gels
Complexing agents	Precipitation of heavy metals

[a] For further information on chemicals derived from inulin see Chapter 5.

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Appendix

PATENTS RELATING TO JERUSALEM ARTICHOKE*

The following is a listing of issued patents that refer to Jerusalem artichoke. The list is not comprehensive, however, because hundreds of other patents concern inulin and fructooligosaccharides, in which Jerusalem artichoke is a potential raw material.

The patents are separated into the following subject categories: medical and veterinary applications; food, drink, and nutraceutical applications; animal feed applications; nonfood industrial applications; genetic manipulation and biotechnology; and cultivation and plant breeding. Within categories the patents are arranged in reverse chronological order over the period from 2006 to 1908. The patent number, country of origin,** date, inventor, applicant, alternative patent numbers, international classification code, and brief synopsis of the patent are presented.

MEDICAL AND VETERINARY APPLICATIONS

1. Composition for prophylaxis and treatment of diseases caused with calcium deficiency (variants)
   Patent number: RU2271822 (2006)
   Inventor and applicant: Zelenkov, V.N. (Russian Federation)
   This invention relates to the production of a curative–prophylactic agent used in the treatment of calcium deficiency. The composition includes dried Jerusalem artichoke.
2. Chinese traditional medicine Jerusalem artichoke preparation
   Patent number: CN1698690 (2005)
   Inventor and applicant: Xu, Mingli (China)
   International classification: A61K35/78
3. Stabilizer for pharmacons
   Patent number: US6841169 (2005)
   Inventor: Hinrichs, W.L.J. and H.W. Frijlink
   Applicant: Rijksuniversiteit Groningen (Netherlands)
   Also published as: WO0078817 (A1), EP1194453 (A1), CA2375241 (A1), EP1194453 (B1), NL1012300C (C2), DE60001744T (T2)
   International classification: C08B37/00, C12N9/96, C12N11/10
   The invention relates to an auxiliary substance to accompany an active substance, such as a pharmacon. The auxiliary substance has a stabilizing action and a positive influence on the bioavailability of the active substance within pharmaceutical preparations. The auxiliary substance is based on a fructan (inulin of degree of polymerization (DP) over 6), obtained from Jerusalem artichoke or other sources.
4. Method for treating diabetic hepatosis
   Patent number: UA69748 (2004)

* *Sources:* European Patent Office, http://www.european-patent-office.org/, accessed May 2–6, 2006; U.S. Patent and Trademark Office, http://www.uspto.gov/patft/, accessed May 8–11, 2006.

** Abbreviations: AT, Austria; CA, Canada; CN, China; CZ, Czech Republic; DE, Germany; ES, Spain; EP, European Patent Office; FR, France; GB, Great Britain; HU, Hungary; JP, Japan; KR, South Korea; MD, Moldova; NL, Netherlands; RO, Romania; RU, Russian Federation; SE, Sweden; UA, Ukraine; US, United States; WO, World Intellectual Property Organization; YU, Yugoslavia.

Inventor and applicant: Neiko, Y.M., V.I. Botsurko, I.H. Babenko, and O.M. Sukholytka (Ukraine)
International classification: A61K35/74, A61K35/66
A method is described for treating diabetic hepatosis. Novel use is made of Jerusalem artichoke powder and live freeze-dried bifidus bacteria in an acid resistance capsule.

5. Bicarbonate process for preparing synanthrin from Jerusalem artichoke
Patent number: CN1359957 (2002)
Inventor: Ji, Ming, Qiwei Wang, and Ling Ji
Applicant: Ji Ming (China)
International classification: C08B37/00
An efficient bicarbonate process for preparing synanthrin from Jerusalem artichoke tubers is disclosed. It involves washing, shredding, leaching, removing impurities by the bicarbonate method, desalting and decoloring, and concentrating. This gives a high yield and quality of synanthrin, for use as a blood stabilizer in medicinal procedures.
6. Method for correcting selenium deficiency in children with exchange nephropathy
Patent number: RU2188030 (2002)
Inventor: Reshetnik, L.A., E.O. Parfenova, and Eva O.V. Prokop
Applicant: Ir G Med Univer (Russian Federation)
International classification: A61P3/00
This patent describes a dry powder of Jerusalem artichoke that can be prescribed per 0.5 g/kg of a child's body weight twice daily. The method enables the body to increase its supply of selenium.
7. Biological preparation for prophylaxis and treatment of young stock animals with gastroenteric diseases
Patent number: RU2180851 (2002)
Inventor: Shcherbakov, P.N., Ju. D. Karavaev, K.P. Jurov, and T.B. Shcherbakova
Applicant: Ural Skaja G Akademija Veterin (Russian Federation)
International classification: A61K35/66, A61K39/07
A biological preparation is described for use in veterinary medicine to treat gastroenteric disease. It comprises a culture of *Bacillus subtilis* 4/97 in nutrient medium. The nutrient medium consists of a decoction of the following medicinal plants: Jerusalem artichoke, common balm, and milfoil in specified ratios. The preparation has a high therapeutic effect and a broad spectrum of action.
8. Method of use of Jerusalem artichoke–base with biologically active additions as dietotherapeutic, curative–prophylactic agents
Patent number: RU2157227 (2000)
Inventor and applicant: Zelenkov, V.N. (Russian Federation)
International classification: A61K35/78
The invention relates to methods of using Jerusalem artichoke–base biologically active additions as curative–prophylactic agents, having broad-spectrum pharmacological action.
9. Plant extract used as cell growth factor medicament with antitumoral and anticancer activity
Patent number: FR2732347 (1996)
Inventor: Rebiere, C.J.P.
Applicant: Bio Media (France)
International classification: C07K14/415, A61K38/00
A plant extract is disclosed that comprises a combination of proteinic and glycoproteinic material, and includes Jerusalem artichoke or other plants.
10. Process for production of compositions for decreasing inflammation, disinfecting, and muscle leasining

Patent number: HU53531 (1990)
Inventor and applicant: Strukkel, I. (Hungary)
A preparation containing plant extract is described that reduces inflammation, disinfects, and relaxes muscle tension. It contains a mixture of dried blood-wort, mint, walnut leaves, Jerusalem artichoke leaves, rose petals, and plantain in specified amounts. The active plant compounds are extracted with ethyl alcohol. They are concentrated and formulated into medicinal or cosmetic preparations.

FOOD, DRINK, AND NUTRACEUTICAL APPLICATIONS

1. Series health care food made from Jerusalem artichoke and barley
   Patent number: CN1718104 (2006)
   Inventor and applicant: Tie, Shunliang (China)
   International classification: A23L1/30
2. Dietary fiber delivery system
   Patent number: US6982093
   Inventor: Licari, J.J. (2006)
   Applicant: Onesta Nutrition (U.S.)
   International classification: A61K 9/20, A61K 31/733
   A delivery system and method for delivering soluble dietary fibers in a chewable tablet form is described. The fiber is inulin from Jerusalem artichoke and other sources.
3. Process for obtaining a pulverulent product from topinambur tubers
   Patent number: MD2696F (2005)
   Inventor: Bantihsh, L.
   Applicant: Chentrul Tekhn Shtiintsifik PE (Moldova)
   International classification: A23L1/22, A23L3/36, A23L3/44, A23L3/40
   The invention is a process for the production of food additives with curative and prophylactic effects from vegetal raw material. The process for obtaining a pulverulent product from Jerusalem artichoke tubers includes peeling, chopping, freezing to temperature of –25°C, vacuum freeze-drying, pulverization, sieving, and packing. This reduces the loss of biologically active components in the raw material.
4. Food biologically active additive for improving human reproduction (variants)
   Patent number: RU2262867 (2005)
   Inventor and applicant: Katkov, J.A. (Russian Federation)
   International classification: A23L1/30, A23C11/00
   The innovation deals with balanced nutrition in children of early age and their parents. The suggested food biologically active ingredient (BAA) includes powder of Jerusalem artichoke tubers. The food promotes the bifidogenic effect.
5. Method of producing dried Jerusalem artichoke
   Patent number: RU2256379 (2005)
   Inventor and applicant: Ostrikov, A.N. and I.A. Zuev (Russian Federation)
   International classification: A23L1/10
   This patent describes the production of powder from tubers of Jerusalem artichoke. The innovative method involves washing, sorting, inspecting, gauging, cleaning, cutting, blanching and exposing to sulfitation, and grinding. The method improves the quality of ready product and increases the thermal efficiency of the drying procedure.
6. Method for manufacturing aromatized tea beverage
   Patent number: RU2249983 (2005)
   Inventor and applicant: Logvinchuk, T.M., V.F. Dobrovol Skij, and O.I. Kvasenkov (RU)
   International classification: A23F3/34, A23F3/14, A23F3/40

The innovation deals with technology for manufacturing different compositions of tea beverages. For instance, a mixture of baikhovi black tea, baikhovi green tea, Jerusalem artichoke flowers, bilberry leaves, fruits of pear and papaya trees, and raisin is prepared with an aromatizing agent.

7. Method for producing sour milk beverage
   Patent number: RU2248711 (2005)
   Inventor and applicant: Poljanskij, K.K., V.M. Bolotov, L.EH. Glagoleva, G.M. Smol Skij, L.I. Perikova, and L.I. Polenova (Russian Federation)
   International classification: A23C9/12, A23C9/13
   A method is disclosed for preparing mixtures of milk and introducing glucose-fructose syrup of plant origin, especially from Jerusalem artichoke. The beverage has increased nutritive and energetic value and stabilized rheological properties during storage.
8. Making of sausage products
   Patent number: UA9008U (2005)
   Inventor: Ulitskyi, Z.Z.
   Applicant: Luhansk Nat Agrarian Universit (Ukraine)
   International classification: A22C11/00
   A novel method of making sausage products is outlined. At the stage of making the mince, Jerusalem artichoke in the native or dry ground state is added at a specified ratio.
9. Butter with immune-protective and diabetic properties
   Patent number: UA8351U (2005)
   Inventor: Ukrainets, A.I., I. Hulyi, T.O. Rashevska, and Y.P. Tasenko
   Applicant: National University of Food Technology (Ukraine)
   International classification: A23C15/16
   A butter having immune-protective and diabetic properties is described; it also contains butter, inulin, buttermilk, Jerusalem artichoke powder, and fructose.
10. Method for producing food and Jerusalem artichoke-containing food
    Patent number: JP2005278459 (2005)
    Inventor: Nakayama, S.
    Applicant: Nippon Tonyo Shokken KK (Japan)
    International classification: A23L1/214, (IPC1-7): A23L1/214
    An innovative processing method is given to make Jerusalem artichoke-containing food safer and more suitable as a health food. The process involves peeling, cutting, drying, roasting, and pulverizing tubers. Peeling before drying and roasting at high temperatures reduce bacterial contamination.
11. Method for producing additive salt
    Patent number: JP2005237258 (2005)
    Inventor and applicant: Honma, C. (Japan)
    International classification: A23F3/14, A23L1/22, A23L1/221, A23L1/237, A23L1/325, A23L1/33, A23L1/333, A23L1/337, A23F3/06
    A method is proposed for producing additive sea salt containing tea extract, squid ink, horseradish, Sergestes, soy sauce, plum pickling sauce, fish broth, seaweed stock, garlic, herbs, dried bonito, perilla, eel and snapping turtle extracts, and turmeric or Jerusalem artichoke extract.
12. A method for producing a prophylactic lactic acid bifidus activating product
    Patent number: RU2243672 (2005)
    Inventor and applicant: Zajtseva, L.A. and V.G. Novikova (Russian Federation)
    International classification: A23C9/12, A23C9/13, A23C9/133
    This patent describes a method of processing milk in which bifidus bacteria and lactic streptococci are introduced, along with a citrus vitamin additive and Jerusalem artichoke juice, powder, or syrup.

13. Dry mixture for milk puddings
    Patent number: UA47272 (2005)
    Inventor: Romodanova, V.O., T.A. Skorchenko, N.V. Remeslo, O.P. Bublyk, and O.M. Khondozhko
    Applicant: National University of Food Technology (Ukraine)
    International classification: A23C9/00, A23L1/187
    A mixture for milk puddings is described that contains a dry milk base, fructose, a stabilizing system, dried chicory, and dried Jerusalem artichoke. The mixture is characterized by a prophylactic action.
14. Novel method for producing inulin using heliangine and cicheriin as raw material
    Patent number: CN1531863 (2004)
    Inventor: Yin, Hong and Guoqiang Yang
    Applicant: Weide Biolog Science and Tech (China)
    International classification: A23L1/214, A23L1/29, A23L3/3571, A23L3/3463
    A process for producing inulin using Jerusalem artichoke or chicory as raw material is described. The method includes pretreatment of plant material, extracting, liquid fermentation and desugarization, and purification of inulin solution to prepare inulin syrup and solid inulin of high purity.
15. Composition of whipped confectionary products of a functional purpose
    Patent number: UA70091 (2004)
    Inventor: Zhovanik, T.M., N.V. Remeslo, V.B. Zakharevych, and V.V. Dorokhovych
    Applicant: National University of Food Technology (Ukraine)
    International classification: A23G3/00
    The composition of a whipped confectionary product is described. It contains foaming and gelling agents, flavoring, aromatic additives, and Jerusalem artichoke syrup with sweeteners.
16. Dietary food supplement containing natural cyclooxygenase inhibitors and methods for inhibiting pain and inflammation
    Patent number: US6818234 (2004)
    Inventor: Nair, M.G., H. Wang, D.L. Dewitt, D.W. Krempin, D.K. Mody, Y. Qian, D.G. Groh, A.J. Davies, M.A. Murray, R. Dykhouse, and M. Lemay
    Applicant: Access Business Group International LLC, Michigan State University (U.S.)
    International classification: A23L1/30
    The invention describes food supplements that contain one or more fruit extracts useful for pain relief and anti-inflammation. Jerusalem artichoke is listed as a potential source of an active ingredient.
17. Composition of an apple jam with functional properties
    Patent number: UA69299 (2004)
    Inventor: Zheplinska, M.M., M.V. Aleksiuk, O.S. Chulanova, and L.V. Zotkina
    Applicant: National University of Food Technology (Ukraine)
    International classification: A23L1/09
    This patent discloses the composition of an apple jam with functional properties, containing apples, sugar, and a Jerusalem artichoke extract.
18. Method for producing cracker-type semifinished food products
    Patent number: RU2221430 (2004)
    Inventor and applicant: Shnejder, T.I., M.A. Kalinina, A.A.Glazunov, and N.K. Kazennova (Russian Federation)
    International classification: A21D13/08, A23L1/16
    A method is disclosed that involves grinding basic materials, mixing with flavoring and enriching additives, gelatinizing the resultant mixture, and extruding and drying. The basic material is product rejected during sorting (e.g., dry cuts of macaroni products

and preliminarily dried cuttings). For obtaining a cracker-type product, the polysaccharide used is citrus, apple, beet, or Jerusalem artichoke.

19. Method for producing a snack product that is fat-free or low in fat
    Patent number: WO2004047542 (2004)
    Inventor and applicant: Schwarzhans, P. (Austria)
    Also published as: AU2003287741 (A1)
    International classification: A23B7/005, A23B7/01, A23B7/02, A23B7/03, A23B7/06, A23L1/01
    The invention relates to a method for producing snack products that are fat-free or low in fat, such as potato chips, Jerusalem artichoke chips and other vegetable chips, and pasty snacks.
20. Methods for reducing cholesterol using *Bacillus coagulans* spores, systems, and compositions
    Patent number: US6811786 (2004)
    Inventor: Farmer, S. and A.R. Lefkowitz
    Applicant: Ganeden Biotech, Inc (U.S.)
    International classification: A61K35/74, C12N1/20, A61K35/66
    The invention describes therapeutic compositions including lactic acid-producing bacteria in combination with bifidogenic oligosaccharides or other cholesterol-reducing agents, for use in reducing LDL cholesterol and serum triglycerides. The compositions include Jerusalem artichoke flour.
21. Low-calorie, palatable, fiber-containing sugar substitute
    Patent number: US6808733 (2004)
    Inventor: Barndt, R.L., S. Liao, C.M. Merkel, W.J. Chapello, and J.L. Navia
    Applicant: McNeil PPC, Inc (U.S.)
    Also published as: WO9849905 (A3), WO9849905 (A2), EP0975236 (A3), EP0975236 (A2), CA2286662 (A1), TR9902826T (T2), NO316758B (B1), AU749025B (B2)
    International classification: A21D2/18, A21D13/08, A23G3/00, A23G3/34, A23G9/32, A23G9/52, A23L1/236, A23L1/308, A21D2/00, A21D13/00
    The invention relates to a palatable, low-calorie, fiber-containing sugar substitute composition, suitable for use as a substitute for table sugar and in the preparation of baked foods and other prepared solid and semisolid foods. The sugar substitute comprises inulin, from Jerusalem artichoke or other sources, and a high-intensity sweetener.
22. A composition of ingredients for herbal elixir (eliksyr prykarpatskyi)
    Patent number: UA68911 (2004)
    Inventor and applicant: Stasiv, T.H. and V.O. Pyptiuk (Ukraine)
    International classification: C12G3/06, C12G3/00
    This patent discloses the composition of an herbal elixir containing St. John's wort, Melilot officinale, and origanum, and extracts, including Jerusalem artichoke.
23. Composition of herbal tea
    Patent number: RU2236789 (2004)
    Inventor and applicant: Logvinchuk, T.M., V.F. Dobrovol Skij, and O.I. Kvasenkov (Russian Federation)
    International classification: A23F3/34, A23F3/00
    The composition of an herbal tea containing leaves of whortleberry and flowers of Jerusalem artichoke in a 50:50 weight ratio is given.
24. Mixed drink comprises combination of ginseng preparation or eleuterococcos extract with mushroom extract, sea buckthorn, Jerusalem artichoke extract or powder, or Topilac
    Patent number: DE10324158 (2004)
    Inventor and applicant: Berg, E.-E. and W. Krohn (Germany)
    International classification: A23L1/0528, A23L1/28, A23L1/30, A23L2/38, A23L1/052

25. Vodka Golden Dozed Lux (Zolotaya Djuzhina Luks)
    Patent number: RU2236450 (2004)
    Inventor and applicant: Arbuzov, V.P., E.A. Stretovich, I.V. Stepanova, and I.I. Burachevskij (Russian Federation)
    International classification: C12G3/06, C12G3/00
    This patent describes vodka made from specified amounts and types of oat flakes, glucose syrup, carbohydrate modulus, Jerusalem artichoke dry extract (Relikt), and aqueous-alcoholic liquid. The vodka is 40% strength with high organoleptic indices.
26. Composition for nonalcoholic prophylactic fermenting beverage, process for preparation thereof and process for preparation of concentrate of the nonalcoholic prophylactic beverage
    Patent number: MD20030068 (2004)
    Inventor and applicant: Ovseannicova, T.N. and E.I. Procopciuc (Moldova)
    Also published as: MD2625 (B2)
    International classification: A23C21/08, A23L2/00, A23L2/38, A23L2/385, A23L2/44, A23L2/52, C12G3/02, A23C21/00, A23L2/42
    The invention refers to the production of nonalcoholic beverages with prophylactic destination. Plants, including extracts from Jerusalem artichoke tubers, are included for their health benefits.
27. Method for manufacturing curd cheese mass and method for manufacturing processed cheese based upon curd cheese mass
    Patent number: RU2242135 (2004)
    Inventor and applicant: Drozdova, L.I., M.V. Orlova, and E.V. Jakush (Russian Federation)
    International classification: A23C19/02, A23C19/082, A23C23/00, A23C19/00
    The patent deals with a method for the thermal treatment of milk and other substances, and the manufacture of curd cheese. Jerusalem artichoke is included in a puree additive used in the manufacture of curd cheese, which helps to improve organoleptic parameters and gives the product restorative and prophylactic properties.
28. A method for preparing Topekh, an herbal fusion
    Patent number: UA64148 (2004)
    Inventor and applicant: Piptiuk, O.V., T.H. Stasiv, and M.I. Derkach (Ukraine)
    International classification: C12G3/06, C12G3/00
    A method for preparing an herbal fusion is described, which includes Jerusalem artichoke and Echinacea.
29. A method for preparing Toprekhin, an herbal fusion
    Patent number: UA64147 (2004)
    Inventor and applicant: Piptiuk, O.V., T.H. Stasiv, and M.I. Derkach (Ukraine)
    International classification: C12G3/06, C12G3/00
    A method for preparing an herbal fusion is described, which includes Jerusalem artichoke, propolis, and Echinacea.
30. Method for producing noodle product containing nutrient of Jerusalem artichoke
    Patent number: JP2004129643 (2004)
    Inventor: Sasaki, S. and Y. Sato
    Applicant: Sasaki Seimenshiyo KK, Sato Yoshie (Japan)
    International classification: A23L1/16
    A method for producing noodles using a fine powder prepared from Jerusalem artichoke is given. The noodles have better long-term preservation and benefit from having inulin, vitamins, and minerals from Jerusalem artichoke.
31. Method for producing glucose-fructose syrup
    Patent number: RU2224026 (2004)

Inventor and applicant: Golubev, V.N. and S.J.U. Beglov (Russian Federation)
International classification: A23L1/09, C13K1/06, C13K11/00
An invention relating to a method for processing Jerusalem artichoke tubers to prepare fructose-glucose syrup is disclosed. Tubers are blanched, milled to pulp, and pressed. Acid hydrolysis of inulin is carried out using orthophosphoric acid, and lime of milk is used to neutralize the hydrolyzate, which is purified by ultrafiltration under pressure, and further ion exchange purification. The solution is evaporated to obtain a syrup with a content of reducing agents of no less than 80%. It can be used as a supplement in the confectionary, baking, and canning industries, in producing beverages, and as a self-contained nutrition product.

32. Method for preparing glucose-fructose syrup from inulin-containing raw materials
Patent number: RU2209835 (2003)
Inventor and applicant: Artem, E.V.D., V.V. Maneshin, and E.J.P. Vasil (Russian Federation)
International classification: C13K11/00
The invention is a method for preparing fructose-glucose syrup from root crops rich in inulin. Juice from Jerusalem artichoke tubers is purified and inulin is hydrolyzed with food acid. The hydrolyzate is cleared and concentrated to prepare the syrup. This simplified method enhances the economy of the process.
33. A composition of ingredients for Zdorovets balsam
Patent number: UA62437 (2003)
Inventor and applicant: Stasiv, T.H. (Ukraine)
International classification: C12G3/06, C12G3/00
A composition of balsam ingredients is disclosed. It contains color, natural honey, milk, nut infusion, nut aromatic alcohol, sugar, Jerusalem artichoke infusion, black chokeberry juice, ashberry juice, St. John's wort, blackcurrant leaves, cherry leaves, echinacea, spiruline, pine (young sprouts), and a cinnamon infusion.
34. Fruit-and-vegetable puree for patients suffering from diabetes
Patent number: RU2202231 (2003)
Inventor: Kupin, G.A., E.G. Najmushina, and G.M. Zajko
Applicant: Sitet, Kuban G T Univer (Russian Federation)
International classification: A23L1/212, A23L1/29
A puree is described, containing Jerusalem artichoke, apple, black chokeberry, walnuts, hydrated wheat bran, and pectin. It is specifically designed for the treating and prophylactic feeding of patients with diabetes mellitus.
35. Gelatinized cereal product containing oligosaccharide
Patent number: US6596332 (2003)
Inventor: Anantharaman, H.G., O. Ballevre, and F. Rochat
Applicant: Nestec S A (Switzerland)
International classification: A23K1/14, A23K1/18, A23L1/0528, A23L1/164, A23L1/18, A23L1/052
The patent describes a gelatinized cereal product, which contains inulin derived from a plant source (e.g., chicory or Jerusalem artichoke). Inulin comprises around 0.25% by dry weight. The cereal product may be used as a pet food or breakfast cereal.
36. Processes for making novel inulin products
Patent number: US6569488 (2003)
Inventor and applicant: Silver, B.S. (U.S.)
A novel method of preparing inulin is disclosed, from Jerusalem artichoke and other plant sources. A settling tank is used to separate high and low molecular weight inulin and fructose fractions.
37. Method of producing pickled vegetable half-finished products for salads

Patent number: RU2197825 (2003)
Inventor: Klevtsova, O.M., T.V. Frampol Skaja, and O.I. Kvasenkov
Applicant: Univ Kubansk (Russian Federation)
Also published as: RU2197824, RU2200418, RU2197823
International classification: A23B7/155, A23L1/214, A23L3/3463, C12N1/20, A23B7/14
The innovation is a new method of vegetable preservation. During preparation, Jerusalem artichoke, carrot, and parsnip are subjected to alkali cleaning, shredded, and mixed with salt and sours (prepared by cultivation of *Lactobacillus plantarum* on a decoction of Jerusalem artichoke wastes). The product is fermented at 18 to 24°C for 5 to 7 days. It is prepacked for consumers and has specific pleasant organoleptical properties.

38. Method of producing preserved salad
Patent number: RU2197847 (2003)
Inventor: Klevtsova, O.M., T.V. Frampol Skaja, and O.I. Kvasenkov
Applicant: Kuban G T Univer, Sitet (Russian Federation)
International classification: A23L1/212
Salad Krasnodarsky is produced using Jerusalem artichoke, beet, carrot, and parsley greens. The components are cut, mixed, and roasted in vegetable oil. Citric acid and salt are added, and the mixture is aged and prepacked as a sterilized product with a long shelf-life and specific organoleptic properties.

39. Method of producing preserved salad Angelina
Patent number: RU2198542 (2003)
Inventor: Klevtsova, O.M., Eh.I. Mamedova, and O.I. Kvasenkov
Applicant: Sitet, Kuban G T Univer (Russian Federation)
International classification: A23B7/10, A23L1/212
Salad Angelina contains Jerusalem artichoke, carrot, and apples and is prepared by an innovative preservation method.

40. Method of producing preserved salad Vesenni
Patent number: RU2198541 (2003)
Inventor: Klevtsova, O.M., E.I. Mamedova, and O.I. Kvasenkov
Applicant: Sitet, Kuban G T Univer (Russian Federation)
International classification: A23B7/10, A23L1/212
Salad Vesenni contains Jerusalem artichoke, greens of parsley and dill, green pea, and sour green head cabbage. It is prepared using an innovative preservation method.

41. Meat-based canned food product for feeding pregnant and suckling women
Patent number: RU2213493 (2003)
Inventor and applicant: Ustinova, A.V., N.V. Timoshenko, M.A. Aslanova, A.V. Verkhososova, and N.P. Perevyshin (Russian Federation)
International classification: A23B4/00, A23L1/31, A23L1/314
The novel canned food product comprises beef, liver, pork, dried milk, melange, buckwheat flour or corn flour, vegetable oil, soya isolate, Jerusalem artichoke, laminaria, caroline, curative and prophylactic salt, bone powder, spice extracts, folic acid, ascorbic acid, and water, in predetermined ratios.

42. Process for ethyl alcohol obtaining from Jerusalem artichoke (*Helianthus tuberosus*) tubers
Patent number: MD2343F (2003)
Inventor and applicant: Baev, O., F. Sepeli, and D. Sepeli (Moldova)
International classification: C12P7/067
This invention relates to alcoholic drinks, specifically a technological process for making ethyl alcohol from Jerusalem artichoke tubers. Processed tubers are heated with mineral acid to complete saccharification, and excessive acidity is neutralized with $CaCO_3$ prior to fermentation and distillation.

43. Direct membrane separating process for producing inulin and oligofructose
    Patent number: CN1389468 (2003)
    Inventor and applicant: Zou, C. (China)
    International classification: C07H1/00, C07H3/00, C08B37/02
    The invention relates to a method for producing oligofructose by direct membrane separation from Jerusalem artichoke or chicory.
44. Method of processing topinambour tubers
    Patent number: RU2218061 (2003)
    Inventor: Golubev, V.N., S. Beglov, N.K. Kochnev, J.P. Karachun, and D.V. Vorobejchikov
    Applicant: Kochnev Nikolaj Konstantinovic, Karachun Jurij Petrovich, Vorobejchikov Dmitrij Vasil EV (Russian Federation)
    International classification: A23L1/09, A23N1/02, A23N1/00
    The patent discloses a method for preparing ground Jerusalem artichoke tubers for processing. Stages include electroplasmolysis, acid hydrolysis, purification using activated carbon, and clarification by lime milk. The syrup is concentrated until it contains at least 50% dry substances. The method is widely applicable in the food industry, and it improves the organoleptic characteristics of fructose-glucose syrup.
45. Method of producing curd dessert
    Patent number: RU2214717 (2003)
    Inventor: Poljanskij, K.K., L.Eh. Glagoleva, G.M. Smol Skij, and V.V. Maneshin
    Applicant: G Obrazovatel Noe Uchrezhdenie, Ezhskaja GTA
    International classification: A23C23/00, A23L1/30
    The patent covers a method for preparing a mixture of milk base, produced with the use of fat-free curd, fructose-glucose syrup separated from Jerusalem artichoke of the Interes type, and edible fibers from sugar beet pulp. This mixture increases the range of curd products, increases the biological and nutritive value of dessert, and stabilizes their rheological properties during prolonged storage.
46. Method for producing Jerusalem artichoke tea bag
    Patent number: CN1435106 (2003)
    Inventor: He, Tian
    Applicant: Lushan Sci & Tech Co Ltd Dalia (China)
    International classification: A23F3/34, A23F3/00
    This patent describes how a Jerusalem artichoke tea is prepared from sliced, dried, and pulverized tubers, which are cured, packed into bags, and radiated with ultraviolet light. The product has high levels of cellulose, vitamins, and trace elements, low levels of fat, and a range of potential health benefits.
47. *Helianthus tuberosus* fine powder, method for producing the same, *H. tuberosus* fine powder-added food, and *H. tuberosus* fine powder product
    Patent number: JP2002306113 (2002)
    Inventor: Nakazato, H.
    Applicant: Shinwa Ind (Japan)
    International classification: A23L1/214
    The invention describes a method for producing a fine powder from *Helianthus tuberosus*, as a product for use in food. The fine powder is easily dissolved in hot water.
48. Method for preparing Jerusalem artichoke beverage
    Patent number: CN1371635 (2002)
    Inventor: Wu, Yunsheng
    Applicant: Lin Yang (China)
    International classification: A23L2/02, A23L2/38
    A method for preparing a health-promoting beverage from Jerusalem artichoke is described. The method includes three technological process steps: preparation of

Jerusalem artichoke hydrolyzate, preparation of a osmanthus flower extract, and blending, packaging, and sterilizing.

49. Inulin fractions
    Patent number: US6419978 (2002)
    Inventor and applicant: Silver, B.S. (U.S.)
    Novel fractions of inulin are disclosed that have improved water solubility and water miscibility at ambient temperatures. The novel fractions are extracted from plant materials, including Jerusalem artichoke. The process for preparing the novel fractions involves holding the inulin-rich extraction water in a settling tank, which causes higher molecular weight polysaccharides to separate from water-soluble lower molecular weight polysaccharides.
50. Fructan-containing composition for the prevention and treatment of colon cancer and method for the prevention and treatment of same
    Patent number: US6500805 (2002)
    Inventor: Van Loo, J. and A. Frippiat
    Applicant: Tiense Suikerraffinaderij NV (Belgium)
    International classification: A61K31/715
    The novel use of fructran (DP over 15) for the manufacture of a composition for the prevention and treatment of colon cancer in nonbovine mammals, particularly in human beings. The composition can be a medicament as well as a functional food. The preferred fructan is inulin, obtained from Jerusalem artichoke or other sources.
51. Processed product of *Helianthus tuberosus* and method for producing the same
    Patent number: JP2002000216 (2002)
    Inventor: Nakayama, S.
    Applicant: Nippon Tonyo Shokken KK (Japan)
    International classification: A23L1/214, A23L1/30
    The manufacture of a processed *Helianthus tuberosus* product, characterized by the addition of natural oily vitamin E, is described. This provides a tableted product that can be easily prepared in desired amounts by diabetics. The tablets are preferably obtained by slicing, drying, and pulverizing *H. tuberosus* tubers and adding citric acid to the powder, and then the natural vitamin E in an amount of about 0.03 wt%.
52. Condiment
    Patent number: RU2195140 (2002)
    Inventor: Kvasenkov, O.I. and E.Ju. Rosljakova
    Applicant: Sitet, Kuban G T Univer (Russian Federation)
    International classification: A23L1/22, A23L1/39
    A new condiment is described that contains soya-bean paste, puree from Jerusalem artichoke and radish, sugar, salt, vegetable oil and extracts of carrot seeds, mustard seeds, rice meal, fennel, basil, creeping thyme, and Grecian laurel. It has improved organoleptic properties and is enriched with biologically active substances.
53. Method of producing powder from Jerusalem artichoke tubers
    Patent number: RU2192761 (2002)
    Inventor: Kochnev, N.K., M.V. Kalinicheva, and S.Ju. Beglov
    Applicant: Kochnev Nikolaj Konstantinovic, Kalinicheva Margarita Vasil EV (Russian Federation)
    International classification: A23L1/214
    The patent describes a method for making a powder-like product from Jerusalem artichoke tubers. The tubers are ground to a puree-like form, heated to 80 to 90°C, cooled, and subject to fermentolysis before being dried and ground repeatedly. This improves the quality of the final product and the homogeneity of its properties.

54. Shaped fruit product based on dried fruit and cereal contains Jerusalem artichoke granules produced by comminuting dried tubers
    Patent number: DE10101871 (2002)
    Inventor and applicant: Koerber, W.E.J. (Germany)
    International classification: A23L1/164, A23L1/308
    A novel consumable product is described that comprises liquid binder, dried fruit, cereal, and Jerusalem artichoke granules (produced by comminuting dried tubers).
55. Filler for meat, fish, or vegetable farces, and also dishes and half-finished products from them
    Patent number: RU2192148 (2002)
    Inventor: Shamkova, N.T. and G.M. Zajko
    Applicant: Sitet, Kuban G T Univer (Russian Federation)
    International classification: A23L1/212, A23L1/30, A23L1/314, A23L1/317, A23L1/325
    A filler is described for use in public catering, which includes numerous ingredients, including dried Jerusalem artichoke.
56. Coloring substance composition and a method of manufacturing same
    Patent number: US6500805 (2002)
    Inventor: Koehler, K., S.J. Jacobsen, C. Soendergaard, and M. Kensoe
    Applicant: Chr. Hansen A/S (Denmark)
    Also published as: WO0070967 (A1), EP1178738 (A1), AU772905 (B2)
    International classification: A23L1/00, A23L1/052, A23L1/27, A23L2/52
    The composition of a coloring agent is disclosed, which comprises beet pectin, chicory pectin, and Jerusalem artichoke pectin. The composition is useful for the preparation of health-improving products or the coloring of food products and nutraceuticals and pharmaceutical products.
57. Oligosaccharide-encapsulated mineral and vitamin ingredients
    Patent number: US6468568 (2002)
    Inventor: Leusner, S.J., J. Lakkis, B.H. van Lengerich, and T. Jarl
    Applicant: General Mills, Inc (U.S.)
    Also published as: WO0205667
    International classification: A23L1/304, A23L1/00, A23L1/10, A23L1/302
    A mineral or vitamin fortification ingredient is disclosed, with mineral and vitamin components encapsulated in a grindable, glassy matrix. The matrix composition includes an oligosaccharide, preferably fructooligosaccharide (FOS) and inulin, from Jerusalem artichoke or other sources, which beneficially increases the fiber content of the food.
58. Coloring substance composition and method of manufacturing same
    Patent number: US6500473 (2002)
    Inventor: Koehler, K., S.J. Jacobsen, C. Soendergaard, and M. Kensoe
    Applicant: Hansen's Lab (Germany)
    International classification: A23L1/00, A23L1/052, A23L1/275, A23L2/58, A23L1/00
    A composition comprising coloring substances is described in this patent. The composition includes beet pectin, chicory pectin, and Jerusalem artichoke pectin or other pectin types having a high degree of acetylation. It has application in the coloring of edible products, including food products and nutraceuticals, and pharmaceutical products.
59. Detoxifying composition for food biologically active additives
    Patent number: RU2179856 (2002)
    Inventor and applicant: Udintsev, S.N. and V.V. Vakhrushev (Russian Federation)
    International classification: A61P39/00
    The patent discloses a suggested food additive composition, containing fiber, vitamins, and mineral substances. The suggested plant sources of pectin and inulin are dandelion

roots, burdock, elecampagne, or Jerusalem artichoke.

60. Composition for producing meat canned products for children
    Patent number: RU2178978 (2002)
    Inventor: Ustinova, A.V., M.A. Aslanova, N.V. Timoshenko, N.A. Ukhova, and A.V. Verkhososova
    Applicant: Vrnii M, Jasnoj Promy (Russian Federation)
    International classification: A23B4/00, A23L1/314
    The composition of improved canned meat with curative and prophylactic properties is given in this patent. It contains poultry meat (mechanically deboned), beef liver, semi-fat pig meat, powder of Jerusalem artichoke, soybean isolate, linseed oil, caroline, vitamin E, and water at determined ratios.
61. Milk serum-based beverage
    Patent number: RU2181248 (2002)
    Inventor: Volkova, O.P., T.V. Frampol Skaja, and O.V. Kichatova
    Applicant: Kuban G T Univer, Sitet (Russian Federation)
    International classification: A23C21/02, A23C21/00
    A beverage is suggested in this patent, which includes Jerusalem artichoke juice. The innovation produces a drink of good prophylactic properties at low cost, with improved organoleptic properties.
62. Process for producing dried preparations from Jerusalem artichoke tubers and chicory roots, and the dried preparations obtained by the process
    Patent number: AT409061B (2002)
    Inventor and applicant: Berghofer, E. and E. Reiter (Austria)
    International classification: A23L1/0528, A23L1/214
    The invention relates to the production of high-fiber dried preparations from Jerusalem artichoke and chicory.
63. Vodka
    Patent number: RU2174549 (2001)
    Inventor: Kalugin, V.D. and S.S. Verkhoturov
    Applicant: Kalugin, V.D., S.S. Verkhoturov, and N.J.A. Porokhova (Russian Federation)
    International classification: C12G3/06, C12G3/00
    The composition of vodka Asia is described. It contains Jerusalem artichoke concentrate.
64. Drink comprising *Helianthus tuberosus* as the main component and process for producing the same
    Patent number: WO0117379 (2001)
    Inventor: Nakayama, S.
    Applicant: Nihon Tohnyo Shokken Co Ltd, Nakayama Shigeo (Japan)
    International classification: A23F3/34, A23L2/44, A23F3/00, A23L2/42
    This patent covers the addition of *Helianthus tuberosus* juice to lemon juice or vitamin C to prevent oxidation. After adding plum extract, the mixture is boiled, filtered, and bottled. The drink is free from starch and therefore can be taken by diabetics as a sweetness source.
65. Method of preparing fructose syrup from Jerusalem artichoke
    Patent number: RU2167198 (2001)
    Inventor: Kantere, V.M., A.J. Vinarov, T.G. Mukhamedzhanova, T.V. Ipatova, V.A. Eremin, and T.E. Sidorenko
    Applicant: Vinarov Aleksandr Jur Evich (Russian Federation)
    International classification: A23L1/09, C13F3/00, C13K11/00
    A method for preparing fructose syrup is described, which involves chopped Jerusalem artichoke tubers. Pectofoetidine is introduced to a hot-water tuber extraction prior to hydrolysis. A clarified hydrolysate is concentrated to fructose syrup. The method

produces syrup with increased biological value, which may be used for alimentation of diabetics.

66. Method for producing soft dietary rennet cheese
    Patent number: RU2166857 (2001)
    Inventor: Liz Ko, N.N., N.I. Bevz, E.A.I. Grigor, and M.S. Belakovskij
    Applicant: Sii Inst Mediko Biolog, G Nts Rossijskoj Federat (Russian Federation)
    International classification: A23C19/068, A23C19/076, A23C19/00
    A method is given that involves pasteurizing normalized milk base, cooling to fermentation temperature, and introducing additives, including lactic acid streptococci and bifidobacteria, and extracts of concentrated Jerusalem artichoke.
67. Macaroni product manufacture method
    Patent number: RU2166863 (2001)
    Inventor: Glazunov, A.A., T.I. Shnejder, N.K. Kazennova, M.A. Podgaetskaja, D.V. Shnejder, A.A. Serdechkina, M.A Kalinina, and V.N. Golubev
    Applicant: Gnin Inst, Khlebopekarnoj Promy (Russian Federation)
    International classification: A23L1/16, A23L1/30
    An innovative method of producing macaroni is outlined, which involves the addition of an enriching additive mixture that includes Jerusalem artichoke powder. The method allows inulin-, vitamin-, and iodine-enriched macaroni products with increased biological value to be produced.
68. Method of production of ethyl alcohol from Jerusalem artichoke
    Patent number: RU2161652 (2001)
    Inventor: Krikunova, L.N., M.M. Aleksandrova, N.G. Il Jashenko, and E.F. Shanenko
    Applicant: Mo Gu Pishchevykh, Proizv (Russian Federation)
    International classification: C12P7/06, C12P7/02
    A novel method for producing ethyl alcohol from Jerusalem artichoke tubers is disclosed. Milled tubers are mixed with water and calcium sulfate, and they are hydrolyzed by endogenous inulinase. The saccharified wort is cooled, nisin is added for aseption with industrial yeast, and the wort is fermented. The method increases the yield of ethanol per raw material unit.
69. Concentrated base (balsam)
    Patent number: RU2170045 (2001)
    Inventor: Filonova, G.L., S.N. Panchenko, N.A. Komrakova, M.V. Kulikova, A.I. Adlin, N.S. Shevyrev, V.I. Postnikov, and V.G. Ugreninov
    Applicant: Soglasie Aozt Fa, Vrnii Pivovarennoj Bezalkogol (Russian Federation)
    International classification: A23L2/385, C12G3/06
    A concentrated base for nonalcoholic beverages is described, which includes Jerusalem artichoke aboveground parts (stems). The concentrated base (balsam) is claimed to provide recovery of metabolism in diabetes mellitus and the restoration of the immune system.
70. Bacteria- and fiber-containing composition for human gastrointestinal health
    Patent number: US6241983 (2001)
    Inventor: Paul, S.M., J.J. Katke, and K.C. Krumhar
    Applicant: Metagenics, Inc (U.S.)
    International classification: A23J3/08, A23L1/305, A23L1/308, A61K9/00, A61K39/395, A61K39/40, A61K39/42, C07K16/04, A23J3/00
    A composition for promoting gastrointestinal health is described that contains an effective amount of a beneficial human intestinal microorganism and an effective amount of dietary fiber. One source of dietary fiber is fructooligosaccharides, obtainable from Jerusalem artichoke.

71. Concentrated drink base
    Patent number: RU2161426 (2001)
    Inventor: Filonova, G.L., S.N. Panchenko, N.A. Komrakova, M.V. Kulikova, A.I. Adlin, N.S. Shevyrev, V.I. Postnikov, and V.G. Ugreninov
    Applicant: Soglasie Aozt Fa, Yshlennosti, Vrnii Pivovarennoj Bezalkogol (Russian Federation)
    International classification: A23L2/385
    The composition of a concentrated base for nonalcoholic drinks is described, which includes aboveground parts of Jerusalem artichoke. The proposed concentrated base is claimed to exhibit antioxidant properties, normalize withdrawal of excess of uric and oxalic acids, and enable rheumatism prophylaxis.
72. Concentrated base for beverage
    Patent number: RU2165225 (2001)
    Inventor: Filonova, G.L., S.N. Panchenko, N.A. Komrakova, M.V. Kulikova, A.I. Adlin, N.S. Shevyrev, V.I. Postnikov, and V.G. Ugreninov
    Applicant: Zao Soglasie Fa, Vrnii Pivovarennoj Bezalkogol (Russian Federation)
    International classification: A23L2/385
    The patent describes the composition of a concentrated base for nonalcoholic drinks, which includes aboveground parts of Jerusalem artichoke. The base is claimed to normalize aqueous salt and carbohydrate metabolism, and improve the function of the gastroenteric tract.
73. Method of preparing inulin–pectin concentrate powder for medicinal and food aims from dried raw materials.
    Patent number: RU2169002 (2001)
    Inventor: Samokish, I.I., N.S. Zjablitseva, and V.A. Kompantsev
    Applicant: Akademija, Pjatigorskaja G Farmatsevtiche (Russian Federation)
    International classification: A23L1/29, A61K31/70, A61K31/715, A61P3/10, C08B37/00
    The novel method involves extraction of inulin from Jerusalem artichoke dry tuber powder by precipitation with ethanol. Pectins are extracted from the remaining powder. The advantage is a simplified and wasteless method of raw processing.
74. Method of preparing inulin and other fructan-containing products from Jerusalem artichoke and other inulin-containing raw materials.
    Patent number: RU2175239 (2001)
    Inventor: Aravina, L.A., G.B. Gorodetskij, N.Ja. Ivanova, E.V. Komarov, N.N. Momot, and M.A. Cherkasova
    Applicant: Gorodetskij Gennadij Borisovic (Russian Federation)
    International classification: A23L1/236
    The invention relates to the preparation of inulin-based biologically active food additions. The method provides for preparing inulin of molecular mass 7000 to 10000 Da and accompanying fructose-containing products. It enhances technological effectiveness and gives a high purity of inulin.
75. Method of preparing dietary curd dessert
    Patent number: RU2166257 (2001)
    Inventor: Volkova, O.P., T.V. Frampol Skaja, and V.N. Chukhlib
    Applicant: Kuban G T Univer, Sitet (Russian Federation)
    International classification: A23C23/00
    The innovative method increases the biological value of curd dessert products. The components include crushed Jerusalem artichoke (particle size, 5 to 7 mm).
76. Paste-like concentrate for drink
    Patent number: RU2161003 (2000)
    Inventor: Filonova, G.L., S.N. Panchenko, E.A. Litvinova, I.L. Kovaleva, A.I. Adlin, N.S.

Shevyrev, V.I. Postnikov, and V.G. Ugreninov
Applicant: Soglasie Aozt Fa, Vrnii Pivovarennoj Bezalkogol (Russian Federation)
International classification: A23L2/385
The compositions of paste-like concentrates for drinks are given. The concentrates include ground chips from Jerusalem artichoke. It is claimed they strengthen the immune system, regulate blood sugar content, and normalize blood pressure.

77. Alcoholic drink
Patent number: RU2158292 (2000)
Inventor: Kukharenko, A.A. and A.Ju. Vinarov
Applicant: Vinarov Aleksandr Jur Evich (Russian Federation)
International classification: C12G3/06, C12G3/00
An alcoholic drink composition is given in this patent, which consists of ethyl alcohol, water, and fructose syrup prepared from Jerusalem artichoke. The proposed drink may have curative properties and can be used by humans suffering with diabetes mellitus.
78. Method of using biologically active food additives in diet of athletes nutrition
Patent number: RU2156086 (2000)
Inventor: Gaptova, J.V., J.V. Orlovskij, M.A. Ul Janova, L.I. Ul Janova, D.A. Fadeev, and I.D. Fadeeva
Applicant: Fadeeva Irina Dmitrievna (Russian Federation)
International classification: A23L1/30, A23L1/30
Jerusalem artichoke syrup is used as an adaptogen in food additives. It shows an ability to overcome immunodeficiency in athletes during a period of maximal loadings.
79. Beer containing concentrated Jerusalem artichoke juice, has fruity, slightly sweet taste
Patent number: DE19924886 (2000)
Inventor: Fritsche, H. and K. Oelschlaeger
Applicant: Klosterbrauerei Neuzelle Gmbh (Germany)
International classification: C12C5/02, C12C5/00
The innovation is the addition of Jerusalem artichoke juice concentrate to beer, after storage and fermentation, but before draining off. A new range of beers with distinctive organoleptic properties can be produced.
80. Method of beer brewing using Jerusalem artichoke
Patent number: RU2149894 (2000)
Inventor and applicant: Zelenkov, V.N. (Russian Federation)
International classification: C12C7/00, C12C12/00
A method of beer production is described that involves using additives from Jerusalem artichoke (aqueous extracts from tubers or aboveground plant parts, or dry powders prepared from various parts of Jerusalem artichoke or its extracts). They are here introduced at various possible stages during the brewing process. The method produces a new type of beer with increased biological value, due to enrichment with inulin and other biologically active components from Jerusalem artichoke.
81. Method of preparing inulin from Jerusalem artichoke tubers
Patent number: RU2148588 (2000)
Inventor: Maneshin, V.V., Ev. V.D. Artem, and Eva J.P. Vasil
Applicant: Ooo Fabrika Biotekhnologija (Russian Federation)
International classification: C08B37/00, C08B37/18
This invention relates to methods of preparing inulin from milled Jerusalem artichoke tubers by crystallization and drying. Water-soluble substances are separated from water-insoluble fibrous components. Following heating (80 to 85°C for 1 to 3 min), filtration, ultrafiltration, and nanofiltration steps remove protein and colored substances. The inulin is crystallized from the concentrated juice.
82. Dietetic baked goods, e.g., bread for diabetics

Patent number: DE19830122 (2000)
Inventor and applicant: Hechler, P. (Germany)
International classification: A21D2/36, A21D13/02, A21D13/04, A21D13/08, A21D2/00
Compositions for dietetic baked goods are given, which include up to 50% Jerusalem artichoke.

83. Method for obtaining food product based on Jerusalem artichoke
Patent number: RU2143823 (2000)
Inventor: Faradzheva, E.I., V.J. Barkhatov, V.A. Bredikhina, and V.S. Ruban
Applicant: Sitet, Kuban G T Univer (Russian Federation)
International classification: A23L1/212, A23L1/29
The method described involves hydrolysis of Jerusalem artichoke polyfructosan and thermal treatment. The method enables increased fructose content to be obtained. It may be used for the treatment of patients suffering diabetes mellitus and obesity.

84. Food additive from Jerusalem artichoke for preparation of food products and beverages with curative and prophylactic properties
Patent number: RU2152734 (2000)
Inventor and applicant: Zelenkov, V.N. (Russian Federation)
International classification: A23L1/052, A23L1/30
This patent describes a food additive made from tuber or aboveground part of plants, including Jerusalem artichoke.

85. Food additive from Jerusalem artichoke with macro- and microelements possessing biological activity
Patent number: RU2152736 (2000)
Inventor and applicant: Zelenkov, V.N. (Russian Federation)
International classification: A23L1/30
A food additive made from dried tubers of Jerusalem artichoke is described. It may be used for dietetic and curative and prophylactic alimentation.

86. Method of producing curative–prophylactic dairy product
Patent number: RU2130731 (1999)
Inventor: Poljanskij, K.K., N.S. Rodionova, and L.Eh. Glagoleva
Applicant: Akademija, Voron G T (Russian Federation)
International classification: A23C23/00
To create the novel product, a protein fraction prepared by diafiltration is mixed with dry concentrate of Jerusalem artichoke. The mixture is pasteurized, cooled, and soured with acidophilic *Bacillus*.

87. Composition for preparing cultured-milk proteinaceous product
Patent number: RU2128444 (1999)
Inventor: Khachatrjan, A.P., R.G. Khachatrjan, A.B. Rodionov, N.A. Jurchenko, and I.G. Lemeshchenko
Applicant: Khachatrjan A P (Russian Federation)
International classification: A23C9/12, A23C9/127, A23C9/133, A23C11/10
The innovative composition includes milk base and powdered concentrate of Jerusalem artichoke.

88. Baby food composition containing fructan and its production
Patent number: JP11332513 (1999)
Inventor: Seuer, R.C. and M.B. Cool
Applicant: Beech Nut Nutrition Corp (U.S.)
International classification: A23L1/09, A23L1/212, A23L1/30
The baby food composition detailed in this patent contains fructans from Jerusalem artichoke, salsify, and *Arctium lappa*. Fructans selectively stimulate bifidobacteria in the colon of a baby.

89. Diabetic species
    Patent number: RU2137491 (1999)
    Inventor and applicant: Sukhanov, A.I. (Russian Federation)
    International classification: A61K35/78
    The patent describes dry mixtures from vegetable raw material for use as prophylaxis and treatment of diabetes mellitus. Jerusalem artichoke tubers are among a wide range of plant species listed — all to be used at particular ratios.
90. Production of Jerusalem artichoke juice concentrate
    Patent number: DE19815085 (1999)
    Inventor: Lienig, H., S. Daehnert, and S. Goworek
    Applicant: Lienig Gmbh (Germany)
    International classification: A23L2/02, A23L2/84, A23L2/70
    A new method for the production of a concentrate from Jerusalem artichoke tubers is given. Among the processing steps, the juice is fermented with *Lactobacillus casei* and *Lactobacillus plantarum*.
91. Cultured-milk product Narine for production of dessert in frozen condition
    Patent number: RU2141766 (1999)
    Inventor and applicant: Khachatrjan, A.P. and R.G. Khachatrjan (Russian Federation)
    International classification: A23C9/12, A23C23/00, A23G9/00
    A milk product is described having prophylactic activity due to cultured-milk strains of microorganisms. It includes several lactic acid bacteria (e.g., *Lactobacillus acidophilus* strain 317/402), and inulin from Jerusalem artichoke.
92. Novel pectin
    Patent number: WO9903892 (1999)
    Inventor and applicant: Van Dijk, G.J., M.E.A. Jaspers, H.W. Raaijmakers, B.W. Walraven, and R. De Vos (Netherlands)
    Also published as: NL1006602C (C2)
    International classification: A23L1/0524, A23L1/22, A23L1/308, B01F17/00, C08B37/00, A23L1/052
    A novel method is described for obtaining pectin from chicory or Jerusalem artichoke, with specified characteristics. The novel pectin is an excellent emulsifier and can also be used as a binder, surfactant, and dietary fiber.
93. Condiment Belyaya
    Patent number: RU2125387 (1999)
    Inventor: Kas Janov, G.I., O.I. Kvasenkovm V.G. Shaposhnikov, and A.I. Nikolaev
    Applicant: Sitet, Kuban G T Univer (Russian Federation)
    International classification: A23L1/22, A23L1/39
    The novel condiment contains soya paste, Jerusalem artichoke puree, sugar, salt, ground coriander, ground red pepper, vegetable oil, flavoring, and sorbic acid in specified amounts. It has improved organoleptical properties.
94. Method of producing medicinal confectionary from Jerusalem artichoke
    Patent number: RU2130273 (1999)
    Inventor and applicant: Zelenkov, V.N. (Russian Federation)
    International classification: A23G3/00, A23L1/052
    A method is disclosed for producing an inulin-enriched confectionary additive, which is combined with plant proteins, vitamins, and microelements. Powder of dried Jerusalem artichoke is added upon cooling of the confectionary mass (temperature not exceeding 80°C at the rate of 1 to 10% by weight of confectionary component). When confectionary filler is to be produced, Jerusalem artichoke may be added in an amount of up to 95% by weight.

95. Method of preparing curative–prophylactic agent from Jerusalem artichoke showing biologically active effect on body
    Patent number: RU2132199 (1999)
    Inventor and applicant: Zelenkov, V.N. (Russian Federation)
    International classification: A61K9/08
    A simplified technology for extracting and purifying extracts from dried Jerusalem artichoke tubers is described.
96. Method of preparing inulin from Jerusalem artichoke for medicinal and food aims (variants)
    Patent number: RU2131252 (1999)
    Inventor: Samokish, I.I., N.S. Zjablitseva, and V.A. Kompantsev
    Applicant: Akademija, Pjatigorskaja G Farmatsevtiche (Russian Federation)
    International classification: A61K31/715
    A novel method for preparing sap and an aqueous extract from fresh or dried milled Jerusalem artichoke tubers is disclosed. Crude inulin is crystallized from evaporating extracts. Inulin precipitates are separated, and additional purification involves a further sequence of stages.
97. Composition for milk pudding Syurpriz
    Patent number: RU2125808 (1999)
    Inventor: Fesjun, V.G., T.B. Cheprasova, I.F. Gorlov, and I.A. Chernavina
    Applicant: Cheskij Inst Mjaso Molochnogo, Ererabotki Produktsii Zhivotno, Volg Ni Skij T, Z Volg, Aktsionernoe Obshchestvo Otkry (Russian Federation)
    International classification: A23C23/00
    The composition described includes sugar, cocoa powder, stabilizer, Jerusalem artichoke powder, and milk base. The pudding has improved taste, higher biological value, and curative and prophylactic properties.
98. Method for producing bakery and farinaceous products by means of Jerusalem artichoke
    Patent number: RU2128439 (1999)
    Inventor and applicant: Zelenkov, V.N. (Russian Federation)
    International classification: A21D8/02, A21D13/08, A21D13/00
    The method described involves introducing biological additive, such as Jerusalem artichoke in dry concentrated powdered state, to kneading dough. Jerusalem artichoke used for obtaining bakery product has residual moisture content of up to 14%. Bakery products obtained by this method are enriched in inulin, pectin, microelements, and other biologically active components.
99. Concentrate of dried Jerusalem artichoke
    Patent number: RU2142239 (1999)
    Inventor and applicant: Zelenkov, V.N. (Russian Federation)
    International classification: A23L1/212, A23L1/30
    A method is presented for producing concentrate of dehydrated Jerusalem artichoke tubers. The novel product is characterized by a high content of micro- and macroelements (e.g., silicon, potassium, phosphorus, and magnesium). It provides a biologically active additive for foodstuffs, a base or component of food products, and can also be a source material for the production of inulin for use in the biotechnological, medicine, cosmetics, and pharmaceutical industries.
100. Gelatinized crop product and manufacture thereof
    Patent number: JP10215805 (1998)
    Inventor: Ballevre, O., H.G. Anantharaman, and F. Rochat
    Applicant: Nestle SA
    Also published as: US5952033 (A1), BR9706448 (A), NO314241B (B1), CA2221526 (C), AU728677 (B2)

International classification: A23K1/14, A23K1/18, A23L1/0528, A23L1/164, A23L1/18, A23L1/052

An innovative method to produce a gelatinized crop product with excellent taste to humans and animals, and capable of being manufactured at low cost, is disclosed. An inulin source (0.25% dry matter weight) is contained in a gelatinized starch matrix, obtained from either chicory or Jerusalem artichoke.

101. Method and composition for inhibiting decomposition of aspartame

Patent number: WO9810667 (1998)

Inventor and applicant: Mitchell, D.C. (U.S.)

Also published as: US5731025 (A1)

International classification: A21D2/24, A23L1/236, A21D2/00

The patent describes a heat-stable aspartame-based sweetening composition, comprising mostly aspartame, with minor stabilizing amounts of manna and Jerusalem artichoke. It may be used to prepare baked goods, hot drinks, and the like.

102. Fructan-containing baby food compositions and methods therefor

Patent number: US5840361 (1998)

Inventor: Theuer, R.C. and M.B. Cool

Applicant: Beech Nut Nutrition Corp (U.S.)

International classification: A23L1/0528, A23L1/212, A23L1/214, A23L1/308, A23L1/052

A baby food composition is disclosed that contains one or more fructan-containing vegetables, including Jerusalem artichoke. The composition selectively stimulates colonic bifidobacteria in the infant.

103. Low-fat spread

Patent number: US5846592 (1998)

Inventor: Alderliesten, L., J.M.M. van Amelsvoort, W.A.M. Castenmiller, N.J. de Fouw, R.A. Schotel, and J.J. Verschuren (Netherlands)

Applicant: Van Den Bergh Foods Co (U.S.)

International classification: A23D7/005, A23D7/015, A23L1/05, A23L1/052, A23L1/09, A23L1/308

A spread is disclosed that contains a fiber ingredient that is nondegradable by enzymes secreted by the human body. The fiber ingredient is a nonstarch polysaccharide (average molecular weight of more than 800). Jerusalem artichoke is one of the raw materials recommended for obtaining the fiber.

104. Nutritional powder composition

Patent number: US5744187 (1998)

Inventor and applicant: Gaynor, M.L. (U.S.)

A composition of natural and herbal products is disclosed, which may be compounded in dry form into a mixture readily soluble in fluid for ingestion by humans. When digested, the mixture provides users with an energy boost and associated feelings of well-being. Jerusalem artichoke is one of many ingredients.

105. Prevention of mammary carcinogenesis and breast cancer treatment

Patent number: US5721345 (1998)

Inventor: Roberfroid, M., N. Delzenne, P. Coussement, and J. Van Loo

Applicant: Raffinerie Tirlemontoise, S A (Belgium)

International classification: A23K1/16, A23L1/052, A23L1/308

The invention relates to the use of inulin, oligofructose, or their derivatives as functional ingredients in food, feed, and pharmaceutical composition to prevent mammary carcinogenesis or treat breast cancer. The active ingredients are obtained by enzymatic hydrolysis of native inulin from chicory or Jerusalem artichoke.

106. Method of preparing fructose-containing product from Jerusalem artichoke
Patent number: RU2118369 (1998)
Inventor: Samokish, I.I., N.S. Zjablitseva, and V.A. Kompantsev
Applicant: Pjatigorskaja G Farmatsevtiche, Akademija (Russian Federation)
International classification: C13K11/00
A method is described for improving the preparation of a fructose-containing paste that contains biologically active substances from Jerusalem artichoke.
107. Manufacture of food product
Patent number: RU2110190 (1998)
Inventor: Kvasenkov, O.I., Eh.I. Faradzheva, V.Ju. Barkhatov, and V.A. Bredikhina
Applicant: Kuban G T Univer, Sitet (Russian Federation)
International classification: A23L1/212, A23L2/84, A23L2/70
A method is described that involves fermenting white cabbage with enzymes of microorganisms of lactic acid fermentation, and mixing with prepared tubers of Jerusalem artichoke.
108. Production of drinks
Patent number: RU2111684 (1998)
Inventor: Barkhatov, V.J., V.A. Bredikhina, O.I. Kvasenkov, and E.I. Faradzheva
Applicant: Sitet, Kuban G T Univer (Russian Federation)
International classification: A23L2/02
A method of preparing Jerusalem artichoke for use in fruit juice drinks is described.
109. Method for producing pulp-like products from Jerusalem artichoke
Patent number: RU2110189 (1998)
Inventor: Bredikhina, V.A., O.I. Kvasenkov, E.I. Faradzheva, and V.J. Barkhatov
Applicant: Sitet, Kuban G T Univer (Russian Federation)
International classification: A23L1/212, A23L1/29
A method is described for mixing fruit pulp with prepared Jerusalem artichoke tubers.
110. Production of food product for dietary alimentation
Patent number: RU2110193 (1998)
Inventor: Faradzheva, E.I., V.J. Barkhatov, V.A. Bredikhina, and O.I. Kvasenkov
Applicant: Sitet, Kuban G T Univer (Russian Federation)
International classification: A23L1/212, A23L1/29
A method is given for the preparation of a product for dietary alimentation from Jerusalem artichoke puree.
111. Method for producing pulped canned product based on Jerusalem artichoke
Patent number: RU2105499 (1998)
Inventor: Bredikhina, V.A. and V.J. Barkhatov
Applicant: Sitet, Kuban G T Univer (Russian Federation)
International classification: A23L1/212, A23L1/29
The innovative method involves many stages, including grinding and mixing Jerusalem artichoke with fruit pulp. The mixture is homogenized, heated, and packed in sterilized cans.
112. Method of inulin preparation
Patent number: RU2121848 (1998)
Inventor: Chepurnoj, I.P., S.M. Kunizhev, E.N. Shvetsov, and V.N. Gejko
Applicant: Stavropol Skaja Kraevaja Diabe (Russian Federation)
International classification: A61K35/78
A method is disclosed for the production of an inulin extract from Jerusalem artichoke tubers. Inulin crystallization is done in two stages. The product is used for preparing diagnostic agents and in the food industry.

113. Method of preparing curative–prophylactic agent from Jerusalem artichoke showing antistress, adaptogenic, immunostimulating, antitoxic, membrane-stabilizing, and antioxidant species of biological activity
Patent number: RU2105563 (1998)
Inventor: Zelenkov, V.N. and V.B. Kazimirovskaja
Applicant: Zelenkov, V.N. (Russian Federation)
International classification: A61K35/78
An improved method for extracting biologically active agents from Jerusalem artichoke tubers is described.
114. Jerusalem artichoke juice free from sugar, salts, and sweeteners and with acid pH and low mineral content
Patent number: DE19546150 (1997)
Inventor and applicant: Alpha Engineering Gmbh Entwick (Germany)
International classification: A23L2/02, A23L2/52
A Jerusalem artichoke juice, obtained from tubers, is described. It excludes sugar, salts, and sweeteners.
115. A process for the preparation of dried particles and flour from Jerusalem artichoke tubers
Patent number: WO9625860 (1996)
Inventor: Walley, B.D. and N. Auty
Applicant: Owenacurra Ltd, Walley, B.D., Auty, N. (Ireland)
Also published as: IE64282 (B2), IE950135 (A1), IE950136
International classification: A23B7/06, A23B7/144, A23B7/157, A23L1/214, A23B7/00, A23B7/14
A novel process for the preparation of flour and dried particles from Jerusalem artichoke tubers is described. Tuber particles are exposing to two applications of dilute sulfur dioxide, with an intermediate blanching. The particles are dried to a moisture content of approximately 7.0% and ground to a fine powder.
116. Hydrogenated fructooligosaccharides
Patent number: US5585480 (1996)
Inventor: Vogel, M., M. Kunz, J. Kowalczyk, and M. Munir
Applicant: Sudzucker Aktiengesellschaft Mannheim/Ochsenfurt (Germany)
A low-calorie, noncariogenic sweetener suitable for diabetics is described. It comprises (fructosyl).sub.n mannitol or (fructosyl).sub.n sorbitol (n = 1 to 6), or a mixture of these compounds, and a process for its preparation. Jerusalem artichoke tubers can be used as a raw material.
117. Juice containing inulin, fructose, and glucose production
Patent number: DE4426662 (1996)
Inventor: Heilscher, K. and B. Fiedler
Applicant: Heilscher Karl (Germany)
International classification: A23L1/0528, C13K1/06, C13K11/00, A23L1/052
The patent describes a method for producing juice containing inulin, fructose, and glucose from Jerusalem artichoke tubers. Tubers are comminuted into mash, inulin is converted into monosaccharides, and oligomers are used to control the release of native plant enzymes. The liquid phase is separated from the quasi-solid phase and pasteurized, and further inulinase or invertase is added after cooling to complete the hydrolysis of inulin and oligomers.
118. Process for manufacturing fructose syrup from Jerusalem artichoke
Patent number: RU2039832 (1995)
Inventor: Ibramdzhi, Z., B.L. Flaumenbaum, and O.I. Kvasenkov
Applicant: Vserossijskij Nii Konservnoj I (Russian Federation)
International classification: C13K11/00

119. Production of sugar alcohol
Patent number: JP7087990 (1995)
Inventor: Kobayashi, S., K. Kainuma, M. Kishimoto, K. Honbo, and K. Nagata
Applicant: Nat Food Res, Nippon Denpun Kogyo KK (Japan)
International classification: A23L1/236, C07C31/26, C07H3/06, C07H15/04, C12P7/18, C12P19/14, C07C31/00, C07H3/00, C07H15/00, C12P7/02, C12P19/00
This patent presents a method for producing fructooligosaccharide alcohol from *Helianthus tuberosus* or other inulin-rich plants. The sugar alcohol is specifically designed for use as a bifidus factor in health foods.

120. Sweetening agent
Patent number: CZ8904180 (1994)
Inventor and applicant: Kantner, V.M. and M. Kovar (Czech Republic)
Also published as: CZ279437 (B6)
International classification: A23L1/0528, A23L1/09, A23L1/221, A23L1/236, C12P19/14, A23L1/052, C12P19/00
Production of sweetening agent from vegetable juices, including Jerusalem artichoke.

121. Fresh pasta product and process of manufacture
Patent number: US5258195 (1993)
inventor and Applicant: Lohan, M.J. (U.S.)
International classification: A23L1/16, A23L1/16, A23P1/08
A fresh pasta product of glutinous flour, preferably durum semolina flour, Jerusalem artichoke flour, and water, and its process of manufacturing, is disclosed.

122. Process for producing high-purity fructose-containing concentrates from inulin-containing basic materials and equipment for producing pure fructose from the semifinished product obtained by the process
Patent number: HU63465 (1993)
Inventor: Barta, J., H. Foerster, K. Magyar, K. Vukov, and I. Rak
Applicant: Interprotein Feherje ES Biotec, Lenin MGTSZ (Hungary)
International classification: B01J47/00, C13K11/00
A method for producing a concentrate of Jerusalem artichoke is described.

123. Polyfructan-containing liquid composition
Patent number: JP4311378 (1992)
Inventor: Harada, T., S. Suzuki, K. Ohata, and F. Yamanaka
Applicant: Ajinomoto KK (Japan)
International classification: A23C9/13, A23L1/03, A23L1/308, A23L1/39, A23L2/00, A23L2/38, A23L2/52, C08B37/00, C08B37/18
A method of obtaining a liquid composed of polyfructans is disclosed. The liquid of desired composition is obtained from polyfructan, produced by incubating conidia of *Aspergillus sydowi* and sugar, or formed from sugar or inulin derived from *Helianthus tuberosus* using fructose transferase. The polyfructan liquid is useful in beverages (e.g., fruit juice) and yogurt, or it can be enriched with fiber.

124. Production of fructose-dianhydride I
Patent number: JP4144692 (1992)
Inventor: Oba, S., H. Ogishi, and R. Sashita
Applicant: Mitsubishi Chem Ind (Japan)
International classification: C12N9/24, C12P19/14, C12P19/00
A method is described for the production of difructose-dianhydride I (DFAI) in high yield, by reacting an inulin-containing solution (e.g., from Jerusalem artichoke) with an inulinase derived from a bacterium of the genus *Streptomyces*.

125. Method for preparing a mixture of saccharides
Patent number: US5127956 (1992)

Inventor: Hansen, O.C. and R.F. Madsen
Applicant: Danisco A/S (Denmark)
A method is disclosed for preparing a mixture of fructose, glucose, and oligosaccharides prepared from tubers or roots, and the use of the mixture as a filler or bulking agent with a sweet taste. Jerusalem artichoke tubers are used as a source for the ingredients.

126. Healthy tea and its preparation
Patent number: JP4008270 (1992)
Inventor: Koyama, A.
Applicant: Marusei Misuzuya Honpo Yuugen (Japan)
International classification: A23L1/30, A23L2/38, A61K31/715
The preparation of a healthy tea, exhibiting both a lean body activity and an intestinal disorder-preventing activity, is described. The tea contains roasted products of the roots and stems of inulin-rich plants such as Jerusalem artichoke, along with a Chinese tea component and a Chinese medicine ingredient (leaves of *Eucommia ulmoides*). Processing causes inulinase to convert inulin into fructooligosaccharides, which promote *Bifidobacterium* activity in the intestines.

127. Method for producing preserved food products of inulin content
Patent number: HU55614 (1991)
Inventor: Olah, I. and L. Szabo
Applicant: Baranya Megyei Tanacs Gyogysze (Hungary)
Also published as: HU203959 (B)
International classification: A23L1/307
A method for preparing long-shelf-life food containing inulin is given. The inulin is prepared from ground Jerusalem artichoke powder.

128. Inulin's insulation from vegetable juices
Patent number: CS8905988 (1990)
Inventor and applicant: Linduska, R., A. Matejka, A. Letenay, F. Hosek, and J. Stuchlik (former Czechoslovakia)
Also published as: CS274145 (B1)
International classification: C07H1/08, C07H1/00
A method is given for extracting inulin from vegetable juices, including Jerusalem artichoke.

129. Method and apparatus for the preparation of root crop
Patent number: EP0401812 (1990)
Inventor and applicant: Gerlach, K. (Germany)
Also published as: DE3918671(A1)
International classification: A23N12/02, B03B5/56, A23N12/00, B03B5/00
The invention separates root and tuber crops, including Jerusalem artichoke, from flotation water carrying soil and other debris.

130. Industrial and edible Jerusalem artichoke sort
Patent number: HU51087 (1990)
Inventor: Bagoly, I., Z. Veress, L. Iklodi, and R. Ferenc
Applicant: Rakoczi Ferenc (Hungary)
International classification: A01H5/06

131. Process for producing a food using Jerusalem artichoke tubers
Patent number: DE3915009 (1989)
Inventor: Juchem, F.J. and G. Lehmann
Applicant: Juchem Franz Gmbh & Co Kg (Germany)
International classification: A21D2/36, A23L1/214, A21D2/00
A method is proposed for steaming Jerusalem artichoke tubers to form a pulp. The pulp is used with cereal flour to form dough for bakery products and can be used in other

food types (e.g., noodles). Bakery products are lighter and have better flavor than products made with Jerusalem artichoke flour.

132. Process for preparing flour from Jerusalem tubers
Patent number: US4871574 (1989)
Inventor: Yamazaki, H., H.W. Modler, J.D. Jones, and J.I. Elliot
Applicant: Canadian Patents Development Ltd/Societe Canadienne Des Brevets (Canada)
Also published as: JP1199554(A), CA1324022(A)
International classification: A23K1/16, A23L1/214
Novel processes are disclosed for preparing flour from Jerusalem artichoke tubers or similar inulin-containing plants. Macerated tubers are subjected to heat and spray dried. The flour comprises a mixture of monosaccharides and small and large oligosaccharides.

133. Alcoholic beverage
Patent number: DE3819416 (1989)
Inventor and applicant: Grueneis Ruediger (Germany)
International classification: C12G3/02
An alcoholic beverage having a dry and fresh taste and health-promoting action is described. It is characterized by a content of fermented aqueous extract of Jerusalem artichoke tubers.

134. Process for producing bakery products using Jerusalem artichoke
Patent number: DE3815950 (1989)
Inventor: Juchem, F.J.
Applicant: Juchem Franz Gmbh & Co Kg (Germany)
International classification: A21D2/36, A21D2/00
A method for producing a bakery product using Jerusalem artichoke tubers is disclosed. Tubers are steamed, mashed, and processed with a cereal flour to form a dough and baked.

135. Production of fructose syrup
Patent number: JP63036754 (1988)
Inventor: Yamazaki, H.
Applicant: Meiji Seika Kaisha (Japan)
International classification: A23L1/236
A method is given for producing syrup from Jerusalem artichoke tubers, with a high content of fructose and fructooligosaccharide, but a low glucose content, usable as a sweetener for the patient of diabetes.

136. Natural coffee substitute
Patent number: US4699798 (1987)
Inventor and applicant: MacLean, M. (Canada)
Also published as: JP59196039 (A), CA1184418 (A)
International classification: A23F5/44, A23F5/00
A process for preparing a natural coffee substitute is provided. It comprises dry roasted Jerusalem artichoke (*Helianthus tuberosus*) and Chinese artichoke (*Stachys affinis*).

137. Method of producing fructose from tubers of Jerusalem artichoke
Patent number: S.E.1300032 (1987)
Inventor: Arkhipovich, N.A., T.Y. Chernyakova, and M.N. Koshevich
Applicant: Ki T I Pishchevoj Promy (Sweden)
International classification: C13K11/00

138. Production of fructooligosaccharide
Patent number: JP61277695 (1986)
Inventor: Kobayashi, S., K. Kainuma, M. Kishimoto, K. Honbo, and K. Nagata
Applicant: Nat Food Res, Nippon Denpun Kogyo KK (Japan)

International classification: C07H1/08, C07H3/06, C08B37/18, C12P19/00, C07H1/00, C07H3/00

A method of producing fructooligosaccharide from Jerusalem artichoke is disclosed. Inulin from tubers is reacted with enzymes, and the resulting compounds separated to obtain fructooligosaccharide useful as a food material.

139. Production of fructose polymer
Patent number: JP61280291 (1986)
Inventor: Kobayashi, S., K. Kainuma, M. Kishimoto, K. Honbo, and K. Nagata
Applicant: Nat Food Res, Nippon Denpun Kogyo KK (Japan)
International classification: C08B37/18, C12P19/04, C08B37/00, C12P19/00
A method for producing large amounts of fructose polymer from Jerusalem artichoke is disclosed. The vegetable material is treated with cellulase, and the resulting liquid extract is centrifuged and concentrated to fructose polymers.

140. Production of Jerusalem artichoke flour
Patent number: US4565705 (1986)
Inventor: Snider, H.K.
Applicant: Show-Me Low Calorie Foods Inc (U.S.)
International classification: A23L1/214
This invention is for a process for the production of flour from Jerusalem artichoke tubers. Tubers are reduced to particles, exposed to acidified water, and subjected to a series of pressings at increasing pressures. After the final pressing the particles are dried.

141. Production of fructose syrup
Patent number: US4613377 (1986)
Inventor and applicant: Yamazaki, H. and K. Matsumoto (Canada)
International classification: C13K11/00
A novel method of producing sweet fructose syrup from pulped Jerusalem artichoke is disclosed. The syrup contains oligofructans as a sweetener, which is ideal for elderly people and diabetics. The pulp remaining after juice extraction is rich in protein and can be used as animal feed.

142. Method for producing dietetic and diabetic vegetable–fruit juices of low-energy content as well as vegetable–fruit cocktails containing Jerusalem artichoke juice
Patent number: HU38236 (1986)
Inventor: Zetelakine, H.K., T.E. Szilagyine, and K. Kovacs
Applicant: Koezponti Elelmiszeripari (Hungary)
International classification: A23L1/09
A process for producing juice from vegetables is described, using endo-polygalacturonase enzymes. The fruit juice is useful for diabetics or people on low-energy diets.

143. Method to prepare improved purified fructan solution
Patent number: JP60160893 (1985)
Inventor: Morita, S., H. Tamaya, S. Hakamata, T. Suzuki, and K. Satou
Applicant: Mitsui Toatsu Chemicals (Japan)
International classification: C08B37/00, C12P19/04, C08B37/00, C12P19/00
The method of preparing a purified fructan solution having improved coloring properties and high purity is disclosed. During preparation, an extracted fructan solution obtained from Jerusalem artichoke is treated with a pectin hydrolyzing enzyme.

144. Method of producing syrup opulent in fructose from Jerusalem artichoke tuber
Patent number: HU37016 (1985)
Inventor: Vukov, K., K. Magyar, J. Barta, K. Sasvari, and G. Szabo
Applicant: Hosszuhegyi Aag, Bardibuekki Aag (Hungary)
Also published as: HU192127 (B)
International classification: A23L1/09

145. Production of high-fructose syrup from inulin involving ultrafiltration
Patent number: US4421852 (1983)
Inventor and applicant: Hoehn, K., C.J. McKay, and E.D. Murray (Canada)
International classification: C12P19/14, C13K11/00, C12P19/00
A method for producing high-fructose syrup from Jerusalem artichoke tubers is disclosed. Inulin is extracted in water and subject to enzymatic hydrolyses to fructose and glucose. The sugars are separated, ultrafiltrated, and evaporated. The fructose syrup (at least 90% dry wt) can be mixed with fructose corn syrup in food applications.
146. Process for the extraction of sugars from plants and fruits thereof, especially sugars from sugar beet and sugar cane, and inulin from topinambur, and the elimination of nonsugar matter from this extraction juice by means of ion exchangers or ultrafiltration
Patent number: YU277381 (1983)
Inventor and applicant: Bozidar, D. (Serbia and Montenegro)
147. Process for extracting the juice from tubers, in particular from the Jerusalem artichoke tuber, and device for carrying out this process
Patent number: DE3211776 (1982)
Inventor: Condolios, E. and L. Berthod
Applicant: Alsthom Atlantique (France)
Also published as: LU84057 (A), FR2502909 (A1), BR8201896 (A), BE892497 (A), IT1155487 (B)
International classification: A23N1/02, C13D1/00, A23N1/00
148. Production method of fructose from Jerusalem artichoke using inulinase
Patent number: KR7900995 (1979)
Inventor: Byen, S.M. and B.H. Nam
Applicant: Korean Advanced Institute of Sciences (South Korea)
149. Process for preparing fructose from Jerusalem artichoke by enzymatic method
Patent number: JP52136929 (1977)
Inventor: Ishibashi, K., S. Amao, S. Higuchi, and T. Watanabe
Applicant: Sankyo Co, Dai Ichi Kogyo Seiyaku Co Ltd (Japan)
International classification: C13K11/00
150. Extraction of flour or starch from tubers, roots, or fruits
Patent number: GB1146854 (1969)
Inventor and applicant: Rolf, H.
Also published as: US3433668 (A1), OA1884 (A)
International classification: A23L1/214, C08B30/04, C08B30/00
151. A process for the production of a fermentation beverage
Patent number: GB714119 (1954)
Inventor and applicant: Vosseler, O. (GB)

ANIMAL FEED APPLICATIONS

1. Method for mixing and introduction of inulin
Patent number: US7001624 (2006)
Inventor: Golz, D.I.
Applicant: Encore Technologies (U.S.)
International classification: A23K1/00, A23K1/16, A23K1/18
A novel method is described for mixing and introduction of inulin in the feed of young animals to promote health, including inulin extracted from Jerusalem artichoke.
2. Prophylactic feed for dogs and method for producing the same
Patent number: RU2264125 (2005)

Inventor and applicant: Gritsienko, E.G., N.V. Dolganova, and R.I. Aljanskij (Russian Federation)
International classification: A23K1/00
A dog's feed is described that contains plant and animal components, with plant components including oats, buckwheat grains, barley, tomato, Jerusalem artichoke green mass, and wheat grits.

3. Piglet feeding method
Patent number: US6387419 (2002)
Inventor: Christensen, B.H.
Applicant: Biofiber-Damino A/S (Denmark)
International classification: A23K1/175, A23K1/18
A method of obtaining optimum performance of piglets without the use of antibiotic growth promoters is disclosed. It involves administering during the entire suckling period feed supplement compositions containing dietary fibers, iron, and other micronutrients, with a third comprising dietary fibers and electrolytes to prevent or cure diarrhea. Jerusalem artichoke fiber is one of the suggested ingredients.
4. Fodder additive on base of Jerusalem artichoke as curative–prophylactic preparation for domestic and farm animals
Patent number: RU2149564 (2000)
Inventor and applicant: Zelenkov, V.N. (Russian Federation)
International classification: A23K1/16
An additive for use in preparing fodder mixtures enriched with Jerusalem artichoke is disclosed, for curative–prophylactic use in ration of domestic and farm animals. As the main component, the fodder additive contains tuber and aboveground parts of Jerusalem artichoke in dried form.
5. Method of sanitation of farm animals
Patent number: RU2140788 (1999)
Inventor: Blokhina, I.N., N.A. Golubeva, V.P. Drjaglov, V.M. Radchenko, A.G. Samodelkin, B.V. Smetov, and E.A. Jakimycheva
Applicant: Ehpidemiologii I Mikrobiologii, Nizhegorodskij Ni Skij I (Russian Federation)
International classification: A61K35/74, A61K35/66
A method is disclosed for the introduction of treatment and prophylactic products to young animals. These products possess a complex of protective factors, including Jerusalem artichoke. They promote weight gain and reduce disturbances in the gastrointestinal tract.
6. Process for treating small intestine bacterial overgrowth in animals
Patent number: US57766524 (1998)
Inventor: Reinhart, G.A.
Applicant: Iams Company (U.S.)
A pet food product useful for reducing the amount of harmful bacteria in the small intestine is described. The pet food composition contains, on a dry matter basis, from about 0.2 to 1.5 wt% of a fructooligosaccharide and is fed to a pet, such as a dog, cat, or horse. Jerusalem artichoke is a potential source of the required fructooligosaccharides.
7. Jerusalem artichoke sort of fodder
Patent number: HU50561 (1990)
Inventor: Bagoly, I., Z. Veress, L. Iklodi, and F.R. Kun
Applicant: Rakoczi Ferenc (Hungary)
International classification: A01H5/06
8. Improved fodder and process for the manufacture of same
Patent number: GB190804565 (1908)

Inventor and applicant: Fodor, G. (Austria)
A fodder to be used as a substitute for oats is described, being prepared by mixing quantities of rye, barley, oats, maize, potatoes, rice, grass, clover, malt germs, food potatoes, topinambur (*Helianthus tuberosus*), horse chestnuts, straw, dried beet, linseed cake, and rape cake.

NONFOOD INDUSTRIAL APPLICATIONS

1. Method of preparing L(+)-lactic acid
   Patent number: RU2195494 (2002)
   Inventor and applicant: Shamtsjan, M.M., V.I. Jakovlev, and K.A. Solodovnik (Russian Federation)
   International classification: C12P7/56, C12P7/40
   A method is given that involves fermenting Jerusalem artichoke tuber with *Streptococcus bovis*. This simplifies and decreases the cost of preparing L(+)-lactic acid.
2. Biologically active additive from Jerusalem artichoke for cosmetic agents
   Patent number: RU2162684 (2001)
   Inventor and applicant: Zelenkov, V.N. (Russian Federation)
   International classification: A61K7/00, A61K7/26, A61K7/50
   A biologically active additive from Jerusalem artichoke is described, made from various plant parts, which is claimed to have a beneficial effect on the skin.
3. Method of ethyl alcohol production from Jerusalem artichoke
   Patent number: RU2144084 (2000)
   Inventor: Krikunova, L.N., E.F. Shanenko, and M.V. Sokolovskaja
   Applicant: Mo Gu Pishchevykh, Proizv (Russian Federation)
   International classification: C12P7/06, C12P7/02
   A novel method is given for treating milled Jerusalem artichoke tubers with endogenous raw inulinases to hydrolyze them. The process is activated with calcium ions, and industrial yeast is added to the must. This simplified process can improve mash quality.
4. Thermoplastic resin composition
   Patent number: JP9048876 (1997)
   Inventor: Okamura, M., T. Kaniwa, and A. Kamata
   Applicant: Mitsubishi Chemical Corp (Japan)
   International classification: C08K3/00, C08K5/15, C08L101/00, C08K5/00, C08L101/00
   A procedure for obtaining thermoplastic resin from plant-derived inulin is disclosed. The resin has excellent mechanical characteristics, heat and chemical resistance, good moldability, and mechanical properties desirable in automotive parts and for recycling. The resin composition includes cyclic inulooligosaccharide (n = 6 to 8), prepared by reacting inulin or vegetable plant extract, obtained from a rhizome of *Helianthus tuberosus* L. or *Cichorium intybus* L., and inulin with an enzyme capable of producing a cyclofructan.
5. Making technology of semicellulose beverage
   Patent number: CN1127261 (1996)
   Inventor and applicant: Lishen, Liu (China)
   International classification: C08B37/14, C08B37/00
   The invention relates to a technological process for preparing hemicellulose, for instance, from Jerusalem artichoke tubers. The tubers are ground (1 to 3 mm grain size), defatted using 30% petroleum ether, washed in a pH 10 to 11 aqueous solution containing 1% Na_2CO_3 and 2% $NaHCO_3$ to dehydrate them, dissolved in 45% C_2H_5OH, sealed in liquid nitrogen, pulverized at low temperature (–120°C), and dried.

6. Building material containing chopped sunflower additive
   Patent number: DE19505989 (1996)
   Inventor: Gerstner, B. and O. Selmigkeit
   Applicant: Hasit Trockenmoertel Gmbh (Germany)
   International classification: C04B18/24, C04B18/04, C04B16/02, C04B24/38
   The patent discloses a building material mix, especially for mortar or concrete, with added vegetable matter. The novelty is that the additive is in the form of chopped stems of sunflower, especially Topinambur (Jerusalem artichoke). Vegetable matter added to the mix retards setting and reduces the density.
7. Curative cosmetics agent containing Jerusalem artichoke extract
   Patent number: RU2138247 (1999)
   Inventor and applicant: Zelenkov, V.N. (Russian Federation)
   International classification: A61K7/48
   The invention relates to agents for curative–prophylactic skin and hair care. The composition includes Jerusalem artichoke extracts from tuber and aboveground parts of stated amounts. The cosmetic agent is claimed to show correcting effects on systemic immune response.
8. Oily cosmetic
   Patent number: JP5097626 (1993)
   Inventor: Shimizu, I. and S. Momose
   Applicant: Kose Corp (Japan)
   International classification: A61K7/00, A61K7/021, A61K7/025, A61K7/027, A61K7/032
   A method for producing a solid or semisolid oily cosmetic uniform is disclosed. The cosmetic contains an oily ingredient and fructooligosaccharide powder, one source of which is Jerusalem artichoke.
9. Production of inulinase
   Patent number: JP3198774 (1991)
   Inventor: Tamaya, H., S. Takahashi, F. Yoshimi, A. Fukuoka, K. Sato, and H. Okuno
   Applicant: Mitsui Toatsu Chemicals (Japan)
   International classification: C12N9/24
   A method for producing highly active endo-type inulinase at low cost is described. Part of the method involves subjecting an inulinase-producing strain of *Penicillium* to an aerated culture comprising an inulin-containing plant material, such as the ground tubers of Jerusalem artichoke.
10. Production method of inulinase
    Patent number: RO103812 (1991)
    Inventor: Dan, Valentina and Lucia Teodorescu
    Applicant: Univ Bucharest (Romania)
    International classification: C12N9/14, C12R1/66
    A method for preparing inulinase is described, in which *Aspergillus niger* is cultured on a substrate containing Jerusalem artichoke powder.
11. Cosmetic compositions having skin-calming and skin-regenerating effects and process for the preparation thereof
    Patent number: US4855137 (1989)
    Inventor: Keri, T. and J. Kristof
    Applicant: Innofinance Altalanos Innovacios Penzintezet (Hungary)
    Also published as: WO8606958 (A1), EP0224550 (A1), NL8620221 (A), GB2186488 (A), FI870264 (A), CH667806 (A5), EP0224550 (B1), SE8700156 (L), SE466733 (B), HU198619 (B), FI81960C (C), FI81960B (B)
    International classification: A61K8/97, A61Q19/00, A61K8/96

This invention relates to cosmetic compositions having skin-calming and skin-regenerating effects, comprising extracts of the aerial shoot or tuber of Jerusalem artichoke as an active ingredient.

12. Process for the production of 2,3-butanediol by aerobic fermentation of a substrate by strains of *Bacillus polymyxa*
    Patent number: EP0162771 (1985)
    Inventor: Wilhelm, J.-L. and J. Fages
    Applicant: Charbonnages Ste Chimique (France)
    Also published as: FR25644 (A1), EP0162771 (B1)
    International classification: C12P7/18, C12P7/02
    The innovative process for making 2,3-butanediol by aerobic fermentation of a substrate by strains of *Bacillus polymyxa* is characterized by the fact that the substrate is Jerusalem artichoke juice.
13. Joint use of acetone–butanol fermentation and alcoholic fermentation for the conversion of sugar-yielding plants into a mixture of butanol, acetone, and ethanol
    Patent number: FR2550222 (1985)
    Inventor: Ballerini, D., R. Marchal, M. Hermann, D. Blanchet, and J.-P. Vandecasteele
    Applicant: Inst Francais Du Petrol (France)
    International classification: C12P7/28, C12P7/24
    A process for the production of a mixture of butanol, acetone, and ethanol from sugar-yielding plants, especially Jerusalem artichoke and sugar beet, is described. The process comprises two stages: (1) seeding with *Clostridium acetobutylicum* and (2) seeding with a yeast that produces ethanol.
14. Improvement to the production of a mixture of acetone and butanol by fermentation of a juice from acidic hydrolysis of Jerusalem artichoke
    Patent number: FR2533230 (1984)
    Inventor: Heyraud, A., M. Rinaudo, F. Taravel, and D. Blanchet
    Applicant: Inst Francais Du Petrol (France)
    International classification: C12P7/28, C12P7/24
15. Production of ethanol from Jerusalem artichokes
    Patent number: US4400469 (1983)
    Inventor and applicant: Harris, F.B. (U.S.)
    International classification: C12P7/06, C12P7/02, A23K1/00
    A novel method of producing ethanol from Jerusalem artichoke is disclosed. Sugar juices are removed from the stalk, before they are reallocated to the tubers, and directly fermented to produce alcohol. The ground stalk mass can be used as animal food.
16. Method for preparing d(-)lactic acid
    Patent number: GB1030740 (1966)
    Inventor and applicant: Kyowa, H. and K.K. Kogyo
    Also published as: US3262862 (A1)
    International classification: C02F1/04, C12P7/56, C12P7/40
17. Preparation of 5-hydroxymethyl 2-furfural
    Patent number: GB817139 (1959)
    Inventor and applicant: Peniston, Q.P.
    International classification: C07D307/46, C07D307/00
18. Improvements in or relating to the production of vegetable fibers
    Patent number: GB410144 (1934)
    Inventor and applicant: Luigi, R.T.
    Also published as: GB408007 (A), FR759454 (A), BE398131 (A)
    International classification: D01C1/02, D01C1/00

19. Improvements relating to the production of propionic acid by fermentation
    Patent number: GB390769 (1933)
    Inventor and applicant: Commercial Solvents Corp
    International classification: C12P7/52, C12P7/40
20. Improved manufacture of organic acids
    Patent number: GB345368 (1931)
    Inventor and applicant: Cahn, F.J.
    International classification: C12P7/48, C12P7/40
21. Improvements in or relating to the preparation of pulp or fibrous material for the manufacture of paper, papier-mache, and the like
    Patent number: GB137105 (1920)
    Inventor and applicant: Skinner, L.H.
    International classification: D21C5/00

GENETIC MANIPULATION AND BIOTECHNOLOGY

1. Transgenic crops accumulating fructose polymers and methods for their production
   Patent number: DE69929676 (2006)
   Inventor: Caimi, G.
   Applicant: Du Pont (U.S.)
   Also published as: WO9946395 (A1), EP1062350 (A1), CA2319759 (A1)
   International classification: C12N15/82, A01H5/10, C12N5/10, C12N9/10
   A method for producing transgenic crops is disclosed, using an enzyme derived from Jerusalem artichoke.
2. Gene encoding protein having aurone-synthesizing activity
   Patent number: US6982325 (2005)
   Inventor: Sakakibara, K., Y. Fukui, Y. Tanaka, T. Kusumi, M. Mizutani, and T. Nakayama
   Applicant: Suntory Flowers Ltd, Suntory Ltd (Japan)
   Also published as: WO9954478
   International classification: C07H 21/04
   The invention relates to genes encoding proteins having aurone synthase activity involved in the yellow color of flowers. Jerusalem artichoke flower color is due to the aurone compound sulfetin.
3. Method for altering storage organ composition
   Patent number: US6930223 (2005)
   Inventor: Higgins, T.J., L.M. Tabe, and H.E. Schroeder
   Applicant: Commonwealth Scientific and Industrial Research Organisation (Australia)
   Also published as: WO 98/13506
   The invention provides a method for altering or modifying the content or composition of one or more metabolites in the storage organs of a plant. The invention extends to plants and genetic constructs used to produce plant material, and is applicable to all tuber crops, including Jerusalem artichoke.
4. Gene engineering for producing fructose by inulase-hydrolyzing *Helianthus tuberosus*
   Patent number: CN1465699 (2004)
   Inventor: Zhang, L. and Y. Wang
   Applicant: Dalian Light Ind College (China)
   International classification: C07H21/04, C12N1/16, C12N9/62, C12P19/02, C07H21/00, C12N9/50, C12P19/00
   The invention relates to a method for producing fructose by engineering an inulase gene to hydrolyze Jerusalem artichoke tubers. The inulase gene inuA1 from *Aspergillus*

niger AF10 expresses INUA1 and provides the means for producing fructose by using GS115/inuA1 inulase to hydrolyze inulin, as well as cane sugar and other raw materials.

5. Separating and recovering components from plants
   Patent number: US6740342 (2004)
   Inventor: Hulst, A.C., J.J.M.H. Ketelaars, and J.P.M. Sanders
   Applicant: Cooperatieve Verkoop-en Productievereniging van Aardappelmeel en derivaten Avebe BA (Netherlands)
   Also published as: WO0040788 (A1), EP1149193 (A1), CA2356880 (A1), EP1149193 (B1), NL1010976C (C2), AU758966 (B2)
   International classification: D01B1/42, D01B1/00
   A method is described for separating cytosolic and parenchyma components from vegetable material, including Jerusalem artichoke.
6. Transgenic plants presenting a modified inulin-producing profile
   Patent number: US6664444 (2003)
   Inventor: Koops, A.J., R. Sevenier, A.J. Van Tunen, and L. De Leenheer
   Applicant: Tiense Suikerraffinaderij NV. (Belgium), Plant Research Int. BV. (Netherlands)
   Also published as: EP0952222 (A1), WO9954480 (A1), AU2003246315 (A1)
   International classification: C12N9/10, C12N15/82
   The patent describes a method for producing transgenic plants with modified inulin-producing profiles. Plants comprise a combination of one or more expressible 1-SST enzyme encoding genes and one or more expressible 1-FFT enzyme encoding genes in their genomes. The invention also relates to a method for modifying and controlling the inulin profile of plants, and to a method for producing inulin from those plants. Furthermore, a novel cDNA sequence of a 1-SST enzyme encoding gene of *Helianthus tuberosus* and a novel cDNA sequence of a 1-FFT enzyme encoding gene of *Cichorium intybus* are disclosed, and novel recombinant DNA constructs and genes derived from them.
7. Nutrient medium for culturing bifidobacteria
   Patent number: RU2214454 (2003)
   Inventor: Amerkhanova, A.M., V.K. Gins, V.A. Aleshkin, A.K. Bandojan, G.V. Khachatrjan, E.S. Zubkova, M.S. Gins, P.F. Kononkov, and L.A. Bojarkina
   Applicant: Sledovatel Skij Inst Ehpidemio, Logii Im G N Gabrichevskogo, G Uchrezhdenie MO N IS (Russian Federation)
   International classification: A61K35/74, C12N1/20, A61K35/66
   The composition of a nutrient medium for culturing bifidobacteria is disclosed that has application in medical research and in the food industry. The medium includes extracts of amaranthus leaves (as a protein source) and Jerusalem artichoke tubers (as a carbohydrate source).
8. Plants with modified growth
   Patent number: US6559358 (2003)
   Inventor: Murray, J.A.H.
   Applicant: Univer Cambridge Tech (GB)
   Also published as: WO9842851 (A1), WO9842851 (A1), CA2282715 (A1), BR9807886 (A), AU751341 (B2)
   International classification: C07K14/415, C12N15/82, A01H5/00, C12N15/29
   This patent covers a range of chimeric genes, containing specified operably linked DNA fragments, and a process to engineer them into plants to obtain altered growth characteristics. The chimeric genes include numerous isolated DNA sequences, including a nucleotide sequence of SEQ ID 4 from nucleotide position 165 to nucleotide position

1109, encoding *Helianthus tuberosus* CYCD1, and the nucleotide sequence of SEQ ID 5 from nucleotide position 48 to nucleotide position 1118, encoding *H. tuberosus* CYCD3.

9. Purified cytochrome P450 polypeptide CYP76B1 from *Helianthus tuberosus* and its application as biocatalyst in particular for the degradation of environmental pollutants and for altering the resistance of plants sensitive to the phenylurea family of herbicides
   Patent number: US6376753 (2002)
   Inventor: Batard, Y., T. Robineau, F. Durst, D. Werck-Reichhart, and L. Didierjean
   Applicant: Centre National de la Recherche Scientifique (France)
   International classification: C12N9/02, C12N15/82, A01H5/00, C12N5/04, C12N15/00, C12N15/29
   This invention relates to the gene CYP76B1 of a cytochrome P450, which has been isolated from a *Helianthus tuberosus* tuber. The expression of this gene in yeast shows that it encodes an enzyme active in catalyzing the *O*-dealkylation of various exogenous molecules with a high efficiency, such as phenylureas. The expression of CYP76B1 is strongly induced in plants brought into contact with certain exogenous metals or organic compounds, which could be exploited for the detection of environmental pollutants, to alter the resistance of plants sensitive to this family of herbicides, or for soil and groundwater bioremediation.
10. Transgenic crops accumulating fructose polymers and methods for their production
    Patent number: US6365800 (2002)
    Inventor: Caimi, P.G.
    Applicant: Du Pont (U.S.)
    International classification: C12N15/82, A01H5/10, C12N5/10, C12N9/10
    A method for producing fructose polymers of various lengths through expression of plant-derived FTF genes in transgenic monocot plants is disclosed. The genes derived from Jerusalem artichoke encode sucrose-sucrose-fructosyltransferase and fructose-fructose-fructosyltransferase.
11. Gene coding for *Helianthus tuberosus*-derived lectin
    Patent number: JP11206386 (1999)
    Inventor: Nakagawa, R., D. Yasogawa, T. Ikeda, and K. Nagashima
    Applicant: Nakagawa Ryoji (Japan)
    International classification: A01H5/00, A01K67/027, C12N1/19, C12N1/21, C12N15/09
    The patent describes the position and base sequence of a gene encoding the amino acid sequence of *Helianthus tuberosus*-derived lectin. The gene is usable in, for example, the separation, removal, and detection of saccharides in microorganisms and cells, and also as a disease-resistant gene. The gene is obtained by the following procedure: a cDNA library is prepared using poly(A)<+> RNA extracted from the callus of *H. tuberosus* and subsequently screened using the antiserum of the above-mentioned lectin.
12. Lectin derived from *Helianthus tuberosus* and method for separating the same
    Patent number: JP8119994 (1996)
    Inventor: Nakagawa, R., D. Yasogawa, T. Ikeda, and K. Nagashima
    Applicant: Nakagawa Ryoji (Japan)
    International classification: C07K1/22, C07K14/42, C07K1/00, C07K14/415
    A method for obtaining a new lectin from Jerusalem artichoke callus is described. The lectin is useful for the separation, removal, detection, and analysis of complex saccharide. Callus is mixed with distilled water containing 2% isoascorbic acid, ground, and centrifuged to recover a supernatant liquid. Fractionation gives a lectin that has a strong affinity for mannose and glucose.

13. Yeast strain for the co-expression of a plant cytochrome P450 monooxygenase activity and an endogenous or heterologous NADPH-cytochrome P450-reductase and use thereof in bioconversion
    Patent number: WO9401564 (1994)
    Inventor and applicant: Kazmaier, M. (France), D. Pompon (France), C. Mignotte Vieux (France), H. Teutsch (Germany), D. Werk-Reichart (France), and M. Renaud (France)
    Also published as: FR2693207 (A1)
    International classification: C12N9/02, C12N15/81, C12P7/42, C12P7/40
    The patent discloses details of a yeast strain for the co-expression of a plant cytochrome P450 monooxygenase activity and an NADPH-cytochrome P450-reductase, and its use with a cDNA sequence coding for cytochrome P450 CA4H of the Jerusalem artichoke for bioconversion purposes.

CULTIVATION AND PLANT BREEDING

1. Method for cultivation of Jerusalem artichoke on salinated semiarid soil with close occurrence of underground water
   Patent number: RU2253221 (2005)
   Inventor and applicant: Dedova, E.H.B. (Romania)
   International classification: A01G1/00, A01G25/00
   A method of cultivating Jerusalem artichoke on salinated soil is disclosed. The method involves planting tubers in autumn, providing care for young crops, applying fertilizer and irrigating to maintain soil moisture, and harvesting green mass and roots in September–October. This results in an increased efficiency in employment of abandoned, oversalinated lands in arid zones.
2. Method for cultivation of Jerusalem artichoke
   Patent number: RU2250585 (2005)
   Inventor and applicant: Starovojtov, V.I., V.I. Chernikov, M.V. Starovojtova, V.V. Rytchenko, and V.V. Khoves (Romania)
   International classification: A01B79/02
   The novel method involves providing autumn preplanting soil cultivation, applying organic and mineral fertilizers, cutting ridges, planting seed tubers, providing interrow cultivation, and harvesting. Plant tops are mown for forage 2 to 3 weeks before harvesting of tubers. The method results in improved growing conditions, reduced damage during harvesting, reduced labor intensity, and reduced probability of sclerotinia disease.
3. Method of contour-strip soil cultivation
   Patent number: UA69229 (2004)
   Inventor: Tymchenko, D.O. and V.I. Didenko
   Applicant: National Scientific Center ON Sokolovsky I (Ukraine)
   International classification: A01B13/16, A01B13/00
   A method of contour-strip soil treatment is disclosed, whereby vegetation is fixed to strips. Fixing a strip is carried out by means of planting long-stemmed agricultural plants, such as Jerusalem artichoke.
4. Breeding method for Jerusalem artichoke
   Patent number: CN1475099 (2004)
   Inventor and applicant: Liu, Junzheng (China)
   International classification: A01G1/00, C05G1/00
   A method for reproducing Jerusalem artichoke by culturing seedlings on a vernalization bed is disclosed. Seedlings are grown to 15 to 20 cm in height, cut into segments, cultured in medium (prepared from humus, fertilizer, trace elements, and macroelements),

and transplanted. The method can provide planting material to combat soil erosion.

5. Method for controlling desert by utilizing *Helianthus tuberosus*
   Patent number: CN1411688 (2003)
   Inventor: Ma, S. and T. He
   Applicant: Beijing Hongju Lugu Desertific (China)
   International classification: A01C1/00, A01G7/00, E02D3/00
   This invention relates to a method for controlling desert spread, by planting Jerusalem artichoke to increase the humic matter of sand. It covers the selection of seed tubers and a sowing procedure involving soaking in pesticide solution.
6. Method of breeding tuber of Jerusalem artichoke in seawater
   Patent number: CN1462576 (2003)
   Inventor: Liu, Z., X. Long, and A. Li
   Applicant: Nanjing Agricultural Univer (China)
   International classification: A01G7/00, A01G9/02, A01G31/00
   This patent describes a method for cultivating the stem tuber of Jerusalem artichoke in seawater. It includes a design for culture bowls, a nutritive liquid prepared from sea salt, the arrangement of stem tuber slices on the surface of paper on an upper-layer soft plastic plate, and the fixing of the upper part of Jerusalem artichoke with the perforated circular disk after it grows to a certain height. Its advantages are high survival rate (60% or more) and high yield.
7. Machine for harvesting of roots, in particular of Jerusalem artichoke
   Patent number: RU2212126 (2003)
   Inventor: Rejngart, E.S., V.V. Rytchenko, I.J. Sigal, L.I. Levchuk, and G.V. Golokolenov
   Applicant: Topiprom Fa O, OOO AGR (Russian Federation)
   International classification: A01D17/04, A01D17/00
   A machine for harvesting tubers is described. It has a frame mounted with tools for digging and a separating elevator with belt, above which a right-hand coil screw and left-hand coil screw are positioned. The machine is further equipped with a clod crusher and conveying and discharging devices; the rotor is arranged in an inclined position with respect to the surface of the conveying device. It results in improved quality of Jerusalem artichoke tubers from soil and their separation from runner and stalk mass.
8. Method of controlling desert by means of kesha Jerusalem artichoke
   Patent number: CN1325617 (2001)
   Inventor: Jiagn, J.
   Applicant: Lushan Package Co Ltd Dalian (China)
   International classification: A01G7/00, E02D3/00
   A method involving the bunch planting of Jerusalem artichoke in the desert is described. It consists of three stages: cutting tubers and planting, sowing later in the spring, and harvesting. Tubers and roots fix the sand firmly, while stems and leaves form a shelter belt.
9. Method for improving desert by planting Jerusalem artichoke
   Patent number: CN1257645 (2000)
   Inventor and applicant: Jiang, J. (China)
   International classification: A01G7/00, E02D3/12, E02D3/00
   A method for improving desert by planting Jerusalem artichoke is described, which includes planting cut stem tubers (up to 1 cm^2) mixed with plant ash in holes (10 to 20 cm deep) in late spring, and harvesting every 2 years. Jerusalem artichoke has high resistance to cold, drought, and wind, and high reproductive potential. Its roots fix sand, and its stems and leaves form a windbreak band.

10. Jerusalem artichoke (*Helianthus tuberosus*) variety, named "compact"
    Patent number: RO113601 (1998)
    Inventor: Diaconu, P., A.F. Badiu, and A. Baia
    Applicant: Inst De Cercetare Si Productie (Romania)
    International classification: A01H5/06
11. Method and apparatus for cleaning roots, tubers, bulbs, and the like
    Patent number: US5824356 (1998)
    Inventor and applicant: Silver, B.S. and R.V. Zimmerman (U.S.)
    Also published as: WO9714514
    International classification: A01D17/06, B07B1/15, A01D17/00, B07B1/12
    A method and apparatus are disclosed for cleaning roots, tubers, bulbs, and the like, for example, Jerusalem artichokes. The apparatus has horizontal rollers with helices on their cylindrical surfaces that scroll articles laterally. The first sets of rollers separate small chips and stones, and loose soil from the articles. The next sets remove adhering soil and mud, weeds, and larger stones. Strategic placement sizing, rotational speed, and direction of rotation of the helices on the rollers are instrumental in removing leaves, stalks, and weeds, breaking up dirt clods and mud balls, and cleaning the articles.

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LATIN BINOMIALS

Biological Sciences

Biology and Chemistry of Jerusalem Artichoke

Helianthus tuberosus L.

A unique plant on many levels, the distinctive properties of the Jerusalem artichoke (*Helianthus tuberosus* L.) present novel answers to some of today's most pressing problems. Jerusalem artichoke is potentially a major source of inulin, a fructose polymer that provides dietary health benefits: as a prebiotic that promotes intestinal health and as a low-calorie carbohydrate to combat obesity and diabetes. Inulin also has myriad industrial applications, including ethanol production — making Jerusalem artichoke a potential source of biofuel. With its ready cultivation and minimal pest and disease problems, Jerusalem artichoke is an underutilized resource that possesses the potential to meet major health and energy challenges.

Gathering a wealth of information into a single volume and drawing on the authors' 25 years of research experience, **Biology and Chemistry of Jerusalem Artichoke** provides a comprehensive, up-to-date resource on this extremely useful crop. Highlighting unique biological and chemical properties, this book—

- Reviews the history, classification, morphology, and anatomy of the Jerusalem artichoke
- Details inulin chemistry including properties, structure, extraction, and modification
- Examines the beneficial role of inulin in relation to obesity and diabetes, and in promoting general good health
- Analyzes the use of Jerusalem artichoke as a biofuel
- Addresses genetic resources, breeding, and the heritability of important traits
- Explains developmental biology in terms of maximizing yield and resource allocation
- Offers practical information on agronomic methods, storage, economics, and future prospects for utilization

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