OPUNTIA FRAGILIS: TAXONOMY, DISTRIBUTION, AND ECOLOGY

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Abstract: *Opuntia fragilis* is the smallest and most cold-hardy species of North American prickly pear, with an unusual distribution. This document is a review of its taxonomy, distribution, and ecology.

Key words: endangered species, Midwestern US, rock outcrop communities

I was not a little surprised to meet with the Cactus Opuntia thus far to the northward, it grew plentifully but in a very dwarf state on the eastern point of the Island which is low flat and dry sandy soil.

—From the Journal of Archibald Menzies, who sailed in 1791–95 with Captain George Vancouver, and was the first European botanist to set foot on the Vancouver Gulf Islands, in May 1792, as quoted by Clark (1976: 318).

Species Description

Opuntia fragilis (Nutt.) Haw., the Fragile Prickly Pear, was first described by Thomas Nuttall in 1819. He named it *Cactus fragilis*, and Haworth later transferred it to *Opuntia fragilis*. The specific name 'fragilis' refers to the ease with which the terminal joint is detached (Clark 1976, p 317), an adaptation for asexual reproduction and dispersal.

Distinguishing characteristics of *O. fragilis* include the small size of the cladodes and their roundness (Fig 1). *O. fragilis* has bluish-green to bright green cladodes 2–6 cm long that are at least half as thick as they are broad. The cladodes readily break off, especially the terminal ones, have strongly barbed spines that are not covered with a sheath, and well-developed glochids. The roots do not have glochids. Flowers are larger than the pads, yellow but may have reddish or greenish centers, and have up to ten stigma lobes. Fertilized flowers produce a dry capsule fruit slightly larger than 1 cm. The entire plant is prostrate, less than 10 cm tall, and larger plants can form dense clusters of 200 or more pads, although whether these plants are still physiologically integrated is doubtful. *O. fragilis* is described in many manuals of the Cactaceae (for instance, Benson 1982, p 394).

O. fragilis cladodes are glaucous whitish-green (Borg 1970) or dark green (Abrams 1951), 1–3 cm wide (Lundell 1969) and 2–6 cm long (Bare 1979). They may be somewhat flattened, especially the older joints (Boissevain and Davidson 1940), but often are cylindrical to obovoid. Older cladodes are more likely to be flattened (Harrington 1964), but still are at least half as thick as broad (Correll and Johnston 1970). Cladodes join to form chains, which generally are prostrate or nearly prostrate (van Bruggen 1976). Undisturbed specimens can form large mats with hundreds of cladodes (Benson 1982, Davis 1952), with branches that are several-jointed, enabling the plant to spread widely (Kearney and Peebles 1964). The younger joints break away from the parent plant and root very easily (Bernshaw and Bernshaw 1984), particularly the terminal joint (Fernald 1950). Pads are often very wrinkled and flaccid (Weniger 1970), although it is my experience this is mostly associated with winter dormancy, which may persist until early June.

Areoles are woolly, especially when young (Bare 1979), 2–3 mm in diameter (Abrams 1951), and are usually closely set (Britton and Rose 1963) at less than 1 cm apart (Harrington 1964), covering most of the pad (Benson 1982). Each areole contains white wool (Boissevain and Davidson 1940), 1–6 (rarely 9) spines (Correll and Johnston 1970), and a few yellowish or brownish glochids. The spines have been described as brownish to grayish, usually with darker tips, up to 3.5 cm long (Borg 1970), up to 0.7 mm in diameter (Lundell 1969), and are round or nearly round in cross section (Weniger 1970). While usually yellowish, spines may be white, reddish, nearly black, or multihued. Spines may even be completely lacking. The spines tend to spread in all directions (Fernald 1950, Haage 1965). The longest spines tend to be found in the upper areoles (Lundell 1969), and the spines are barbed (Davis 1952). McGregor and others (1986) noted that the longest spines are often longer than the stem is wide. Munz and Keck (1959) described the areoles of *Opuntia fragilis* in California as being closely set, circular, woolly, with 1–5 spines, these 15–25 mm long, whitish to brownish, and slender. Figure 2 is a close-up of two pads; the spines and glochids are clearly visible.

Abrams (1951) described *O. fragilis* as having light yellow glochids 1–4 mm long. Benson (1982, p 394) noted that the glochids can be "tan or brownish, 2 mm long," a length echoed by Lundell (1969) and McGregor and others (1986). Correll and Johnston (1970) stated that *O. fragilis* is distinguished by having glochids that are well-developed, barbed, and effective. Weniger (1970) described *O. fragilis* glochids as being "very few and short, and yellowish in color."

Gibson and Nobel (1986: 176) included a black-and-white picture of *O. fragilis* wood. The caption reads: "*Opuntia fragilis*: A low plant that has short-lived shoots in which only very small patches of libriform wood fibers can be seen; thus, most of the wood is unlignified. The dark structures in the vascular rays of the figures are druses; the large, clear cells contain mucilage." *O. fragilis* roots are fibrous (Weniger 1970), and do not bear glochids (Correll and Johnston 1970, Lundell (1969). Burger and Louda (1994) noted that *O. fragilis* plants have extremely shallow roots, which seldom penetrate below the top 10 cm of soil. *O. fragilis* pads, when developing, carry small leaves up to 3 mm long (Benson 1982). The leaves (Fig 2) are soon abscised (Davis 1952).

The flowers of *O. fragilis* (Fig 3) are formed from upper spine-bearing areolae (Davis 1952). The hypanthium is short, with a corolla up to 5 cm long (van Bruggen 1976), and bears areolae (Davis 1952). The flowers are greenish to yellow (Clark 1976, Cullmann and others 1986), and sometimes have orange centers (Weniger 1970). They are 3–4 cm long (Abrams 1951, p 148), and about 5 cm broad (Britton and Rose 1963, p 193). They have no fragrance (Bernshaw and Bernshaw 1984) or a subtle fragrance (David Ferguson, pers. comm.), and several authorities say they are rarely produced (Bare 1979, p 240; McGregor and others 1986). Flowering is probably very common in the more central portions of *O. fragilis'* range, but flowering is certainly rare in many peripherally distributed populations (pers. obs.).

O. fragilis flower petals are 1.5–2 cm long (Munz and Keck 1959), yellow or greenish (Bare 1979, Correll and Johnston 1970), or occasionally bronze, or violet (Welsh 1984), and thin (Pojar and MacKinnon 1994). Benson (1982: 394) wrote "Sepaloids green, edged with yellow, the smaller ovate-acute, the intermediate semicircular, the larger nearly orbiculate, 5–15 mm long, 4.5–15 mm broad, acute to broadly rounded and short-acuminate to mucronate, undulate," and Lundell (1969) describes *O. fragilis* petals as: "petaloid perianth parts yellow or greenish or reportedly sometimes magenta, cuneate or cuneate-obovate, 1.5–2.5 cm long, 1.2–2 cm broad, truncate to rounded, entire."

O. fragilis stamens are yellow or brown (Boissevain and Davidson 1940), or bright red. The filaments are reddish brown (Abrams 1951) or yellow (Lundell 1969), 6 mm long (Benson 1982, p 394), and the yellow anthers are 1.5 mm long (Lundell 1969). There are conflicting descriptions of the stigma. Davis (1952) stated that the stigma has five to seven lobes, whereas Correll and Johnston (1970) state that there are ten stigmas, and Boissevain and Davidson (1940, p 31) described *O. fragilis* as having four to six green stigmas, as did Weniger (1970). The style is 10–15 mm long, about 4 mm in diameter, and greenish-yellow (Benson 1982). The stigmas are green (Parfitt 1998), and about 2 mm long. The ovary is "small and almost spherical" (Weniger 1970: 217).

O. fragilis fruit is green or reddish-green when immature (Benson 1969b), but becomes tan when mature (Gleason and Cronquist 1991). It is ovoid (Bare 1979), dry, 1.5–2.5 cm long (Fernald 1950, Lundell 1969), 10 mm in diameter (Correll and Johnston 1970), tubercled (Boissevain and Davidson 1940), and has both glochids and spines (Bare 1979), with a slightly depressed cuplike umbilicus (Abrams 1951; Lundell 1969) and an apical rim of divaricately-spreading, strongly barbed spines (Correll and Johnston 1970). Dry fruits are unusual in the genus *Opuntia*. When mature, the fruit is a rather woody brown capsule (pers. obs.), and acts as a burr-like structure, dispersing by attaching to passing animals. Fruits may be rare; Britton and Rose (1963) only saw one fruit from *O. fragilis*, and I have found no fruits on any of the Midwestern populations I have examined.

Flowers are open, and pollination is likely to occur as a result of many different possible insect visitors. Anderson (2006) found that the average flower in Illinois opened by 10 AM, and observed insects from eight different major taxonomic groups visiting flowers. The most frequent visitors were solitary bees (Halicidae). Flowers are typically open for just one day.

There are usually only five or six seeds in each fruit. Seeds are yellow (Boissevain and Davidson 1940), or bone-colored (Lundell 1969), 5–6 mm broad (Abrams 1951), and more or less circular in outline (Bare 1979). They are often rough and irregular (Correll and Johnston 1970) with a conspicuous margin (Benson 1969b, Parfitt 1998).

Taylor and MacBryde (1977) reported that the chromosome number for *O. fragilis* is 11. However, all others reported that *O. fragilis* has a (gametophytic?) chromosomal count of $2n = 66$ (Gleason and Cronquist 1991, McGregor and others 1986). Bowden (1945), in a study of over 100 different species of flowering plants, determined that *O. fragilis* has a chromosomal count of $2n = 66$, and included a drawing of the chromosomes in mitotic metaphase. Löve and Löve (1982) (the only reference cited by Goldblatt and Johnson 2003), as well as Pinkava and others (1977), reported 66 chromosomes, consistent with a base gametophytic number of 11. Eleven is a common chromosome number in *Opuntia* (Pinkava and others 1977), so a count of 66 probably indicates that the plant is hexaploid.

Subspecies and Hybrids

Several subspecies have been described. Benson (1969a, 1982) separated *Opuntia fragilis* (NUTT.) HAW. into two varieties. In his descriptions, *Opuntia fragilis* var *fragilis* generally has smaller terminal joints with shorter spines colored gray, tan, or brown, whereas *Opuntia fragilis* var *brachyarthra* (ENGELM. & BIGELOW) J.M. COULT. has longer spines that are always reddish or reddish-brown. Furthermore, *O. fragilis* var *fragilis* has a widespread distribution, whereas *O. fragilis* var *brachyarthra* can be found only in extreme north-central Arizona, western Colorado, and northwestern New Mexico. *O. fragilis* var *fragilis* is found at lower elevations, mostly in sagebrush desert, but also in a wide variety of other habitats. Boissevain and Davidson (1940, p 31) described *O. fragilis* var *brachyarthra* as a western-slope variety of *O. fragilis*, having spines that are 2–5 cm long and with yellow or pink flowers. On the western slope the *brachyarthra* variety is larger than the plains form of var *fragilis*, and it has longer and stouter brownish needles. It is otherwise similar to *O. fragilis* var *fragilis*. Haage (1965) explained that *Opuntia fragilis* var *brachyarthra* differs from *O. fragilis* var *fragilis* by having "more uneven stem surfaces, more spines and smaller flowers." The spines could also be white with brown tips, and the range of var *brachyarthra* was indicated as north-central Arizona, northwestern New Mexico, and western Colorado up to 2500 m elevation.

Figure 1. *Opuntia fragilis* growing in Michigan.

Hunt (1999) placed *Opuntia fragilis* var *brachyarthra* into a separate species, *Opuntia brachyarthra* ENGELM & BIGELOW. Luc Bulot (pers. comm.) wrote "*O. brachyarthra* was published as a distinct species by Engelmann and Bigelow back in 1856 from plants collected by Bigelow at the foot of Inscription

Rock near Zuni (New Mexico) under pinetrees. The holotype is kept at MO under cat no. POM 317.98." There have been various opinions on the status of this plant in the US literature. Coulter (1896, p 440) regarded the taxon to be a subspecies of *O. fragilis* and was the first to publish the combination *O. fragilis* var *brachyarthra* that was accepted afterward by Benson. On the other hand, Boissevain and Davidson (1940) refer to this plant as the western slope variant of *O. fragilis*. Weniger (1970, 1984) considered the two plants as synonyms. Hunt's opinion in CITES Cactaceae Checklist (2nd edition, 1999) is most probably derived from the paper of Crook and Mottram (1995) that also lists *Opuntia brachyarthra* as a separate species. Unfortunately, those authors do not explain the reasons why they keep the species distinct.

Supporting this view, Britton and Rose (1963: 193) considered *O. fragilis* var *brachyarthra* as not separable from *O. fragilis* var *fragilis*, and stated that "An examination of the type material [for *brachyarthra*] now preserved in the Missouri Botanical Garden does not warrant a separation of any kind." Dave Ferguson does not think this is a valid variety, and wrote (pers. comm.) "the only distinction of the 'variety' is darker spines. Benson implies it is large, but the plants at the type locality are very small even for *O. fragilis*." While the species certainly exhibits much variation, I do not see real evidence of any systematic differentiation. As a nonsystematist who is sympathetic with the "lumpers," I would also like to see some evidence of functional or ecological differences between different varieties, and it is my opinion that until such evidence is produced these varieties should be discarded.

One potential complication is hybridization. *O. fragilis* apparently hybridizes readily with many other *Opuntia* species. True *O. fragilis* only have yellow flowers, or yellow flowers with a red to orange center. Often in hybrids the stems are elongated, and the flowers are pink. Hybrids are often larger than *O. fragilis* (Barr 1983). *O. fragilis* has been known to hybridize with *Opuntia humifusa* (Raf.) Raf., *Opuntia macrorhiza* Engelm., and *Opuntia polyacantha* Haw. where the ranges overlap (Barr 1983), and Benson stated "Hybrids of this species are common in Washington, Oregon, Idaho, eastern Utah, and western Colorado" (1969a: 73). Boissevain and Davidson (1940) remarked that it is possible to find hybrids between *Opuntia rutila* Nutt. and *O. fragilis*. According to Britton and Rose (1963: 193), a hybrid with *Opuntia tortispina* Engelm. & Bigelow has been found in Kansas. Welsh (1984) stated that *O. fragilis* forms hybrids "presumably intermediate with both *Opuntia erinacea* Engelm. & Bigelow ex Engelm. and *Opuntia polyacantha*."

In eastern Washington, a variety of prickly pear which Griffiths (1916) named *Opuntia columbiana* was formally defined by Parfitt (1998) as a hybrid species, *Opuntia ×columbiana* Griffiths, involving *O. fragilis* and *Opuntia polyacantha* var *polyacantha* with the type specimen from Franklin County, Washington, in 1910. Dringman (1997, 1998) calls this variety *Opuntia erinacea* Engelm. & Bigelow ex Engelm. var *columbiana* (Griffiths) L.D. Benson, and described how it can be found in the Yakima River area of eastern Washington.

Geographic Distribution

O. fragilis populations are spread widely across North America. Most are west of the Mississippi River (Fig 4). *O. fragilis* is not generally found in areas experiencing the high temperature regimes most people associate with cacti. Its northernmost extension is in British Columbia. *O. fragilis* occurs up to latitude 58° N in northern Alberta and British Columbia (Benson 1982); Benson (1982) remarked that the most northern location for *O. fragilis* is Fort Saint John, in British Columbia, at a latitude of 58°15' N. Moss (1959) stated that *O. fragilis* grows in the Peace River region. These populations apparently regularly flower, fruit, and produce viable seed; *O. fragilis* seeds can be purchased from several Canadian sources.

In Canada, *O. fragilis* populations grow in British Columbia, Alberta, Saskatchewan, Manitoba, and Ontario. Within British Columbia, *O. fragilis* is found in three separate locations: the Peace River district of northeastern British Columbia, the northern Puget Sound and southeastern Vancouver Island in southwestern British Columbia, and as the westernmost extension of the Great Plains population. *O. fragilis* grows on southeastern Vancouver Island and many of the Gulf Islands, usually on low exposed rocky shorelines (Pojar and MacKinnon 1994), although there are several reports indicating that these island populations are in serious decline, especially in Washington. Bernshaw and Bernshaw (1984) reported that *O. fragilis* in British Columbia is found in the greatest concentration in the dry belt that comes up from the US, south of Osoyoos, including the entire Okanagan Valley, and continuing over to Kamloops and the Thompson River Valley to Lytton.

Moss (1959) stated that *O. fragilis* grows on hillsides, knolls, and clay flats in southern Alberta in the rain shadow of the Rocky Mountains. Similarly, *O. fragilis*, according to Benson (1982), is found in Saskatchewan. Scoggan (1979) noted that "*Opuntia fragilis* grows on dry prairies, sandhills, and rocks in S. Saskatchewan (north to Swift Current)." Colonies are found in two separate regions in Manitoba (Frego and Staniforth 1986a). The southwest and south-central parts of the province have *O. fragilis* colonies that inhabit dry sand hills and alkaline prairies (Frego and Staniforth 1986a), while in the southeast isolated colonies are found in the largely coniferous Boreal Forest Zone (for instance, Whiteshell Provincial Park) (Bernshaw and Bernshaw 1984; Frego and Staniforth 1986a). Frego and Staniforth (1986a) noted that these two regions are separated by a 180 km-wide zone that does not contain cactus colonies.

There are scattered populations in Ontario, but *O. fragilis* is rare enough that Argus and White (1977) include *O. fragilis* in their list of the rare vascular plants of Ontario, and Consaul and others (1998) state that *O. fragilis* is considered a vulnerable species in Ontario, recorded from three or four sites in the province. In Ontario it is found in two regions (Scoggan 1979): In Western Ontario *O. fragilis* is found in the Rainy River District, and in eastern Ontario near Kaladar (Benson 1982). The Western Ontario populations of *O. fragilis* are extensions from eastern Manitoba into Ontario on a number of gneiss outcrops on rocky islands in Lake of the Woods and the nearby Rainy Lake area (Bernshaw and Bernshaw 1984; Consaul and others 1998). Lakela (1965) stated that *O. fragilis* plants without flowers were collected by Ardis Erickson in August 1956 from a rocky ledge on Sand Point Island, Rainy Lake, Ontario, about a mile from the Minnesota border, and subsequent discoveries have confirmed this population. The eastern Ontario population of *O. fragilis* is a disjunct rock-outcrop colony in southeast Ontario, 11.5 km south of Kaladar (Staniforth and Frego 2000) on the shore of Mellon Lake. It is almost 1000 km from the nearest Canadian or US site, has experienced some vandalism, and there has been speculation about whether or not its origin is anthropogenic.

In the United States *O. fragilis* is most abundant in the western Great Plains, especially Colorado, Nebraska, and the Dakotas. It is found sporadically to commonly in all western states except those directly south of Iowa. East of the Mississippi it is restricted to three states: Illinois, Wisconsin, and Michigan.

O. fragilis grows in all three states along the west coast. It is rare in California, found only in Siskiyou County (Abrams 1951, Lundell 1969), which is along the Oregon border (Benson 1969b). Munz and Keck (1959) described *O. fragilis* in California as occupying northern Juniper woodlands from 2000–6000 feet elevation. Abrams (1951) described *O. fragilis* as occupying dry flats and hillsides in the Transition and Upper Sonoran Zones from southern British Columbia south to Siskiyou County, California. In these three states, it is most common in Washington. *O. fragilis* occurs along northern Puget Sound in the rain shadows of the Olympic Mountains in Washington and the mountains of Vancouver Island (Benson 1982: 147), and is a "species of local concern" in San Juan County, Washington. Hitchcock and Cronquist (1973) state that *O. fragilis* is found on dry open ground in Washington, mostly in the east Cascades, but also in the Pacific trough. Pojar and MacKinnon (1994) show *O. fragilis* occurring along the shores of Puget Sound and southeastern Vancouver Island on dry open sites in sandy or gravelly soils at low elevations. It is growing on the Hanford Site and in the Columbia Basin. Domico (Domico 1996, cited by Staniforth and Frego 2000: 98) noted "a recent 'alarming decline' in numbers of individuals in disjunct populations of *O. fragilis* in Washington."

In the Intermountain region, *O. fragilis*, according to Benson (1982), is found in Idaho. Davis (1952) includes *O. fragilis* in his *Flora of Idaho*, but gives no specific locality information except to state that it can be found on dry plains and hills. Welsh (1984: 62) described *O. fragilis* in Utah as "a taxon of unusually great latitude of habitat types ranging from low elevation marshlands and riparian sites upwards to pinyon-juniper, ponderosa pine, sagebrush, mountain brush, and aspen communities at 1370 to 2565 m in Box Elder, Carbon, Duchesne, Emery, Garfield, Piute, San Juan, Sanpete, Sevier, Uintah, Utah, and Weber Counties." McPherson (1975) stated that *O. fragilis* is reported in southern Nevada near Las Vegas. Benson (1969) states that in Arizona *O. fragilis* is mostly found from 3000 to 5000 or 8000 feet elevation in sagebrush desert but also sparingly in a number of other sites. Kearney and Peebles (1964: 581) reported that *O. fragilis* is found in Arizona from "Apache County to Coconino County, 6500 to 7500 feet elevation, with pines," and

Lundell (1969) described *O. fragilis* in northern Arizona as occurring chiefly in the deserts at from sea level to 600 m elevation on northward slopes or at 900–1500 (or 2400) m on southward slopes.

In the Rocky Mountain states, *O. fragilis* is mostly found on the eastern slopes or in the plains east of the Rockies. It is one of four species of cacti commonly found on the plains of Montana (Benson 1982). McGregor and others (1977) show *O. fragilis* as being present in eastern Montana. In Wyoming, Dorn (1977: 160) states that *O. fragilis* is found on "plains and hills, NW, NE, SE Wyoming." Nelson (1969: 199) wrote that "it grows on sunny, rocky slopes of the foothills." Shaw (1976) noted that "*Opuntia fragilis* in the Grand Tetons area is frequent on gravel banks of the Snake River in area of Deadman's Bar, also at Kelly Warm springs."

Colorado has a split distribution. Boissevain and Davidson (1940) described *O. fragilis* var *fragilis* as occupying the plains of eastern Colorado, whereas *O. fragilis* var *brachyarthra* is found in western Colorado. *O. fragilis* var *brachyarthra*, according to Benson (1982, p 395), is restricted to Utah, Arizona, northwestern New Mexico, and western Colorado. Clements and Clements (1920) included *O. fragilis* in their list of Rocky Mountain wildflowers. Harrington (1964) stated that *O. fragilis* occurs on dry plains and hills, scattered over Colorado at 4500–7500 feet but that most of the eastern records are rather doubtful, and McGregor and others (1977) show *O. fragilis* as being present in the two counties of extreme northeastern Colorado. Weber (1976: 90) stated that *O. fragilis* in the Rocky Mountains occupies "open ponderosa pine forests on the mesas."

O. fragilis, according to Benson (1982), is found in New Mexico. Lundell (1969) describes *O. fragilis* as occurring in northern New Mexico, and Weniger (1970) described *O. fragilis* as having a range extending north from "extreme northern New Mexico."

Farther east Correll and Johnston (1970) state that in Texas *O. fragilis* is restricted to the panhandle region, and Lundell (1969) describes *O. fragilis* as occurring in the Texas panhandle and Oklahoma. Weniger (1970: 217) described *O. fragilis* as having a range from "extreme northwestern Texas across the Oklahoma panhandle and on into Kansas." He wrote that "in Texas it can occasionally be found in the sandy breaks along the Canadian River north of Amarillo… It appears from old accounts that the cactus may have been more widespread in the past in the Oklahoma and Texas panhandles, but it is my theory that it has been practically eliminated by the farming which has been practiced on almost all of that area, or where there has not been farming, by the drifting sand of the dust bowl days."

O. fragilis becomes more common to the north, the center of its range. Bare (1979: 240) wrote that *O. fragilis* is "scattered in the west half of Kansas." McGregor and others (1977) show numerous populations in western Kansas. McGregor and others (1977) show *O. fragilis* as being present in western Nebraska. Pound and Clements (1900: 82) noted that *O. fragilis* has a "regular and abundant occurrence" in Sheridan County and western Cherry County. They stated that *O. fragilis* is frequent, though rarely abundant, in the peppergrass-cactus formation that extends over vast stretches of mesa and tableland, especially north of the North Platte River, where it occupies a belt 8–20 km wide and 75–100 km long. In the badlands of Scott's Bluff County this formation is characteristic of the flat tops of peaks and buttes. Keeler and others (1980)

Figure 2. *Opuntia fragilis* new growth, with leaves.

reported an annotated list of vascular flora of the Arapaho Prairie. They state that *O. fragilis* is abundant on slopes and ridges, and flowers in summer (June–July). It is listed as a subdominant slope species, and the third-most-abundant forb in the ridge community. McGregor and others (1977) show *Opuntia fragilis* as being present throughout South Dakota. van Bruggen (1976: 320) wrote that *O. fragilis* was "Frequent in dry prairies and sandy, exposed areas over the state." In North Dakota, McGregor and others (1977) show *O. fragilis* as being present throughout the state. Bergman (1912) reported that in North Dakota *O. fragilis* grows in dry soil and stony knolls of the prairie.

O. fragilis rapidly becomes rarer to the east. Carter (1960) and Christiansen and Müller (1999) described *O. fragilis* in Iowa occurring only on Sioux Quartzite (Pipestone) outcrops in extreme northwest Iowa. McGregor and others (1977) show *O. fragilis* as being present in a few spots in northwestern Iowa. Ownbey and Morley (1991) indicate that *O. fragilis* is mostly found in Minnesota in scattered locations along the Minnesota River, with several populations in St. Cloud, another on the St. Croix River, and abundant populations on rock outcrops in the southwestern parts of the state. Lakela (1965) stated that *O. fragilis* is found in western Minnesota, and McGregor and others (1977) show *O. fragilis* as being present in a few scattered locations in Minnesota, although it is probably quite common on rock outcrops throughout the southwestern portion of Minnesota. *O. fragilis* grows in a number of small isolated populations within Wisconsin. The Wisconsin Department of Natural Resources lists *O. fragilis* as threatened in Wisconsin. In Wisconsin, *O. fragilis* is found in dry sand prairies and thin dry soil over rock outcrops in Adams, Buffalo, Burnett, Columbia, Dunn, Green, Green Lake, Jackson, La Crosse, Marquette, Monroe, Pepin, Polk, Sauk, Trempealeau, Waupaca, and Waushara Counties (Freckmann Herbarium, http://wisplants.uwsp.edu). It is known from only one location in Illinois: Mohlenbrock (1986) states that *O. fragilis* in Illinois is rare, found on sandy soil in Jo Daviess County. The most eastern population in the United States is located in Michigan. Wagner (1976) included *O. fragilis* in the list of Michigan's rare and endangered plant species, and reported that it is found within Michigan only at one locality in the Huron Mountains. Voss (1985: 604) confirmed the Huron Mountain location, stating that "*O. fragilis* is thriving on Huron Mountain in Marquette County on sunny rock surfaces," and added a second location, in Ogemaw County, "of uncertain status on a hill east of St. Helen (collected in 1967)." Figure 5 shows typical Midwestern habitat: an igneous rock outcrop. *O. fragilis* plants, while not visible in this picture, are abundantly nestled in the moss and lichen cover.

Legal Protection Classifications

While this species is not on the US List of Endangered or Threatened Species, it is on several state lists, and should be on some other state lists. For example, California has not listed it, despite its obvious rarity. It is protected in Nevada. In Arizona, it is on the Highly Safeguarded Protected Plants list created by the Arizona Department of Agriculture. Its range barely extends into New Mexico, where it is not listed. It probably should be listed by Oklahoma and Texas. It is also on four Midwestern state lists: Wisconsin, Michigan, Illinois, and Iowa, and is protected in Canada as well. Because each state has its own protocol and interpretation of rarity, while *O. fragilis* is on many lists, these lists should not be considered as equivalent in status, meaning, or the degree of actual resulting protection.

Reproductive Ecology

Since *fragilis* refers to the tendency of terminal cladodes to break away easily, it is not surprising that many writers have commented on this trait. Even Lewis and Clark complained that the brittle prickly pears were a nuisance ("The prickly pear is now in full blume and forms one of the beauties as well as the greatest pests of the plains." Meriwether Lewis, July 15, 1805, writing during the Lewis and Clark Expedition, probably about *Opuntia fragilis* (DeVoto 1953: 155)). The spines are strongly barbed and hold very firmly to passing animals (Boissevain and Davidson 1940). In addition to using animals as a dispersal vector, *O. fragilis* has also been known to disperse via gravity (Frego and Staniforth 1985) and by floating in rivers (Domico 1996, Frego and Staniforth 1985). Weniger (1970: 217–218) stated that some say *O. fragilis* cladodes "can even be loosened and distributed by the wind." Frego and Staniforth (1985) determined that about 6% of the pads produced in their site were dispersed away from the outcrop.

In many areas where *O. fragilis* grows, it does not appear to reproduce sexually. For example, when Frego and Staniforth (1985) studied *O. fragilis* at Bird River, Manitoba, (50°25' N, 95°41' W), they wrote "propagules studied were stem units (pads) because this cactus propagates entirely by vegetative means in this region." Frego and Staniforth (1986a) reported that *O. fragilis* colonies in southeastern Manitoba flower irregularly and fruits are sterile. Their intensive searches failed to find any new seedlings. Based on this they conclude that all reproduction in southeastern Manitoba is asexual. Ribbens and Myrom (1997) found that in Stearns County, Minnesota, "several pads flowered, but none of the flowers set seed, indicating that persistence of these populations probably occurs primarily via asexual reproduction." Bennett and others (2003) studied a large population growing on a sandy outwash plain in western Wisconsin and reported that flowering was much more likely to occur when *O. fragilis* was growing in the presence of several lichen species. They proposed that the lichens lowered the soil temperature slightly, which would conserve soil moisture. However, even in the areas where flowering did occur, it was apparently quite uncommon (19 out of 265 clumps flowered).

Across its range *O. fragilis* blooms between May and July (Abrams 1951, Gleason and Cronquist 1991). However, the timing is strongly dependent on location, and usually the duration of flowering is only a few days (Bernshaw and Bernshaw 1984). In Canada *O. fragilis* blooms in late June or early July (Bernshaw and Bernshaw 1984). In the United States, Munz and Keck (1959) described California *O. fragilis* as flowering in May–June, and Christiansen and Müller (1999) stated that in Iowa *O. fragilis* flowering is from mid-to late-June and fruiting begins in early July. van Bruggen (1976: 320) wrote that *O. fragilis* flowers in South Dakota in "May–June." Clark (1976: 317) wrote that in the Pacific northwest "each May and June the unpromising prickly pears expand their quite incredible blooms." McGregor and others (1986) stated that in the Great Plains *O. fragilis* flowers are produced in June and July.

O. fragilis does not bloom frequently in many locations. McGregor and others (1986) state that *O. fragilis* flowers are seldom observed, and Weniger (1970: 217–218) described *O. fragilis* as a species which "does not flower at all unless very well situated, often relying upon the scattering of the little joints to propagate it for years at a time before every factor of season and soil pleases it and it blooms." Frego and Staniforth (1986a) reported that *O. fragilis* colonies in southeastern Manitoba flower irregularly and that its fruits are sterile. Britton and Rose (1963) mentioned that they have only seen one fruit from *O. fragilis*, and Borg (1970: 79) noted that *O. fragilis* flowers are "rarely borne." When it does bloom, flowers are open only for a day or two. I have observed that the stamens bend toward the stigma when touched. In Illinois the flowers are visited by a variety of pollinating insects (Anderson 2006), including several species of bees. The flowers also attracted juvenile grasshoppers, which often consumed much of the floral tissue by mid-afternoon.

Opuntia fragilis appears to be geographically parthenogenetic. Anderson (2006) found that, in Illinois, pollen grains germinate, but then are blocked from further growth, which she attributed to a self-incompatibility mechanism. In many peripheral populations *O. fragilis* does not appear to be sexually reproducing, while there is extensive evidence that in populations more central to its distribution it does produce fruit with viable seed (David Ferguson, pers. comm.) *O. fragilis* seeds need to be cold-stratified to germinate. Scarification may also help.

Adaptations to Cold

Ecologically, *O. fragilis* has been most intensively studied for its ability to tolerate cold winters. *O. fragilis* occurs up to 58° N in northern Alberta and British Columbia, where winter temperatures can reach –40° C (Benson 1982, Nobel 1994). Benson speculated that the prostrate growth form and thickened pads of *O. fragilis* are both adaptations to cold climate; the low growth form means the plant is quickly covered by protective snow, and thick pads decreases the surface to volume ratio. Benson (1969a) mentions that some species of *Opuntia* (including *O. fragilis*) native to higher altitudes, where winter temperatures are low, go through a water-losing process which reduces the hazard of frost injury. This process has all the appearance of wilting, but the plant fills out and becomes entirely healthy upon the return of warm weather the following spring.

Loik and Nobel (1993a) reported that fourteen days after shifting the plants from day/night air temperatures of 30/20° C to 10/0° C, chlorenchyma water content decreased for *O. fragilis*. This temperature shift caused the freezing tolerance (measured by vital stain uptake) of chlorenchyma cells to be enhanced by 14.6° for *O. fragilis*. Injecting water into plants reversed the acclimation. Abscisic acid (ABA) concentration increased to 49 pmol g^{-1} fresh weight for *O. fragilis*, enhancing freezing tol-

Figure 3. *Opuntia fragilis* in flower. Notice the greenish stigma and the reddish center of the flower.

erance. Decreases in plant water content and increases in ABA concentration appear to be important for low-temperature acclimation.

Loik and Nobel (1993b) studied *O. fragilis* populations at 20 locations as far north as 56°46' N latitude and at elevations up to 3029 m in Canada and the United States, most of which experience extreme freezing temperatures each winter. Freezing tolerance averaged –29° C for the 20 populations, indicating that *O. fragilis* has the greatest cold acclimation ability and the greatest freezing tolerance reported for any cactus. Moreover, freezing tolerance and cold acclimation were both positively correlated with the minimum temperatures at the 20 locations ($r^2 = 0.7$). Plants lost water during low-temperature acclimation, leading to 30% decreases in cladode and chlorenchyma thickness; the decrease in water content was greater for the five warmest populations than for the five coldest ones. Over the same period the average osmotic potential of the chlorenchyma decreased from –1.42 to –1.64 MPa, and the relative water content decreased from 58% to 49%, but the average osmotic potential of saturated chlorenchyma was unchanged, indicating no net change in solute content during acclimation. Although the role of water relations in freezing tolerance is unclear, the substantial freezing tolerance and cold acclimation ability of *O. fragilis* permits its distribution in regions of Canada and the United States that experience minimum temperatures below –40°C during the winter.

Competitive Ability

O. fragilis declines or dies with almost any competition. Ribbens and Myrom (1997) described *O. fragilis* as occupying a narrow ecotone between bare granitic rock and soil deep enough to support a grass community. In the Midwest *O. fragilis* can also occasionally be found on sandy outwash prairies; for example, the Illinois population is found on a sandy outwash supporting a rather sparse bunchgrass prairie (Gleason 1923). Burger and Louda (1995) found that when *O. fragilis* was released from competition with surrounding vegetation, it grew significantly larger in the second growing season, both in terms of number and size of new cladodes. Ramets grown within live prairie vegetation averaged no net growth.

Burger and Louda (1994) studied *O. fragilis* in a sandhills prairie in western Nebraska. They concluded that variations in cladode herbivory, mediated by grass canopy cover, increased cladode mortality underneath the grass canopy. Ramets under grass were more frequently fed upon by the larvae of two internally feeding cactus insects. As a result, insect herbivory reinforced the competitive suppression of the cactus by grasses. Water supplementation had no significant effect, either on cactus growth or on insect herbivory. They conclude that the mechanism by which dense prairie vegetation influenced net growth of *O. fragilis* was both direct, through competition for non-water resources such as light, and indirect, through its mediation of feeding by specialized insect herbivores.

Frego and Staniforth (1986b) examined the vegetation sequence on granite outcrops containing *O. fragilis* at three sites in southeastern Manitoba. The primary factor determining the sequence was substrate depth, presumably because of its effect on moisture retention. *O. fragilis*, a stress-tolerant perennial, was the first vascular plant in the sequence and colonized mats of moss and lichen. It did not persist once stress-tolerant perennial vascular plants moved in. They reported that *O. fragilis* occurs on highly organic nutrient-poor soils with low pH, and that the soil depth under *O. fragilis* has a mean of 2.09 cm with a standard deviation of 1.84 cm.

Dispersal Characteristics

Toumey (1895) argued that the spines of many species of *Opuntia*, in addition to providing protection against herbivory, are also designed to promote vegetative dispersal of cladodes. He does not specifically mention *O. fragilis* in this context. This point has been echoed by many authors in regard to *O. fragilis*. Bare (1979) wrote that in late summer and fall the season's new *O. fragilis* joints have matured and will detach easily from the plant when brushed by a passing animal or person. If caught in fur or clothing they may be carried some distance before dropping or being thrown to the ground, where they may root and start a new plant. Similarly, Barr (1983: 48) said "*O. fragilis* has equipped itself with sharp and prolonged spines which effectively hook onto the hide of animals, to detach the end joint from the older stems. Thus it hitches a ride of indefinite length and surely by this means has enlarged its territory." McGregor and others (1986: 157) remarked that *O. fragilis* stems readily detach and cling to fur and clothing by barbed spines, and commented that "this inconspicuous little cactus makes its presence known by its easily detached stem segments that cling tenaciously to clothing, including shoes. Sometimes the spines are longer than the stem is wide."

Within the Great Plains, this habitat of fragmentation and epizoochory is associated with herds of grazing ungulates. Harrington (1964) stated that *O. fragilis* terminal joints easily break off and are often carried away on the pelts of animals, and Britton and Rose (1963: 193) wrote "this species is of wide distribution and is especially common on the plains. It usually grows low, often being hidden by the grass. In the grazing country

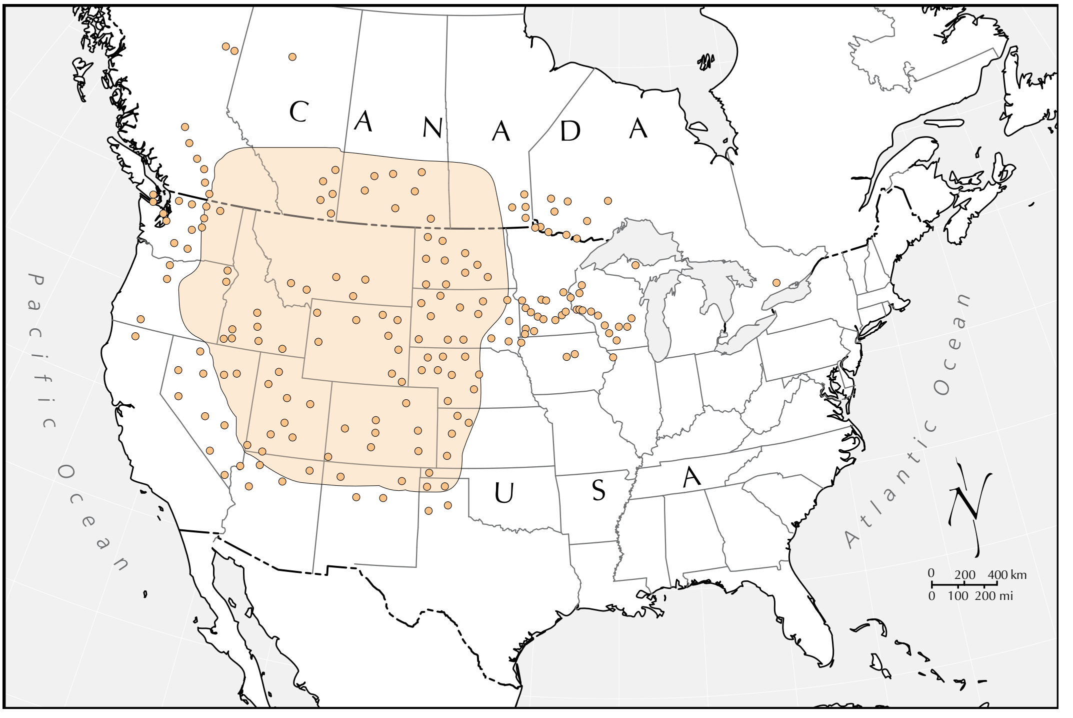

Figure 4. Distribution of *Opuntia fragilis.* This map represents an attempt to compile a wide range of locality information. For Midwest regions dots represent known or documented localities, although not all are shown. For instance, I know of 42 Minnesota populations, which cannot be shown with sufficient accuracy at the scale of this map. Localities shown for California, Oregon, Washington, and British Colombia are accurate to county.

The species can occur throughout states in the upper Midwest (western Nebraska, the Dakotas, and Colorado), and it occurs sporadically in many other states and provinces. In the Rocky Mountain states the distrubution is affected by elevation. The species probably occurs in many areas below 9000' in Colorado, for example.

Verbal descriptions of range information have been compiled from various floras and David Ferguson and are only accurate to the extent that they indicate general areas where *Opuntia fragilis* may be found (shaded area). Throughout its range *O. fragilis* is poorly collected. It has probably been extirpated from the southeast completely. There may be none left in Texas, due to agricultural development, and I suspect none remain in Oklahoma.

it is a most troublesome weed, for the joints easily break off and become attached by their spines to passing objects, thus greatly annoying and pestering all animals on the range, even frightening horses. The wide distribution of the species is doubtless largely due to the fact that the joints are so easily scattered." Borg (1970: 79) notes that the joints "drop off at the least touch," and Dawson (1963: 44) states that *O. fragilis* is "widely distributed over the great plains from Wisconsin to central Kansas and NW Texas, westward through northern Arizona, Utah, Montana, and to the drier parts of Oregon and Washington. It is a troublesome grassland pest to grazing animals."

Benson (1982, p 147) also mentions that the dry fruits are capable of epizoochorous transportation, and says that in his opinion the reason for the wide northern range of *O. fragilis* is because of the easy fragmentation of the pads: "The plains buffalo occurred in enormous herds, and their great hairy bodies would have been ideal for transporting the small cactus joints. The places where buffalo lay down probably included many plants of *O. fragilis*". According to Jack E Schmautz, US Forest Service (pers. comm. 1976), the cactus is common at the edges of 'slick spots' formed on solodized solonetz soils in eastern Montana and western North Dakota. These areas…"were probably buffalo wallows." Finally, it is also possible that epizoochorous transport occurs in aquatic systems as well. Staniforth and Frego (2000: 100) cited Domico (1996) when they wrote "burrs are distributed by otters and as floating stem segments," and Bernshaw and Bernshaw (1984) noted that these colonies are "unhealthy environments" for cacti, and speculated that some of the *O. fragilis* colonies on islands in the Puget Sound may have been established by birds moving seeds from the basin and range populations in eastern Washington.

Ethnobotany

Pojar and MacKinnon (1994: 157) stated in regard to *O. fragilis* that "the succulent stems of the prickly pear were roasted and eaten as a green vegetable by interior peoples, but were apparently little used on the [Pacific northwest] coast." The Secwepemc Indian Nation of British Columbia included this extensive description of traditional uses of *O. fragilis*: "The stems were gathered, mainly in the spring. They ate the inner stem boiled, roasted or pit-cooked. The stems were used in soup or mixed in with fat and berries to bake in cakes. They also boiled the flesh into syrup for use as a cough medicine. When bones were unavailable, they joined two cactus spines together in a V–shape or four together in a cross to make a temporary hook" (discontinued Secwepemc website). I have also heard speculations that the needles were used by fur trappers or native Americans in tattooing.

Growth Rates

Burger and Louda (1994) found that 52% of the cladodes in their study were new (that is, produced during the current growing season), and they state that this implies that cladode mortality is likely to be high as well. Similarly, when Frego and Staniforth (1985) studied *O. fragilis* in the boreal forest of southeastern Manitoba, they found from censuses (1979–1982) of an established colony that pad number was increasing by 51% per year. Frego and Staniforth (1985) aged plants by assuming that a new cladode was added every year to the end of a cladode chain. Anderson (2006) found this to be an unreliable method at Lost Mound Illinois. Some plants that appeared healthy did not add new growth each growing season, while other terminal cladodes produced more than one new cladode within a single growing season. Furthermore, some plants added new growth but the new growth was produced by cladodes other than the terminal cladode.

Habitat

Often the conjunction of drought and rock indicate *O. fragilis* habitat. For example, McGregor and others (1986) state that *O. fragilis* prefers sandy to rocky prairies and hillsides. Similarly, Munz and Keck (1959) described California *O. fragilis* as occupying dry places from 2000 to 6000 feet within the northern Juniper woodland habitat, and Nelson (1969: 199) wrote that "the brittle cactus, *O. fragilis*, grows on sunny, rocky slopes of the foothills [in Wyoming]." Pojar and MacKinnon (1994) show *O. fragilis* occurring only along the shores of Puget Sound and southeastern Vancouver Island on dry open sites on sandy or gravelly soils at low elevations, and Gleason and Cronquist (1991: 95) stated that *O. fragilis* occupies "Dry prairies and plains."

O. fragilis inhabits rocky outcrop communities in Manitoba (Frego and Staniforth 1985, 1986a), Ontario (Catling and Brownell 1999, p 401), Idaho, Minnesota (Ribbens and Myrom 1997), Washington, and Wisconsin. It is found on dry sandy prairies in Manitoba (Frego and Staniforth 1986a), Illinois (Gleason 1910), Kansas (Bare 1979), Minnesota, Nebraska (Keeler and others 1980, Pound and Clements 1900), North Dakota, and Wisconsin. In Alberta, British Columbia, and Montana, *O. fragilis* is found as a component of the shrub-steppe habitat.

In general, *O. fragilis* prefers light shade to full sun, and is the most cold-tolerant of all *Opuntia* species (Loik and Nobel 1993a). Loik and Nobel (1993b) reported that as they moved north, the altitude at which *Opuntia fragilis* was found dropped by about 80.1 meters for every degree change in latitude ($r^2 = 0.69$). For example, Harrington (1964) stated that *Opuntia fragilis* is scattered over Colorado at 4500–7500 feet. The preference for a slightly cooler climate was noted by Weniger (1970: 217–218) when he described *O. fragilis* as "growing in very sandy soil, and anyone who has tried to treat it to the same soil and extreme heat as he does most other cacti will find it is fragile indeed. It just will not grow in the typical hot desert situation or in heavy soil. But it is not fragile in regard to cold. It is one of our most northern cacti."

Herbivory

Boissevain and Davidson (1940) stated that *O. fragilis* would be even more abundant if it were not subject to insect attacks. They described a green bug, *Chelinidea vittiger*, a close relative of the squash bug, which attacks the joints of *O. fragilis* and destroys them. It will attack other cacti but prefers *O. fragilis*. However, in the midwest populations I have studied I have rarely seen evidence of herbivory except on floral tissue.

Burger and Louda (1994, 1995) state that the three most common cactus-feeding insects in the Arapaho Prairie (western Nebraska) are a pyralid moth borer, *Melitara dentata*, a coreid sucking bug, *Chelinidea vittiger*, and a stem-boring curculionid weevil, *Gerstaeckeria* sp. The moth is univoltine, feeding internally on cladodes in August and September

Figure 5. Typical Midwestern *Opuntia fragilis* rock outcrop habitat. All photos by Eric Ribbens.

and leaving them dead and hollowed when it exits. The sucking bug feeds throughout the growing season, leaving chlorotic rings on the cladodes. Adult weevils create a hollow beneath the epidermal tissues, which heal but leave black scars 2–3 mm in diameter. Weevil larvae feed internally and are common in decaying cladodes. They found that the moth and the weevil larvae were more commonly encountered under a grass canopy, whereas the hemipteran sucking bug was more common on new cladodes in the open.

Maw and Molloy (1980) identified 20 species of insects associated with *Opuntia polyacantha* and *O. fragilis*. They fed *Cactoblastis doddi* and *Cactoblastis bucyrus* moth larvae prickly pear pads. They reported that they had to wound the pads before the moth larvae would enter, and larvae would not leave pads after consuming all available tissue. Thus, they concluded that introducing them to control cacti would be a failure. They mentioned that in Canada cactus provide food for at least 44 species of birds and mammals, seeds may be 65% of the diet of the Harris Ground Squirrel and up to 5% of browse for deer and antelope. During the summer, cactus may be 30% of the food of the black-tailed jack rabbit and the main food of the pocket gopher.

O. fragilis has several anti-herbivory mechanisms. First, the numerous minutely barbed glochids are easily dislodged when the plant is touched. They then become stuck to the skin where they are difficult to see and remove. Second, *O. fragilis* may contain unspecified alkaloids which may be chemical herbivory deterrents. However, when Abramovitch and others (1968) analyzed the chemical constituents of *O. fragilis*, they reported that alkaloids were absent. Abramovitch and others (1968) found that "ethanol extraction of *O. fragilis* gave neutral and acidic material. Column chromatography of the neutral material yielded two major fractions, a mixture of saturated long-chain aliphatic esters and a mixture of unsaturated long chain aliphatic esters… saponification of the acidic material followed by methylation and gas chromatographic analysis indicated the presence of p-hydroxybenzoic acid, vanillic acid and ferulic acid in addition to undecylic, lauric, myristic, pentadecylic, palmitic, and stearic acids in this fraction."

Future research

O. fragilis, while extensively studied, still hides a number of interesting ecological and taxonomic secrets. We know little about the evolutionary relationships between *O. fragilis* and the other species in the Polycanthae subgroup to which *O. fragilis* has been assigned (for instance, Benson 1982). Furthermore, the number of varieties is in doubt. Are varieties *fragilis*, *brachyarthra*, and *denudata* different varieties or not? Is there molecular or ecological evidence for subspecific differentiation? We need a reliable molecular technique to verify genuine *Opuntia fragilis*; while morphological characters are useful, *O. fragilis* is polymorphic enough that a molecular technique such as genetic barcoding would be helpful.

We know that in some parts of its range *O. fragilis* is sexually reproducing, whereas in other parts it apparently does not reproduce sexually. Are plants from asexually reproducing regions capable of sexual reproduction? What physiological cues determine whether or not flowers are produced? If flowers are produced, is the species self-compatible? Speirs (1989) asserts that the stamens of *O. fragilis* may be responsive to touch to facilitate self-pollination. Anderson (2006) confirms that stamen movements do occur, but flowers are probably self-incompatible and thus this is not likely to be a pollinating mechanism. Flowering appears to be correlated with the presence of larger plants that have accumulated ample resources.

In particular, reciprocal transplants would help to clarify the relationships between environment and flowering. Do plants from non-flowering populations flower when grown in more appropriate environments? How large do plants need to be before flowering? Do plants that flower repeat with more flowers the next year? Will flowers that do not set seed produce viable fruits when cross-pollinated with plants from other populations?

While *O. fragilis* is abundant in the central portions of its range, more information is needed about populations in the periphery. Where are they? Are the populations expanding or declining? In Minnesota, I have observed stable or expanding populations, but there are reports of declines in other regions (Washington Pacific islands, for example). We know very little in particular about populations in California, Texas, Oklahoma, Iowa, Michigan, and Ontario. For example, in the process of collecting information about Iowa populations, we have discovered that three of the six putative populations were not *O. fragilis* at all.

Information about rates of growth and cladode reproduction are also scanty. Several references indicate approximately one new cladode is produced per existing cladode per year, but little or no data exists to describe patterns of branching or which correlate cladode production and survival with plant health or size. Anderson (2006) describes transition probabilities for pad and plant survival in Illinois, but we have no indication how generalizable these probabilities are. We also do not know whether pads are equally likely to detach, or if detachment is a function of pad position, time of year, or other variables.

The degree of spininess seems to vary from population to population. Are these variations genetic or do they vary due to phenotypic plasticity?

Some references indicate that snow cover might be an important variable in cladode survival, although whether or not snow might be beneficial is completely unclear. Benson (1982) speculates that snow cover might promote overwintering survival, while Loik and Nobel (1993b) claim that snow cover is completely uncorrelated with freezing tolerance. Watson (1981) proposed that snow cover, at least of wet snow in mild climate conditions, may adversely affect pads and have been the cause of his high observed winter mortality. Certainly the Illinois population, which regularly experiences heavy wet snows combined with winter thaws, has substantially more stressed plants than populations further north (pers. obs.).

Opuntia molecular genetic studies are complicated by the presence of complex polysaccharides that make DNA extraction difficult. Griffith and Porter (2003) describe a good method to extract DNA from cacti. We have successfully obtained DNA by floating a pad in water. After four to six weeks, pads respond by producing roots. The roots, which are free of polysaccharides, can then be harvested for analysis. Tissue culturing has also been used to obtain good tissue for DNA sampling (Kitrina Carlson, pers. comm.).

Does *O. fragilis* experience varying levels of polyploidy across its range? What levels of differentiation between plants are necessary before cross-pollination can successfully occur? Loik and Nobel's work on cold-hardiness has been criticized; their methods of inducing cold-hardiness were strange, and the data they collected thus unreliable. However, they did document varying levels of cold-hardiness between different populations. What physiological processes cause these variations?

In Illinois, *O. fragilis* pads frequently host a number of different species of fungi. Are there fungi on other populations? Are the fungi detrimental or commensal? Are they more likely to appear on stressed pads? Are spines hosting fungi less sturdy than spines that do not carry fungi?

Finally, how are patterns of distribution of *O. fragilis* populations changing in response to human impact? Lundell (1969) believed that in Oklahoma and Texas *O. fragilis* is much less common today than it was in the past, largely due to agricultural conversion of prickly pear habitat. Some of the populations on the perimeter of the global distribution of *O. fragilis* appear to be declining (for instance, Domico 1996; Staniforth and Frego 2000). The origin of the midwest population extensions is uncertain. Gleason (1923) believed they were evidence of a warmer period a few hundred years ago; others have speculated that the pads were moved deliberately or accidentally by humans.

Western Illinois University: *Opuntia fragilis* research

At Western Illinois University we have been exploring the ecology of *Opuntia fragilis* in Illinois. Illinois has one large population, located on a sandy outwash prairie in northwestern Illinois (Jo Daviess County). Barbara Anderson tracked individual pads and plants for several years, building a transition model that shows that terminal pads are much more likely to die or disappear than other pads on the plant. She also showed that in Illinois flowers do not produce fruits. We are currently attempting to analyze the genetic diversity of this population and to determine if there are spatial patterns to genetic variability within the site.

We have also been studying the sole population of *O. fragilis* in Michigan. A completely different population, it is much smaller, less disturbed, and apparently healthier. Like the Illinois population, plants occasionally flower, but flowers never produce fruits.

We are in the midst of gearing up for a Midwestern metapopulation analysis. We have been developing a database of every known population in five Midwestern states (Illinois, Iowa, Michigan, Minnesota, and Wisconsin), from which we plan to build a comprehensive collection of herbarium voucher specimens (still the best way to document the existence of a population), measure the approximate size (geographic and number of individuals) of each population, document the site with a series of photographs, and identify land owners, site management histories, and other site-specific information. Some of these sites are likely to be good locations for further studies. For example, there are two sites in Sherburne County, Minnesota, where we know that a specific number of *O. fragilis* plants were transplanted a few years ago. These populations are good candidates for monitoring population expansion rates, and in particular may enable us to better understand the degree to which fragmentation and dispersal enables populations to spread.

We are also attempting to collect DNA from each population. While these samples will not provide any information about within-population variability, they may shed light on the degree of genetic relatedness between Midwestern populations and may thus enable us to develop better theories about patterns of Holocene expansion into the eastern portion of its range.

These projects are hardly a comprehensive list of work to be done. While we generally understand cold-hardiness, for example, someone should study the role of snow protection and the effects of fall moisture and winter freeze-thaw cycles on pad survival. Provenance trials and between-population cross-pollinations would greatly enhance our understanding of flowering and fruiting. How resistant is *O. fragilis* to fire, an increasingly common management tool on prairie sites? What are the effects of herbivory on flowering success? How can we guide site managers attempting to prevent further decline of this lovely cactus species?

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