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Assimilate partitioning and distribution in fruit crops: A review

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Abstract

Productivity in fruit crops is dependent upon assimilate supply and storage, and on the ability to translocate and partition carbon into reproductive structures in an efficient manner that does not compromise vegetative development to sustain growth during the current season, or in the future. In this article we have reviewed carbohydrate supply and partitioning, source sink manipulation to increase assimilate partitioning towards major sink and have indicated the effect of environmental factors on those processes. The interrelationship between the various sinks at different times during the season is especially important if abiotic or biotic stresses occur. It is only with this understanding that a researcher or producer can make intelligent decisions to optimize economic yield over a sustained period.

Keywords: Assimilate partitioning, distribution, Productivity, vegetative development

Introduction

In higher plants, leaves function as the principle site of resource acquisition by utilizing the free energy captured in photosynthesis for the reductive assimilation of oxidized forms of carbon and nitrogen into carbohydrates and amino acids, respectively. Photosynthate are subsequently partitioned to the many heterotrophic tissues of the plant with as much as 80 per cent of the carbon acquired in photosynthesis is transported in the plant's vascular system to the import dependent organs. Sucrose is the principal metabolite in this scheme of resource allocation as it is the major end product of photosynthetic carbon metabolism and, in majority plants; it is the predominant form of carbon transported to the heterotrophic tissues. This systemic distribution of photosynthate is known as '*assimilate partitioning*,' a crucial process associated with plant growth and productivity. (H. Ravishankar, 2014) ^[25]

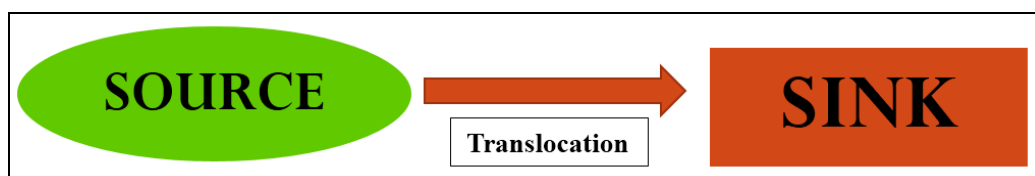
Source A source of organic material is a region in which organic materials are synthesized. example leaf, root, tuber, or tuber during development.

Sinks Any non-photosynthetic organ or an organ that does not produce enough photosynthate to meets its own needs. Example root, seed, fruit, root tuber and tuber during developing.

Leaves are the most important organ for photosynthesis, in which light energy is captured by green plants (mainly by the chlorophyll in leaves) and used to synthesize reduced carbon compounds from CO₂ and water. Photosynthesis produces carbohydrates for growth and energy and photosynthates constitute up to 90% of a plant's dry matter and both growth and cropping depend on a ready supply of carbohydrates and nutrients.

2. Source and Sink relationship

The terms source and sink in relation to the transportation of organic molecules in the phloem of plants.



Source = Photosynthesis (PS), **Sink** = Growth and development

Food conduction may be in any required direction unlike the water conduction which is unidirectional process. Pressure flow/ mass flow hypothesis of food/ sucrose translocation – given by. E Munch (1930). This is the most accepted theory of food conduction in plants.

Correspondence

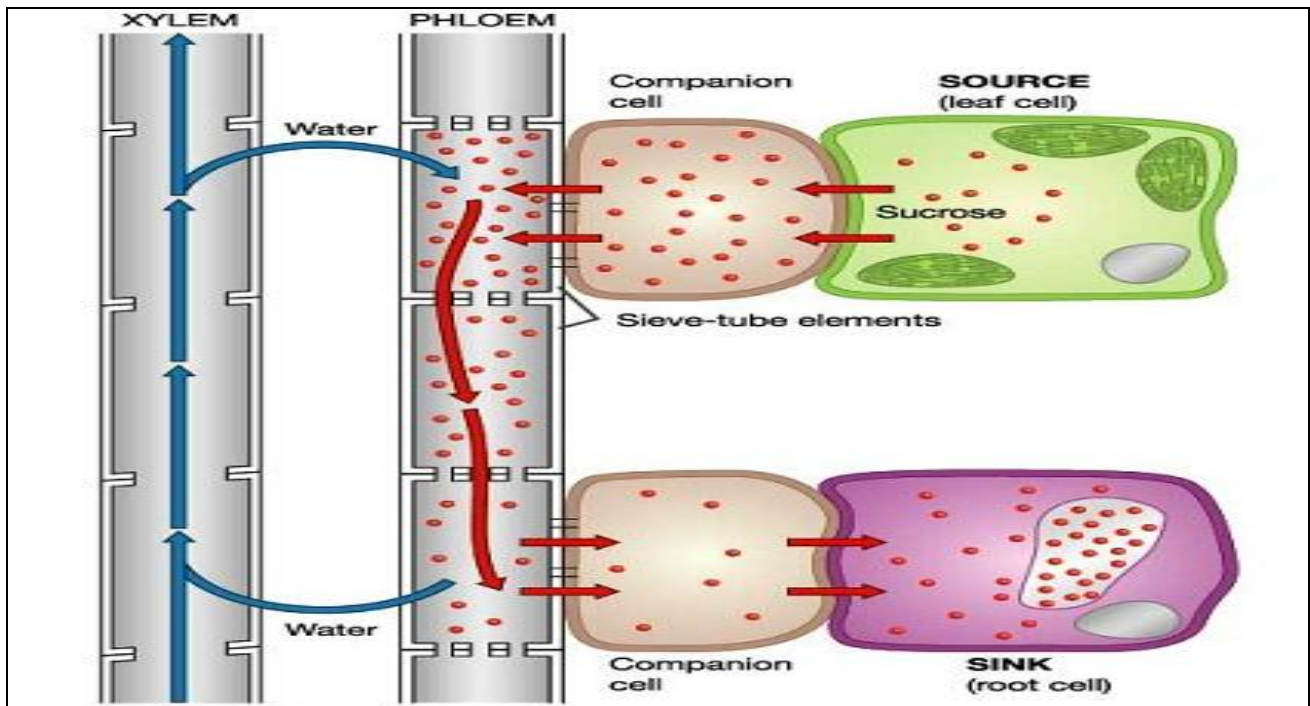
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According to it food translocations occurs in between source and sink in order of turgor pressure gradient i.e. high turgor pressure to low turgor pressure.

3. Phloem loading/ sucrose loading at source-

It is an active process helped by carrier molecules. At source due to phloem loading concentration of sieve cells increase,

results in increase in osmotic pressure and water will moves from nearby xylem into sieve cells results in increase in turgor pressure and increase in water potential. It is establish a higher T.P. at source and sieve tubes. Sucrose moves from source in sieve tubes towards sink from high T.P/ High water potential to towards the low T.P./Low water potential.



4. Phloem unloading/ sucrose unloading at sink

It is an active process helped by carrier molecules. At sink sucrose is unloaded results in decrease in O.P., it results in exit of water into nearby xylem leads to decrease in T.P. and water potential of phloem. In sink cells the unloaded sucrose is either changed into starch or consumed, to maintain low O.P. and continuous unloading.

So the process of sucrose loading at source and unloading at sink continues. This turgor pressure difference will maintained and water will continue to move in at source and out at sink.

According to evidences of modern research phloem conduction is an active process and it required metabolic energy in phloem cells. Munch hypothesis described by

Thornley and Johnson (1990) [23], Minchin *et al.*, 1993 & Genard *et al.* 2007) [20, 10]

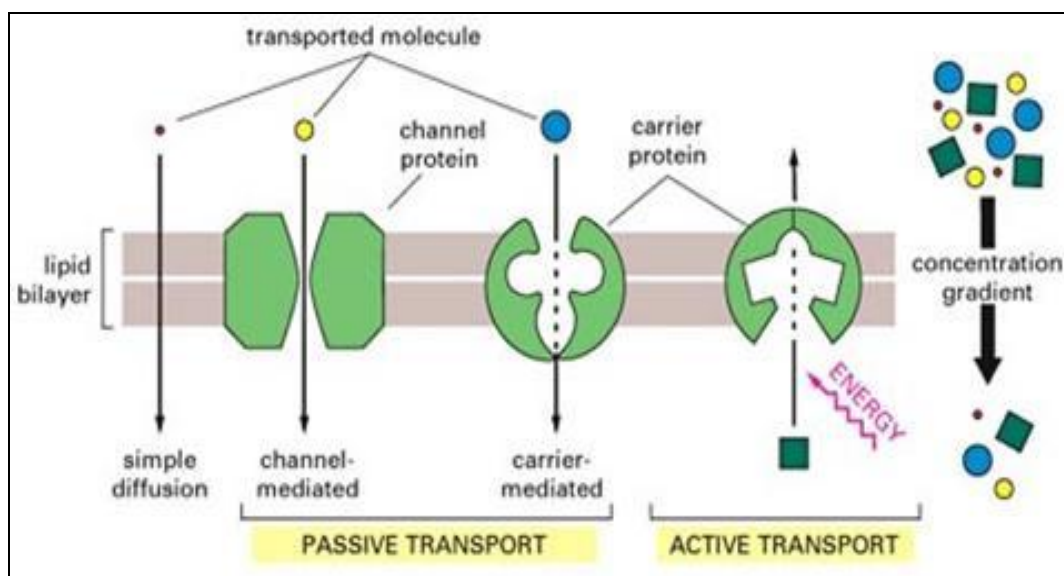
5. Passive v. active transport

Passive transport

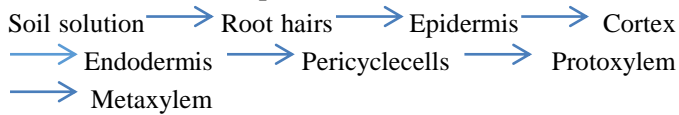
- Movement *down* the electrochemical gradient
- From a more positive electrochemical potential
- to a more negative electrochemical potential

Active transport

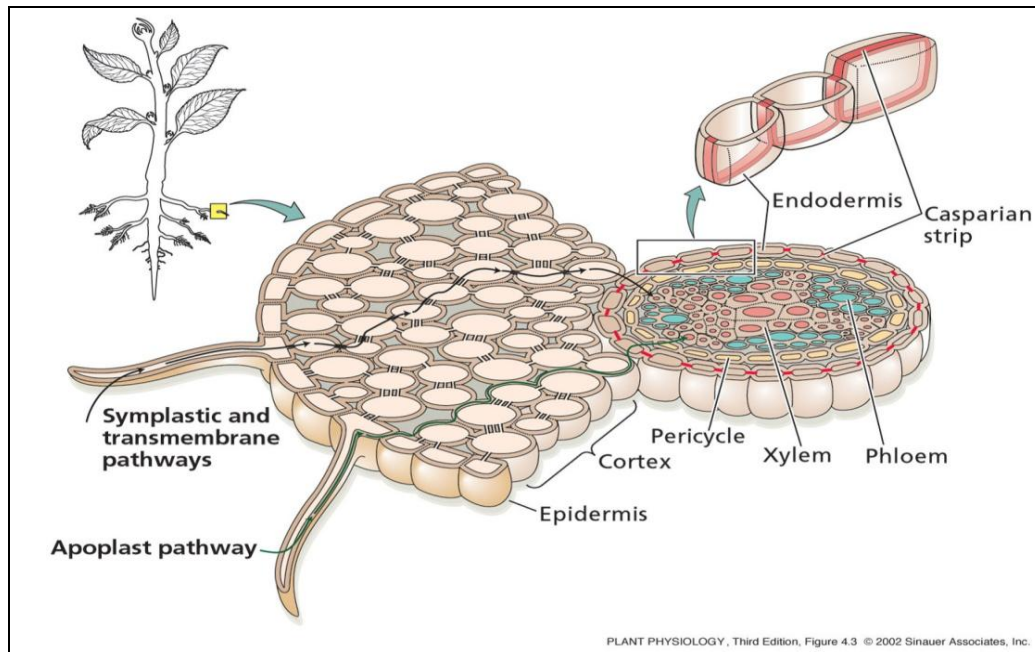
- Movement *against* electrochemical gradient
- From a more negative electrochemical potential
- to a more positive electrochemical potential



6. Path of water absorption



The path of water from root hair to cortex, may be apoplastic or symplastic. Casparian strips blocks the apoplast, thus water must pass through passage cells via symplast.



PLANT PHYSIOLOGY, Third Edition, Figure 4.3 © 2002 Sinauer Associates, Inc.

Symplast

A sustainable living path is known as symplast. This is the living passage. The movement of water from cell to cell through plasmadesmata is called symplastic path in plant.

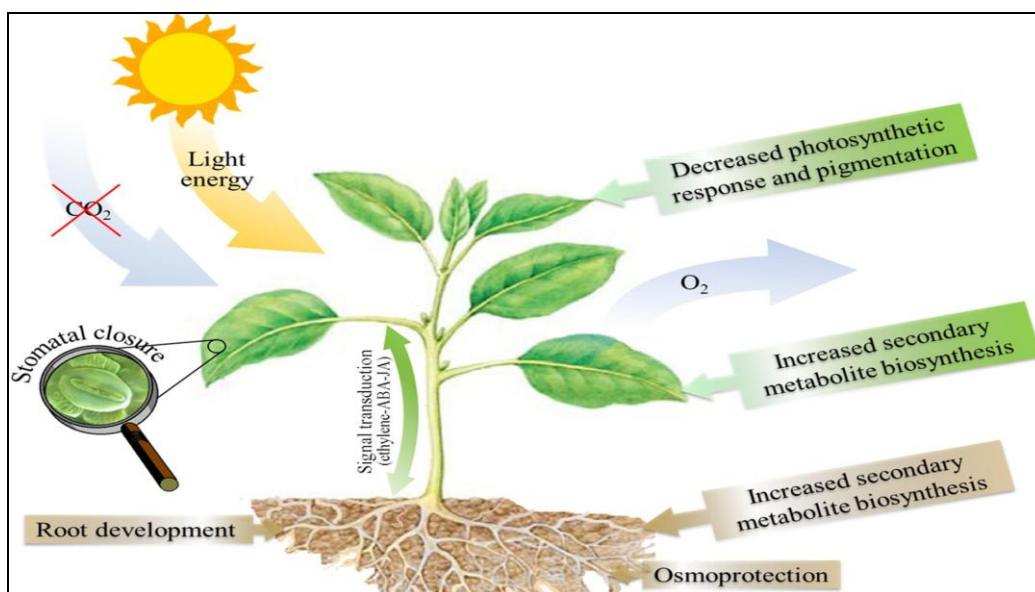
Apoplast

This is non-living path in plants. Watered cell wall, intercellular space and xylem cavity bassociate to getherbto form apoplast

7. Assimilate partitioning

Assimilate supply is dependent on photosynthesis (Marschner, 2012) [22]. The distribution of assimilate

determines the amounts and patterns of plant growth and yield (Lakso and Flore, 2003) [17]. Translocation dependent on developmental state of the plant. Transport direction and volume depend on sink position and relative attraction strength. 90% of sap solute molecules are carbohydrate that travel at a speed of about 50-100 cm/h (Friedrich and Fischer, 2000) [9]. Sucrose is main form of translocation. (Teiz and Zeiger 2006) [28] Partitioning within a tree is not a genetically programmed process, but a result of the unique combination of competing organ and their relative abilities to compete for limited carbohydrates. The degree of competition among various sinks depends on the organ activity and distance from the carbohydrate source.



8. Partitioning priorities and sink competition

Herbaceous crop plants accumulate photosynthates in source leaves during the photoperiod and evacuate them during

night, leaving the leaf "empty" toward morning. Goldschmidt and Koch (1996) [12]. Competition for photosynthate is evident among different organs (e.g., fruit-shoot) as well as among

individual units of the same type of organ (e.g., fruit-fruit). In citrus, the spring flush gives rise to vegetative shoots, leafy inflorescences, and pure, leafless inflorescences. Shoot elongation and leaf expansion occur mostly before anthesis and fruit set; direct competition is thus prevented. Moreover, leafy inflorescences reveal higher rates of fruit set and persistence, indicating that the leaves support the reproductive organs by provision of photosynthate, hormones, or some other mechanism. The leaves close to developing fruits exhibit increased photosynthetic capacity as compared to the remaining leaves of the tree. (Urban *et al.*, 2003) ^[29]. The calyx has significant photosynthetic capacity, so in the cape gooseberry, the green calyx that completely covers the fruit during its development plays an important role in the production and translocation of carbohydrate during the first 10-20 days of fruit development.

On the other hand, in the presence of a heavy crop the vegetative summer flush is poor or absent altogether, suggesting sink priority of the developing fruit. The retardation of root growth during periods of shoot flush emergence has been interpreted in terms of root-top competition for photosynthate, with tops having the priority (Bevington and Castle, 1985) ^[2]. Competition between fruit is apparent in citrus, as in other fruit trees. The progressive reduction in fruit numbers during early fruit development (fruitlet abscission) has been linked to the carbohydrate status. The inverse relationship between fruit number and size is another facet of fruit-fruit Competition.

9. Source-sink manipulations

Fruit load adjustment improves the fruit quality in same year and ensures the accumulation of reserves which can positively influence tree development for subsequent years. But alternate fruit bearing is a major problem that can result in serious economic losses for fruit producers. A high fruit load probably main cause of alternate bearing. (Iglesias *et al.*, 2007) ^[15].

Heavy crop load, as occurs during the "on" year of alternate-bearing cultivars, involves depletion of both carbon and mineral reserves which may culminate under extreme conditions in tree collapse. Photosynthate production is often unable to satisfy the demands during fruit set and fruit growth following heavy and prolonged flowering (Chacko *et al.*, 1982) ^[4].

Fruit removal in apple trees favors more leaf area development compared to those with intact fruits and subsequent fruiting in young trees reduces leaf area. (Lenz, 2009). Furthermore, fruitless growing strawberries produced 61.1% assimilates in leaves, but only 39.2% and 21.1% of the assimilates occurred in plants growing with 6 and 12 fruits, respectively. Defoliating trees partially increases the rate of photosynthesis in the remaining leaves because they provide a relatively larger sink and this depends on the defoliation degree.

10. Some special practices which divert the assimilates to developing organs (by Glaustus Horticulture)

1. Root pruning- removal of roots 40cm. Away from the plant. Exa. Guava and Citrus
2. Ringing- removal of complete ring of bark from a branch or a trunk. Exa. Mango and grapes
3. Dehorning – to removal of overcrowding & intermingling of branches.

4. Notching – partial ringing of a branches above a dormant lateral bud. Exa. Poona fig
5. Nicking- partial ringing of a branches below a dormant bud. exa. Apple and Poona fig
6. Bending- bending of branches or shoot. Exa. Guava
7. Leaf pruning- removal of old and senescence leaves. Exa. Datepalm.
8. Skirting- removal of low hanging branches. Exa. Mango

11. Girdling

Although most orchard management practices influence the tree's carbohydrate economy one way or the other, girdling and fruit thinning evidently achieve their goals through alteration of the source-sink relationship.

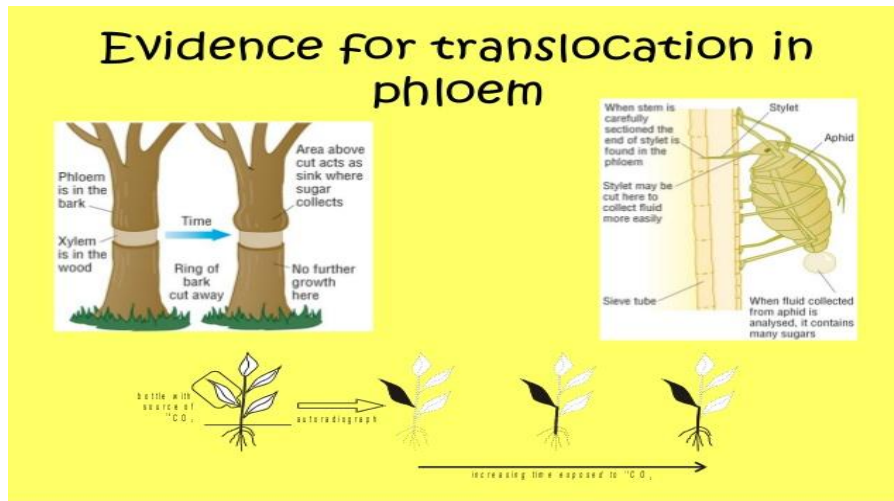
Girdling has repeatedly been shown to cause accumulation of carbohydrates and particularly starch in tree organs above the girdle. It is highly suggestive, therefore, that the beneficial effects of girdling are brought about by the increased availability of carbohydrates although the involvement of other hormonal and nutritional systems cannot be excluded (Wu *et al.*, 2008) ^[31].

Fruit thinning is a widely used agrotechnique which clearly operates via modification of source-sink relationships. Following partial removal of fruit, the same leaf area now supports less fruit, making more photosynthate available for each fruit unit, leading to increased fruit size (Dejong and Grossman, 1995) ^[5] The dependence of fruit growth on the available leaf area was investigated by manipulation of fruit and leaf numbers on girdled grapefruit branches.

From a source-sink point of view it should be emphasized that the total amount of dry matter partitioned to the fruit is greatly dependent upon the number of fruit sinks. In fact, only a small fraction of the dry matter "saved" by fruit thinning is diverted to the remaining fruit. One may wonder what happens to the excess photosynthate which does not find its way into the fruit.

Since photosynthetic rates were not reduced even when trees were completely defruited, the excess photosynthate is in all probability partitioned to other sinks. Drought has profound influences on plants' carbohydrate economy. Leaves of water stressed Valencia orange trees had lower starch and sucrose contents, due to reduced photosynthesis, but somewhat higher levels of reducing sugar than controls. It is not clear, however, whether this increase in reducing sugar contributes to the ability of citrus leaves to endure water stress, as there is no clear evidence of osmotic adjustment in citrus.

The fruit enlargement period is another phase of heavy demand for photosynthate. Under heavy crop loads the carbohydrates reserves are depleted to the extent that root starvation and tree collapse take place. Although reserves are recruited from all tree organs root reserve levels appear to be most closely related to crop load. The term sink strength is used here to describe as the competitive ability of an organ to attract assimilates. Sink strength can be quantified by a the potential growth rate of a sink, i.e. the growth rate under non-limiting assimilate supply (Hevelink, 1997 & Marcellis *et al.*, 1998) ^[6, 19]. Moreover, sink strength depend on sink age rather than sink size (Marcellis, (1996) ^[16] Whereas, molecular processes involved in determining sink strength may alter dynamically with development and also differ with the function of the respective sink tissue (Herbers and Sonnewald 1998) ^[14].

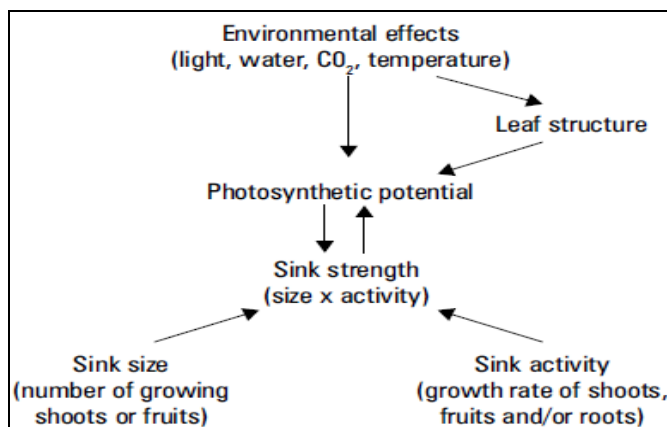


12. Leaf area index (LAI)

LAI in conjunction with sunlight interception is useful as a basis for analyzing canopy productivity. Apart from cultural practices, agro-ecological conditions and age of plants can influence LAI development. The rapid LAI development at 2,300 m a.s.l. allowed early and higher fruit production throughout the culture compared to the higher site. The leaves close to developing fruits exhibit increased photosynthetic capacity as compared to the remaining leaves of the tree.

13. Training and pruning

Training and pruning alters the balance between vegetative growth and reproductive fruiting by the allocation of resources, such as carbohydrates, water and growth regulators. (Myers, 2003) [24]. Heavy pruning diminishes leaf area, whole tree photosynthesis and translocation of photosynthates to fruits and roots, increasing the root/shoot (Casierra-Posada) ratio and favoring vegetative growth. In guava (*Psidium guajava*), mid- and light pruning provide greater fruit weight ratios in contrast to heavy pruning (Serrano *et al.*, 2007) [27]. During the reproductive phase, “fruiting pruning” is used because this pruning type improves fruit load, regulates the physiological balance (vegetative-reproductive), ensures a harmonious and rational distribution of high quality production, maintains a constant production over time, and contributes to fruit thinning. In pruning, it is important to cut off (thinning) upright water sprouts which direct photosynthates, among other substances, to the growing shoot tip at the expense of reproductive growth. (Arjona and Santinoni, 2007 & Flore and Layne, 1999) [1, 8].



Schematic illustration of factors affecting net photosynthesis and photosynthate translocation (after Faust, 1989. This material is reproduced with permission of ©John Wiley & Sons, Inc.).

14. Factor affecting net photosynthesis and photosynthate translocation

Temperature plays an important role in CH partitioning. The optimum temperature for transporting CH in most species is between 20 and 30 °C and, according to Guardiola and Garcia-Luis (1993) [13], translocation diminishes with decreasing temperatures (due to the viscosity of the phloem solution); however, in species not sensitive to low temperature conditions, the sieve tubes are functional at temperatures close to the freezing point and even lower. Night temperature is of great importance for carbohydrate translocation. This is because CH are translocated during night hours and therefore, as in the case of the Rosaceae, it has been reported that most growth occurs during night than day.

Water stressed plants delay CH transport due to an increase in the viscosity of the solution translocated. Prolonged water deficits cause the accumulation of abscisic acid, a hormone that inhibits phloem loading in leaves (Guardiola and García-Luis, 1993) [13]. The distribution of assimilates may be affected by a deficiency or imbalance of mineral nutrients and, furthermore, by the initiation and development of sink organs and for source functioning, the plant requires an adequate supply of nutrients. Potassium is claimed to be essential in the process of loading and unloading the phloem (due to high concentrations of K in companion cells of sieve elements). Potassium deficiency affects vegetative growth because the plant alters the distribution of K to improve the growth of the fruit (Teiz and Zeiger 2006) [28].

Future Prospects

Source sink relationships of plants have become one of the most exciting research areas in recent years. The subject encompasses broad array of physiological and biochemical processes, with significant crop management ramifications. Assimilate partitioning in plants is controlled by a number of factors that include photosynthesis, the number and location of competing sinks, storage capacity and vascular transport. Although there is considerable knowledge on individual processes in plants such as photosynthesis, translocation and cell growth, it appears that the controls actually regulating the assimilate partitioning at the whole plant level are still poorly understood (Wardlaw 1990; Le Roux *et al.* 2001) [32, 33]. Indeed, many processes are closely interrelated and more integrative research work based on modelling is greatly needed.

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