

# **BASIC AND PRACTICAL ASPECTS OF CITRUS TREES' CARBOHYDRATE ECONOMY**

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Source sink relationships of plants have become one of the most exciting research areas in recent years. The subject encompasses a broad array of physiological and biochemical processes, with significant crop management ramifications. The interplay of sources and sinks involves complex regulatory loops, operating at biochemical as well as genetic levels (Koch, 1996).

Fruit trees in general and citrus, in particular, are by no means the most convenient experimental system for studies of source - sink relationships. However, as citrus researchers we must address these aspects, interpret the behavior of trees and provide agrotechnical solutions to what might be defined as 'carbohydrate economy' problems. A broader, comprehensive review of citrus source - sink relationships has recently been provided by Goldschmidt and Koch (1996).

## **Diurnal and Annual Fluctuations**

Herbaceous crop plants accumulate photosynthates in source leaves during the photoperiod and evacuate them during night, leaving the leaf "empty" toward morning. The diurnal pattern of citrus leaves is quite different. Although starch and soluble sugar levels show some daily fluctuation, this indicates that, in addition to their photosynthetic role, citrus leaves serve as a storage organ, as already noted by Kriedemann (1969). One may wonder whether the use of the leaf as a storage organ does not interfere with its photosynthetic capacity by way of "product inhibition", although compartmentalization of the storage carbohydrates might preclude such interference.

The annual changes in carbohydrate levels represent a combination of developmental and seasonal trends with the demand exerted by developing vegetative and reproductive sink organs.

In fully expanded leaves starch and soluble sugar levels decline and stay low during summer and autumn, because of the heavy demand of developing fruit. Soluble sugars increase toward midwinter in cool areas, as an osmotic, cryoprotective measure against cold injury (Jones and Steinacker, 1951; Toritaka et al., 1974). Cold hardening treatments of citrus trees also bring about a rise in soluble sugar levels (Yelenosky and Guy, 1977), which is caused in part by conversion of starch to soluble sugar (Yelenosky, 1985). The seasonal follow-up observation of carbohydrate levels in lemon leaves conducted by Dugger and Palmer (1969) emphasized the inverse relationship between the soluble sugar fraction, which peaks by midwinter, and the starch, which reaches a minimum at that time. Starch level increases in the old leaves toward the end of winter and then drops again concomitantly with the emergence of the spring flush (Jones and Steinacker, 1951; Sharples and Burkhart 1954). Starch attains markedly higher levels in roots than in other tree organs (Sharples and Burkhart, 1954; Goldschmidt and Golomb, 1982). Starch accumulation takes place in roots throughout autumn and winter and seems to be highly dependent upon the demand made by the fruit (Shimizu et al., 1978).

Apart from varietal and climatic factors (Jones and Steinacker, 1951; Dugger and Palmer, 1969) the time of harvest (Hilgeman et al., 1967) and the crop load (Shimizu et al., 1975; Goldschmidt and Golomb, 1982) have large, overriding effects on carbohydrate levels in all tree organs.

### **Partitioning Priorities and Sink Competition**

How does the plant direct the partition of photosynthate among all potential sinks? How are partition priorities established? These are some of the intriguing questions which may also hold the key to improvement of productivity.

Actively growing organs are strong sinks, as clearly shown by CO<sub>2</sub> labeling experiments. 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).

Competition between vegetative and reproductive organs has been described for various crops (e.g., avocado). 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 (Moss et al., 1972; Erner, 1989; Ruiz and Guardiola, 1994). 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).

As observed in other species, the presence of fruit interferes most strongly with growth of roots. After CO<sub>2</sub> labeling of source leaves on potted Murcott trees, the vast majority of the label resided in the roots. When fruit were present, although by the third day roots were labeled rather strongly, after 10 days more than 90% of the label had reached the fruit (Ein Guedy, Goldschmidt, and Monselise, unpublished data). This may suggest that roots have higher priority in this short term, but in the long term the fruit wins the race. Under heavy crop load, as during the "on" year of alternate bearing cultivars, root growth seems to be completely arrested (Jones et al., 1975; Smith, 1976; Goldschmidt and Golomb, 1982). Fruit - root partitioning priorities have recently been examined with pot-grown Calamondin trees (Bustan et al., 1996).

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 (Goldschmidt and Monselise, 1977; Schaffer et al., 1985; Goldschmidt et al., 1992). The inverse relationship between fruit number and size is another facet of fruit-fruit competition, as will be discussed later.

Allocation of carbohydrates to storage compartments is generally believed to have lower priority than the needs of developing organs. Nevertheless, even during the high-demand fruit enlargement period some starch reserves build up in the subtending twigs (Fishler et al., 1983).

## Source - Sink Manipulations: Girdling and Fruit Thinning

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 consists of removal of a ring of bark from the trunk or scaffold branches, thereby blocking the downward transport of photoassimilates. Effects of girdling on citrus tree performance have been reviewed by Cohen (1977). Autumn girdling enhances flower formation (Goldschmidt et al., 1985), full bloom girdling improves fruit set (Monselise et al., 1972), and summer girdling increases fruit size (Fishler et al., 1983; Cohen, 1984). 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.

In the absence of fruit (or another active sink) leaves of girdled trees develop severe chlorosis (Stewart and Wheaton, 1967), attributed by Cohen (1977) to excessive accumulation of photosynthetic products. Schaffer et al. (1986) further characterized this phenomenon, showing that in the absence of a sink outlet, chloroplasts of source leaves became packed with starch to the extent that thylakoid systems were damaged and the chlorophyll degraded. This may be regarded as a special, extreme case of inhibition of leaf photosynthesis by product accumulation.

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. The dependence of fruit growth on the available leaf area was investigated by manipulation of fruit and leaf numbers on girdled grapefruit branches (Fishler et al., 1983). When fruit size was plotted against the leaf area/fruit ratio a logarithmic curve was obtained, saturating at  $2.0 \pm 0.5$  m<sup>2</sup> leaf area per fruit. This value varies, of course, according to fruit size of different cultivars.

The results of a typical fruit thinning experiment are shown in Fig. 1. The negative correlation between fruit number and fruit size is evident, but the relationship is not linear. Meaningful increase in fruit size is obtained only after massive reduction of fruit number (Goldschmidt and Monselise, 1977; Guardiola, 1988). The lower part of Fig. 1. illustrates another important aspect of fruit thinning, also pointed out by Guardiola (1988). Even when economically profitable as a result of increase in fruit size, fruit thinning always involves a serious reduction in total yield. 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. Does the reduction of fruit-sink demand lead to reduced production of assimilates or is this photosynthate allocated to other sinks? Since photosynthetic rates were not reduced even when trees were completely defruited (see Goldschmidt and Koch, 1996), the excess photosynthate is in all probability partitioned to other sinks.

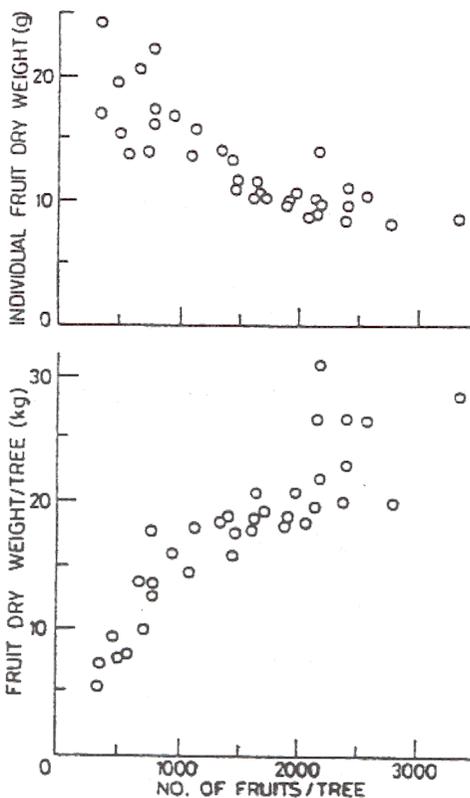


Figure 1. Dry weight (g) of individual 'Wilking' mandarin fruit (upper) and total fruit dry weight (kg) per tree (lower), plotted against the number of fruits per tree. (Adapted from data of a thinning experiment by Galliani et al., 1975.)

### Water and Mineral Nutrient Stress

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 (Vu and Yelenosky, 1989). 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 (Syvertsen and Albrigo, 1980).

Little is known about the relationship between carbohydrate metabolism and mineral nutrition. 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 (Stewart et al., 1968; Smith, 1976; Golomb and Goldschmidt, 1987). Whereas Stewart et al. (1968), assumed that N and K deficiencies are the primary cause of tree collapse, Smith (1976) indicated that root carbohydrate starvation is the triggering event; this view has also been adopted by Monselise and Goldschmidt (1982).

The effect of K, Mg and Ca deficiencies on leaf carbohydrate pools and metabolism was recently investigated by Lavon et al. (1995). K deficiency results in lower starch and higher soluble

sugar content, as well as a several-fold increase in  $\beta$ -amylase and acid invertase activities. Recent evidence suggests that K-deficiency damages the sensitivity of citrus' stomatal apparatus, thereby interfering with trees' response to drought stress and reducing photosynthetic yields (Bower and Wolstenholme, 1996).

### Reserves and Their Utilization

All the perennial organs of a woody plant may serve a storage function, and for an evergreen like citrus this includes the leaves. Bark and pith rays are the principal starch depots in branches (Margalith, Goren and Goldschmidt, unpublished data). The highest concentration of carbohydrate reserves is usually found in roots (Loescher et al., 1990), and in citrus is no exception (Goldschmidt and Golomb, 1982).

Starch is the major storage carbohydrate in all citrus tree organs. Starch concentrations of 180 and 123mg g<sup>-1</sup> dry matter were determined in minor roots and leaves, respectively, during the "off" year of alternate-bearing Wilking mandarin trees (Goldschmidt and Golomb, 1982).

The soluble sugar pool (which as usually determined includes reducing sugars and sucrose) is less dependent upon crop load (Goldschmidt and Golomb, 1982) and is not depleted to the same extent as of starch. Flavanoid glucosides have been suggested to function as reserve carbohydrate in lemon leaves (Dugger and Palmer, 1969), but the general significance of this finding needs further confirmation.

Evaluation of the total amount of the tree's reserve pool is complicated, since it requires determination of organs' carbohydrate concentrations as well as estimates of the total amounts of each organ per tree, a goal particularly difficult to achieve with regard to the roots. Dissection of "off" and "on" Wilking mandarin trees was carried out by Goldschmidt and Golomb (1982) in order to calculate the size of the reserve pool and the extent of its depletion under heavy crop load. A medium-size tree was found to contain during its "off" year, 13.26 kg starch and 10.66 kg soluble sugar, the vast majority of which would be mobilized into the fruit during the forthcoming "on" year. The availability of the stored carbohydrates for fruiting needs was highest in roots, lowest in trunk, and intermediate in leaves and branches.

Allocation of carbohydrates to reserve compartments is believed to have a low priority compared with supporting the needs of actively developing organs. The buildup of reserves is most prominent, therefore, in the absence of competition by vegetative or reproductive sinks.

Dependence upon reserve carbohydrates has been considered with regard to two phases of the annual cycle of mature citrus trees: the spring flush and fruit enlargement.

The spring flush, soon followed by floral development, anthesis, and fruit set, demands large amounts of photosynthate for organ growth as well as for high rates of respiration (Bustan, Goldschmidt and Erner, unpublished data). The persistence of the previous year's foliage in citrus undoubtedly plays a critical role in provision of photosynthate during the emergence of the spring flush, at least prior to full expansion of the new leaves (Shimizu et al., 1978). And yet, the decline in carbohydrate levels throughout the flowering and fruit set period (Jones and Steinacker, 1951;

Hilgeman et al., 1967; Gonzalez-Ferrer et al., 1984), which is accentuated by heavy flowering (Garcia-Luis et al., 1988), indicates that reserve carbohydrates are also utilized to sustain the early stages of reproductive development (Shimizu et al., 1978).  $^{14}\text{CO}_2$ -labeling experiments indicated that reserve carbohydrates were utilized mainly to support the reproductive development, while old leaves' photosynthesis supplied the needs of vegetative growth (Akao et al., 1981).

The fruit enlargement period is another phase of heavy demand for photosynthate. Under heavy crop loads the carbohydrate reserves are depleted to the extent that root starvation and tree collapse take place (Smith, 1976). Although reserves are recruited from all tree organs (Goldschmidt and Golomb, 1982) root reserve levels appear to be most closely related to crop load (Shimizu et al., 1975).

### Discussion

It has often been questioned whether carbohydrate supplies restrict citrus vegetative and reproductive development. While it seems beyond doubt that carbohydrate depletion is a major problem under heavy crop load (Smith, 1976; Goldschmidt and Golomb, 1982); it may still be argued that there should be no carbohydrate limitation under regular bearing conditions (Garcia-Luis et al., 1988).

At first glance there seems to be no reason why citrus trees should be deficient in carbohydrate supplies. As an evergreen growing mostly under mild climate conditions citrus has ample time for photosynthesis, and relatively large starch reserves are usually present in various tree organs. And yet, several lines of evidence strongly indicate that citrus trees are "source-limited" and that the availability of photosynthate restrict their growth and development.

Flower formation, fruit set, and fruit enlargement have been identified as three major processes along citrus' annual reproductive cycle (Goldschmidt and Monselise, 1977), all of which are strongly enhanced by girdling. The only common denominator for all girdling treatments is the resultant upsurge in carbohydrate levels. Whereas flower formation may require only a threshold level of carbohydrates (Goldschmidt et al., 1985; Garcia-Luis et al., 1995), fruit set and fruit enlargement seem to be quantitatively correlated with carbohydrate levels (Schaffer et al., 1985; Goldschmidt et al., 1992; Fishler et al., 1983). By saying this we do not mean to deny the involvement of plant hormones and other regulatory systems in the control of these developmental events. Nor do we imply that every developmental trait (such as the advantage of "leafy" over "leafless" inflorescences in fruit set [Sanz et al., 1987; Erner, 1989]) must be explicable in terms of carbohydrate limitations. Evidently, the links between the source-sink balance and other regulatory signals require further study.

Overwhelming evidence in support of the existence of a "source limitation" in citrus emerges from  $\text{CO}_2$  enrichment studies. Both vegetative (above ground as well as below ground) (Ideo et al., 1991) and reproductive development (Downtown et al., 1987) are strongly promoted by  $\text{CO}_2$  enrichment. As shown by Ideo and Kimball (1994), under lack of root restriction there is a large and persistent increase in photosynthetic capacity, followed by remarkable growth increments. Fruit set, which is believed to be limited by carbohydrate availability (Schaffer et al., 1985; Garcia-Luis et al.,

1988), has been increased by 70% after CO<sub>2</sub> enrichment (Downtown et al., 1987). All this strongly indicates that under most normal growth conditions citrus trees are "source-limited".

The prevalence of high starch levels in citrus organs does not imply that there is a surplus of carbohydrates. Reserve accumulation takes place even while the needs of developing fruit are not fully satisfied (Fishler et al., 1983). The accumulation of reserve carbohydrates seems to have a high priority in citrus, as part of a general survival strategy (Goldschmidt and Koch, 1996).

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