

## ***What do Carbohydrate Reserves Tell us about Avocado Orchard Management?***

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### **ABSTRACT**

*Carbohydrate reserves (stored mainly as starch) in tree crops represent the currently unutilized and stored component, mainly in the trunk, branches and leaves of avocado trees. They are the difference between manufacture (in photosynthesis) and utilization (growth and respiration). They follow a seasonal pattern, peaking just before flowering, declining rapidly during flowering and fruit set, remaining low until mid-summer, and rising through autumn and winter. It has been suggested that the levels of starch reserves at critical periods can be used in orchard management decisions.*

*Data are presented, mainly from delayed harvest trials in KwaZulu-Natal and Queensland, to indicate that there is a broad relationship between starch concentration and key aspects of tree performance, e.g. yield and root growth. However, carbohydrate reserves are but one of many factors, potentially limiting, which affect yield, and by themselves provide only some useful information. A far more meaningful guide to tree performance, and an aid to management, is the pheno-physiological model of Whiley (1994), of which the starch reserves are but one component. Avocado trees appear to accumulate high levels of carbohydrate reserves as an adaptation to water stress and drought.*

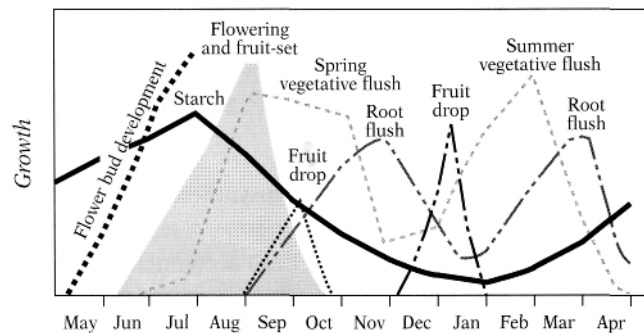
### **INTRODUCTION**

Carbohydrates are the first products of photosynthesis, in which carbon dioxide (CO<sub>2</sub>) from the atmosphere is 'fixed', by combining with water and energy from solar radiation, into simple sugars (chemical energy), with the liberation of oxygen. These simple carbon (C), hydrogen (H) and oxygen (O<sub>2</sub>) containing molecules in turn form the carbon skeletons for more complex carbohydrates, proteins and lipids, which collectively make up over 90% of the dry mass of plants. Carbohydrates themselves can constitute over 65% of the dry mass of tree crops. They are 'storehouses of energy' which can be used in respiration for synthesis, metabolism, and growth in general. Small wonder then, that knowledge of plant carbohydrate status is a useful barometer of tree health and performance potential.

The concept of 'carbohydrate management' of evergreen tree fruit crops has been strongly promoted by Maroochy Horticultural Research Station in Queensland, Australia, initially by Cull (1989). At the same time the phenological growth cycle

concept was popularized by Whiley *et al.* (1988), and has since been adopted by many countries, including South Africa. In 1989, Wolstenholme and Whiley suggested integrating the two concepts to provide greater management understanding. Whiley and Wolstenholme (1990) elaborated on the relationship between the seasonal starch curve (i.e. storage carbohydrates) and tree phenology (figure 1). At the time, trials on the effect of late hanging of avocado fruit (delayed harvesting) on, *inter alia*, the starch curve, were under way in both countries. The prospect of being able to define a 'critical' starch concentration at some growth stage, as a guide to potential yield, was mooted.

A decade has now passed and much research has been conducted on the carbohydrate economy of avocado trees. This brief review attempts to put it into perspective from the grower's point of view. Are we at a stage where carbohydrate or starch analyses become as routine as leaf or soil analyses, for guiding orchard management? Will this ever be likely?



**Figure 1**  
The total growth cycle of cv Fuerte showing the relationship between vegetative and reproductive growth and reserve starch in the trunks of trees (Whiley & Wolstenholme, 1990)

## CARBOHYDRATES IN TREE CROPS: STORAGE RESERVES VS CURRENT PHOTOSYNTHATE

### Current photosynthate

Carbohydrates (CHO's) manufactured during photosynthesis can immediately be used for growth processes, either in the (young) leaf itself, but overwhelmingly to meet the needs of other growing organs and tissues ('sinks'). The latter requires translocation out of the leaf, typically as (soluble) sucrose but also in avocado as the 7-carbon sugar alcohol called perseitol. We refer to such CHO's and other metabolites as 'current photosynthate'. Whiley (1990) and Finazzo *et al.* (1994) showed that individual avocado leaves change from being nett sinks to nett sources (i.e. suppliers) of CHO when about 80% expanded, after  $\pm 25$  days for spring flush leaves while whole shoots require ca. 40 days to make the transition. Furthermore, leaves reach peak photosynthetic efficiency while still relatively young. The ability of individual leaves or shoots to supply CHO 'energy' to nearby sinks, in particular setting and growing fruits, is obviously extremely

critical to yield, fruit size and quality. It is affected however by many variables, including root health, nutrition, water relations, and canopy architecture and leaf position, especially shading.

For an 'energy-expensive' (Wolstenholme, 1986) fruit such as avocado, it is evident that a comparatively large number of well-lit leaves is needed to support the growth of a single fruit. This figure is not shown, but certainly exceeds the more than 30 leaves per fruit quoted by Chacko *et al.* (1982) for mango, or the  $2.0 \pm 0.5\text{m}^2$  leaf area per fruit needed for a large-sized grapefruit (Fishier *et al.*, 1983). The question arises as to whether avocado is 'source-limited', i.e. whether CHO supplies restrict vegetative and reproductive development. An excellent review by Goldschmidt and Koch (1996) provides overwhelming evidence that this is so in citrus. For example, fruit set, believed to be limited by CHO availability in citrus, is increased 70% by CO<sub>2</sub> enrichment (Downton *et al.*, 1987). The contrary debate about 'feedback inhibition' of photosynthesis by *inter alia* accumulation of unused CHO's in leaves, undoubtedly occurs in some plant species (Goldschmidt & Huber, 1992) especially after girdling. However, it is probably not a big factor in the avocado canopy as a whole, which is likely to be light-limited in mature orchards. Other factors which are relevant to avocado canopy photosynthesis are the short life of avocado leaves (10-12 months, according to Whiley and Schaffer, 1994) and the composite canopy with leaf cohorts of different age, photosynthetic efficiency and light regime.

### **Stored carbohydrates**

CHO's in excess of immediate requirements of the numerous competing sinks, the largest of which comprises the fruits, are stored. It is generally accepted that the priority ('pecking order') in allocation of CHO's is developing seeds > fleshy fruit parts = shoot apices and leaves > cambium > roots > storage. Storage can take place in leaves, twigs, branches, trunk and roots, and we need a definitive study on avocado to quantify these storage pools over a range of conditions, including crop load. Both concentration and amount of CHO in particular plant parts need quantification. A useful analogy is to liken CHO reserves (usually starch) to a bank balance, viz:

Balance = Income - Expenditure

CHO Accumulation = Gross Photosynthesis - (Growth + Respiration)

We have previously pointed out that CHO accumulation is especially significant in perennial crops, since the excess or deficiency of one season will influence tree performance the following season. In this respect the avocado can accumulate more CHO's than other evergreens such as citrus, but usually not as much as deciduous trees (Chandler, 1957). Deciduous trees are totally dependent on stored reserves (CHO and other) for early spring growth (reproductive and vegetative), whereas evergreens have overwintered leaves to at least partly reduce this dependence. We will see however, that avocado trees vary in their relative dependence on stored vs current photosynthate, and that overwintered leaves are likely to be photo-inhibited and limited by feeder root attrition accompanying flowering (Whiley, 1994).

## **THE SEASONAL CARBOHYDRATE CYCLE General Pattern**

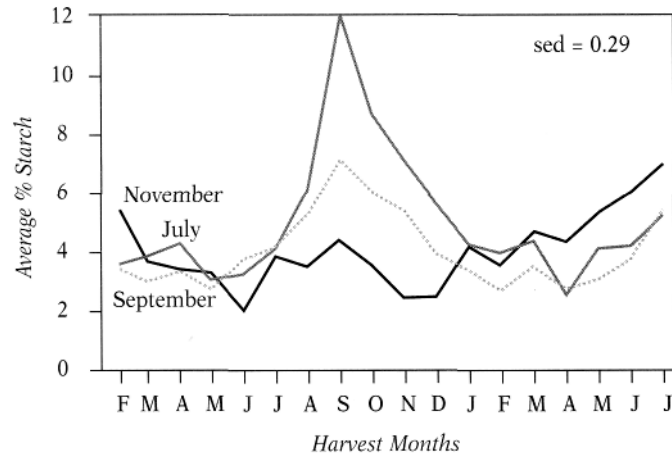
The number of studies on the seasonal CHO cycle (the starch curve) in avocado trees has increased dramatically in the past 10 years. The study of Scholefield *et al.* (1985) in the cold, semi-arid interior of S.E. Australia established the general pattern of a mid-summer low and a late winter high, with a severe decline starting with flowering and fruit set. Furthermore, late winter peak starch concentrations (in the trunk) were related to the following season's crop. High concentrations led to a high ('on') crop, and vice versa for an 'off' crop. This led to interest in a possible 'starch index' system as a crop predictor. Whiley and coworkers in Queensland initiated two detailed studies on the consequences of late harvesting, while locally in KwaZulu-Natal similar studies were conducted by Graham and later by Kaiser. Renewed interest in girdling as a manipulative tool also led to various trials at Everdon Estates and at the ITSC, Nelspruit, *inter alia*.

### **Environmental Aspects**

Whiley (1994) and Whiley *et al.* (1996a, b) noted the importance of climate in starch cycling in avocado trees. In semi-arid, cold winter areas such as the interior of S.E. Australia, California and Israel, there is a distinctly wider seasonal flux in starch reserves. Scholefield *et al.* (1985) noted pre-anthesis peaks of + 18% trunk starch in S.E. Australia. In contrast, peaks of ca 8% are more likely in the humid subtropics of Queensland and South Africa. Whiley (1994) explained this on the basis of reduced vigour (less growth) in cold semi-arid climates, so that there was more time for CHO build-up in autumn and winter. Furthermore, avocado trees in such environments are semi-deciduous, with heavy leaf loss at anthesis. Obviously, such trees will be far more dependent on stored reserves during fruit set, very similar to deciduous fruit trees. Conversely, trees in the humid subtropics (with higher yield potential) will depend on both current photosynthate and stored reserves during the critical fruit set period. It is apparent that the environment markedly affects the stored reserves.

### **Late Harvesting Trials**

In the cool, moist midlands of KwaZulu-Natal, neither Graham and Wolstenholme (1991) or Kaiser and Wolstenholme (1993) were able to show significant yield declines from late as compared to early harvesting of Fuerte or Hass. This was in spite of obvious depletion of starch reserves to lower pre-anthesis peaks and subsequent spring and early summer levels by delayed harvest (figure 2). The assumption therefore was that the leaves 'worked harder' and photosynthates were moved more efficiently out of them to fruits (less feedback inhibition or 'constipation' of leaves). This study also noted that there was not a distinct differentiation into spring and summer shoot flushes in this mesic environment.



**Figure 2**  
 Mean monthly % trunk bark starch levels of July, September and November harvested trees for Everdon (Howick) from February 1991 to July 1992 (Kaiser & Wolstemholme, 1993)

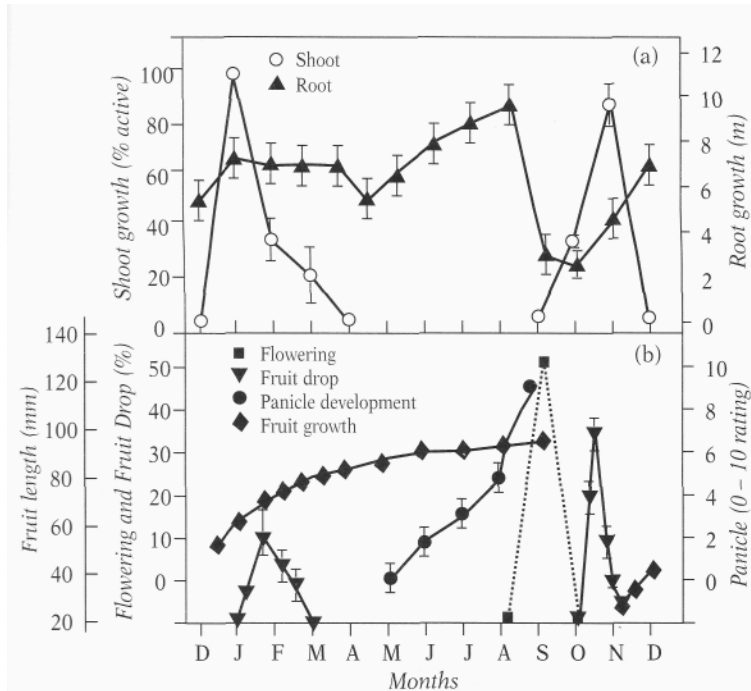
Whiley's studies in Queensland, however, over a longer timespan and including a more stressful locality, clearly showed that late harvesting significantly lowered yields of both Fuerte and Hass, although the impact was reduced by harvesting half the crop early and half late. A strong relationship ( $r^2 = 0,86$ ) between July trunk starch concentration in Hass and next season's yield was found at a relatively cool locality, but for a hot locality the relationship was weaker ( $r^2 = 0,52$ ). In Hass, where alternate bearing was already established at the start of the trial, early harvest was insufficient to break this pattern. For Fuerte, wood starch concentrations from trunks and bearing shoots fluctuated seasonally in the established pattern, but could not be related to harvest treatment. It is also noteworthy that high starch levels were accompanied by greater root growth in avocado trees.

Although Whiley (1994) and Whiley *et al.* (1996b) found a significant relationship between July starch concentration and subsequent crop in Hass trees, the reduced yields from late harvested trees and during 'off' years could not be attributed only to threshold concentration of starch at critical phenological stages. Crop failure was more related to poor flowering, possibly due to inadequate root growth during floral induction.

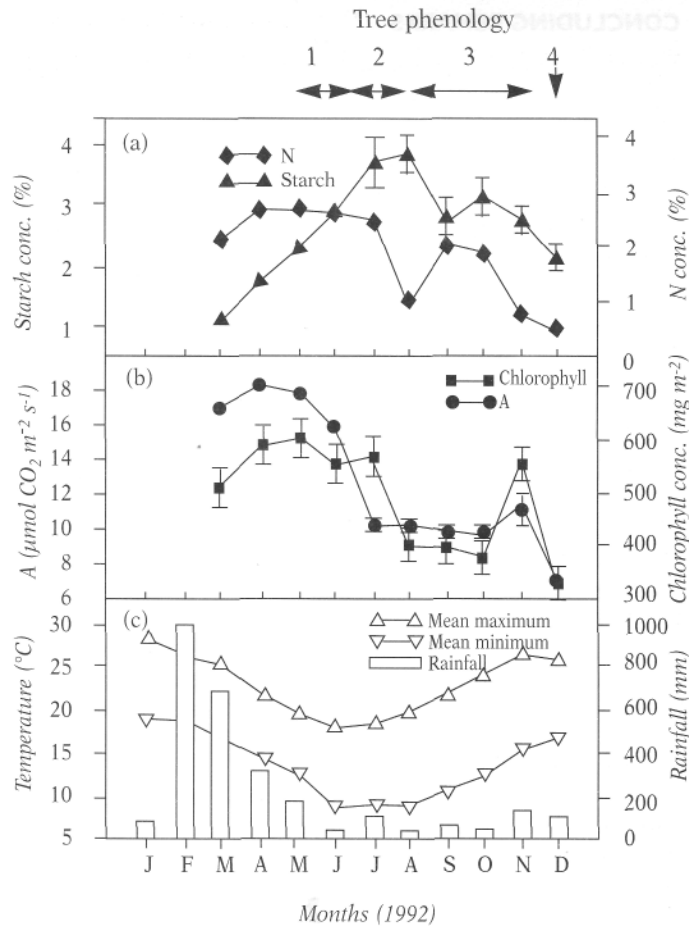
## **WHILEY'S PHENO-PHYSIOLOGICAL MODEL: AN INTEGRATOR OF TREE POTENTIAL**

From our brief discussion of some research results, it is clear that the seasonal starch cycle tells us much about the potential of an avocado tree, particularly if environmental differences are appreciated. It would appear that the starch cycle is of greater value in the cooler, drier Mediterranean climates, where avocado trees are less vigorous, have lower and less predictable yields, and are semi-deciduous. However, in the humid subtropics it was equally clear that stored reserves are less closely correlated with yield potential, although more so in Hass than Fuerte. High yields were possible with a fairly

wide spread of peak starch concentrations at anthesis, provided that orchards are well managed. The answer lies in the fact that in such areas stored CHO reserves are probably less important, and current photosynthate from healthy well-lit leaves more important in overall tree performance.



**Figure 3**  
 Phenology of cv. Hass on cloned Velvick rootstock growing at Maleny, S.E. Queensland where: (a) is the seasonal relationship between shoot and root growth; and (b) is the relationship between floral development and fruiting. Data points are mean values from five trees  $\pm$  vertical SE bars which are obscured by symbols at some points (Whiley, 1994)



**Figure 4**

Seasonal changes in nitrogen and chlorophyll concentrations and net  $\text{CO}_2$  assimilation (A) of summer grown leaves of cv. Hass in relation to phenology (1 = inflorescence development; 2 = anthesis; 3 = fruit set and shoot growth; 4 = leaf senescence) and temperature where: (a) are mean leaf nitrogen and starch concentrations ( $n = 5$ ); (b) is the total chlorophyll concentration and A ( $n = 3$ ); and (c) are the mean monthly temperatures and the exceptionally high rainfall recorded at the experimental site. Data are mean values of five trees  $\pm$  vertical SE bars which are obscured by symbols at some points (Whiley, 1994)

This also emphasises the concept of limiting factors. While there is a broad relationship between stored CHO's and flowering, yield, consistency of bearing, and root growth, there are other potentially limiting factors at critical periods such as flowering and fruit set. Temperature, water stress and *Phytophthora* root rot are the most obvious, as well as mineral deficiencies or toxicities, and they will impact not only on energy (carbon) supply but also on plant growth substances and other metabolites. Excessive emphasis on just one factor is dangerous, as trees are highly complex entities with feedback and feed forward controls.

Whiley (1994) has extended his phenological growth model into a pheno-physiological model (figures 3 and 4). This incorporates quantitative data on not just the main

phenological events, but also key physiological events. The latter includes the starch cycle, but also factors such as leaf nitrogen and chlorophyll content, and the seasonal rate of photosynthesis (figure 4). His study has highlighted other problem areas at key phenological growth stages such as flowering and fruit set. These include nitrogen and chlorophyll loss and photo-inhibition of overwintered leaves, leading to a decline in their photosynthetic efficiency. With the accompanying severe loss of feeder roots as flowering proceeds, the tree is placed under considerable stress at fruit set. CHO stress is certainly part of the picture, but several other stresses will, to varying degrees depending on conditions, impact on overall tree performance. The greater understanding which this model gives us, permits more intelligent 'fine-tuning' of management.

## CONCLUDING REMARKS

There is no doubt about the importance of carbohydrates in the yield performance of tree crops. Similarly, there are logical reasons for the typical seasonal starch curve, with its pre-anthesis maximum and summer minimum. It has become clear however, at least in healthy well-managed orchards, that the winter starch peak is not necessarily always correlated with subsequent yield it is but one of several factors which can be limiting. At best we can say that a high level at this time increases the chances of good flowering and good fruit set. With poorly managed and especially *Phytophthora* infected orchards, the picture of course is totally different genuine and severe CHO stress will then be evident, even to the extent of shoot collapse and dieback. Similarly, a relatively heavy crop load on a tree recovering from *Phytophthora* root rot will delay recovery, by appropriating CHO's which could have gone into root and shoot renewal (Wolstenholme, 1987). Girdling, in all its forms, which encourages CHO accumulation above the girdle for shorter or longer periods, similarly alters the picture, and is a complex topic in its own right (Davie *et al.*, 1995; Hackney *et al.*, 1995).

As is the case for citrus (Goldschmidt & Koch, 1996), it is highly likely that avocado trees are in fact 'source-limited', i.e. CHO-starved, and that management should attempt to reduce the impact by providing better conditions for whole-orchard photosynthetic efficiency.

Why then do avocado trees accumulate 'excess' CHO reserves, usually in fact even more than other evergreen fruit trees such as citrus under similar conditions? The answer is that, as in citrus, a high starch level does not imply that there is a surplus of CHO's. Fishler *et al.* (1983) showed in citrus that reserves continue to build up even when the needs of the developing fruit are not fully met. If, according to Goldschmidt & Koch (1996), the accumulation of reserve CHO's has a high priority in citrus, this is even more so in avocado.

In discussing the reasons for the CHO accumulation in citrus trees, Goldschmidt & Koch (1996) note that even if citrus progenitors evolved in a mesic tropical rainforest, as is commonly believed, they have many 'xerophytic' features which adapt them to drought stress. The same is true for the 'subtropical' avocado its origin was in a subtropical or highland tropical rainforest, but periods of drought, especially in winter, were common. Avocado leaves are comparatively large, short-lived, and leathery with a thick cuticle.



While they are capable of high photosynthetic rates when conditions are mesic (low level of environmental stress), they also adapt to exeric (high stress) conditions and adopt water conservation strategies. Like citrus trees, it seems that avocado trees maintain a large pool of reserve CHO's as a protective measure against recurrent droughts, even at the expense of maximizing photosynthetic gains through water conservation priorities.

The message for the grower would appear to be that reserve CHO's are important, and the tree will use a high percentage of its reserves to support growth and development witness the decline of trunk starch reserves to as low as 2 or 3% in mid to late summer. However, in our humid subtropics we should probably be equally concerned about current photosynthate from healthy, well-lit leaves, made possible by a healthy root system. Both the spring and summer leaf renewal flushes have important roles to play. The challenge is to manage them to best advantage in a canopy situation for the orchard as a whole. The Whiley pheno-physiological model is the most sophisticated tool so far suggested to guide us in the endeavour, incorporating not just the starch curve but other physiological factors such as nitrogen and chlorophyll concentrations, and photosynthesis rate. A more balanced and holistic assessment of tree performance and manipulation potential then becomes possible.

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