

Carbohydrate and phenological cycling as management tools for avocado orchards

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ABSTRACT

The reason for low average avocado yields are summarized, and it is concluded that the grower will have to increase yield ha⁻¹ to remain competitive. The concept of the phenological growth model is explained and its value to understanding orchard management discussed. Carbohydrates are sources of energy for growth and respiration and components such as starch, undergo seasonal changes which can be related to tree performance. The writers motivate an international research programme on these concepts which is currently underway.

UITTREKSEL

Redes vir die lae gemiddelde oeste in avokadoboorde word opgesom. Die gevolgtrekking word gemaak dat oeste ha⁻¹ hoer moet wees as kwekers mededingend wil bly. Die fenologiese groeimodelkonsep en die waarde daarvan vir 'n begrip van boordbestuur word bespreek. Koolhidrate is energiebronne vir plantgroei en respirasie en veral die styselkonsentrasie is aan seisoenskommelings onderhewig wat met boomgedrag in verband staan. Die skrywers motiveer 'n internasionale navorsingsprogram volgens hierdie konsepte, wat tans ingewy word.

INTRODUCTION

Low yields of avocado orchards, calculated on a per hectare basis over a number of years, are a problem worldwide. Reports of low average yields have come *inter alia*, from California (Bergh, 1967; Rock, 1977); Florida (Ruehle, 1963); Israel (Lahav *et al*, 1971); Australia (Trochoulis & O'Neill, 1976; Whiley, 1987) and South Africa (Kotzé, 1986). The problem is often expressed as alternate bearing, with a heavy crop followed by a light crop (Hodgson, 1946; Chandler, 1957), or by irregular bearing.

The reasons for low average yield are complex, multi-faceted and affected by many interacting factors. Wolstenholme (1985; 1987) has discussed the role of evolutionary history, stage of domestication, *Phytophthora* infection of roots, and the energy cost of fruiting in a high oil/large seeded fruit. Whiley & Winston (1987) noted the importance of temperature during flowering and fruit-set in the adaptation (and yield potential) of cultivars in different parts of Australia. Recent research has focused on controlling

vegetative/reproductive growth competition at critical stages (Köhne & Kremer-Köhne, 1987; Wolstenholme *et al*, 1989). The long-term solution is of course, breeding of cultivars and rootstock to adapt the tree to the requirements of modern orchard management (Bergh, 1987).

Avocado growing industries face increasing costs and increasing marketing problems. Several countries face over-production, although world-wide the avocado is only in the development stage. This paper emphasises that competitiveness of individual growers can only be assured by a higher production of saleable fruit per ha, thereby reducing unit costs through greater efficiency. The roles that a knowledge of orchard phenology, as well as carbohydrate cycling, could play in manipulating the tree to the best advantage, is also discussed.

The concept of phenological cycling and the growth model

Phenology has been defined, as the relationship between climate and periodic biological phenomena. Tree crops show development phases (or pheno-phases) with the passing of a season, eg flower initiation and maturation, shoot growth flushes, fruit-set, fruit-drop, fruit-growth and maturation, root growth flushes, leaf-drop. If these pheno-phases are recorded in relation to the calendar year and to meteorological data, the manager is provided with clues to optimize plant productivity.

A first attempt to construct what amounted to a partial phenological model of the avocado, was that of Kotzé (1979). This was derived largely from the morphogenetic studies of Fuerte flower and fruit at Nelspruit by Robertson (1969). Kotzé referred to three phases of seasonal growth of the avocado tree, based on the reproductive events from floral differentiation to fruit maturity. He defined the critical period as being from pollination to completion of fruit-drop in mid-summer. This concept was taken considerably further by Whiley *et al*, (1988). They diagrammatically represented the distinct seasonal growth patterns of Fuerte avocado in SE, Queensland, Australia (Figure 1). These patterns are essentially similar for bearing trees of different cultivars and in different localities, although the time scale and the intensity of the responses will, of course, vary somewhat.

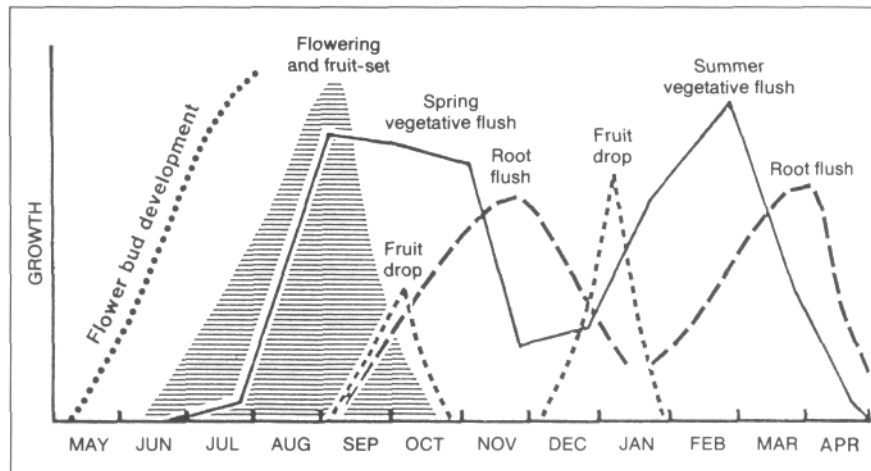


Fig 1 The total growth cycle of cv Fuerte avocado at Palmwoods. Growth forms are dependent on each other, but all compete for tree resources. Management of this cycle leads to improved fruit yields (Whiley *et al*, 1988).

The main components of Figure 1 are two shoot growth flushes (in spring and summer), each followed by a root growth flush). Superimposed on these vegetative phenological events are the reproductive events of flower initiation and development into buds in autumn, flowering and fruit-set in late winter and spring, and two major periods of fruit-drop (spring and mid-summer). The value of such a model is that it is easy to conceptualise which phenological and competitive events are occurring at any one time, and what occurred before and what will take place subsequently. Orchard managers come to recognize and understand critical growth changes and are then better equipped to apply management decisions most likely to increase tree productivity (Whiley *et al*, 1988). This includes timing and amount of irrigation, application of individual nutrient elements, and timing of *Phytophthora* fungicides and mulches.

Vegetative - reproductive growth competition

Vegetative/reproductive growth competition in early spring has been recognized as a major limitation to avocado yield potential (Embleton *et al*, 1959; Biran, 1979; Blumenfeld *et al*, 1983; Zilkah *et al*, 1987). From the growth model (and from an understanding of the Ruah architectural model of Halle *et al*, 1978), we note that although flowering starts before spring shoot growth, there is a period of overlap and intense competition for the nutrient (including carbohydrate), mineral elements and water resources of the tree. (It may, therefore, be necessary to control the vigour of the spring flush, especially, in vigorous cultivars such as Fuerte, to improve the sink strength of setting flowers and fruitlets, so that more are retained and fewer abscise.

This control has been achieved with varying degrees of success by managed nitrogen nutrition (Embleton *et al*, 1959). Leaf analysis should ideally take account of cultivar, growing conditions, 'on' vs 'off' cropping, spring vs summer flush samples, and degree of *Phytophthora* infection (Whiley *et al*, 1987). Israeli workers have shown the value of spring flush spot-tipping (pruning) in increasing fruit-set (Biran, 1979; Blumenfeld *et al*,

1983; Zilkah *et al*, 1987). Bertling & Köhne (1986) also showed that 'determinate' flower clusters (where the terminal bud does not grow out) had better fruit-set than indeterminate clusters.) In South Africa, it may well be economical and practical to physically tip-grow spring shoots in young trees, in order to allow well-placed avocado fruitlets to establish their mobilizing ability better and set into fruits (J G Cutting & J P Bower, 1989, pers comm).

Control of vegetative vigour of the spring flush at the critical period of fruit-set is also the rationale behind research on growth retardants, especially paclobutrazol (Cultar®). Soil applications are directed more at overall vigour control, whereas foliar applications can theoretically be timed to improve initial fruit-set (Köhne, 1986, 1988; Wolstenholme *et al*, 1988, 1989). The calcium content of fruits can theoretically also be increased in such less-vigorous trees (Witney *et al*, 1986).

The phenology approach to orchard management, therefore, helps us to understand growth events and their interactions in the tree, as well as the concept of critical periods, when factors influencing yield must be optimised. If this approach can be integrated and quantified with that of carbohydrate cycling, we may well have a more finely-tuned management tool for growers.

The concept of carbohydrate cycling and management

Carbohydrates (in this case simple sugars) are the first products of photosynthesis. In turn, they can be synthesized into more complex carbohydrates, as well as undergo transformations into proteins and lipids. Collectively, these compounds constitute over 90 per cent of the dry mass of plants, while carbohydrates themselves can constitute over 65 per cent of the dry mass of tree crops.

Carbohydrates, therefore, provide the carbon skeletons for structural components of plants, including cell walls, as well as for the synthesis of components of the living cytoplasm. They also serve as a major source of substrate for the process of respiration, which provides energy for synthesis and growth of plants.

Interest in carbohydrates (CHO's) in tree crops arise because they are the chief source of plant energy, even in plants which store lipids. Plants can accumulate CHO's in excess of their immediate needs, in a manner which can be likened to a bank balance, viz:

Balance = Income - Expenditure

CHO Accumulation = Gross Photosynthesis - (Growth + Respiration)

CHO accumulation is especially significant in perennial crops, since the excess products of one season remain to influence the performance of the plant the following season. This applies particularly in deciduous trees, but also in evergreens. The total CHO content of tree crops show marked seasonal rhythms, reflecting the changing balance between supply (source) and demand (sinks) (eg Stassen, 1980; Figure 2).

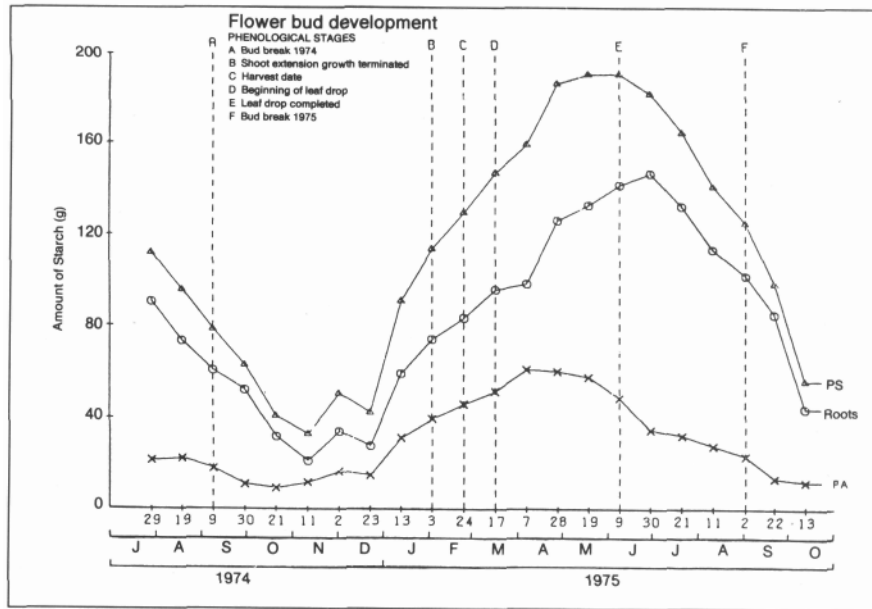


Fig 2 Seasonal changes in starch content of the roots, permanent aerial parts (PA) and permanent structure (PS) of young Kakamas peach trees (Stassen, 1980).

CHO's available for plant growth consist of the products of current photosynthesis and the storage or reserve forms. The living plant is a dynamic entity, and rapid inter-conversions occur in response to short-term demand (Date, 1985). However, the authors concern lies more with the storage or reserve CHO's, which are more stable, although following predictable seasonal trends. In addition, the authors are interested in the available or useable CHO's, ie those which can be recycled, rather than the structural CHO's.

Total available reserves and resources

Various CHO fractions can be analysed. The concept of '**total available carbohydrates**' or 'total non-structural carbohydrates' is well established (Priestley, 1962; Smith, 1969; Dey & Dixon, 1985). '**Total CHO reserves**' or '**storage CHO's**' are likewise CHO's which accumulate during a period of abundance and are subsequently available when required by the tree. They are stored in shoots, trunk, leaves, roots and even fruits,

Since CHO's derived from storage reserves are indistinguishable from those produced in current photosynthesis, Priestly (1962; 1965) preferred the term '**resources**' for all available CHO's present at one stage of growth.

In all of the above cases, the materials of interest are only CHO's. Priestley has shown that CHO's constitute only 1/3 to 2/3 of the total resources or reserves (dry matter) in apple trees. He notes that other reserves include amino acids, proteins, and lipids. His '**total available resources**' is therefore a broader concept, and includes all resources extractable with boiling 5 per cent trichloro-acetic acid and 35 per cent methanol. Today

this is regarded as a very drastic extraction procedure.

All the above terms have been used where broad estimates of reserves or resources are required as a management tool, without reference to the individual fractions of non-structural CHO's.

Carbohydrate fractions in plants

In the past decade a feast of modern texts on the biochemistry of the wide range of plant storage CHO's have appeared, eg Duffus & Dixon (1985).

In most plants, sucrose is the major form in which carbon is **translocated**, but it is usually relatively unimportant as a storage CHO (except in sugarcane, sugarbeet and a few other plants). In some plants, two sugar alcohols are important translocation forms, eg sorbitol in apple and mannitol in olive, in avocado, the seven-carbon sugar alcohol perseitol has been shown to be important in translocation (A Blumenfeld, 1988 - pers comm.).

Starch is undoubtedly the most common and important reserve (storage) form of CHO in most higher plants. It can accumulate to 20 per cent or more of the dry mass of some tissues. It is the most useful indicator of seasonal CHO trends in tree crops, and is most closely related to the aspects of the tree performance of interest to horticulturists. There are a number of 'fringe' compounds with less clearly defined storage roles, eg mannans and fructans.

Storage carbohydrates in avocado trees

Few studies have been conducted on the carbohydrate cycle of avocado trees. Cameron *et al*, (1952) reported on starch and sugar changes in young shoots under California conditions. The most detailed study is that of Scholefield *et al*, (1985) in south-east Australia. They showed that CHO levels were lowest after the second (summer) vegetative flush and just prior to floral initiation in autumn. Levels increased during winter and reached a maximum just before flowering. A steep decrease in CHO levels, especially starch, occurred during flowering, shoot growth and fruit development. Starch levels could also be closely related to alternate bearing. A High yield followed high starch levels during the previous season. This resulted in lower levels during the following winter and spring, with a consequent poor crop.

The above study has suggested that the peak starch concentration during the dormant season may well be a useful quantitative index to the **potential** yield the following season, assuming no climatic upsets, and a good level of management. It should then be possible to superimpose a CHO (or starch) graph into the phenological growth model, and to specify target levels and critical concentrations.

Some cautionary remarks

The scenario presented above is undoubtedly a gross simplification of a complex subject. Plant growth and fruiting are dependent on many factors, of which energy

partitioning is only one aspect. It ignores the regulatory role of plant growth substances, and glosses over the topics of assimilate partitioning and relative sink strength. According to Cannell (1985), the evidence indicates that the priority order for allocation of assimilates is:

developing seeds > fleshy fruit parts = shoot apices and leaves > cambium > roots > storage organs.

In other words, assimilates (including storage CHO's) are partitioned preferentially to young reproductive structures, and storage comes last in the 'pecking order'. In practice, the demand for assimilate by each component of the tree depends on its current metabolic rate, mediated by plant hormones (Landsberg, 1988; Figure 3). The whole question of timing, therefore, becomes important - this is where phenological matching of critical developmental phases of roots, shoot and fruit to relative source and-sink strengths, needs in-depth study (Wolstenholme, 1987).

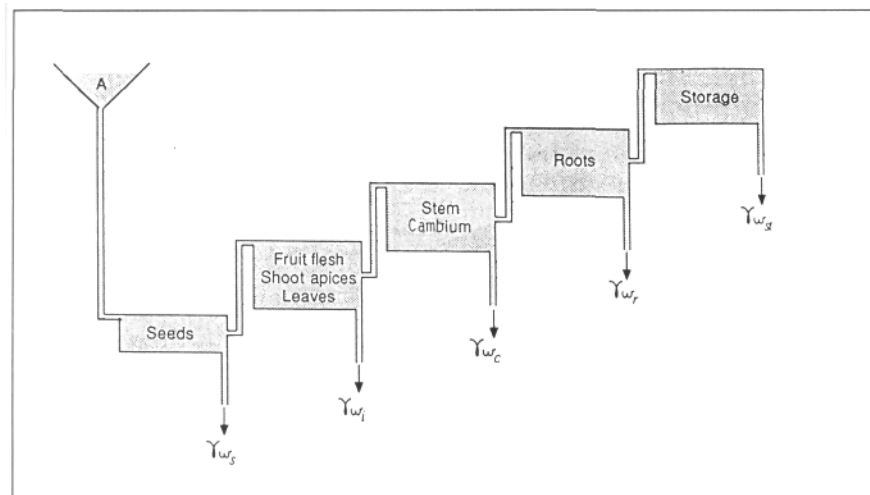


Fig 3 A hydraulic analogue to illustrate the concept of priority areas for assimilate allocation. It demonstrates clearly that if the rate of supply is not sufficient to meet the demand for all organs in the system, the lower priority components (with smaller gradients, higher resistance) will suffer. The loss terms (γw_i , where i denotes any organ) represent respiration (rate γ), which is a function of the mass of each component, and of temperature (Landsberg, 1988).

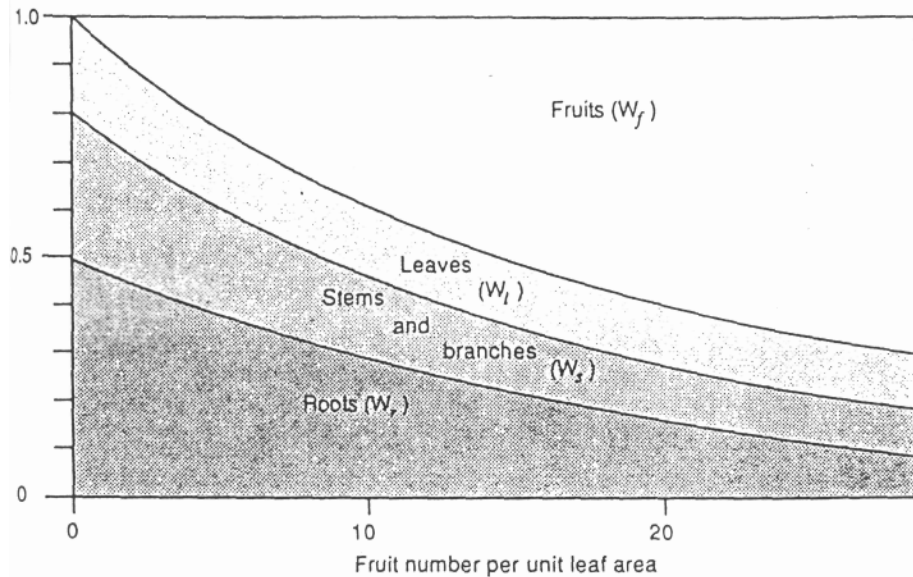


Fig 4 Diagram showing the changes in patterns of carbon allocation as the number of fruits carried by a tree increases relative to the leaf area. The diagram has been re-drawn from that produced by Heim *et al* (1979), describing relationships obtained for apple trees. The fruit (nut) production cycle of macadamias is very similar to apples and the same relationships can be expected to hold: as fruit numbers increase the growth of all other parts of a tree is reduced (Landsberg, 1988),

Priestley (1987) has also cautioned that CHO sources (leaves) often have the potential to supply more than are normally utilised by sinks, i.e. there can be constraints on assimilate utilisation. On the other hand, the manner of leaves or leaf area required to support the growth of a normal-sized fruit is not known for the 'energy-expensive' (Wolstenholme, 1986) avocado. Similarly, as in the apple (Heim *et al*, 1979), it would be useful to obtain data on changes in carbon allocation, as fruit number increases relative to leaf area.

Even if studies of carbohydrate cycling and assimilate partitioning are simplifications, they still represent what is today fashionably called 'the bottom line'. For an understanding of the whole tree we have nothing better at present - nothing which integrates across all physiological processes and gives us a simple but good measure of overall tree health and potential. Simplicity can be a virtue in such circumstances.

An international research programme initiated

The Maroochy Horticultural Research Station in Queensland, Australia has developed both the phenological growth model (Cull, 1986; Whiley *et al*, 1988) and the carbohydrate cycling concepts in their research programmes on subtropical fruit crops. The senior author's sabbatical leave in Australia during 1986/87, will soon be reciprocated by study leave in South Africa for Whiley. The latter initiated a comprehensive study on carbohydrate cycling in avocados in 1987, including the effect of late hanging on subsequent tree performance. Similar research was initiated in the late maturity areas of the Natal midlands in 1989. The CSFRI, Nelspruit, is also involved

in this cooperative programme.

Locally in Natal, the main objective is to characterize the carbohydrate cycle in Hass trees at a very cool and warm locality. Secondly, the author will attempt to quantify the effect of late hanging of fruit on tree performance (including yield) in the following season. Finally, the endeavour will be to produce a model whereby the grower has an index to tree health and yield potential by sampling his trees at key growth stages.

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