

# INTERACTION OF PLANT GROWTH REGULATOR AND CARBOHYDRATE IN FLOWERING AND FRUIT SET

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## Summary

Biennial or alternate bearing is common in many tree crops. This is particularly problematical in avocados. Some researchers have attempted to use stored carbohydrate levels, particularly of the trunk or roots, to predict the potential yield of the next season's crop. Those favouring a plant growth regulator approach, however, are of the opinion that a healthy tree can compensate photosynthetically, for a high fruit load, and that suppression of flowering and fruit set following a heavy crop is PGR controlled. A hypothesis integrating both aspects in the regulation of flowering and early fruit retention is presented.

## 1. Introduction

Accurate crop prediction is essential for both grower and industry. The earlier this can be done, the more valuable. From a horticultural viewpoint, yield prediction prior to flowering and fruit set, has considerable advantages, as many managerial aspects can be altered to cater for the expected crop size, thereby optimising inputs. A number of subtropical fruit industries have recently expressed a wish to see research aimed at developing such a prediction system. Field observations of floral intensity have been used to predict fruit set and subsequent yield, but a more objective diagnostic technique is desired.

Research thus far has emphasized two potential mechanisms in the regulation of flowering and fruit set with little integration between the two areas of study. On the one hand, there are those researchers who have concentrated on plant growth regulators; while on the other hand, a number of workers have demonstrated a role for energy reserves prior to flowering, as the factor determining the extent of flowering and controlling fruit set and early fruit growth (Wolstenholme & Whiley, 1969).

The aim of this paper is to review the potential role of PGR's and carbohydrate in the regulation of flowering and fruit set within the context of our own research into tropical and subtropical tree fruits,

and to develop a hypothesis that integrates the two mechanisms. It is not intended to review the physiology of alternate bearing, which has been adequately covered by Monselise & Goldschmidt (1982).

## 2.1 Carbohydrates

Much of the published work relating to the control of flowering and fruiting concerns deciduous trees, and must therefore be treated with considerable caution in extrapolating to evergreen tropical and subtropical trees. Nevertheless, guidelines may be obtained.

The woody tissues of trees, such as trunks, large shoots and roots, accumulate carbohydrates, particularly starch, which serves as an energy reserve (Yoshioka et al., 1988). These authors further indicated that with the onset of flowering and fruiting, such reserves can be mobilised in the form of soluble sugars, and be moved to areas of utilisation. Sedgley et al., (1985) considered that poor flowering of avocados in tropical areas of Australia was linked to a lack of carbohydrate reserves, possibly due to high respiration rates under hot environmental conditions. Girdling which increases reserves within the girdled limb (Jackson & Sweet, 1972) also increases flowering and fruit set (Trochoulis & O'Neill, 1976). This has been used as evidence that carbohydrates play a vital role in flower development and fruit set. A similar approach to mango flowering was taken by Gazit (1960). Scholefield et al., (1985) recorded carbohydrate levels in alternately bearing avocado trees. It was found that in all cases, carbohydrate (primarily starch) levels changed through the season, being lowest after the summer flush and prior to floral bud initiation. Thereafter, reserves increased until flowering, when a considerable decrease again occurred. The major build-up was thus during the winter, after flower initiation. While floral initiation probably was not dependant on carbohydrate concentration directly, the authors obtained a good correlation between yield and the level of carbohydrate reserves at the time of flowering. It was postulated that carbohydrate requirements for flowering and fruit set compete with that of the spring flush, with increased fruit and flower drop occurring if reserves were insufficient. Our own research on avocados and citrus does not always support this hypothesis. Further, it is evident from a review of avocado flowering by Davenport (1986) that carbohydrates may not be related to the initiation of flowering, and that flowering intensity may not be related to the eventual crop load.

Goldschmidt & Golomb (1982) examined the carbohydrate balance of alternately bearing mandarin trees. Considerable reserves, particularly starch, built up in the roots of "off" year trees, when compared with trees carrying a heavy crop. Trees with high reserves flowered well, and set a good crop, while those with low reserves did not flower. Davis & Sparks (1974) found similar results for pecans. Goldschmidt & Golomb (1982) showed that partial removal of a fruit crop allowed for an intermediate build-up of carbohydrate reserves plus an intermediate intensity of flowering. It was, therefore, concluded that carbohydrates play a vital role in flower initiation, fruit set and fruit growth, although they may not act alone, with both mineral nutrition and plant growth regulators having an influence.

Goldschmidt & Golomb (1982) suggested that flower initiation was not energy intensive, while flowering, fruit set and fruit growth were, and might, if the crop was heavy, require more energy than the tree could supply during the season. If photosynthetic output can be enhanced or reduced in response to fruit load as demonstrated by Monselise and Lenz (1980), then the tree should not suffer a depletion of reserves to the extent that future flowering and fruiting is affected. Further, the fruit may itself contribute to carbon fixation. A recent review into this still largely unexplored field by Blanke & Lenz (1989) indicates that carbon fixation within the fruit may influence not only fruit growth, but also fruit drop and even subsequent ripening. The degree to which re-fixation of fruit respiratory carbon dioxide might occur, varies with fruit age. Blanke et al., (1987) found that in the case of apples, the carbon dioxide reassimilation potential could exceed its loss by several fold at the time of harvest, but was considerably less at fruit set. Blanke & Leyhe (1989) showed that reassimilation made a significant contribution to the total carbon economy of developing grape flowers and fruits. In contrast, apple fruits are known to withdraw almost all the assimilates produced by leaves on the same spur (Hansen, 1967). Clearly more research in these areas is required.

Ban-Tai (1985) mentions that vegetative growth cessation is essential for the promotion of flowering and fruit set. This is clearly shown in the case of citrus and mango, which do not flower well nor set crops in tropical areas in the absence of stress which causes growth cessation. This does not necessarily mean, however, that alteration in carbohydrate production or partitioning is the all important criterion. Contrary to popular belief, neither starch nor glucose accumulated in leaves of Washington navel orange trees during a low temperature stress treatment which promoted flowering in this variety (Lovatt et al., 1983b). Despite the fact that leaf carbohydrate content did not change in response to stress, there was a significant correlation between the number of floral shoots produced and leaf starch content at the end of the stress period. At the same time, there was no significant relationship between leaf carbohydrate content (starch or glucose) and the number of vegetative shoots produced. Demonstration that tree carbohydrate status influenced the number of floral shoots produced but not the number of vegetative shoots suggests that starch is not simply serving as an energy source to support budbreak (Lovatt et al., 1983b).

While the carbohydrate status of the canopy did not change in response to stress, nitrogen metabolism in citrus leaves did. The result was an increased production and accumulation of ammonia (measured as the combined pool of ammonia-ammonium) that paralleled the duration of the low temperature treatment. In addition there was a significant correlation between the content of ammonia in the leaves at the end of the stress period and floral intensity ( $P < 0.0001$ ) (Lovatt et al., 1983a, b). Evidence of a cause and effect relationship between leaf ammonia content and floral intensity was provided by demonstration that foliar-applied urea increased leaf ammonia levels and caused a concomitant and equal increase in flower number.

Little is known about changes in carbohydrate and nitrogen metabolism in the roots during stress-induced flowering. Concentrations of glucose and starch (sucrose was undetectable) in citrus roots changed dramatically during the year independent of increases and decreases in root biomass (Hamid *et al.*, 1985). Starch was highest just before flowering, disappeared at the time of spring bloom, and increased again until the first root flush occurred.

Assimilate partitioning affects many physiological processes. Subsequent changes in root metabolites in relation to flowering and fruit has received limited attention. A better understanding of root metabolism, including changes in carbohydrate, nitrogen and plant growth regulators moving from the roots during flower induction, initiation and development of the ovary through fruit set is needed.

## 2.2 Plant growth regulators (PGR)

When a plant changes from the vegetative to the reproductive phase, many previously quiescent genes must be activated in a large number of cells in localised areas of the shoot apex (Naylor, 1984). Once started, the activation of other genes follows in an orderly sequence. Since plant hormones have the potential to alter expression of the genome, it is thought that plant hormones play a role in flower initiation.

Application of plant growth regulators to trees has provided evidence suggesting that changes in endogenous hormones may be more important than differences in carbohydrate status *per se*, in the control of flower initiation (Hoad, 1984). This is supported by the work of Whaley (*et al.*, 1989) which demonstrated that PGR levels and ratios were influenced by the present season's crop, primarily via gibberellins. Changes in shoot and root growth occurred with resultant changes in carbohydrate partitioning.

The application of gibberellins to woody angiosperms such as apple, pear and grape have shown a strong inhibiting effect on flowering. In addition, growth retardants (such as paclobutrazol) which block the gibberellin biosynthesis pathway, promote flowering. In apples, the seed are known to be a major source of gibberellins (Luckwill *et al.*, 1989) and there is considerable evidence of their role in inhibiting return flowering (Ebert & Dangert, 1981). Our own research has shown that the injection of gibberellin into avocado shoots results in a vegetative flush (Cutting & van Vuuren, 1983) with a concomitant inhibitory effect on flowering (Cutting & Bower, unpublished results).

Initially, cytokinins were not thought to play a role in flower induction (Duban & Faust, 1982). However, more recent evidence has indicated that cytokinins can overcome the inhibitory effects of GA4+7 on flowering in apples (McLaughlin & Greene, 1984). Certain anti-cytokinin compounds have also been shown to inhibit flower induction in apple (Hoad & Abbot, 1983). Root pruning is known to stimulate flowering in apple (Abbot, 1983). This corresponds to our previously mentioned work on citrus, where the indications are that the production of new roots plays a crucial role in flowering and fruiting.

Cytokinins are usually considered to be root produced. Therefore, the root growth and metabolism plus availability of water, will influence the cytokinin content of xylem sap. The cytokinin content of roots and xylem is reduced by withholding irrigation (Itai & Vaadia, 1965), while irrigation after a water stress was shown to cause a rise in cytokinin-like compounds in the xylem fluid of coffee (Browning, 1973). There is also strong evidence that cytokinins increase mitotic activity (Bernier et al., 1977). Vince-Prue (1985) stated in a review that the possible role of cytokinin in flower initiation deserves further attention.

The role of indoleacetic acid (IAA) and abscisic acid (ABA) in the regulation of flowering and fruiting is not well documented. Bangerth et al. (1986) found ABA concentrations in shoots correlated positively with flowering intensity in apples. Jones et al. (1976) found high levels of t-ABA (believed to be an ABA precursor) in "on year" Valencia buds. In our own recent research we observed root-produced ABA, moving in xylem sap, in response to flower induction treatments. The significance of these findings still need clarification.

### 3. Discussion

Within the group of evergreen tropical and subtropical crops of interest, there are arguments for and against both the photosynthate and plant growth regulators as mechanisms controlling flowering and fruiting. A recent review by Bernier (1988) perhaps summarises the situation most adequately, by stating that a multifactorial approach best accounts for the complexity at all steps in the process. Both the role of assimilates as well as those favouring plant growth regulators can be accommodated. Bernier's (1988) review shows that the balance between the various systems differs in different plant types. A simple diagnostic procedure for prediction of yield or cropping potential is thus not possible until we understand how PGR's and carbohydrate interact in the regulation of flowering and fruit set.

As far as the tropical and subtropical fruits, avocados, citrus and mangoes, are concerned, for which we have some experience of flowering and fruiting, we believe that root physiology may be a key factor. We propose that vegetative growth, flowering and fruit set are regulated by both PGR's and carbohydrate as depicted in figure 1 and as described below.

In the absence of low temperature or water-deficit stress, root production provides active root apices which synthesize cytokinins. The cytokinins move in the xylem to the shoot and cause bud break leading to vegetative shoots. The more new root tips, the more cytokinins, the more buds that break, the more vegetative shoots. The new shoots produce gibberellic acid (GA) or IAA, which moves to the roots and inhibits root initiation. The more shoots produced, the more GA, the more complete the inhibition of root growth. Thus no cytokinins, and no new shoots, which leads to a reduction in GA production as the shoots mature. The reduced level of GA moving from the shoots to the roots allows root growth to start again. Thus, an alternating pattern of shoot and root growth prevails.

While PGR's promote root or shoot growth, the amount of available carbohydrate, nitrogen compounds, water and nutrients, determines the extent of that growth.

With low temperature and water-deficit stress, the same events occur but there is the additional production of ABA in the roots in response to stress. The ABA converts the vegetative shoot apex to a flower and thus regulates floral shoot development.

The reason that tree starch content parallels the number of floral shoots induced by stress but is slightly negatively correlated with the number of vegetative shoots produced in response to stress is as follows. Available starch level determines the numbers of new roots that can be produced in the absence of shoot growth which is inhibited during the stress. The more starch, the more new roots, the more cytokinins and the more ABA. The cytokinins increase bud break so there should be more vegetative shoots but the ABA converts the vegetative shoots to floral shoots. There is thus no net increase in vegetative shoots, in fact, there is a slight decrease in the number of vegetative shoots at higher starch due to increased availability of ABA, causing the conversion of more vegetative shoots to floral shoots.

The high transpiration rate of flowers, and PGR's produced by the developing ovaries create sink strength that mobilizes carbohydrates, water and nutrients to the fruit. While PGR's promote fruit set and fruit growth, the capacity to set and grow can only be expressed fully if carbohydrate, nitrogen compounds, water and nutrients are available in sufficient quantity.

A diagnostic technique for yield which ignores any of the aspects discussed, is likely to be inconsistent in its long-term reliability. It is clear that more research of an integrated nature will be necessary before the objective of long-term yield prediction, quantification and manipulation will be possible.

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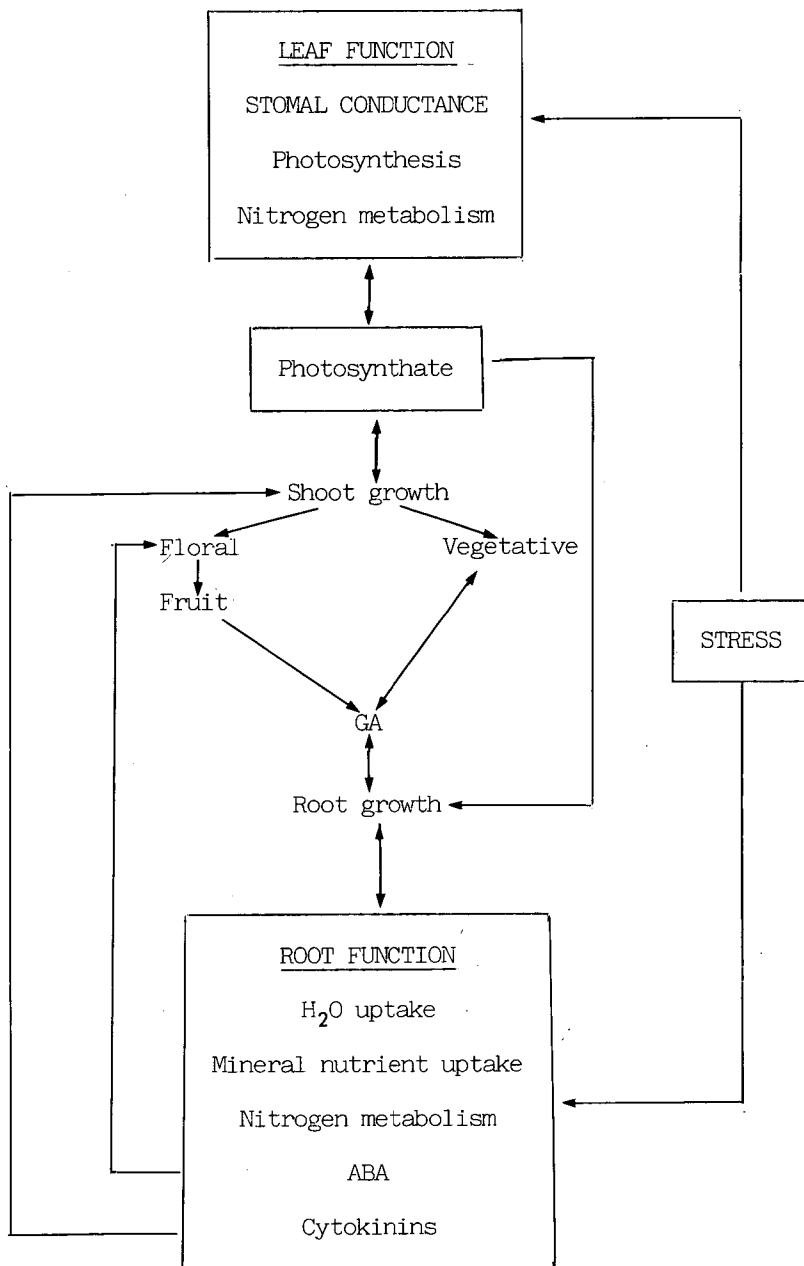


Figure 1: A simplified schematic representation of the interaction between plant growth regulators and carbohydrates in influencing flowering and fruiting. GA = Gibberellic acid, ABA = abscisic acid.

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