

GENERAL DISCUSSION AND CONCLUSIONS

DISCUSSION

Internationally, avocados are grown across a wide range of environments (Whiley and Schaffer 1994), however for the most part research reported in this thesis was carried out in humid subtropical regions. Although the attributes of phenological modelling assist in the translation and interpretation of growth responses to changing environments, caution is necessary when translating specific principles across diverse climatic conditions. While it is thought that some results from this research will be of benefit to avocado production in semi-arid cooler climates, its greatest impact will be felt in subtropical regions.

Low average yields are a feature of avocado production in most countries which grow this tree as a commercial orchard crop (Monselise and Goldschmidt 1982; Wolstenholme 1987). There is little doubt that unfavourable climatic conditions in some situations (southern Australia, California, Chile, Israel) are largely responsible for continued poor performance which leads to economically unsustainable production of avocado, e.g. California (L. Francis, pers. comm.[‡]) and Israel (Dr O. Reuveni, pers. comm.^{‡‡}). Strong alternate bearing cycles precipitated by either climatic stress or poor management (Monselise and Goldschmidt 1982) introduce economic uncertainty into avocado production which impacts on the confidence of producers and their ability to reliably service markets. The present rate of planting of new production areas in Australia will inevitably increase pressure on domestic markets where most of the fruit is currently sold. For sustainable economic growth new markets, both processing and export, must be developed. Reliable and more cost-effective production is needed to achieve this goal which may be realised through improved production technology and its implementation in the orchard.

Phenology and Rootstocks

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Since the late 1970s the author has been developing phenology models for avocados which have become increasingly sophisticated with time. These models have been used to gain a greater understanding of the synchrony of growth, resource competition within the tree and genotypic responses to diverse environments (Whiley and Winston 1987; Whiley *et al.* 1988a). Results presented in this thesis have extended this holistic approach with the development of a pheno/physiological model which integrates related growth events and physiological changes in trees. As a research approach, modelling growth and key physiological changes assists with identification of factors limiting growth and production, spatial and temporal relationships of sinks and sources (vegetative:reproductive competition), and critical pheno/physiological events which may have a large impact on yield and fruit quality.

The seasonal flux of new root growth and related starch concentrations in roots and scions are the first long-term studies reported for avocado trees. The extension of root growth through winter, at least under the mesic high rainfall conditions at Maleny, has not been previously identified and has implications for long-term tree health and performance. The substantial loss of “feeder” roots from the onset of flowering through to maturation of the spring flush which this study has highlighted, occurs during the critical period of fruit set and early ontogeny. The related decline in starch content suggests that the flower sink either diverts assimilates or remobilises carbon products from roots, which in either case leads to assimilate starvation of this organ. Loss of root surface at a time of competitive reproductive:vegetative growth (Biran 1979; Wolstenholme 1990) potentially reduces the uptake of water and minerals and may limit cytokinin production. This is also a time of the year when *Phytophthora* root rot stress is greatest as roots may have been damaged in late summer (Pegg *et al.* 1982) thereby reducing the potential volume approaching flowering. The objective of the fertiliser program recommended by Whiley *et al.* (1988a) was to optimise the requirements of the tree during summer and autumn so that recyclable nutrients are available to support spring growth from endogenous sources (e.g. leaves and stems), at a time of reduced root volume. Subsequent studies reported in this thesis have validated and reinforced the concepts on which the recommendations were based.

Differences between the two rootstock/scion combinations were pronounced with cropping efficiency comparatively increased for the cloned ‘Velvick’/‘Hass’ which also carried a higher percentage of fruit on determinate inflorescences. The seedling ‘Velvick’/‘Hass’ trees produced

more roots which accumulated higher concentrations of starch than the cloned 'Velvick'/'Hass' trees, which accumulated more in the scion. Rootstock manipulation of growth and cropping is highly developed in apples (Lockard and Scheider 1981). Dwarfing of avocado trees (cv. Fuerte) has been reported by Barrientos Priego *et al.* (1987) who found that using Colin V-33 as an interstock reduced growth by ca. 30%, although no yield data were supplied to indicate tree performance. Results with the 'Velvick' rootstocks give a clear indication that genetic manipulation of tree performance with avocado can be achieved and is worthy of further investigation in the future. Both rootstock and scion require attention, and in view of the paucity of horticultural research on avocado rootstocks, it is likely that investment in this area will be more rewarding in the short and medium term.

Reproductive:vegetative competition

Reproductive:vegetative competition during spring shoot development has been previously reported (Biran 1979; Blumenfeld *et al.* 1983; Köhne and Kremer-Köhne 1987; Adato 1990; Cutting and Bower 1990; Wolstenholme *et al.* 1990). Shoot tipping and chemical manipulation have both increased fruit retention on spring shoots. Results from studies reported in this thesis have contributed to knowledge on photoassimilate supply, presumably one of the limiting factors, during early fruit and shoot ontogeny. Increased sample size in some studies would improve confidence in the results reported, however there were limitations with respect to resources (labour) available to assist with the detailed field aspects of the research. Despite these limitations some assurance can be taken from the repeatability of the studies and support given by previous research (Biran 1979; Blumenfeld *et al.* 1983; Köhne and Kremer-Köhne 1987; Adato 1990; Cutting and Bower 1990; Wolstenholme *et al.* 1990).

The dynamics of carbon dioxide efflux of fruit during ontogeny showed that a small contribution is made from fruit photosynthesis towards the fruits own carbon requirements for growth. On a g_{dw}^{-1} basis fruit photosynthesis was highest during early ontogeny and progressively declined as fruit mass increased. While carbon fixation from fruit photosynthesis is negligible in terms of total fruit requirement for growth it may be a significant factor during the first few weeks of ontogeny - a period of strong competition for assimilate resources.

The importance of retention of over-wintered (previous spring and summer flush) leaves during anthesis through to sink:source transition of the renewal spring shoots was clearly demonstrated with 'Hass' trees and is probably due to low starch reserves in heavily cropping trees. Pre-anthesis starch concentrations determined in trees growing in the subtropics were much less (ca. 8%) than reported in similar tissues by Scholefield *et al.* (1985) (ca. 18%) where avocados were growing in a cool, semi-arid Mediterranean climate. These differences are likely due to successive heavy crops on trees in the subtropics which reduce investment into carbohydrate reserves (Whiley *et al.* 1992) and the longer period of quiescence and the smaller crops carried on trees growing in cooler interior climates which promote the accumulation of starch (Scholefield *et al.* 1985; Whiley and Winston 1987; Whiley *et al.* 1988a). In cool, semi-arid Mediterranean climates there is significant leaf loss during anthesis (Scholefield *et al.* 1985; Bergh 1986; Sampson 1986) and it is likely that the remaining over-wintered leaves have irreversible physiological damage due to prolonged exposure to mean minimum temperatures of $\leq 4^{\circ}\text{C}$. In southern California, starch accumulation in avocado trees during winter is much higher than citrus and more akin to that expected in deciduous fruit tree species (Chandler 1958). It is suggested that avocados in these more stressful cool climates are dependent on the "storage pool" of carbohydrates to sustain fruitlets from set through to the sink:source transition of the spring shoot growth as the supply of current photoassimilates during this period would be negligible. Furthermore, premature leaf senescence would be more likely to be aggravated by salinity stress in semi-arid areas.

With respect to the importance of the over-wintered canopy to yield of avocados in subtropical climates brought to light in this study, knowledge on leaf dynamics in orchard situations is limited. Longevity, rate of turn-over, acclimation to changing PPFs and stress recovery cycles are areas of leaf dynamics worthy of further research, with the potential to develop management strategies promoting higher yield. In particular, the determination of genotypic responses to photo-inhibiting winter temperatures, common to all subtropical regions, has the potential to identify sources of cold tolerance useful in future plant improvement programs.

Preliminary results from research which increased the photosynthetic efficiency of over-wintered leaves following anthesis (pre-anthesis N plus mid-anthesis paclobutrazol) were encouraging in that a trend for a substantial increase in cumulative yield was demonstrated. Prior

recommendations have targeted summer as opposed to pre-anthesis applications of nitrogen to avoid invigorating renewal spring shoot growth at the expense of developing fruitlets (Whiley *et al.* 1988a). Results indicate that these recommendations remain valid in the absence of growth inhibition treatments to counter the effects of nitrogen applied during late winter. However, it remains to be seen if pre-anthesis nitrogen with appropriate suppression of shoot growth can be developed into manageable strategies at the production level. Further research should be pursued in this area in respect to improving the photosynthetic efficiency of the over-wintered canopy with increased partitioning of photoassimilates to developing fruitlets.

Influence of harvest time on sustainable production

Results in this thesis are the first long-term studies reporting on the effects of harvest time on sustainable yield with experiments continuing from three to six consecutive years. It was conclusively shown that long-delayed harvest of 'Fuerte' caused significant yield reduction the following season, with trees driven into alternate bearing cycles. However, 'Hass' appeared more tolerant of late harvesting and took longer to develop alternate bearing cycles. Once biennial cropping patterns had developed they could not be broken by early harvesting of fruit, and more severe strategies will be required to moderate cropping patterns, e.g. early fruit thinning or strategic pruning.

Ecological significance of phenological and physiological characteristics of avocado trees

The high net CO₂ assimilation (A) for avocado reported in this thesis ($> 17 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) is contradictory to the common held rubric for evergreen fruit trees ($A_{\text{max}} \leq 12 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in the literature. A probable explanation is that leaf longevity and the dynamics of canopy replacement suggest that many aspects of avocado phenology and physiology are more typical of deciduous than evergreen species.

Avocados evolved in the subtropical and highland tropical rainforests of Central American and have many features identifying them as climax species (Whitmore 1990), colonising small gaps when the forest canopy is disturbed. Successful capture of canopy space by a forest species is initially dependant on the presence of viable seed or seedlings when gaps are formed; the latter

being a feature of the abundance and distribution of the reproductive propagule and its ability to germinate and survive for a considerable time in low light regimes (Denslow 1987; Whitmore 1990). Avocado seed is large, 40 to 80 g_{fw} and represents 20 to 35% of the fresh fruit mass (A.W. Whiley, unpublished data). Due to the large fruit size (300 to 700 g), seed dispersal would require large mammals such as were present in the Americas during the Pleistocene age (Janzen and Martin 1982), with the energy-rich pulp a substantial attractant and reward. Germination of the seed can occur in darkness or at low light intensity and the rich store of energy in the fleshy cotyledons (Wolstenholme 1986, 1987) provides reserves for the initial establishment of seedlings in understorey strata. Light environments of understorey strata are characterised by irradiance levels of 0.4 to 3% of full sunlight (Björkman and Ludlow 1972; Pearcy 1983; Chazdon and Fletcher 1984). Plants permanently occupying this niche are extremely shade tolerant (light saturation level for $A \approx 3$ to 4 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$; A at saturating PPFs from 3 to 4 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$), and are able to regularly flower and fruit despite minimal interception of light (Chazdon 1986). As the Q_0 for avocado is ca. 30 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$, PPFs penetrating to the understorey strata would preclude growth once seed reserves were depleted.

The plasticity of the light response of avocado is more typical of small gap colonisers which are usually deciduous trees or those evergreens with leaves which live for less than a year (Grubb 1992). While tolerant of shade, for these species A at saturating PPFs is $\geq 10 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$, allowing moderate to fast growth and capture of space when opportunities arise (Langenheim *et al.* 1984; Oberbauer and Strain 1984; Pearcy and Francheschi 1986; Denslow 1987). As rainforest environments are at least in part resource-rich, trees grow rapidly in the vegetative phase and usually produce several cohorts of leaves in a season. Leaf redundancy is rapid as they quickly become shaded by successive cohorts, senesce and fall to the forest floor. Thus, plant investment in short-lived leaves is returned by higher A when compared with the “true” evergreen species with extended longevity of leaves (Chabot and Hicks 1982), e.g. 2 years for citrus; several years for mango (Erickson 1968; Verheij 1991). The relatively high A_{max} of avocado compared with other rainforest species (although A_{max} for the pioneer species *Ochroma lagopus* (balsa) is $\approx 27 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$; Whitmore 1990), is likely due to its spatial and temporal organisation of reproductive and vegetative sinks (described in this thesis) and its comparatively large investment into high-energy fruit (Wolstenholme 1987).

CONCLUSION

In the past 20 years or so, probably the most important limiting factor to higher avocado yields was *Phytophthora* root rot. The application of fungicide technology based on trunk injection of phosphonates has largely removed this potent threat. Yet even in this instance the principles on tree manipulation developed in pheno/physiological modelling were found to be eminently relevant for strategic timing of fungicide injections. This thesis has mainly highlighted the horticultural aspects of tree manipulation, and in several respects the research represents pioneering work on this often recalcitrant crop. The payoff in funds invested has undoubtedly been high, but much remains to be done.

The application of pheno\physiological principles developed throughout this research program and implemented as management strategies, have demonstrated the ability to sustain orchard yields $> 20 \text{ t ha}^{-1}$ for an extended number of years in subtropical environments. This level of production is double that of the current Australian industry average for bearing avocado orchards and indicates opportunities for substantial improvement for the majority of growers. However, it is acknowledged that in some areas of Australia more severe environmental conditions will limit this yield potential. Despite this considerable improvement in crop production, sustainable yield remains lower than the potential target yield of ca. 32 t ha^{-1} estimated for avocados by Wolstenholme (1986, 1987).

It is the author's opinion that current sustainable production of 23 to 25 t ha^{-1} has reached the genetic limit of cultivars and rootstocks currently available to the industry. Significant improvement in yield is likely from breeding new cultivars and the development of superior rootstocks and rootstock/cultivar combinations. By their nature, breeding programs are high risk and long-term in respect to committed resources. Future developments in biotechnology areas may improve the potential for results, but to date no serious investment has been made in this field for avocados. In the short-term, rootstock improvement offers the greatest opportunities for improving tree performance (Whiley 1991) and this neglected area deserves an investment of resources so that its potential may be realised.