

STRATEGIES FOR MAXIMISING AVOCADO PRODUCTIVITY: AN OVERVIEW

B.N. Wolstenholme

Department of Horticultural Science University of Natal Pietermaritzburg,
South Africa

A.W. Whiley

Department of Primary Industries Queensland
Maroochy Horticultural Research Station
Nambour, Queensland, Australia

Summary

The extent of the avocado productivity problem varies regionally. In spite of greater tree vigour in the warm, humid subtropics, sustained yields of 20 to 25 t ha⁻¹ have been achieved. More typical yields in the cooler, semi-arid winter rainfall areas are 8 to 12 t ha⁻¹. A target sustainable yield with current germplasm of 30 t ha⁻¹ still appears realistic. The majority of growers average less than half of these yields.

Causes of low yield are both genetic and climatic, with the latter recently quantified in Israel. A concerted breeding and selection program is necessary to further modify residual evolutionary adaptations which are counter-productive in orchards. Scion requirements should emphasise yield, fruit quality, tree complexity and semi-dwarf growth; rootstocks must have both disease tolerance and impart favourable horticultural characteristics. A growing perception that phosphonate trunk injection technology is less effective than when initially developed requires investigation. ,

The expanded pheno-physiological growth model of Whiley (1994) sheds new light on productivity constraints in the humid subtropics. Fruit set can be limited not only by temperature and moisture stress, but also by reduced photosynthetic efficiency of over-wintered leaves, and attrition of feeder roots during flowering. Stored carbohydrates become increasingly important as environmental stress increases. Opportunities for managing shoot vigour at critical periods, optimising balanced root, shoot and fruit relationships are discussed. Evidence of cross-pollination benefits must be reconciled with orchard practicalities.

Orchard design and canopy management strategies remain controversial. Initial high density plantings (200 - 800 tree ha⁻¹) are generally accepted, usually with one or two orchard thinnings at onset of crowding. Staghoming, hedgerowing and tree containment by pruning or chemicals, to optimise light interception and canopy bearing throughout the productive life of the orchard, would benefit from ecophysiological research. Guidelines from deciduous orchards are mentioned for possible relevance to avocado.

Additional Index Words: *Persea americana* Mill., breeding, pheno-physiological model, canopy management.

1. Introduction

Globally, avocado production is dominated by Mexico and tropical countries. Its coming-of-age as a world fruit crop has however, been facilitated by research conducted in subtropical countries or areas, notably California and Israel (relatively cool, semi-arid Mediterranean climates), and South Africa and Australia (warm, humid, summer rainfall subtropics), although the research base in many other countries is expanding rapidly. This overview of productivity constraints and strategies to maximise productivity will have a subtropical, southern hemisphere bias, but the main principles should be globally applicable with modification.

2. The avocado yield problem

The avocado yield problem was discussed in our paper at the Second World Avocado Congress (Wolstenholme and Wilely, 1992). National average yields are in the 4-8t ha⁻¹ range, depending on the proportion of young trees. Good growers in the cool, semi-arid, winter-rainfall subtropics can average 8-12 t ha⁻¹, or 12-16 t ha⁻¹ in the warmer, humid summer-rainfall subtropics. Respective averages for best growers are 12-15 and 20-25 t ha⁻¹. Our target yield of >30t ha⁻¹ still appears realistic, but probably unattainable on a large scale over a period of years with current germplasm and technology.

2.1 Main reasons for low productivity

2.1.1 Evolutionary adaptive strategies

The avocado tree (Guatemalan and Mexican subspecies or ecological races, Bergh and Ellstrand, 1986) originated in subtropical to highland tropical mesic rainforests of Mexico and Guatemala. It has a long history of use and the fruit has undoubtedly been vastly improved by indigenous selection. However, according to modern criteria cultivar selection is still in its infancy and the tree has many residual features that are counter-productive to the requirements of a modern orchard.

This potentially large canopy tree has ecophysiological features suggesting a late successional to climax adaptive strategy. It can be characterised as a small gap species, shade-tolerant in the juvenile phase (Wilely, 1994). The vegetative bias, antagonistic to fruiting, is still evident in vigorous cultivars on invigorating rootstocks under favourable growing conditions. Rhythmic growth in two or three flushes is associated with surprisingly short-lived leaves which are readily abscised under stress (including shade). Normally a wintergreen tree, it can become deciduous or semi-deciduous during flowering under conditions of water, cold, overbearing, salinity, or Phytophthora-induced stress (Wilely and Schaffer, 1994). The shallow, fibrous but desiccation-sensitive feeder root system, with its high oxygen requirement and intolerance of saturated soils, is an adaptation to "litter feeding" on the forest floor.

Associated with these factors is an energy-expensive, oil-storing fruit with a large carbohydrate-rich seed, collectively imposing a relatively low ceiling on yield (Wolstenholme, 1986, 1987). In its native habitat, fruiting was much delayed and irregular. In response to moderate cold and drought stress, accompanied by high (for an evergreen tree) starch storage in the above-ground structural framework, heavy flowering led to strong crop load adjustment through spring and summer fruit drop episodes, so that ultimate fruit set is only about 0.001% of the flowers produced. A heavy crop however severely depletes stored carbohydrates and sets the scene for alternate bearing (Scholefield et al., 1985).

2.1.2 Tree architecture and branching pattern

The main features of Rauh's growth model (Halle et al., 1978) affecting avocado productivity relate to the potential for vigorous growth which may compete with reproductive growth at critical periods. The model specifies that although flowering is on the periphery of the tree from over-wintered shoots, it is actually pseudoterminal, as a terminal bud can give rise to competitive vegetative growth in the spring flush. Such indeterminate flowering panicles certainly predominate in existing cultivars (Thorp et al., 1994; Whiley, 1994) but determinate, entirely reproductive flowering panicles are also present. The required partial separation of vegetative and reproductive growth peaks, to reduce competition for resources therefore varies among shoots within the tree (Verheij, 1986).

Spatial separation will be absent in indeterminate, and partial in determinate inflorescences. Temporal separation will be minimal in indeterminate, and substantial in determinate inflorescences. It is widely accepted that fruit set and retention is lower in indeterminate inflorescences (Blumenfeld et al., 1983; Whiley, 1994), especially in conditions promoting spring flush vigour. Whiley (1990) established that the sink- source transition in developing spring shoots takes ca 27 days during which most of the initially set fruit drops. The fact that determinate flowering shoots set and hold more fruit, and also produce larger fruit (Whiley, 1994), suggests that competition for both current and stored carbon is substantial, and that determinate shoots are advantaged. The tree architecture studies of Thorp and Sedgley (1993) and Thorp et al. (1994), while contributing to our understanding of avocado branching patterns, need to be related to the yield potential of different cultivars under varying environmental conditions.

2.1.3 Environmental constraints

The recent study of Lomas and Zamet (1994) has highlighted climatic parameters limiting Israeli national yields over a 27 year period, when the mean yield was $6.8 \pm 2.5 \text{ t ha}^{-1}$ with an annual C.V. of 36.7%, and a range from 1.4 to 12.9 t ha^{-1} . Seasonal (winter) rainfall reduced yield ($r^2 = 0.43$) by an average $7 \text{ kg ha}^{-1} \text{ mm}^{-1}$ rainfall, probably through poor soil aeration and root function, lower soil temperature, changed soil nitrogen cycle, and alternative flowers (weeds etc) during pollination. They also noted that frost (over 6 years), and especially the lowest minimum temperature being below -1.5°C , strongly reduced yield ($\pm 2.4 \text{ t ha}^{-1} \text{ }^\circ\text{C}^{-1}$ below -1.5°C). Other factors reducing yield were low spring (flowering) temperatures (five night av. min. $<10^\circ\text{C}$); and low soil temperature (low root activity?) in March (September in SH) before peak flowering. A high spring heat stress index (maximum temperature $>33^\circ\text{C}$) and high vapour pressure deficit during fruit set were also detrimental.

2.1.4 Other factors

Historically, avocado trees in their native habitat did not have to cope with *Phytophthora cinnamomi*, the root rot fungus. The introduction of this pathogen into nurseries and orchards proved to be devastating to tree health and productivity into the late 1970's. The development of trunk injection technology of phosphonate fungicide has greatly reduced the impact of *Phytophthora* root rot (Darvas and Bezuidenhout, 1987; Pegg et al., 1987; Whiley et al., 1995). However, more recently there are growing perceptions that it is becoming less effective.

There is no doubt that other diseases (sunblotch viroid, *Verticillium* wilt, fruit diseases) and a range of insect pests have the potential to limit production, but control is relatively simple.

Similarly, poor technology and understanding of the needs of the crop along with extreme climatic events including hail, wind and drought, contribute to low yields.

3. Ecophysiology and pheno-physiology: widening the knowledge base'

In the past five years, our knowledge of avocado ecophysiology has increased dramatically, as exemplified in the review by Whiley and Schaffer (1994). The original phenological growth model of Whiley et al. (1988), which assisted in guiding research, extension and orchard management, has been expanded into a pheno-physiological model (Whiley, 1994; Whiley et al., 1995), which has already led to innovative new manipulatory strategies to increase productivity.

Modern portable instrumentation allows us to report on carbon dioxide assimilation (A) for single, well-lit avocado leaves with confidence (Whiley, 1994; Whiley and Schaffer, 1994). Full leaf expansion occurs ca 30 days after bud-break, with sink-source *transition* at 80% leaf expansion (24 days). Leaves reach A_{\max} at ca 50 days. Orchard trees in warm, mesic climates on good soils have a leaf A_{\max} , of $17 \mu\text{mol m}^{-2} \text{s}^{-1}$, which is in the high range compared with other fruit trees. Cold temperatures ($< 10^{\circ}\text{C}$) result in photoinhibition and some loss of chlorophyll, with A_{\max} dropping to $10 \mu\text{mol m}^{-2} \text{s}^{-1}$. Light compensation point is $30 \mu\text{mol m}^{-2} \text{s}^{-1}$, indicative of shade tolerance, while light saturation of A occurs at $1270 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ in (ca 60% of full sunlight). However, these data are preliminary and there is a need to develop whole tree models to provide insights into how best orchard canopies can be developed and maintained for optimum production.

For a 'Hass' shoot in the spring flush, Wiley (1994) found that the sink phase of leaves lasted 42 days, during which 86% loss of initially set fruits occurred. The carbon budget of whole avocado trees under orchard conditions has not been studied. The best integrator available is the seasonal starch cycle, popularised by Scholefield et al. (1985) for a cold, stressful climate where avocado trees are less vigorous, accumulate higher starch levels, are semi-deciduous, and where fruit set is more dependent on stored carbohydrate than current photosynthate than in the humid, warm subtropics (Whiley, 1994). There is abundant evidence that excessive crop load, long delayed harvest, climatic upsets and poor management can lead to severe carbohydrate depletion and initiate alternate bearing, which is then difficult to control unless drastic measures are taken (eg. pruning, fruit thinning) (Whiley, 1994).

4. Opportunities for orchard and tree manipulation

4.1 Pollination, interplanting

The alternating (complementary) synchronous dichogamy (protogyny) of avocado flowering appears to be an outcrossing mechanism, albeit with a fail-safe back-up (Gazit, 1977; Davenport, 1986). Numerous studies have shown that environmental factors modify flower opening. Low temperatures disrupt group '13' cultivars ('Fuerte', 'Sharwil', 'Ettinger') more than group 'A' cultivars ('Hass', 'Gwen', 'Pinkerton', 'Reed') (Sedgley, 1977; Whiley and Winston, 1987), partly due to slower pollen tube growth (Sedgley and Grant, 1983). The demise of 'Fuerte' in California was mainly due to low yield under cool flowering conditions. Whiley and Winston (1987) were able to predict the performance of 'A' and '13' group cultivars in different areas of Australia, based on mean temperatures during flowering. It is now accepted in the subtropics that group 'A' cultivars will yield better in cool climates, and that 'Fuerte', 'Sharwil' etc only achieve high yields in warm (spring) environments. Lahav and Gazit (1994) point out the significant

preference for group 'A' cultivars in California, and that among the 12 new semi-commercial cultivars selected in Israel in the last decade, only two (both late-flowering) belong to the B group. The ability to delay flowering of group '13' cvs into a warmer time slot (perhaps through a rootstock effect), may significantly increase their yield potential.

The necessity for interplanting cultivars of complementary groups and overlapping flowering times is still equivocal (Davenport and Lahav, 1992). The issue has been debated over several decades (Bergh 1977; Gazit and Gafni, 1986; Davenport et al., 1994). The work of Degani et al. (1989) with genetic markers shows that 'Ettinger' (B) is a good cross-pollinator of 'Hass' (A), and that under environmental stress and vegetative growth competition it is the hybrid progeny rather than the self-pollinated fruitlets which develop the greater sink strength to survive the massive abscission. By implication and common observation, solid blocks of single cultivars (selfs) are more likely to yield adequately under low stress conditions at fruit set. Lahav and Gazit (1994) summarise succinctly: "Interplanting cultivars that belong to complementary flowering groups and bloom at the same time tends to increase pollination rates and promote cross-pollination and hence fruit set; yields are usually improved". Widespread adoption of interplanting is prejudiced by practical issues such as the need for closeness of pollinator and pollinated, their often incompatible management and requirements; and also by insufficient research on the best pollinators.

4.2 Ameliorating fruit set bottlenecks

Comprehensive pheno-physiological studies in the warm and cool humid subtropics of S.E. Queensland by Whiley (1994) have highlighted a number of resource limitations during the critical fruit set period. The first comprehensive rhizotron studies identified major attrition of feeder roots from flowering until spring flush maturity. This means reduced water and mineral uptake, and probably also reduced root synthesis of cytokinins and gibberellins at a time of increased demand. Over-wintered, partially photoinhibited leaves have reduced carbon assimilation potential, while starch reserves decline precipitously during early fruit ontogeny. Untimely and over-vigorous spring flushing especially from indeterminate flowering shoots, aggravates the drain on resources.

That such a situation is amenable to sophisticated manipulation was shown by Whiley (1994). Pre-anthesis soil nitrogen application successfully increased 'Hass' leaf N, chlorophyll concentration and A during fruit set and early ontogeny. The subsequent and potentially competitive spring shoot growth was controlled by a mid-anthesis foliar paclobutrazol application. Preliminary results showed a substantial increase in yield over two seasons. The importance of retaining over-wintered leaves until the sink:source transition of the new cohort of spring flush leaves was also demonstrated.

4.3 Manipulation of vegetative-reproductive competition

That untimely and over-vigorous spring flushing can be detrimental to avocado fruit set is overwhelmingly accepted (Blumenfeld et al., 1983; Whiley and Schaffer, 1994). Such vegetative competition has been reduced by decreased or delayed N fertilisation and the strategic use of paclobutrazol (Köhne and Kremer-Köhne, 1987; Whiley et al., 1991). Excessive retardation of the spring flush is counter-productive - these leaves are necessary to help meet the needs of developing fruits (Cutting and Bower, 1990; Wolstenholme et al., 1990). Similarly, encouragement of the summer shoot flush still seems beneficial, in view of the high carbon demand of fruits, the short longevity of leaves (especially stressed leaves), the need for starch

accumulation during autumn and winter; the importance of root growth during autumn and winter, and finally the necessity for a new cohort of more efficient leaves to help cope with the demands of flowering and fruit set the following spring.

Girdling (ringing, scoring, cincturing) is an ancient manipulatory tool which may be coming back into fashion in the "clean and green" modern world. It has been researched in Israel, Australia and recently in other countries, as a means of inducing precocity in over-vigorous trees, increasing yield, inducing a "death crop" in trees before tree thinning, and possibly increasing fruit size. Effects vary according to the size of the girdle, the proportion of the tree affected, the timing of the treatment, the health of the tree and duration of treatment (Lahav et al., 1971; Trochoulas and O'Neill, 1976). It can be a drastic treatment affecting not only carbohydrate apportionment but also plant growth substances, and some degree of root starvation is inevitable. It needs to be used judiciously and with a clear understanding of tree responses.

4.4 Canopy light interception, utilisation and management

It stands to reason that economic yield is a function not only of total canopy net carbon assimilation, on a per ha basis, but also on the apportionment of that fixed carbon among competing sinks, and particularly the relative share to the economic end product, the fruits. Light and photosynthesis relationships of single well-lit leaves differ dramatically from those of a full canopy, where most leaves are shaded. Givnish (1988) notes the importance of the costs of producing and maintaining leaves and other sinks, and of energetic trade-offs. He notes that in *Liriodendron* trees the traditional leaf light compensation point (CP) has little meaning for net carbon gain. The effective "ecological compensation point" takes into account additional costs, e.g. night leaf respiration, and construction of leaves and the associated support and root tissue. Thus in a single leaf the light CP was $13 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$; in a 1 m tall tree 153 and in a 30 m tall tree $1350 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ ($\pm 75\%$ of full sunlight), i.e. the light level at which total leaf benefits and costs just balance.

We have no comparable estimates for avocado, and the questions of spacing, crowding, canopy surface and bearing volumes, light requirements for seasonal carbon gain and flower initiation remain open to innovative research. Jackson's (1985) injunction to quickly achieve a yield ceiling is especially pertinent - the logic of discounted cash flow analysis makes early yield more valuable economically than later yield with high real interest rates, i.e. precocity of yield. South African researchers and growers have perhaps been the most adventurous in translating this concept into high density plantings, especially for 'Hass'. Köhne and Kremer-Köhne (1990) clearly show the benefits of close initial spacing (400-800 trees ha^{-1}) and precocity-inducing rootstocks ('Duke 7' vs 'Martin Grande') on cumulative yield and recovery of financial investment, at least where land is expensive and nursery trees relatively cheap. Tree crowding is delayed by growth retardants, and early fruiting, but initial tree thinning may be necessary in the fifth year, and a second thinning a few years later, with growth rates of 1 m p.a. possible in the humid subtropics. Further research on the reasons for consistently high and low yielding trees (Smith and Köhne, 1992; Steyn et al., 1993) will be instructive.

Even with less intensive management, tree crowding is inevitable, with reduction in light interception and loss of yield and fruit quality. Growers respond with a variety of strategies, including chemical priming; staghorning (preferably of orchard blocks rather than alternate rows - a form of orchard renewal or "recycling"); hedgerowing with mechanical pruning devices; and pruning for tree size containment (especially height reduction) and opening up the canopy.

Scientific and economic guidelines are sadly lacking, perhaps because long-lived avocado orchards are a recent luxury (successful control of *Phytophthora*).

Rom (1994) summarises light interception and utilisation guidelines for deciduous tree orchards, discussing concepts of canopy surface area and volume, and their optimum ratio for cumulative yield. The importance of relatively small tree size, and of limiting tree height (also emphasised by Givnish, 1988) are emphasised. The guidelines that tree height should not be more than 1.5 to 2 times the inter-row space (usually 2m) seems particularly important. However we have a long way to go in evergreen fruit tree research.

5. Conclusions

This limited overview has dealt only with certain aspects of the avocado yield problem, and only with subtropical avocados. The problem varies regionally, with higher yield potential (but greater management inputs) in the humid warm subtropics. The current cultivar and rootstock options are very restricted, and national breeding programmes for semi-dwarf scions and rootstocks remain high priorities. Further exploration of the fast disappearing indigenous gene pool in Central America is surely of international concern.

Amongst the most significant advances since the previous World Avocado Congress are the expansion in ecophysiological knowledge, and the development of a pheno-physiological growth model. Sustained yields of above 20 t ha⁻¹ have been shown to be achievable for both 'Hass' and 'Fuerte'. However canopy management research lags sadly. Environmental issues, including rising CO₂ levels associated with global warming, less predictable weather, and "clean and green" resource sustainability, will test us into the next millennium. Improved germplasm, also using the largely unexploited but potentially powerful tool of a range of horticulturally and pathologically superior clonal rootstocks, remain the greatest challenge.

References

- Bergh, B.O., 1977. Factors affecting avocado fruitfulness. In: J.W. Sauls, R.L. Phillips and L.K. Jackson (eds.). Proc. 1st Internat. Trop. Fruit Short Course: The avocado. Univ. of Fla, Gainesville.
- Bergh, B.O., and Ellstrand, N., 1986. Taxonomy of the avocado. Calif Avocado Soc. Yearb. 70: 135-145.
- Blumenfeld, A., Gazit, S., and Argaman, E., 1983. Factors involved in avocado productivity. Special Publ. No. 222. Department of Subtropical Horticulture, Center, Bet-Dagan, Israel. Pp. 84-85.
- Cutting, J.G.M. and Bower, J.P., 1990. Spring vegetative flush removal: The effect on yield, size, fruit mineral composition and quality. S. Afr. Avocado Growers' Assoc Yearb. 13: 33-34.
- Darvas, J.M., and Bezuidenhout, J.J., 1987. Control of *Phytophthora* root rot of avocados by trunk injection. S. Afr. Avocado Growers' Assoc. Yearb. 10: 91-93.
- Davenport, T.L. 1986. Avocado flowering. Hort. Rev. 8: 257-289.
- Davenport, T.L., and Lahav, E., 1992. "Is a pollinator required to maximise avocado production?" Proc. Second World Avocado Congr. II: 667-668.
- Davenport, T.L., Pamitzki, P., Fricke, S., and Hughes, M.S., 1994. Evidence and significance of self-pollination of avocados in Florida. J. Amer. Soc. Hort. Sci. 119: 1200-1207.

- Degani, C., Goldring, A., and Gazit, S., 1989. Pollen parent effect on outcrossing rate in 'Hass' and 'Fuerte' avocado plots during fruit development. *J. Amer. Soc. Hort. Sci.* 114:106-111.
- Gazit, S., and Gafni, E., 1986. Effect of hand pollination with different pollen donors on initial fruit set in avocado. *Israel Agresearch* 1: 3-17.
- Givnish, T.J., 1988. Adaptation to sun and shade: a whole-plant perspective. *Aust. J. Plant Physiol.* 15: 63-93.
- Halld, F., Oldernan, R.A.A., and Ton-dinson, P.B., 1978. Tropical trees and forests: an architectural analysis. Springer-Verlag, Berlin. Pp. 221-228.
- Jackson, J.E., 1985. Future fruit orchard design: Economics and biology. In: Attributes of trees as crop plants. M.G.R. Cannell and J.E. Jackson (eds.). Institute of Terrestrial Ecology, Huntington, U.K.. Pp. 441-59.
- Köhne, J.S., and Kremer-Köhne S., 1987. Vegetative growth and fruit retention in avocado as affected by a new plant growth regulator (paclobutrazol). *S. Afr. Avocado Growers' Assoc. Yearb.* 10: 64-66.
- Köhne, J.S., and Kremer-Köhne S., 1990. Results of a high density planting. *S. Afr. Avocado Growers' Assoc. Yearb.* 13: 31-32.
- Lahav, E., and Gazit, S., 1994. World listing of avocado cultivars according to flowering type. *Fruits* 49: 299-313.
- Lahav, E., Gefen, B., and Zamet, D., 1971. The effect of girdling on the productivity of the avocado. *J. Amer. Soc. Hort. Sci.* 96: 396-398.
- Lomas, J., and Zamet, D., 1994. Longterm analysis and modelling of agroclimatic effects on national yields in Israel. *Agric. For. Meteor.* 71: 315-336.
- Pegg, K.G., Whiley, A.W., Langdon, P.W., and Saranah, J.B., 1987. Comparison of phosetyl-Al, phosphorous acid and metalaxyl for the long-term control of phytophthora root rot of avocado. *Aust. J. Exp. Agri.* 27: 471-474.
- Rom, C.R., 1994. Pomology 10 1, balancing growth and cropping: which comes first, the canopy or the crop? *Compact Fruit Tree* 27: 53-59.
- Scholefield, P.B., Sedgley, M., and Alexander, D.McE., 1985. Carbohydrate cycling in relation to shoot growth, floral initiation and development and yield in the avocado. *Scientia Hort.* 25: 99-110.
- Sedgley, M., 1977. Flowering, pollination and fruit set of avocado. *S. Afr. Avocado Growers' Assoc. Yearb.* 10: 42-43.
- Sedgley, M., and Grant, W.J.R., 1983. Effect of low temperatures during flowering on floral cycle and pollen tube growth in nine avocado cultivars. *Scientia Hort.* 18: 207- 213.
- Smith, D.G., and Köhne J.S., 1992. Production potential of Fuerte on seedling rootstocks. *S. Afr. Avocado Growers' Assoc. Yearb.* 15: 83-85.
- Steyn, E.M.A., Robbertse, P.J., and Smith, D., 1993. An anatomical study of ovary-to-cuke development in consistently low-producing trees of the 'Fuerte' avocado (*Persea americana* Mill.) with special reference to seed abortion. *Sex. Pl. Reprod.* 6: 87-97.
- Thorp, T.G., and Sedgley, M., 1993. Architectural analysis of tree form in a range of avocado cultivars. *Scientia Hort.* 53: 85-98.
- Thorp, T.G., Aspinall, D., and Sedgley, M., 1994. Preformation of node number in vegetative and reproductive proleptic shoot modules of *Persea* (Lauraceae). *Ann. Bot* 73: 13-22.
- Trochoulis, T., and O'Neill, G.H., 1976. Girdling of 'Fuerte' avocado in subtropical Australia. *Scientia Hort.* 5: 239-242.
- Verheij, E.W.M., 1986. Towards a classification of tropical tree fruits. *Acta Hort.* 175: 137-150.

- Whiley, A.W., 1990. CO₂ assimilation of developing fruiting shoots of cv. Hass avocado (*Persea americana* Mill.) - A preliminary report S. Afr. Avocado Growers' Assoc. Yearb. 13: 28-30.
- Whiley, A.W., 1994. Ecophysiological studies and tree manipulation for maximisation of yield potential in avocado (*Persea americana* Mill.). Unpubl. PhD Thesis, Dept. Hort. Sci., Univ. Natal, Pietermaritzburg.
- Whiley, A.W., and Schaffer, B., 1994. Avocado. In: CRC Handbook of environmental physiology of fruit crops. Vol. 2, Subtropical and tropical crops. B. Schaffer and P.C. Anderson (eds.). CRC Press Inc., Boca Raton. Pp. 3-35.
- Whiley, A.W., and Winston, E.C., 1987. Effect of temperature at flowering on varietal productivity in some avocado growing areas in Australia. S. Afr. Avocado Growers' Assoc. Yearb. 10: 45-47.
- Whiley, A.W., Saranah, J.B., Cull, B.W., and Pegg, K.G., 1988. Manage avocado tree growth cycles for productivity gains. Qld Agric. J. 114: 29-36.
- Whiley, A.W., Saranah, J.B., Wolstenholme, B.N., and Rasmussen, T.S., 1991. Use of paclobutrazol sprays at mid-anthesis for increasing fruit size and yield of avocado (*Persea americana* Mill. cv. Hass). J. Hort. Sci. 66: 593-600.
- Whiley, A.W., Hargreaves, P.A., Pegg, K.G., Doogan, V.J., Ruddle, L.J., Saranah, J.B., and Langdon, P.W., 1995. Changing sink strengths influence translocation of phosphonate in avocado (*Persea americana* Mill.) trees. Aust. J. Agri. Res. 46: 1079- 1090.
- Wolstenholme, B.N., 1986. Energy costs of fruiting as a yield-limiting factor with special reference to avocado. Acta Hort. 175: 121-126.
- Wolstenholme, B.N., 1987. Theoretical and applied aspects of avocado yield as affected by energy budgets and carbon partitioning. S. Afr. Avocado Growers' Assoc. Yearb. 10: 58-61.
- Wolstenholme, B.N., and Whiley, A.W., 1992. Requirements for improved fruiting efficiency in the avocado tree. Proc. Second World Avocado Congr. 1: 161-167.
- Wolstenholme, B.N., Whiley, A.W., and Saranah, J.B., 1990. Manipulating vegetative:reproductive growth in avocado (*Persea americana* Mill.) with paclobutrazol foliar sprays. Scientia Hort. 41: 315-327.