

AV033

**The relationship between carbohydrate
levels and productivity in the avocado and
impact of management practices**

**A Wiley
Queensland Department of Primary
Industries**



Know-how for Horticulture™

AV033

This report is published by the Horticultural Research and Development Corporation to pass on information concerning horticultural research and development undertaken for the Avocado industry.

The research contained in this report was funded by the Horticultural Research and Development Corporation with the financial support of the Avocado industry.

All expressions of opinion are not to be regarded as expressing the opinion of the Horticultural Research and Development Corporation or any authority of the Australian Government.

The Corporation and the Australian Government accept no responsibility for any of the opinions or the accuracy of the information contained in this Report and readers should rely upon their own inquiries in making decisions concerning their own interests.

Cover Price \$20.00

HRDC ISBN 1 86423 187 4

Published and Distributed by:



Horticultural Research and Development Corporation
Level 6
7 Merriwa Street
Gordon NSW 2072

Telephone: (02) 418 2200
Fax: (02) 418 1352

© Copyright 1996

Final Report



The relationship between carbohydrate levels and productivity in the avocado and impact of management practices, particularly time of harvest

A W Whiley¹, J.B. Saranah¹ and T.S. Rasmussen²

¹ Maroochy Horticultural Research Station, Department of Primary Industries Queensland, PO Box 5083 SCMC, Nambour 4560, Australia

² Agricultural Chemistry, Department of Primary Industries Queensland, Meiers Road, Indooroopilly 4068, Australia

A Department of Primary Industries Queensland project with additional financial support from the Australian Avocado Growers Federation, the Horticultural Research and Development Corporation, Queensland Fruit and Vegetable Growers and the Rural Industries Research and Development Corporation



Industry Summary

This report covers two areas of closely aligned research which have been funded in part by the Avocado industry and are:

- Relationship between carbohydrate levels and productivity in the avocado and impact of management practices, particularly time of harvest; and
- Root growth studies in avocado trees.

The 'Time of Harvest' study was carried out with early ('Fuerte') and late ('Hass') maturing cultivars growing in subtropical environments in S.E. Queensland. With 'Fuerte' treatments were imposed on the same trees for 6 consecutive seasons. Although there were seasonal changes in the levels of storage carbohydrate (starch) concentrations in the tissues of the trees there was no predictable relationship between starch and subsequent yield. Early harvesting of all fruit from trees (either 21% or 24% dry matter) gave the highest average yield over the six years of the experiment (21.5 t/ha/yr). Delaying harvest of all fruit until 30% dry matter was accumulated reduced average yield by 26% and caused a strong biennial bearing pattern to develop. Split harvesting of fruit at 21 or 24% dry matter with the rest of the crop at 30% dry matter reduced yield by 12.5% and only had a minimal effect on biennial cropping patterns. Split harvesting is the most practical for larger production units however, harvesting strategies will need to be formulated with consideration of market price. Delayed harvesting also increased mean fruit size in most years of the study.

There were two separate shorter-term studies carried out with 'Hass'. In the first study alternate bearing was already entrenched due to a previous severe hail storm. This biennial cycle was not broken by early harvesting of fruit (24% dry matter). In the second study with 'Hass' early harvesting of fruit (24% dry matter) sustained the highest yield (18.3 t/ha/yr) while later harvesting reduced production by about 20%. A biennial bearing cycle developed when fruit was harvested late (35%) which is not an uncommon practice in some production areas. Fruit size also increased when harvesting was delayed. In both studies either trunk or shoot starch concentrations were directly related to the subsequent yield and this relationship has potential to be used in a crop prediction model.

The results from these time of harvest studies will be incorporated into the AVOMAN software.

Root and whole tree studies clearly demonstrated that the rootstock/scion combinations have different patterns of starch accumulation in various tissues in trees which may account for the differences in tree performance. The rootstock/scion combination which accumulated high starch concentrations in the trunk of the scion ('Hass' on clonal 'Velvick') had greater production efficiency than the combination which accumulated high starch concentrations in the roots ('Hass' on seedling 'Velvick'). This research has given a new insight into the manipulation of avocado trees by the choice of rootstocks and indicates that rootstock development offers opportunities for improving tree performance. This neglected area deserves an investment of resources so that its potential may be realised.

Technical summary

Effects of delayed harvest were investigated in 'Fuerte' avocado over six consecutive seasons at Childers, S.E. Queensland, a warm subtropical environment conducive to high mean yields exceeding 20 t ha^{-1} . Early harvesting at 21 and 24% fruit flesh dry matter (DM) resulted in highest cumulative average yield ($21.5 \text{ t ha}^{-1} \text{ yr}^{-1}$). A harvest delay of ca. two months, until flesh D.M. was 30%, reduced average yield by 26 % and initiated an alternate bearing cycle. Early harvest of half the crop and late harvest of the other half did not significantly reduce yield. Trunk and bearing shoot wood starch concentrations fluctuated seasonally but could not be related to harvest treatment. Late harvest led to significantly larger fruit in three of the six seasons.

Effects of early and delayed harvest were investigated in 'Hass' avocado, at Childers a slightly suboptimal (too warm) site (4 seasons), and at Maleny, a close to ideal cool mesic site (3 seasons) in subtropical S.E. Queensland. Early harvesting at 25 to 30% flesh dry matter (DM) sustained high productivity (especially at the cooler site), but a delayed harvest up to 4 months later at 35% flesh DM eventually depressed yield (at Childers) and precipitated alternate bearing. Split harvests (early and late) were less detrimental to sustainability of high yields ($> 20 \text{ t ha}^{-1}$). Where alternate bearing was already entrenched at the start of the experiment at the cooler site, early harvest was insufficient to break this pattern. Starch cycling in trunk wood and new shoots followed predictable seasonal patterns, and peak concentrations were reduced by heavy fruiting. However, relatively low avocado yields are more likely due to other environmental and resource constraints at critical phenological growth stages.

The phenological growth model for avocado cv. Fuerte of Whiley *et al.* (1988) has been internationally accepted as a basis for understanding growth rhythms and guiding research and extension. However, it is based on growth measurements and is qualitative in scope and applicability. We report on detailed quantitative research conducted since 1988 to improve the physiological basis of the model. Root growth studies over 5 seasons in rhizotrons installed in a commercial orchard, using cv. Hass on clonal and seedling 'Velvick' rootstocks, confirmed a late spring/early summer and late summer/autumn peaks of feeder root activity. However, root activity down to 0.85m depth was shown to continue at a high level through winter until anthesis during early spring flowering, when a pronounced die-off of feeder roots occurred. Rootstock differences in growth and in starch concentration were noted, with slight scion:rootstock incompatibility on the clonal rootstock associated with smaller trees and greater fruiting efficiency. Fruiting markedly decreased root growth.

Publication Schedule

- Whiley, A.W., Saranah, J.B. and Rasmussen, T.S. 1990. The relationship between carbohydrate levels and productivity in the avocado and impact of management practices, particularly time of harvest. *Talking Avocados*, May/June, 12. **(Appendix 1)**
- Whiley, A.W., Rasmussen, T.S. and Saranah, J.B. 1992. Effect of time of harvest on fruit size, yield and trunk starch concentrations of Fuerte avocados. *World Avocado Congress II Proceedings*, Orange, California (April 1991). 1, 155-9. **(Appendix 2)**
- Whiley, A.W. and Saranah, J.B. 1992. Managing fruit harvest for sustainable yield. *Proceedings of the AAGF Conference '92 'Management into the future'*, Gold Coast (September 1992). **(Appendix 3)**
- Whiley, A.W. 1994. Ecophysiological studies and tree manipulation for maximisation of yield potential in avocado (*Persea americana* Mill.). Chapters 2 & 6 in a PhD Thesis, Department of Horticultural Science, University of Natal (accepted 30 March 1995).
- Whiley, A.W., Rasmussen, T.S. and Saranah, J.B. 1995. Avocado crop prediction - usefulness and methods. *Proceedings of the AAGF Conference 1985 'The Way Ahead'*. Freemantle, May 1995. **(Appendix 4)**
- Wolstenholme, B.N. and Whiley, A.W. 1995. Prospects for increasing 'Hass' fruit size - a southern hemisphere perspective. *Proceedings of the AAGF Conference 1985 'The Way Ahead'*. Freemantle, May 1995. **(Appendix 5)**
- Whiley, A.W., Rasmussen, T.S., Saranah, J.B. and Wolstenholme, B.N. 1995. Delayed harvest effects fruit size, yield and starch cycling in avocado (*Persea americana* Mill.) in two subtropical environments. I. The early-maturing cv. Fuerte. *Scientia Horticulturae* Manuscript submitted for internal refereeing.
- Whiley, A.W., Rasmussen, T.S., Saranah, J.B. and Wolstenholme, B.N. 1995. Delayed harvest effects fruit size, yield and starch cycling in avocado (*Persea americana* Mill.) in two subtropical environments. II. The late-maturing cv. Hass. *Scientia Horticulturae* Manuscript submitted for internal refereeing.
- Whiley, A.W., Saranah, J.B., Wolstenholme, B.N. and Rasmussen, T.S. 1995. Verification and quantification of a growth model for avocado (*Persea americana* Mill.). I. Root and rootstock components. *Journal of Horticultural Science*. Manuscript submitted for internal refereeing.
- Whiley, A.W., Saranah, J.B., Wolstenholme, B.N. and Rasmussen, T.S. 1995. Verification and quantification of a growth model for avocado (*Persea americana* Mill.). II. Shoot and fruit growth and a synthesis. *Journal of Horticultural Science*. Manuscript submitted for internal refereeing.
- Wolstenholme, B.N. and Whiley, A.W. 1995. Avocado productivity: strategies for balancing growth and cropping. *Proceedings of the World Avocado Congress III*. Tel Aviv, October 1995. Abstract submitted. **Invited paper. (Appendix 6)**
- Whiley, A.W., Saranah, J.B. and Wolstenholme, B.N. 1995. Pheno/physiological modeling in avocado - An aid to research planning. *Proceedings of the World Avocado Congress III*. Tel Aviv, October 1995. Abstract submitted. **(Appendix 7)**

Acknowledgments

We wish to thank Spencer and Lyn Gray of Maleny and John and Jay Dorrian of Childers who provided trees and at considerable personal cost assisted with the collection of data reported for this project. Dr C. Searle and Messrs D.R. Simpson and R.J. Nissen assisted with data collation.

Source: Whiley, A.W. 1994. Ecophysiological studies and tree manipulation for maximisation of yield potential in avocado (*Persea americana* Mill.). Unpublished PhD Thesis, Department of Horticultural Science, University of Natal (accepted 30 March 1995).

Effect of delayed harvest on subsequent yield and fruit size of early ('Fuerte') and late ('Hass') maturing avocado (*Persea americana* Mill.) cultivars

A.W. Whiley¹, J.B. Saranah¹ and T.S. Rasmussen²

¹Maroochy Horticultural Research Station, Department of Primary Industries Queensland, Nambour 4560, Australia

²Agricultural Chemistry, Department of Primary Industries Queensland, Indooroopilly 4068, Australia

Introduction

Competition with other trees in forest stands during evolution has increased the complexity of woody perennials to the extent that they have developed life-cycle strategies which optimise competitive fitness within the plant community (Dickson 1991). The storage of minerals and carbohydrates surplus to current requirements and their remobilisation during periods of critical demand, enhance the tree's competitiveness in terms of growth and reproduction. Avocados have the capacity to store significant quantities of minerals and carbohydrates which are largely recycled during flowering, fruit set and spring growth (Cameron and Borst 1938; Cameron *et al.* 1952; Scholefield *et al.* 1985). While mineral nutrients are essential for vegetative growth, the requirements for avocado fruit development are comparatively small (Wolstenholme 1991). However, there is large investment of "energy" to produce oil-rich fruit with large carbohydrate-rich seeds, compared with sugar-storing species, e.g., apples, citrus, peaches, mangoes (Wolstenholme 1986; 1987). Avocado fruiting therefore places high demand on the carbon-based products of photo-assimilation.

During a current cropping cycle, biotic and abiotic factors can have a substantial impact on tree performance. Biotic factors such as shoot vigour, leaf to fruit ratios and the incidence of pests and diseases (Quinlan and Preston 1971; Chacko *et al.* 1982; Whiley *et al.* 1986), and the environmental variables such as temperature (particularly in relation to critical phenological events), humidity, light, wind and storms (Proctor and Creasey 1971; Sedgley and Annells 1981; Whiley and Winston 1987; Issarakraisila and Considine 1994; Crane *et al.* 1994) all contribute to the quality and quantity of the harvest.

The inability of mature avocado fruit to ripen while attached to the tree (Schroeder 1952) has been widely utilised as a "tree storage" strategy to take advantage of marketing opportunities. As lipids continue to accumulate in fruit well after horticultural maturity (Eaks 1990; Kaiser and Wolstenholme 1994), this practice undoubtedly will have some impact on the total carbon economy of the tree. In some circumstances, delayed harvest of late maturing cultivars such as 'Hass', may result in the tree simultaneously carrying mature fruit while flowering and setting the

following season's crop. In cooler climates where 'Hass' is grown, e.g. California, Israel and New Zealand, simultaneously carrying two seasons crops on trees is a "normal" event and may be the main cause of the pronounced alternate bearing experienced in these countries.

While currently there are no published reports on the long-term effect of delayed harvest of avocado on subsequent productivity, the consequences of this practice have been reported for 'Valencia' orange. This fruit may also be "stored" on trees in cool areas for up to eight months after legal maturity has been reached, with several months overlap of successive crops. The consequences are reduced yields of smaller fruit in subsequent crops, with the likelihood of the onset of alternate bearing (Hilgeman *et al.* 1967; Monselise and Goldschmidt 1982).

Fruit size of avocado is also an important component of yield as premium prices are often paid for larger fruit, and small size can be problematic with some cultivars, e.g. 'Hass' (Lahav and Adato 1990; Köhne 1991; Cutting 1993). This study investigates the impact of delayed harvesting on starch cycling within the tree, and the subsequent effect on fruit size and yield of early and late maturing cultivars growing in Australia.

Materials and Methods

Avocados growing in commercial orchards at Childers (latitude 25°S, altitude 40 m) and Maleny (latitude 26.5°S, altitude 520 m) in S.E. Queensland were used in this study over six seasons from 1988 until 1994. The research was carried out with the two most important avocado cultivars grown in Australia - the early maturing 'Fuerte' and the late maturing 'Hass'. The 'Fuerte' experiment was located at Childers which has a warm, subtropical climate best suited to this cultivar. There were two 'Hass' experiments, one located at Childers and the other at Maleny. The climate at Childers is considered marginally too warm for 'Hass', with small fruit at maturity consequently a serious commercial problem. This cultivar is much more suited for production in the cool, mesic subtropical climate of Maleny. At Childers, seven-year-old 'Fuerte' and 'Hass' trees grafted to seedling Guatemalan rootstock spaced at 9 x 7 and 8 x 6 m respectively, were chosen while at Maleny 10-year-old 'Hass' trees grafted to seedling 'Velvick' spaced at 12 x 8 m were used. The 'Hass' at Maleny had previously been affected by hail and had developed a strong alternate bearing pattern prior to starting the experiment. At each location, fertilisation and pest and disease control were according to recommendations of Whiley *et al.* (1988a) and Banks (1992). Irrigation at Childers was by under-tree sprinklers (two per tree each delivering 14 l hr⁻¹) and was scheduled with tensiometers to supplement rainfall (annual average of 900 mm) while at Maleny trees relied solely on rainfall (annual average of 2000 mm).

Percentage dry mass of fruit flesh was selected as the maturity index for harvest. As maturing avocado fruit maintain a constant relationship between the percentage oil and water in the flesh (Swarts 1976; Lee 1981a; Lee *et al.* 1982), the determination of flesh dry matter is a reliable method of judging maturity with respect to the previously defined oil content standard (Lee 1981b). In Australia and South Africa this (or the reciprocal, flesh moisture percentage) has been commercially utilised for some time for determining minimum fruit maturity standards (Swarts 1978; Brown 1984). In Australia the minimum maturity standard for avocados is 21% dry matter (Brown 1984) though commercially 'Hass' is generally harvested when it reaches 23 to 25% dry matter. In many instances fruit is stored on trees for market opportunities, so that pulp dry matter

may exceed 30 to 35% when harvested. Thus treatments selected spanned those of normal commercial practice and were:

for 'Fuerte'

1. All fruit harvested at 21% dry matter (21%);
2. All fruit harvested at 24% dry matter (24%);
3. Half of the fruit harvested at 21% and half at 30% dry matter (21/30%);
4. Half of the fruit harvested at 24% and half at 30% dry matter (24/30%);
5. All fruit harvested at 30% dry matter (30%); and

for 'Hass'

1. All fruit harvested at 25% dry matter (25%);
2. All fruit harvested at 30% dry matter (30%);
3. Half of the fruit harvested at 25% and half at 35% dry matter (25/35%);
4. Half of the fruit harvested at 30% and half at 35% dry matter (30/35%);
5. All fruit harvested at 35% dry matter (35%).

To determine the correct stage of maturity for harvesting, random fruit samples were periodically collected for pulp dry matter determination. In addition, at harvest pulp dry matter of five fruit from each tree was measured to establish the actual maturity of fruit from each treatment when picked.

Tree phenology was detailed by recording the date of floral bud-break; the duration of anthesis and the periods of active shoot growth. Wood samples were collected from trunks and the most recently produced shoots at regular intervals for starch analyses. Samples of wood were taken from five sites on each tree by first removing a plug of bark and then drilling 40 mm into the trunk with a 9 mm bit. The shavings were collected for analysis. Approximately 6 cm samples were removed from mature summer grown shoots and the leaves discarded. Ten non-fruiting shoots were randomly collected from each tree and sampling continued until the completion of anthesis. Starch was determined by a two stage enzymatic hydrolysis of the starch to glucose and the concentration measured colorimetrically using a coupled glucose oxidase/peroxidase/chromogen system as described by Rasmussen and Henry (1990).

Data from each experiment were analysed by ANOVA, and covariance analysis was used to separate the effect of yield on fruit size. Where applicable, the relationship between trunk starch concentration in July and subsequent yield was established using linear regression analysis (TableCurve™, Jandel Scientific, Calif., USA).

Results

'Fuerte' at Childers

Depending on the year, fruit reached 21% dry matter from late March until mid-April; 24% dry matter from late April until mid-May and 30% dry matter from late May until mid-June (Table 1). All fruit over the duration of the study were harvested within $\pm 1\%$ of the target dry matter for the respective treatments.

Table 1 Maturity of cv. Fuerte fruit at Childers indicated by dry matter at the different times of harvest in 1988 to 1993. Data are the means \pm SE ($n = 5$) from each treatment when harvested at their respective maturity times.

1st Harvest		2nd Harvest		3rd Harvest	
Date	Dry matter (%)	Date	Dry matter (%)	Date	Dry matter (%)
14.04.88	21.5 \pm 0.3	06.05.88	24.6 \pm 0.4	17.06.88	31.1 \pm 0.3
28.03.89	21.1 \pm 0.2	26.04.89	24.9 \pm 0.5	08.06.89	29.8 \pm 0.4
24.04.90	21.4 \pm 0.3	15.05.90	25.4 \pm 0.4	19.06.90	29.7 \pm 0.3
11.04.91	21.7 \pm 0.1	09.05.91	24.8 \pm 0.2	21.05.91	30.4 \pm 0.4
09.04.92	21.2 \pm 0.2	29.04.92	24.6 \pm 0.2	18.06.92	30.6 \pm 0.3
14.04.93	21.7 \pm 0.2	04.05.93	25.7 \pm 0.6	24.05.93	30.0 \pm 0.5

On an annual basis, there was no significant treatment effect on yield except in 1991 where trees that were strip-harvested at 21% and 24% or picked at 24/30%, had significantly higher yield than trees where fruit was harvested at 21/30% or 30% (Fig. 1a). Due to carry-over effects and natural tree to tree variation, it is unusual to demonstrate yield responses from agronomic treatments in tree crops over an annual cycle (Schaffer and Baranowski 1986). In this case significant differences were likely due to pre-conditioning of the trees following the application of treatments over a number of years.

Trunk and shoot starch concentration data have been pooled as there were no significant differences between treatments. The concentration flux of trunk starch over three years was in the order of 5% (from ca. 2 to 7%) (Fig. 1b). Starch levels peaked during each winter and declined after flowering. The lowest trunk starch concentrations were during the summer and autumn of 1990 when trees were carrying their heaviest crop (Figs. 1a & 1b). The seasonal concentration flux of starch in summer grown shoots was higher than in the trunks of trees (ca. 8% varying from < 1% to > 7%) and followed a defined seasonal pattern (Fig. 1b). Peak concentrations of starch accumulated during the autumn/winter period when shoot growth had ceased and the tree was in a relatively quiescent phase (Figs. 1b, 1c & 1d). During the flowering and spring flush periods shoot starch levels dropped rapidly to < 1% by the end of spring.

There were two periods of shoot growth activity in trees during a cropping cycle, viz. in spring and summer (Fig. 1d). Spring shoot growth was synchronised by flowering with most terminals flushing simultaneously in early September. Shoot growth was relatively quiescent after 60 days, followed by more sporadic summer and autumn flush growth from late December through to late April-May when all shoot growth activity ceased.

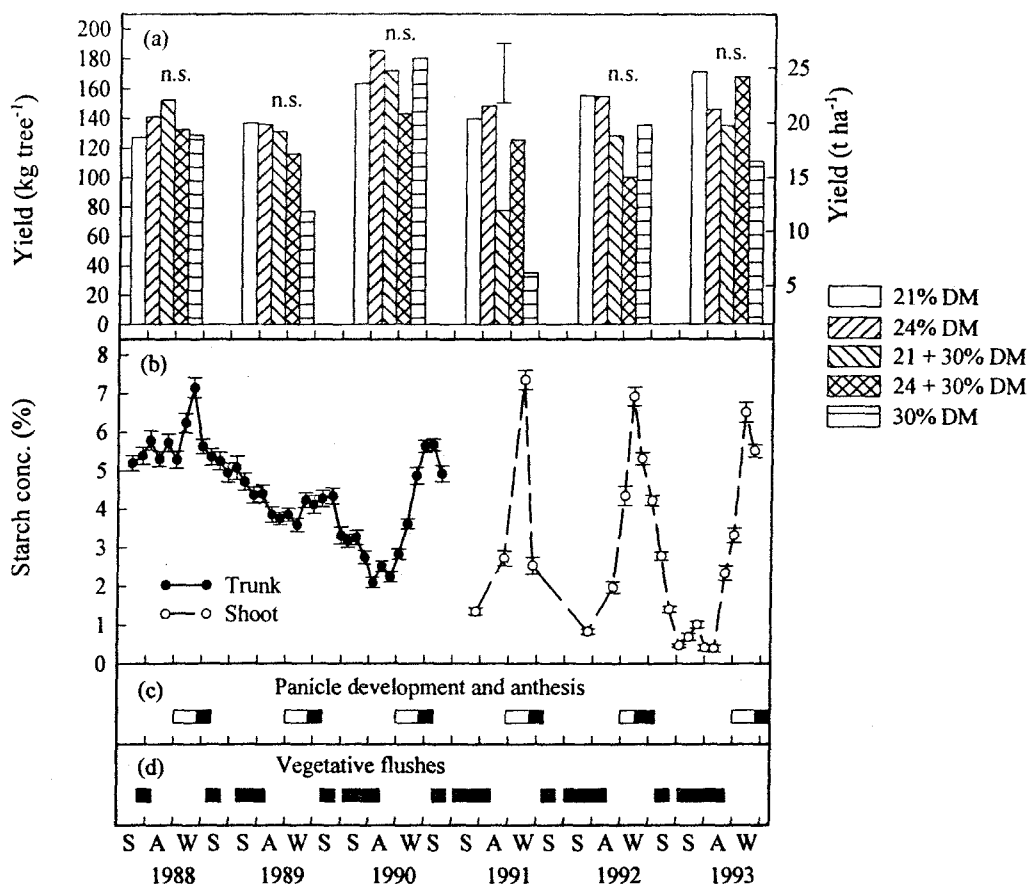


Figure 1 Relationship between yield, seasonal starch concentration flux and tree phenology of cv. Fuerte at Childers where: (a) is yield of fruit which were harvested at different stages of maturity as judged by dry matter (DM), vertical bar indicates LSD ($P \leq 0.05$); (b) is the mean starch concentration of all treatments ($n = 30$), SEs are represented by vertical bars; (c) is periods of panicle growth represented by open horizontal bars, and periods of anthesis represented by closed horizontal bars; (d) is periods of vegetative growth represented by closed horizontal bars.

Mean fruit size was dependent on the time of harvest although significant differences were not apparent for every year of the study (Table 2). In general fruit size increased in those treatments where harvest was delayed, either by removing part of the crop early and the balance later or leaving the fruit until they had reached 30% DM. In three years out of six for example, fruit size of the 21/30% and 30% DM treatments were significantly larger than the 21% DM treatment.

From the second year of the study treatments began to affect the cumulative yield of trees (Fig. 2). Treatments with the earliest harvest times, i.e. 21% and 24% DM, had significantly higher yields than where fruit was allowed to hang until 30% DM. The yield increment increased with time, though the earliest harvested treatments never significantly out-yielded those where fruit were harvested at 21/30% or 24/30% DM. Expressed differently, split harvests did not prejudice cumulative yields over the six seasons.

Table 2 Effect of time of harvest on fruit size of cv Fuerte at Childers. Data are mean values ($n = 6$) of treatments for each year of the study and have been analysed by covariance analysis adjusting for yield. Values in columns not sharing a common letter are significantly different ($P \leq 0.05$) (ANOVA).

Treatments	Fruit mass (g)					
	1988	1989	1990	1991	1992	1993
1. 21% DM	269.3 c	306.6 c	318.9 a	339.4 a	309.3 b	290.9 a
2. 24% DM	309.5 b	313.6 abc	312.3 a	338.2 a	313.0 b	321.8 a
3. 21/30% DM	343.9 a	331.2 ab	329.3 a	330.6 a	343.6 a	334.4 a
4. 24/30% DM	340.2 a	357.9 a	340.6 a	351.8 a	320.2 ab	314.3 a
5. 30% DM	339.8 a	343.0 ab	327.2 a	344.8 a	345.5 a	335.8 a

The effect of the time of harvest on yield becomes more apparent when the annual patterns for each treatment are examined over the duration of the study (Fig. 3). In the first year of this experiment treatments had no significant effect on yield, indicating absence of bias in the experimental population (Fig. 1a). The continued early harvesting of fruit at 21 and 24% for six years resulted in cropping patterns wherein annual variation was insignificant, and limited to fluxes which most likely expressed environmental conditions at critical periods of development (Fig. 3). In contrast, delayed harvesting of fruit, either 50% or all of the crop, resulted in the development of an alternate bearing cycle where the amplitude increased with time. Examination

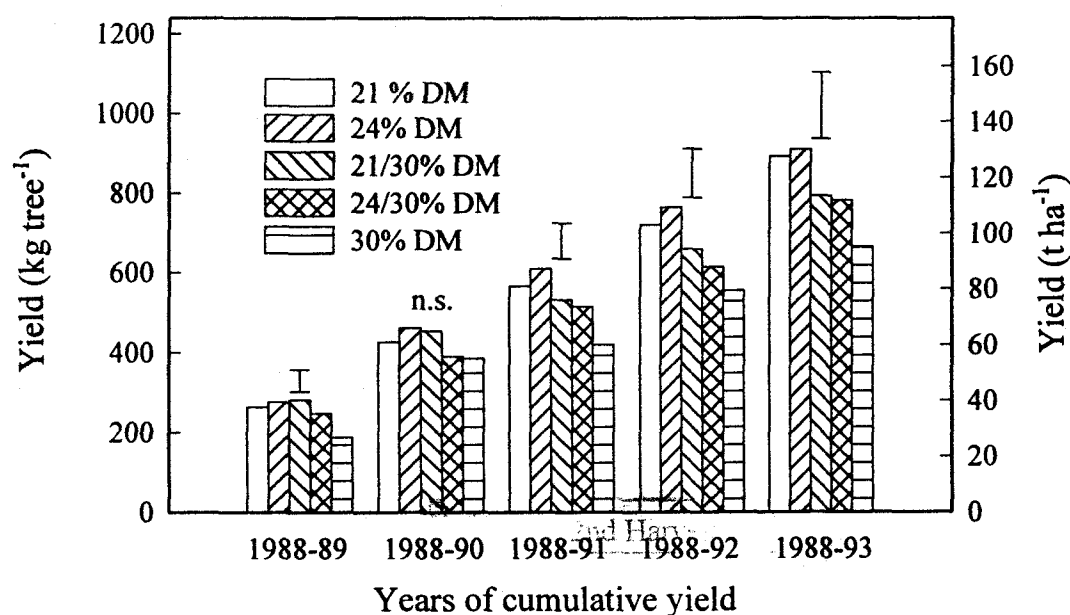


Figure 2 Effect of time of harvest, based on fruit dry matter (DM), on the cumulative yield of cv. Fuerte avocado trees at Childers over six consecutive years. Columns are treatment means ($n = 6$) and vertical bars indicate LSDs ($P \leq 0.05$).

of the data show that the cycle was atypical from 1992 to 1993 where yields for the 21/30% and 30% treatments were almost identical (Fig. 3). This may be explained by the severe tropical storm experienced in the orchard in February 1992 when a significant portion of the crop was lost when fruit was about 60% grown. This effectively amounted to an unscheduled early harvest across all treatments allowing a similar sized crop to be carried the following year.

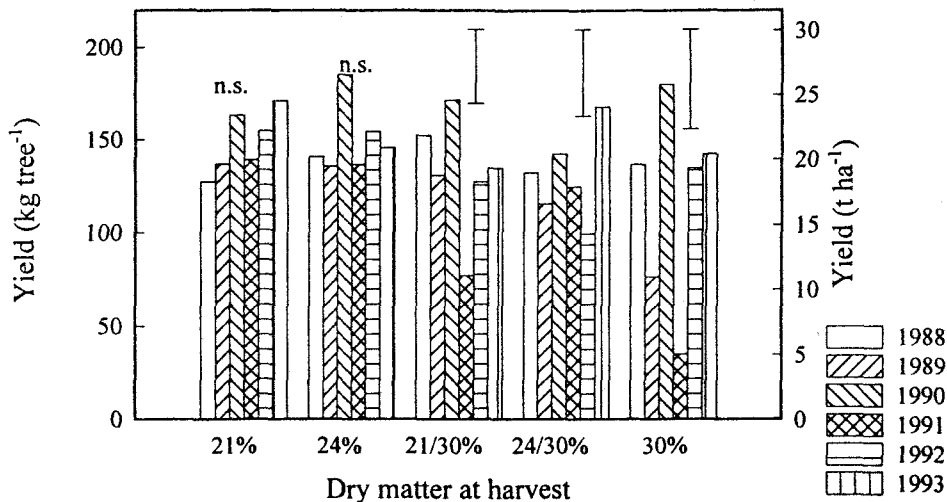


Figure 3 Effect of time of harvest on the sustainability of yield of cv. Fuerte avocado trees at Childers over six consecutive years. Columns are mean values ($n = 6$) and vertical bars indicate LSDs ($P \leq 0.05$).

'Hass' at Childers

'Hass' fruit at Childers reached 24% dry matter from mid to late May over the duration of the study (Table 3). From mid- to late July, fruit had accumulated 30% dry matter with 35% being reached from late August to mid-September. All fruit were harvested within $\pm 1\%$ of the target dry matter for the respective treatments.

Table 3 Maturity of cv. Hass fruit at Childers indicated by dry matter at the different times of harvest in 1991 to 1994. Data are the means \pm SE ($n = 5$) each of treatment when harvested at their respective maturity times.

1st Harvest		2nd Harvest		3rd Harvest	
Date	Dry matter (%)	Date	Dry matter (%)	Date	Dry matter (%)
12.05.91	24.8 \pm 0.2	03.07.91	31.6 \pm 0.4	22.08.91	35.1 \pm 0.4
18.05.92	24.7 \pm 0.3	06.07.92	30.6 \pm 0.3	07.09.92	34.8 \pm 0.3
25.05.93	24.9 \pm 0.4	27.07.93	29.4 \pm 0.3	17.09.93	35.2 \pm 0.4
30.05.94	24.7 \pm 0.4	04.07.94	30.7 \pm 0.4	28.08.94	34.8 \pm 0.4

There was an increase in crop load from the start to the finish of the study, particularly in the last two years of the experiment (Fig. 4a). However, fruit yield was lower than expected in 1992 due to the effects of a tropical cyclone. There were no significant differences between treatments in annual yield except for 1993 when trees harvested at 25%, 30% and 25/35% DM out-yielded those in which harvest was delayed until 35% DM. In this case, carry-over effects from the storm may have enhanced the magnitude of treatment effects thereby precipitating a conclusive result. There were no significant differences in fruit size between any of the treatments in each of the four years of the study (Table 4). However, there were trends present, stronger in some years than others, which indicated the potential for fruit size to increase the longer it is left on the tree.

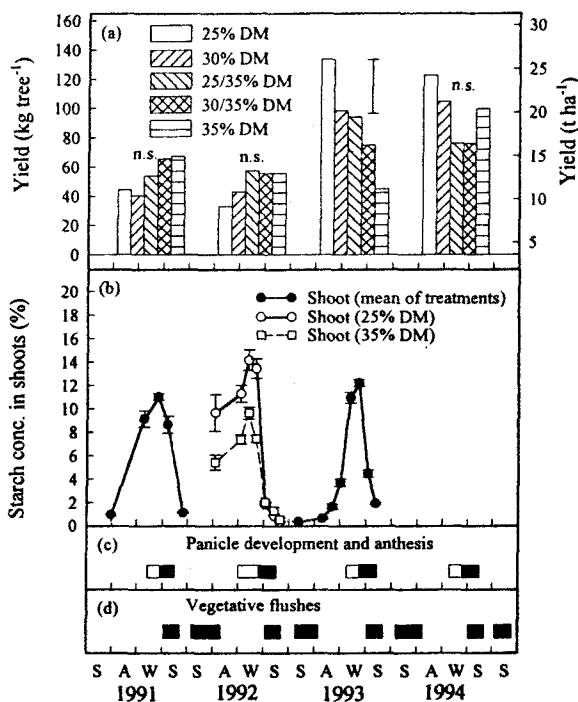


Figure 4 Relationship between yield, seasonal starch concentration flux and tree phenology of cv. Hass at Childers where: (a) is yield of fruit which were harvested at different stages of maturity as judged by dry matter (DM), the vertical bar indicates LSD ($P \leq 0.05$); (b) is starch concentration of shoots of all treatments (\bullet , $n = 15$), or 25% DM (\circ , $n = 3$), or 35% DM (\square , $n = 3$), SEs are represented by vertical bars; (c) is periods of panicle growth represented by open horizontal bars, and periods of anthesis represented by closed horizontal bars; and (d) is periods of vegetative growth represented by horizontal closed bars.

With respect to seasonal starch concentrations in shoots, there were no significant differences during 1991 and 1993 so data for all treatments were pooled. However, in 1992 shoot starch concentrations were significantly different and data have been presented separately for the 25% and 30% DM treatments (Fig. 4b). Starch levels for the 30%, 25/35% and 30/35% DM treatments in 1992 fell between concentrations for the 25% and 35% DM treatments and were not significantly different (data not presented). Starch concentrations in the shoots followed similar

Table 4 Effect of time of harvest on fruit size of cv. Hass growing at Childers. Data are mean of 6 trees for each treatment for each year of the study and have been subjected to covariance analysis adjusting for yield. Figures in parenthesis are the unadjusted fruit size means. There were no significant differences between values in columns as tested by ANOVA.

Treatment	Fruit size (g)			
	1991	1992	1993	1994
25% DM	172.9 (179.8)	169.1 (164.8)	230.2 (203.8)	188.9 (183.8)
30% DM	178.6 (188.3)	146.5 (144.7)	239.6 (241.5)	194.0 (195.2)
25/35% DM	186.2 (186.4)	160.3 (163.0)	244.8 (240.4)	192.5 (195.5)
30/35% DM	185.4 (177.6)	162.7 (164.6)	236.4 (242.5)	192.8 (195.8)
35% DM	202.1 (193.0)	176.3 (178.2)	238.5 (253.2)	206.9 (205.7)
Regression coefficient	-0.692**	0.253	-0.553**	-0.174

seasonal patterns for the first three years of the study when they were measured. Levels were initially low at the completion of summer shoot growth but increased rapidly as shoots entered a period of quiescence and peaked prior to flowering (Figs. 4b, 4c & 4d). Concentrations declined rapidly during flowering and spring shoot growth.

Shoot growth occurred during two periods over each cropping cycle; a relatively short term of activity in the spring concomitant with the termination of flowering followed by intermittent growth during the summer. The spring flush was generally concluded by mid- to late November while shoot growth during summer began in early January and had ceased by mid-March.

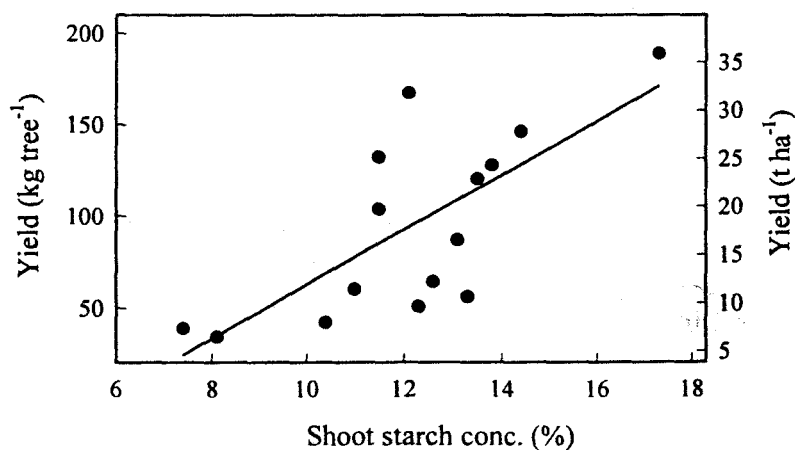


Figure 5 Relationship between yield (1993) and July shoot starch concentration (1992) of cv. Hass growing at Childers. The regression is represented by the equation $y = 14.84x - 85.63$, $r^2 = 0.52^*$.

The light crop due to storm damage and the different harvesting times of fruit are the factors most likely contributing to higher accumulation of starch in the 25% DM treatment in 1992. While all treatments lost a considerable percentage of their crop in February, the earlier harvesting of the 25% treatment (18.05.92) provided these trees with a greater period without strong sinks to accumulate starch in shoot tissues. The 1992 starch concentration in shoots was positively related to fruit yield in 1993 (Fig. 5).

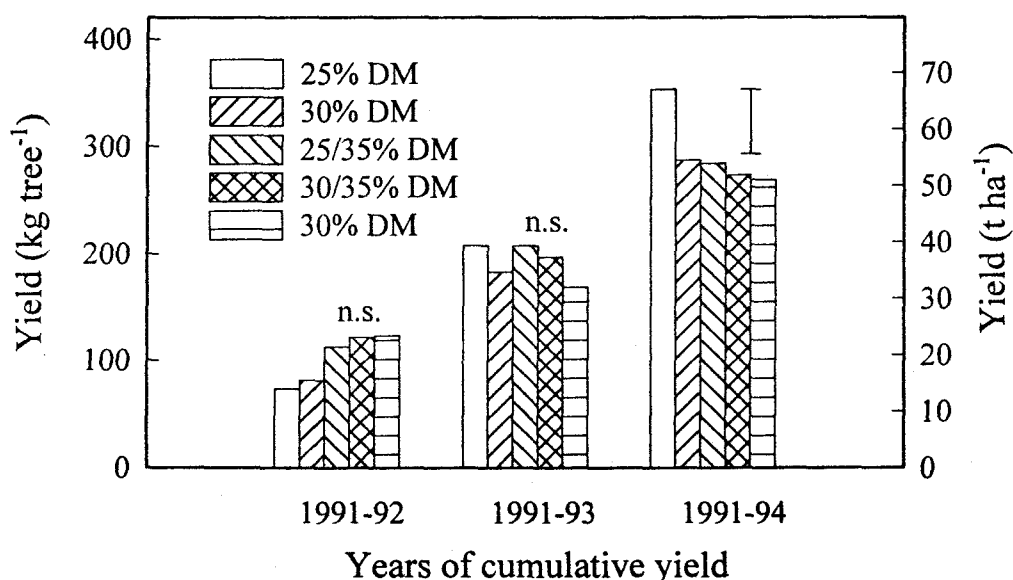


Figure 6 Effect of time of harvest, based on fruit dry matter (DM), on the cumulative yield of cv. Hass avocado trees at Childers over four consecutive years. Columns are mean values of 6 trees for each treatment and vertical bar represents LSD ($P \leq 0.05$) determined by ANOVA..

While there were no significant differences in cumulative fruit yield until the fourth year of the study, the combined yield of the first and second years was higher for treatments which were harvested late (Fig. 6). This was undoubtedly due to the non-significant trend for an increase in size of late harvested fruit (data not presented) and before any impact was made by these fruit on the following year's crop. By the end of 1993 (three years) this trend was changing slightly favouring the earlier harvested fruit and after four years, those trees harvested at 25% dry matter produced more fruit than all the other treatments (Fig. 6).

With respect to the sustainability of production there was little impact made on yield by any of the treatments during the first two years of the study (Fig. 7). This in part may be due to the storm damage to the trees during the 1992 season. However, in the third and fourth years there is an indication that treatments were beginning to affect production sustainability. Where fruit were harvested at 25% and 30% DM, yield increased substantially in 1993 and 1994 and was similar for both of these years. There were no significant differences in yield from year to year in those treatments harvested at 25/35% and 30/35%. However, in those trees where all fruit were harvested at 35% there was a reduction in the 1993 yield compared with production in 1994. It is

suggested that this may be the beginning of a biennial fruiting pattern similar to that induced with 'Fuerte' growing in the same orchard.

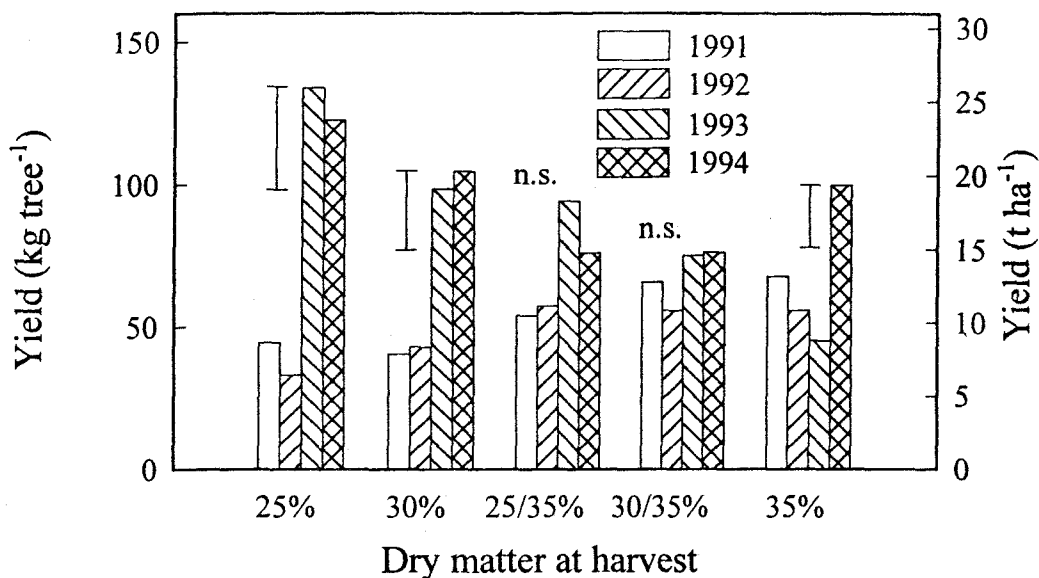


Figure 7 Effect of time of harvest, as judged by fruit dry matter (DM), on the sustainability of yield of cv. Hass at Childers. Columns represent mean values of 6 trees for each treatment and vertical bars LSDs ($P \leq 0.05$) determined by ANOVA.

'Hass' at Maleny

At Maleny fruit reached 25% dry matter from late June to mid-July; 30% from early August to late September; and 35% in early November (Table 5). For the most part treatments were harvested within 1.5% of their defined maturity, the exceptions being the November 1989 and September 1990 harvests at which fruit were slightly more mature than planned. Some fruit were tree-stored for over 4 months, well into a second growing season.

Table 5 Maturity of cv. Hass fruit at Maleny indicated by dry matter at the different times of harvest in 1988 - 1990. Data are the means \pm SE of five fruit from each of the trees when harvested at their respective maturity times.

1st Harvest		2nd Harvest		3rd Harvest	
Date	Dry matter (%)	Date	Dry matter (%)	Date	Dry matter (%)
14.07.88	24.5 \pm 0.3	28.09.88	31.6 \pm 0.4	09.11.88	35.5 \pm 0.3
28.06.89	24.2 \pm 0.4	02.08.89	31.1 \pm 0.5	01.11.89	37.4 \pm 0.3
18.07.90	25.0 \pm 0.2	19.09.90	32.6 \pm 0.5	07.11.90	35.4 \pm 0.5

There were no significant differences among treatment yields in any of the three years of the study (Fig. 8a). However, there was a very strong biennial effect across all treatments with high yields in the first and third years of the experiment (equivalent to 39.2 and 37.0 t. ha⁻¹, respectively) and low yield (equivalent to 9.6 t. ha⁻¹) in the second year.

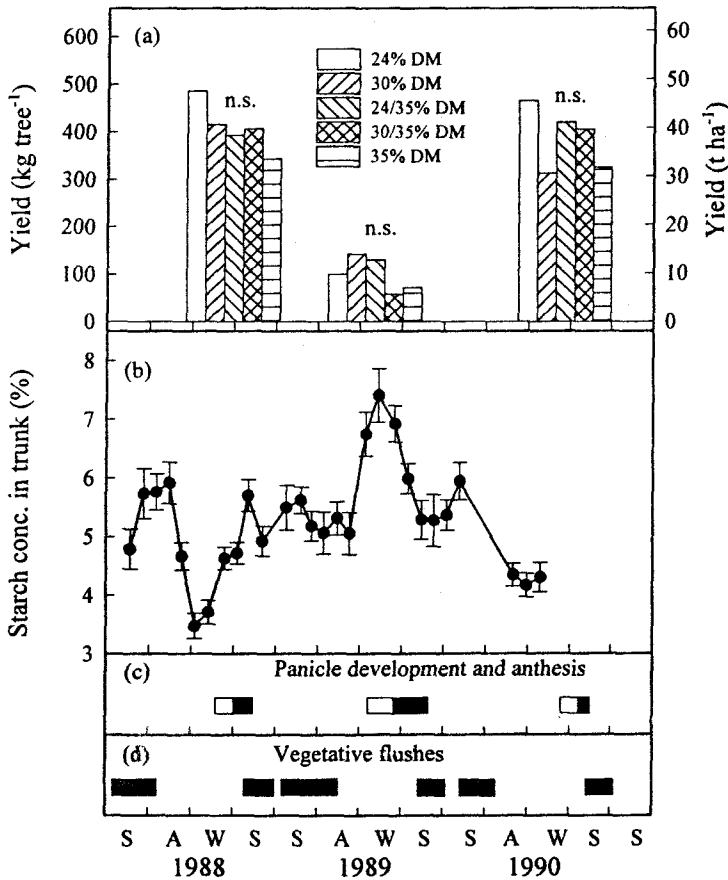


Figure 8 Relationship between yield, seasonal starch concentration flux and tree phenology at Maleny where: (a) yield of fruit which was harvested at different stages of maturity as judged by dry matter (DM); (b) is starch concentration ($n = 30$), of all treatments, SEs are represented by vertical bars; (c) is periods of panicle growth represented by open horizontal bars, and periods of anthesis represented by closed horizontal bars; and (d) is periods of vegetative growth represented by horizontal closed bars.

As there were no significant differences in trunk starch concentrations between treatments throughout the three years of the study data have been pooled. Seasonal fluctuations in trunk starch levels ranged from ca. 3.5 to 7.4% and maximum concentrations occurred just prior to (1988 & 1990) or during flowering (1989) (Figs. 8b & 8c). Starch concentrations tended to be relatively stable during shoot growth and were in the vicinity of 5 to 6% (Figs. 8b & 8d). The low starch concentrations in 1988 and 1990 were likely due to very heavy crop loads which were not harvested until June/July or later for some of the treatments. The highest concentration of starch occurred during winter 1989 after shoot growth had ceased and when the crop load was light (Figs. 8a & 8b).

Panicle emergence began in mid- to late July each year with anthesis mainly during September and extending into October (Fig. 8c). The flowering intensity was noticeably greater and extended for longer in the spring of the off-year preceding heavy cropping. Shoot growth occurred in two major periods over each crop cycle (Fig. 8d). In spring growth was synchronised by flowering and began near the conclusion of anthesis in early October. By late November of each year shoots had matured and following a short rest, sporadic flushing occurred over the summer months. In 1989, summer growth began in mid-December and extended through until mid-April while in 1990 summer growth had ceased by the middle of March.

Trunk starch concentration in July of 1988 and 1989 were directly related to the yields in 1989 and 1990, respectively (Fig.9). These data show "low" yields of ca. 100 kg tree⁻¹ (10 t ha⁻¹) after July trunk starch concentrations of ca. 3 to 4%, rising to ca. 500 kg tree⁻¹ (50 t ha⁻¹) at ca. 9 to 10% trunk starch the previous July.

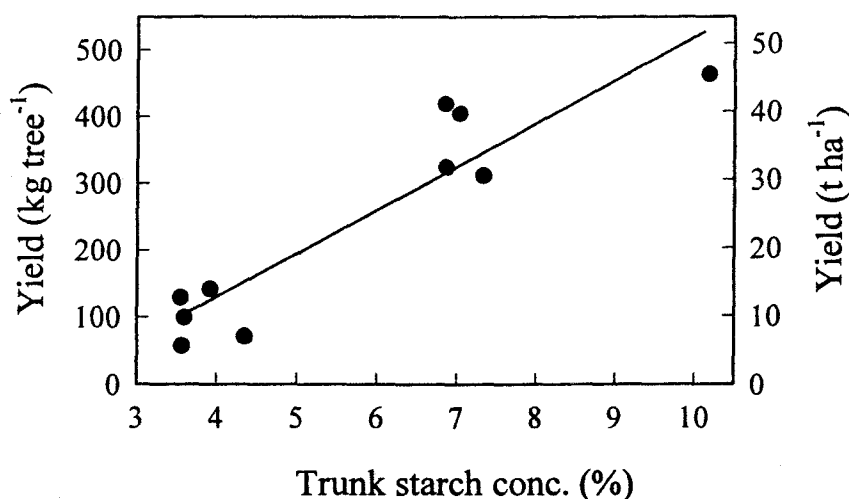


Figure 9 Relationship between July trunk starch concentration and next season's yield of cv. Hass growing at Maleny. The regression is represented by the equation $y = 64.90x - 129.04$, $r^2 = 0.86^{**}$.

The effect of harvest time on fruit size is detailed in Table 6. General trends for each year indicate that delayed harvest increased fruit size, however a near significant ($P \leq 0.06$) increase was only recorded in the low crop year of 1989. In this season fruit which was allowed to hang late on the tree were 23% heavier than the earliest fruit harvest. This increase in fruit size was achieved without any significant reduction in fruit yield, either in the 1989 or 1990.

Table 6 Effect of time of harvest on fruit size of cv. Hass growing at Maleny. Data are means of 6 trees for each treatment for each year of the study and have been subjected to covariance analysis adjusting for yield. Values in parenthesis are the unadjusted fruit size means. Means in columns not sharing a common letter were significantly different at $P \leq 0.06$ as tested by ANOVA.

Treatment	Fruit mass (g)		
	1988	1989	1990
25% DM	219.8 a (214.0)	259.3 a (255.2)	219.2 a (214.3)
30% DM	233.5 a (233.0)	227.2 ab (214.5)	217.9 a (222.5)
25/35% DM	222.5 a (223.7)	251.2 a (243.4)	230.3 a (228.1)
30/35% DM	225.3 a (225.5)	210.3 b (214.7)	210.8 a (209.6)
35% DM	217.3 a (222.2)	236.7 ab (240.5)	237.7 a (241.4)
Regression coefficient	-0.075	-0.167*	-0.062

Discussion

Yield and fruit size

Results presented in this Chapter have shown that avocado yields are strongly influenced by the synergism of fruit load and duration of the crop on the tree. With early and late maturing cultivars growing at Childers, removal of fruit within reasonable time of reaching maturity maintained yield performance over a number of seasons. However, prolonged delayed harvesting of fruit caused strong alternate bearing cycles to develop. This was particularly evident with 'Fuerte' which began this cycle the first year after starting treatments, i.e. shown in the 1989 yields. The development of the alternate bearing pattern at Childers was delayed with 'Hass', as yields were relatively low across all treatments over the first two years of the study. This was most likely due to the previous history of the trees which had suffered from *Phytophthora* root rot and boron deficiency prior to starting the treatments, and damage caused by the tropical storm in 1992. Nevertheless, in the final two years of the study there were signs that a biennial cycle had developed in trees where delayed harvesting was practiced. This result contrasts with that reported by Kaiser and Wolstenholme (1994) who found that late harvesting of 'Hass' in the cool, mesic, subtropical Natal midlands did not depress yields the following year. There are three possible reasons why results differ: the length (number of years) of the Kaiser and Wolstenholme experiment was insufficient to induce biennial patterns; theft of fruit from trees distorting yield data which was suggested by the authors to explain unexpected results; or environmental differences between the sites significantly changing comparative tree and fruit performance. With respect to the latter, the Childers site in Queensland is significantly warmer than Everdon in Natal. Higher mean temperatures would increase the 'cost of fruiting' at Childers through increased respiratory losses (Blanke and Whiley 1995) thereby limiting photo-assimilates for fruit growth and subsequent crops.

Picking date is also reported to have affected yield in other tree crops. In a study with apples, fruit were picked over an eight week period from when they were judged to attain maturity until they had begun to fall naturally from the trees (Williams *et al.* 1980). It was shown that fruit set the following spring was highly correlated to the harvest dates of the previous year. Early picking promoted more flower clusters which consequently set more fruit. Similarly, harvest time has been shown to affect cropping patterns of 'Valencia' oranges. After a 14-year study, Jones and Cree (1954) concluded that late picking decreased the following year's yield and increased the severity of alternate bearing. Later studies showed a curvilinear relationship between harvest date and the size of the next year's crop and suggested that 'Valencia' oranges crop to the limit of their available carbohydrates (Jones *et al.* 1964b).

'Hass' trees at Maleny were in a hail-induced biennial bearing cycle when treatments were started and this cycle, represented by "on", "off", "on" years continued for the duration of the study. Climatic stresses have been reported responsible for biennial bearing in other fruit species. For instance, spring frosts which destroy bloom have caused synchronised alternate cropping over large areas in apples, pecans and mangoes (Singh *et al.* 1974; Williams and Edgerton 1974; Sparks 1975). Unseasonably cool temperatures during flowering have also led to large scale failure of fruit set of 'Valencia' oranges in Australia thereby initiating an alternate cropping cycle (Gallasch *et al.* 1978).

The crop at Maleny in the first year (ca. 39 t. ha⁻¹ averaged across treatments) was extremely high by physiological standards for avocados (Wolstenholme 1986; 1987). It was associated with depletion of trunk starch content as the crop matured during winter, which contrasts with previously described patterns (Cameron and Borst 1938; Rodrigues and Ryan 1960; Scholefield *et al.* 1985; Kaiser and Wolstenholme 1994). Flowering, which led to a small crop in 1989, was of low intensity and short duration compared with the same event in 1989 which subsequently produced a 37 t. ha⁻¹ crop (averaged across treatments). In this case the effect of harvest time on yield had no apparent impact on the pre-determined cycle, and it appears that more rigorous procedures earlier in the crop cycle of an "on" year will be necessary to break strong alternate bearing patterns. For instance, Jones *et al.* (1974) were able to influence the cropping cycle of alternate bearing 'Valencia' oranges by thinning fruit at different stages of development in an "on" year. The subsequent crop was directly related to the amount and time after set that fruit was removed, e.g. removal of 66% of the current crop three months after anthesis produced more fruit the following year than the removal of 33% of the current crop seven months after anthesis. Similarly, El-Zeftawi and Thornton (1975) showed that stripping fruit from 'Valencia' trees within four months of setting their first commercial crop, moderated alternate bearing for six years without decreasing total yield over that period. Strategic pruning of trees may also be an alternative practice to modulate biennial cropping patterns in avocado. There is currently no information available on this topic but severe pruning (topping along with tree removal) of large trees in Florida improved yield compared with non-pruned crowded trees (Crane *et al.* 1992).

There was a trend of increased fruit size with delayed harvest though results were not significant in all years or at all sites. For 'Fuerte', fruit size increased in the order of 8 to 18% with later harvested treatments. However, these gains must be balanced against lower yields as small fruit are generally not an issue in well managed 'Fuerte' orchards. There was no significant difference in fruit size with 'Hass' grown at Childers once data had been adjusted for yield, though there was

a consistent trend each year suggesting larger fruit with delayed harvest. Although delayed harvest at Maleny increased fruit size by ca. 23% in the "off" year ($P \leq 0.06$), no differences were recorded when heavy crops were carried on the trees. This may be due to assimilate limitation due to over-loading trees with fruit. Other studies have reported increased fruit size when harvesting was delayed. For instance, the size of 'Bramley's Seedling' apple improved appreciably with late harvesting (Williams *et al.* 1980), and Kaiser and Wolstenholme (1994) found larger 'Hass' fruit when harvesting was delayed. This is consistent with the well-known fact that cell division continues as long as avocado fruits are firmly attached to the tree, with effects likely to be greater in fruit in which seed coats do not abort prematurely (Schroeder 1952; Valmayor 1967).

It is worth noting the difference in 'Hass' fruit size between Childers and Maleny after adjustment for yield at both sites (Tables 11 & 13). At Childers the mean fruit size over the four years of the study was 195.0 ± 6.5 g while for the three years at Maleny mean fruit size was 227.9 ± 3.6 . This represents an increase of ca. 17% in the size of the fruit at Maleny. Due to different time frames for the two experiments statistical analysis cannot be applied to the data, however these results support industry perceptions that in warmer climates the 'Hass' small fruit problem is more severe. During the first 12 weeks of fruit ontogeny (October/December) the mean min/max temperature at Childers was 3.5°C higher than at Maleny. This is the period of most rapid cell division and growth (Valmayor 1967) when respiration rates of fruit are highest (Whiley *et al.* 1992; Blanke and Whiley 1995). Blanke and Whiley (1995) have suggested that the high rates of R_d measured for 'Hass' fruit may be a contributing factor to their smaller size in warmer climates.

Seasonal starch cycling

Starch is the most common and ubiquitous reserve carbohydrate in plants and there are numerous reports on its role in alternate bearing in fruit crops (Grochowska 1973; Davis and Sparks 1974; Jones *et al.* 1975; Goldschmidt and Golomb 1982; Scholefield *et al.* 1985). It has been repeatedly confirmed that starch levels are higher during the winter of the "off" year compared to levels when the tree has cropped heavily. The three year study of Scholefield *et al.* (1985) clearly indicated a direct relationship between winter starch levels and subsequent yield of 'Fuerte' avocado trees growing in a cool, dry Mediterranean climate in southern Australia. In this six year study with 'Fuerte' there was no clear correlation between starch concentrations (measured in the trunk or shoots) and yield, although in all years trunk or shoot levels declined rapidly during flowering and early fruit development. The small seasonal change in starch concentration relative to yield compared with that reported by Scholefield *et al.* (1985), suggests a low dependence on reserve carbohydrate of 'Fuerte' trees to maintain yield in subtropical climates. It is suggested that carbohydrates from current photo-assimilates play a proportionally more important role in cropping than is the case in cooler regions where avocados are grown. Observations at Childers indicated the trees retained most summer grown leaves through until spring shoot growth was fully developed, thereby ensuring continuity of photo-assimilate supply during the flowering and fruit set period. However, Scholefield *et al.* (1985) reported that summer grown leaves were shed from March onwards at a rate faster than new ones were produced, probably as a consequence of salinity and environmental stress. Thus the assimilation surface was substantially reduced at flowering (a period of critical demand) and setting fruit were largely dependent on storage carbohydrate until the sink/source transition of the spring growth occurred.

Starch concentrations in either the trunk or shoots of trees were a better indicator of crop performance for 'Hass'. At Childers, a direct relationship between shoot starch concentrations in July and the subsequent crop was established for the 1992/93 cycle when large differences in treatment yields were recorded. Similarly, at Maleny trunk starch and subsequent yield were directly related across two seasons when strong biennial bearing was present. Shoot starch concentrations at Childers reached higher levels in 'Hass' (ca. 14%) than 'Fuerte' (ca. 7%). The reasons for this are not clear but may be associated with magnitude and temporal differences in phenology. 'Fuerte' showed more vegetative vigour than 'Hass' and flushed longer during summer (Figs. 26 & 29). Although 'Fuerte' fruit were harvested earlier in the year, floral bud development and anthesis were also advanced compared with 'Hass'. Strong root growth could also be expected from the cessation of summer flushing through to anthesis (see Chapter 2) and this combination of sinks together with decreased CO₂ assimilation efficiency during the winter, may have produced the lower peak concentrations.

The reduced yields detailed in these experiments cannot be solely attributed to threshold concentrations of starch at critical phenological stages. Crop failure was most often related to poor flowering with either a reduced number of floral sites or expression of flowering intensity (observed but no data recorded). The reasons for flowering failure are beyond the scope of data presented in this chapter, but can possibly be explained by the theory of "multifactorial control" which postulates that several compounds - assimilates and known phytohormones - participate in floral induction (Bernier *et al.* 1981; Bernier 1988). Bernier *et al.* (1993) suggest a complex series of physiological signals between shoots and roots which precipitate floral induction. Roots are the primary source of cytokinins which participate in the floral stimulus at apical buds. Root studies presented in this thesis (Chapter 2), clearly show suppression of root growth during the autumn/winter period, a time of floral induction in avocado (Davenport 1982; Whiley *et al.* 1988a), when trees carry heavy crop loads. Poor root growth resulting in reduced cytokinin supply may well be a factor contributing to the diminished flowering observed in trees where delayed harvesting reduced the subsequent yield.

Conclusions

Alternate bearing in fruit crops disrupts continuity of supply to markets and reduces farm cash flow. Results reported herein indicate that harvesting time with respect to avocado fruit maturity, is an important criteria with respect to maintaining productivity on a yearly basis. Early removal of fruit from trees between 21 to 24% ('Fuerte') or 25 to 30% ('Hass') flesh dry matter sustained production levels in otherwise well managed orchards, but markedly delayed harvesting of fruit precipitated strong alternate cropping patterns. Early harvesting of 'Hass' where biennial bearing was entrenched, did not release the tree from this cropping pattern and more extreme practices such as fruit thinning or pruning may be needed to moderate the cycle. Indeed, where storm damage effectively removed crop load five months after fruit set, cropping patterns were modified in cv. Fuerte (see Childers data). In both cultivars the concentration flux of starch closely followed changes in phenological events and generally peaked in winter during an extended quiescent period. Although heavy fruiting depressed winter starch accumulation which resulted in reduced yield, production is more likely to be constrained by other environmental, resource and management bottlenecks at critical phenological stages.

References

- Banks, A., 1992. Growing avocados in Queensland, Department of Primary Industries, Brisbane. Pp. 1-36.
- Bernier, G. 1988. The control of floral evocation and morphogenesis. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 39, 175-219.
- Bernier, G., Havelange, A., Houssa, C., Petitjean, A. and Lejeune, P., 1993. Physiological signals that induce flowering. *The Plant Cell* 5, 1147-55.
- Bernier, G., Kinet, J.M. and Sachs, R.M., 1981. *The Physiology of Flowering*, Vol. II. CRC Press, Boca Raton, Florida.
- Blanke, M.M. and Whiley, A.W., 1995. Bioenergetics and water relations of developing avocado fruit. *J. Plant Physiol.* 145, 87-92.
- Brown, B.I., 1984. Market maturity indices and sensory properties of avocados grown in Queensland. *Food Technol. Aust.* 37, 474-6.
- Cutting, J.G.M., 1993. The cytokinin complex as related to small fruit in 'Hass' avocado. *S. Afr. Avocado Growers' Assoc. Yrbk.* 16, 20-1.
- Cameron, S.H. and Borst, G., 1938. Starch in the avocado tree. *Proc. Amer. Soc. Hort. Sci.* 36, 255-8.
- Cameron, S.H., Mueller, R.T. and Wallace, A., 1952. Nutrient composition and seasonal losses of avocado trees. *Calif. Avocado Soc. Yrbk.* 36, 201-9.
- Chacko, E.K., Reddy, Y.T.N. and Ananthanarayanan, T.V., 1982. Studies on the relationship between leaf number and area and fruit development in mango (*Mangifera indica* L.). *J. Hort. Sci.* 57, 483-92.
- Chandler, W.H., 1958. The avocado. In: *Evergreen Orchards*. Lea and Febiger, Philadelphia. Pp. 205-28.
- Crane, J.H., Balerdi, C., Campbell, R. and Goldweber, S., 1994. Managing fruit orchards to minimize hurricane damage. *HortTech.* 4, 21-7.
- Crane, J.H., Schaffer, B., Davenport, T.L. and Balerdi, C., 1992. Rejuvenation of a mature, non-productive 'Lula' and 'Booth 8' avocado grove by topping and tree removal. *Proc. Fla. State Hort. Soc.* 105, 282-5.
- Davenport, T.L. 1982. Avocado growth and development. *Proc. Fla State Hort. Soc.* 95, 92-6.
- Davis, J.T., and Sparks, D., 1974. Assimilation and translocation patterns of carbon-14 in the shoot of fruiting pecan trees. *J. Amer. Soc. Hort. Sci.* 99, 468-80.
- Dickson, R.E., 1991. Assimilate distribution and storage. In: *Physiology of Trees*. A.S. Raghavendra (ed). Wiley. Pp. 51-85.
- Eaks, I.L., 1980. Respiratory rate, ethylene production, and ripening response of avocado fruit to ethylene or propylene following harvest at different maturities. *J. Amer. Soc. Hort. Sci.* 105, 744-7.
- El-Zeftawi, B.M. and Thornton, I.R., 1975. Effects of rootstock and fruit stripping on alternate bearing of Valencia orange trees. *J. Hort. Sci.* 50, 219-26.
- Gallasch, P.T., Bevington, K.B., Hocking, D. and Moss, G.I., 1978. Ethephon thinned heavy crops of 'Valencia' oranges in three widely spaced districts of Australia. *Proc. Intern. Soc. Citriculture* Pp. 273-6.
- Goldschmidt, E.E. and Golomb, A., 1982. The carbohydrate balance of alternate-bearing citrus trees and the significance of reserves for flowering and fruiting. *J. Amer. Soc. Hort. Sci.* 107, 206-8.

- Grochowska, M.J., 1973. Comparative studies on physiological and morphological features of bearing and non bearing spurs of apple tree. I. Changes in starch content during growth. *J. Hort. Sci.* 48, 347-56.
- Hilgeman, R.H. Dunlap, J.A. and Sharples, G.C., 1967. Effect of time of harvest of 'Valencia' oranges on leaf carbohydrate content and subsequent set of fruit. *Proc. Amer. Soc. Hort. Sci.* 90, 111-6.
- Issarakraisila, M and Considine, J.A., 1994. Effects of temperature on microsporogenesis and pollen viability in mango cv. Kensington. *Ann. Bot.* 73, 231-40.
- Jones, W.W. and Cree, C.B., 1954. Effect of time of harvest on yield, size and grade of Valencia oranges. *Proc. Amer. Soc. Hort. Sci.* 64, 139-45.
- Jones, W.W., Embleton, T.W., Barnhart, E.L. and Cree, C.B., 1974. Effect of time and amount of fruit thinning on leaf carbohydrates and fruit set in Valencia oranges. *Hilgardia* 42, 441-9.
- Jones, W.W., Embleton, T.W. and Coggins Jr, C.W., 1975. Starch content of roots of 'Kinnow' mandarin trees bearing fruits in alternate years. *HortScience* 10, 514.
- Jones, W.W., Embleton, T.W., Steinacker, M.L. and Cree, C.B., 1964b. The effect of time of fruit harvest on fruiting and carbohydrate supply in the Valencia orange. *Proc. Amer. Soc. Hort. Sci.* 84, 152-7.
- Kaiser, C., and Wolstenholme, B.N., 1994. Aspects of delayed harvest of 'Hass' avocado (*Persea americana* Mill.) fruit in a cool subtropical climate. II. Fruit size, yield, phenology and whole-tree starch cycling. *J. Hort. Sci.* 69, 447-57.
- Köhne, J.S., 1991. Increasing 'Hass' fruit size. *S. Afr. Avocado Growers' Assoc. Yrbk.* 14, 38.
- Lahav, E. and Adato, I. 1990. Increasing the size of 'Hass' avocado fruit. *Rep. Inst. Hort. Sci. Activities 1981-1984.* Volcani Centre, Bet Dagan, Israel.
- Lee, S.K., 1981a. Methods for percent oil analysis of avocado fruit. *Calif. Avocado Soc. Yrbk.* 65, 133-41.
- Lee, S.K., 1981b. A review and background of the avocado maturity standard. *Calif. Avocado Soc. Yrbk.* 65, 101-9.
- Lee, S.K., Young, R.E., Schiffman, P.M. and Coggins, C.W., 1982. Maturity studies of avocado fruit based on picking dates and dry weight. *J. Amer. Soc. Hort. Sci.* 108, 390-4.
- Monselise, S.P. and Goldschmidt, E.E. 1982. Alternate bearing in fruit trees. *Hort. Rev.* 4, 128-73.
- Proctor, J.T.A. and Creasey, L.L., 1971. Effect of supplementary light on anthocyanin synthesis in McIntosh apples. *J. Amer. Soc. Hort. Sci.* 96, 523-6.
- Quinlan, J.D., and Preston, A.P., 1971. The influence of shoot competition on fruit retention and cropping of apple trees. *J. Hort. Sci.* 46, 525-34.
- Rasmussen, T.S. and Henry, R.J., 1990. Starch determination in horticultural plant material by an enzymic colorimetric procedure. *J. Sci. Food Agric.* 52, 159-70.
- Rodrigues, J. and Ryan, G.F., 1960. The influence of season and temperature on carbohydrates in avocado shoots. *Proc. Amer. Soc. Hort. Sci.* 76, 253-61. Wolst.
- Schaffer, B. and Baranowski, R.M., 1986. Sample size estimates for avocado yield experiments. *J. Amer. Soc. Hort. Sci.* 111, 985-7.
- 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.

- Schroeder, C.A., 1952. Floral development, sporogenesis, and embryology in the avocado. *Persea americana*, *Bot. Gaz. (Chicago)* 113, 270-8.
- Sedgley, M. and Annells, C.M., 1981. Flowering and fruit-set response to temperature in the avocado cultivar 'Hass'. *Scientia Hort.* 14, 27-33.
- Singh, R.N., Majumder, P.K., Sharma, P.K., Sinha, G.C. and Bose, P.C., 1974. Effect of deblossoming on the productivity of mango. *Scientia Hort.* 2, 399-403.
- Sparks, D., 1975. The alternate fruit bearing problem in pecans. *65th Annu. Proc. Northern Nut Growers' Assoc.* 1974. Pp. 145-58.
- 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. *Sexual Plant Reproduction* 6, 87-7.
- Swarts, D.H., 1976. 'N praktiese avokado-oliebepalingsmetode vir produsente. *Citrus and Subtropical Fruit J.* 8-14.
- Valmayor, R.V., 1967. Cellular development of the avocado fruit - blossom to maturity. *Philippine Agriculturist* L, 907-76.
- Whiley, A.W., Pegg, K.G., Saranah, J.B. and Forsberg, L.I., 1986. The control of Phytophthora root rot of avocado with fungicides and the effect of this disease on water relations, yield and ring neck. *Aust. J. Exp. Agri.* 26, 249-53.
- Whiley, A.W., Rasmussen, T.S. and Saranah, J.B., 1992. Effect of time of harvest on fruit size, yield and trunk starch concentrations of Fuerte avocados. In: *Proc. of the World Avocado Congress II*, Los Angeles. Pp. 155-9.
- Whiley, A.W., Saranah, J.B., Cull, B.W. and Pegg, K.G., 1988. Manage avocado tree growth cycles for productivity gains. *Queensland Agric. J.* 114, 29-36.
- 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. Yrbk* 10, 45-7.
- Williams, R.R., Arnold, G.M., Flook, V.A. and Jefferies, C.J., 1980. The effects of picking date on blossoming and fruit set in the following year for the apple cv Bramley's Seedling. *J. Hort. Sci.* 55, 359-62.
- Williams, M.W. and Edgerton, L.J., 1974. Biennial bearing of apple trees. *Proc. XIX Intern. Hort. Congr. Warsaw* 3, 343-52.
- Wolstenholme, B.N., 1986. Energy costs of fruiting as a yield-limiting factor with special reference to avocado. *Acta Hort.* 175, 121-6.
- Wolstenholme, B.N., 1987. Theoretical and applied aspects of avocado yield as affected by energy budgets and carbon partitioning. *S. Afr. Avocado Growers' Assoc. Yrbk* 10, 58-61.
- Wolstenholme, B.N., 1991. Making an avocado fruit: energy expensive but mineral cheap. *Avokad* 11, 8-9.
- Wolstenholme, B.N. and Whiley, A.W. 1995. Prospects for increasing Hass fruit size - A southern hemisphere perspective

Source: Whiley, A.W. 1994. Ecophysiological studies and tree manipulation for maximisation of yield potential in avocado (*Persea americana* Mill.). Unpublished PhD Thesis, Department of Horticultural Science, University of Natal (accepted 30 March 1995).

Root growth and phenology of cv. Hass avocado (*Persea americana* Mill.)

A.W. Whiley¹, J.B. Saranah¹ and T.S. Rasmussen²

¹Maroochy Horticultural Research Station, Department of Primary Industries Queensland, Nambour 4560, Australia

²Agricultural Chemistry, Department of Primary Industries Queensland, Indooroopilly 4068, Australia

Introduction

To enhance competitive fitness, perennial plant species typically display seasonal variation in the production of new leaves, flowers and fruit due to genetically imprinted growth patterns (van Schaik *et al.* 1993). In individual species, biotic influences have generally selected for temporally staggered, or clumped phenological activities. For instance, some species vulnerable to seed predation have developed strongly clumped fruiting sequences by storing carbohydrate reserves to produce larger crops at longer intervals (Janzen 1971); and leaves produced in synchronised flushes sustain less insect damage than those grown asynchronously (Lieberman and Lieberman 1984).

Environmental factors have a major impact on plant growth and dictate seasonal change, within genetically determined limits. For instance, many deciduous species of seasonally dry tropical forests drop all their leaves before the dry season and re-leaf about one month before the onset of rain, thereby minimising the impact of water stress (Frankie *et al.* 1974; Wright and Cornejo, 1990). Irradiance and water stress have been identified as the most important environmental factors shaping the phenology of tropical woody plants in natural communities (van Schaik *et al.* 1993). However, with the domestication of fruiting species temperature has become equally important as production has been extended into more hostile environments (Sedgley and Grant 1983; Whiley and Winston 1987; Issarakraisila and Considine 1994).

These introductory remarks are perhaps an over-simplification of the complexity of plant responses and interactions in mixed communities, and ecologists are still grappling to gain a meaningful understanding of the phenological processes and the agents which control them. As horticulturists dealing with monoculture systems we are not concerned with the complexities of mixed communities. However, by recognising and appreciating the evolutionary factors which dictate the organisation of growth and seasonal change in natural plant communities we become better equipped to modify and adapt spatially and temporally separated phenological events for commercial gain.

The significance of phenological modelling to the horticulturist is that it provides a practical holistic approach to understanding plant growth and as such can be utilised as a powerful research

and extension tool. It is particularly useful when dealing with the complexities of tree fruit research, where crop performance integrates carry-over effects from previous physiological activity. Yield management involves fundamentally resource (assimilate) allocation between the reproductive and vegetative structures of the tree. In subtropical and tropical evergreen fruit trees, it appears that direct source/sink relationships (spatial separation) are less important than tree phenology, which represents a temporal separation of potentially competing sinks (vegetative vs. reproductive) although exceptions occur. Under appropriate conditions, phenological events can be manipulated so that the impact of potentially competing sinks is lessened (Wolstenholme *et al.* 1990; Whiley *et al.* 1991). The focus of this paper is devoted to the concepts of phenological modelling and the understanding of significant physiological changes concurrent with growth and quiescence in avocado trees.

Avocado phenology

The earliest description of seasonal growth of avocado trees and its significance to crop management was by Chandler (1958) and Venning and Lincoln (1958). They observed that shoot growth occurred in cycles (commonly called flushes) separated by periods of relative quiescence. In California, avocado trees generally produced two major shoot flushes each season, in spring and in summer/autumn (Chandler 1958). Trees growing in the tropical regions of Florida and Cuba may have up to four distinct flushes each season of which the first is associated with flowering. With respect to the management of growth of these trees, Venning and Lincoln (1958) concluded that shaping of young trees via tip pruning of succulent shoots could be advantageous through increasing shoot complexity. However, pruning of mature trees was discouraged due to the unpredictable nature of the growth response.

Kotzé (1979) compiled a simple model for the annual growth of avocado (cv. Fuerte) to promote discussion and encourage research initiatives. Tentative suggestions were made with respect to irrigation and the timing of fertiliser applications. However, his model focused on the reproductive cycle from floral initiation through to fruit maturity, and failed to recognise the dynamics of seasonal contributions from competitive and complementary shoot and root growth. A more holistic approach to the dynamics of tree growth was presented by Wolstenholme (1981) who speculated on the interactions between root, shoot and fruit growth. The implications of physiological changes and their effect on the "rhythmic" growth patterns of trees were discussed and conclusions drawn on potential management strategies to improve and sustain avocado yields.

A further significant development in avocado phenology was a detailed account of above-ground growth sequences for 21 avocado cultivars growing in southern Florida (Davenport 1982). His observations on floral development, flowering and fruit set, and vegetative flushes were mostly reported in a single time dimension (seasonal change). Of particular interest were the reported relationships between tree phenology and some associated physiological changes, e.g. observations that leaf senescence was precipitated by flowering, which exposed new opportunities in relating tree physiology and phenology as a research tool. However, the dynamics of root growth were not studied.

The senior author began whole-tree phenology studies with avocados in the late 1970's and despite prototype models being used to assist with research approaches and as an extension tool, details were not published until 1988 (Fig. 2) (Whiley *et al.* 1988a). By this time the concept had wide recognition as an extension aid by the Queensland avocado industry, and interest in the application of the models was being shown by other avocado producing states in Australia and later internationally. The published models were based on data sets collected in a time sequence from orchard trees, superimposed with the interpretation of research results and drawn as a conceptualised framework to provide management strategies at farm level. The incorporation of root growth patterns, even though these were deduced from simple non-destructive "surface root mat" techniques, was of particular significance to the holistic understanding of rhythmic growth patterns.

The basic phenology model (Fig.1) is two dimensional, integrating a time scale (x-axis) with the magnitude of response (y-axis). It illustrates the sequence of growth events over a full

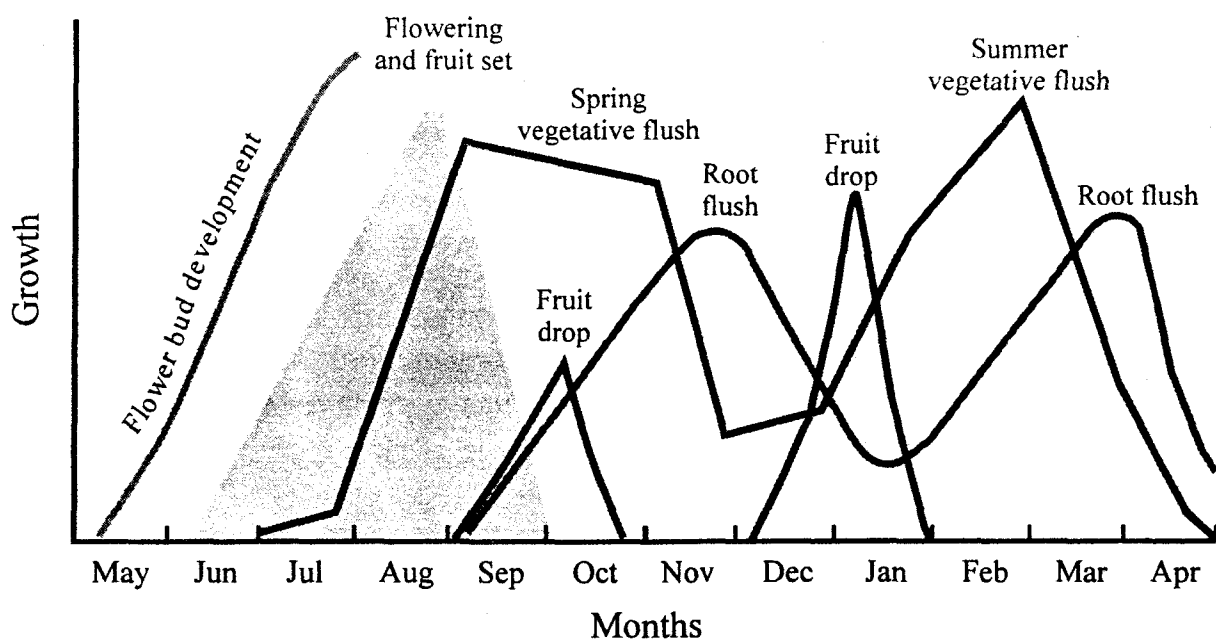


Figure 1 Phenology model developed for cv. Fuerte avocado growing in a warm, subtropical climate at Nambour, S.E. Queensland. Redrawn from Whiley *et al.* (1988a).

fruiting cycle and the relationship between the reproductive effort and root and shoot growth. Due to the plasticity of phenological responses across environments, the model is a useful tool for providing management strategies to growers in diverse regions. The timing of the key phenological events moves left or right along the x-axis in response to warmer and cooler climates dictated by changing latitude or altitude. As orchard management should be timed by growth event rather than by calendar month, strategies which target major phenological changes can be recommended irrespective of where the tree is growing. However, as a cautionary note, experience has shown that at outer environmental extremes (latitudes 12° & 33° S in Australia) plasticity may fail wherein there is a requirement to redefine the model. As

researchers or managers, we are limited in the control we can exert on displacement along the x-axis once a cultivar has been selected for a given environment.

While there is undoubtedly an interaction with prevailing environmental conditions, it is the magnitude of each growth event which can be manipulated through management strategies to have the greatest impact on tree performance. It is largely in this area that horticultural research has been focused, defining water, nutritional and crop protection requirements and the time sequence in which they should be applied in relation to phenological events.

Integration of physiology with phenology models

The previous section has reviewed the development of phenological modelling for avocado and the implications for its use in research and extension programs. However, the model of Whiley *et al.* (1988a) was qualitative and based solely on growth measurements, and as a research tool there were limitations in the interpretation of relationships between phenological events which could only be improved by more detailed physiological knowledge. Objectives with the research reported herein were (i) to re-examine root growth with respect to whole tree phenology; and (ii) to study seasonal changes in net CO₂ assimilation (*A*), leaf nitrogen and chlorophyll concentrations and starch levels, with a view to providing further information on physiological limitations during critical phenological events.

Materials and Methods

A commercial 'Hass' avocado orchard at Maleny in S.E. Queensland (latitude 26.5°S, altitude 520 m) was chosen for the phenological/physiological study. The climate is cool, mesic subtropical with a high mean annual rainfall of 2000 mm in a summer/wet: winter/dry pattern. The soils of the area are of basaltic origin and are described as krasnozems. Physically they are well drained clay loams (ca. 60% clay fraction) to between 10 to 16 m deep and show no obvious physical limitations to root growth.

Roots were observed from a rhizotron facility especially constructed for the study. It consisted of 10 wooden boxes 1.0 x 1.2 x 2.1 m, each with a 10 mm thick 690 x 845 mm clear plexiglass (polymethyl methacrylate) panel built into the two opposite 1.2 m sides: 20 panels in total. Disadvantages of this approach to root study have been enumerated by Rogers (1934) and were ameliorated as far as practicable by replication of the viewing panels, planting trees after the facility had been installed and excluding light from the viewing panels. Root measurements obtained with this technique on fruit trees have compared favourably with those obtained by other methods, e.g. tracer uptake (Atkinson 1974) and excavation or water depletion (Atkinson 1978). This is believed to be the first detailed study of this nature and scope and duration (4½ yr) on avocado trees anywhere in the world, incorporating non-fruiting and fruiting trees, and light and heavy cropping.

Holes slightly larger than the boxes were excavated and the rhizotrons installed in October 1988. They were aligned in one row, 4 m apart with the plexiglass panels in each box facing outwards and the top of each window at soil level. To ensure good contact with the plexiglass, the top-soil was carefully packed against each of the viewing panels to the same dry bulk

density as the surrounding soil (1.1 t m^{-3}). Once in position the rhizotrons were fitted with solid lids with an upper silver surface to block light and reflect heat. Apart from removal for access to the panels each month (ca. 30-45 mins. to collect data) the covers remained closed for the duration of the study. After installation, the soil 3 m either side of the rhizotrons was deep-ripped to 1 m, and planting sites adjacent to each window prepared by incorporating 9 l of chicken manure, 250 g of superphosphate (9% P) and 500 g of dolomite m^{-2} surface area.

During 1988 'Velvick', a Guatemalan race seedling selected in Queensland; 'G755A', a *Persea schiedeana* x *P. americana* hybrid rootstock, and 'Duke 7', a Mexican race selection both from California (Coffey *et al.* 1988) were clonally propagated using the nurse-seedling technique (Frolich and Platt 1971-72, modified by Brokaw), and were grafted to 'Hass' scions. A number of seedling 'Velvick' rootstocks were also grafted to 'Hass' scions. All propagation material used in this study had been previously tested and certified free of Sunblotch viroid, a potentially serious disease of avocado (da Graca 1985). In March 1989, five 'Hass' trees on each of the four rootstocks were randomly planted in central positions 1 m from the windows. To control weed growth and assist in reducing fluctuations in soil matric potential (ψ_s), trees were mulched with barley straw spread 1 m from the trunk and to a depth of 100 mm, within a week of planting. This mulch was maintained for three years after planting by which time tree canopies provided sufficient ground shade and became self-mulching through the accumulation of leaf litter.

At the time of planting, under-tree mini-sprinklers (10 l hr^{-1}) were installed at each site to supplement natural rainfall. Soil matric potential was monitored 0.5 m from rhizotron walls using permanently installed tensiometers at 30 and 75 cm depth. During dry periods tensiometers were checked at weekly intervals and irrigation given to maintain $\psi_s \leq 40 \text{ kPa}$ at 30 cm and $\leq 50 \text{ kPa}$ at 75 cm depth. Trees were fertilised according to the schedule for tree age developed for avocados growing in S.E. Queensland (Banks 1992). The exception to this program was the additional 4 g m^{-2} of canopy of Solubor (22% elemental B) soil-applied in spring and summer each year due to known boron deficiencies and the high buffering capacity of the soil at this site (A.W. Whiley, unpublished data).

Root measurements were made only of the white, unsuberised "feeder" roots. Data were collected at monthly intervals by tracing the outline of roots visible at the soil-panel interface onto transparent sheets of acetate with a black indelible pen. Only those portions of roots that were visible at the interface were recorded. No distinction was made between roots of different diameters. Only some of the white "feeder" roots became suberised (browning) after which they were no longer measured. The information on the acetate sheets was digitised by scanning to an electronic file using a Hewlett Packard ScanJet Iic. Root lengths were determined by computerised image analysis (Sci-Scan Image Analysis System, Delta T, UK). This method gave a total length (m) of visible white root at the soil-panel interface (0.58 m^2 vertical window area) each month.

Beginning in 1991 trunk girth measurements were taken during July of each year in positions demarcated by white acrylic paint marks, above and below the graft union. In 1992, the first year of heavy cropping, the diameter and height of the trees were measured and the canopy volume calculated using the models for a half sphere and a cylinder. This was the only year

that canopy measurements were taken as trees began to crowd in 1993 and side canopies had to be pruned.

Reproductive and vegetative phenology data were collected for four seasons at monthly intervals, or more frequently when necessary, using the system of Whiley *et al.* (1988a). Floral bud development was ranked on a 0 to 10 scale where 0 = no visible development and 10 = opening of the first flower. Flowering was judged by recording the first and last dates of anthesis and estimating the time that 50% of the flowers had opened. All qualitative estimates were made independently by two people and the mean of the scores used for fitting the data. Fruit drop in spring was estimated by counting fruit on three tagged shoots on each of five trees at weekly intervals from the end of anthesis until numbers were relatively stable. The weekly data were calculated as a percentage of the total fruit that dropped from the tagged shoots. In summer, fallen fruit under each tree were counted and removed at weekly intervals. These data were calculated as a percentage of the total number of fruit on the tree at harvest, reflecting the crop loss after a substantial growth investment (30-40% of full size). At the completion of anthesis three indeterminate and three determinate inflorescences on each of five trees were tagged and individual fruit lengths on each shoot measured with electronic callipers at weekly intervals for the first five months after fruit set and then monthly until harvest. When harvesting the two "on" crops (1992 & 1994), fruit which developed on either indeterminate or determinate shoots were recorded separately.

For nitrogen and starch analysis, the most recently matured summer-flush leaves were selected at monthly intervals from May until December 1992. Thirty leaves were randomly collected from each tree and equally divided into sub-samples; one for nitrogen and the other for starch analysis. Leaves for nitrogen analysis were washed in a solution of mild detergent (1 ml l^{-1}) and acetic acid (0.6 ml l^{-1}), rinsed in distilled water, dried at 52°C for three days, milled and re-dried at 105°C immediately prior to determinations. Nitrogen was measured using a Kjeldahl digest of sulphuric acid, sodium sulphate and selenium catalyst (McKenzie and Wallace 1954). The digestate was diluted prior to automatic colorimetric analysis using the indophenol reaction with salicylate and sodium dichloroisocyanurate (Berthelot 1959).

Wood samples were collected for starch analysis from the large roots radiating from the crown of the rootstock and from the scion region of the trunk after June 1992, when it was judged that trees were large enough to support a monthly program of this nature. For each organ, samples were obtained from five sites around the tree by first removing a plug of bark and then drilling 40 mm into the wood with a 9 mm diameter bit. The drilled shavings from each hole were bulked for analysis.

Starch samples were placed in a cool, insulated box for transport back to the laboratory and within 3 hrs of collection, were transferred to a convection oven at 60°C and dried to constant mass. Dried samples were ground at 100 mesh in a Udy Mill (Udy Corporation, USA) and stored in an airtight container. Starch was determined by a two stage enzymatic hydrolysis of the starch to glucose and the concentration measured colorimetrically using a coupled glucose oxidase/peroxidase/chromogen system as described by Rasmussen and Henry (1990).

Photo-assimilation studies were carried out from March to December 1992 on 'Hass' trees growing in the rhizotron and grafted to cloned 'Velvick' rootstocks. When summer-flush shoots were nearing maturity, five fully expanded sun-exposed leaves were tagged on the northern sides of trees. At the time of selection the leaves were ca. 40 days old and fully expanded, and to lessen "sink" effects were at least 0.5 m from the nearest fruit. Net CO₂ assimilation (*A*) was measured at monthly intervals with a LICOR LI-6200 portable photosynthesis meter configured as a closed system (LICOR, Nebraska, USA) and using a LI-6000-11, 1 l chamber. All measurements of *A* were made at or above PPFs of 1200 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ and between 0830 to 1030 h, a low stress time of day (Whiley *et al.* 1988b). Photosynthetic rates were derived from LI-6200 Software Version 2.00.

Chlorophyll concentrations were determined from five leaves on the northern side of the same trees used for photo-assimilation studies. Two discs totaling 1.0 cm² were sampled from either side of the midrib of each leaf and the discs pooled for each tree. Chlorophyll was extracted with 85% acetone from the discs kept in darkness at 25°C for 48 h. Measurements were made spectrophotometrically as described by Proctor (1981).

An automatic weather station (Monitor Sensors, Caboolture, AUST.) was positioned at the site to record rainfall and air and soil temperatures. The soil temperature sensor was installed at 450 mm below the surface in a position equi-distant between the top and bottom of the recording field. Data presented in the figures are the means \pm SEs of pooled values from five trees.

Results and Discussion

Some trees on 'Duke 7' and 'G755A' rootstocks died in the second and third years of the project (Verticillium wilt). Therefore only data for trees propagated on cloned and seedling 'Velvick' rootstocks are presented.

Rootstocks and Root Phenology

Twenty-seven months after planting an over-growth of the scion, expressed by a scion/rootstock girth ratio of > 1.0 , was detected in trees grafted to cloned 'Velvick' rootstocks (Table 1). The over-growth in this scion/rootstock combination persisted for the duration of

Table 1 Scion/rootstock girth ratios of cv. Hass trees grafted to cloned and seedling 'Velvick' rootstocks. The ratios were calculated from girth measurements taken above and below the graft union. Data are mean values of five trees \pm standard errors.

Rootstock	Scion/rootstock ratio			
	1991	1992	1993	1994
Cloned 'Velvick'	1.15 \pm 0.04	1.21 \pm 0.04	1.20 \pm 0.05	1.17 \pm 0.01
Seedling 'Velvick'	0.94 \pm 0.02	0.97 \pm 0.01	0.98 \pm 0.01	1.00 \pm 0.01

the study indicating mild incompatibility. In contrast, trees grafted to seedling 'Velvick' were near normal (slightly favouring the rootstock) with respect to scion/rootstock relationships. The compatibility of graft unions between the same species is ultimately a function of biochemical events (Leakey 1985). In *Pinus contorta*, scion overgrowth has been attributed to translocation incompatibility wherein a degree of phloem degeneration and necrosis is evident (Copes 1975). Compatibility of this type does not necessarily indicate that the combination is without merit and indeed it may be exploited for horticultural gain.

The first roots were visible at the soil-panel interface in some boxes by March 1990, but due to insufficient numbers recording did not begin until July 1990 when all windows were colonised. Note that where time is plotted as the abscissa in Figs. 2 & 3 it refers to time elapsed since 1 June 1990 (June is early winter in the southern hemisphere); thus each calendar season refers to a three month period, e.g. spring is from September through November.

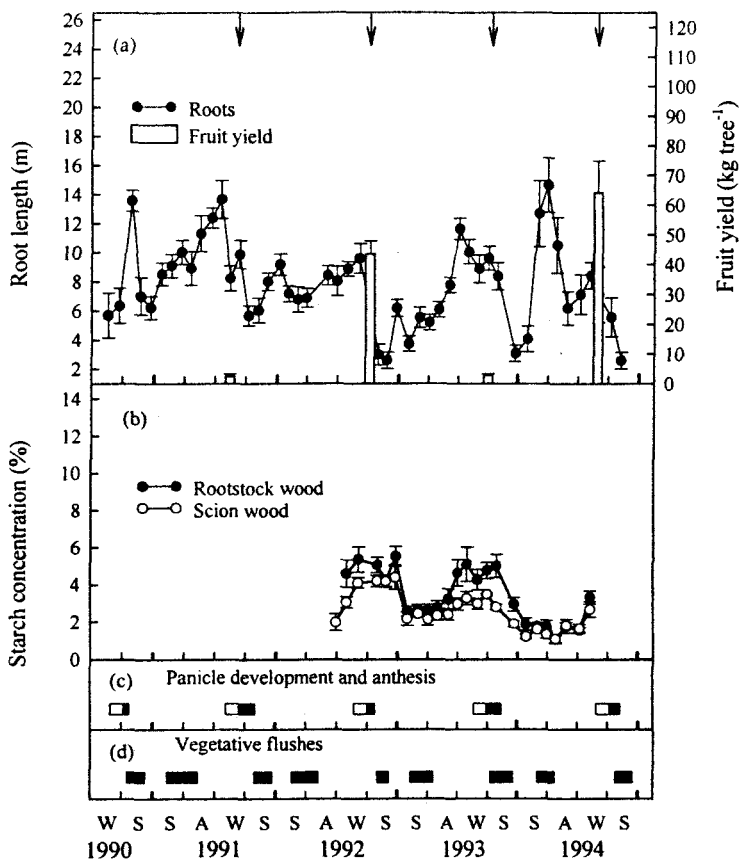


Figure 2 Root growth and starch cycling over a 4½ yr period in cv. Hass grafted to cloned 'Velvick' rootstock as they relate to above ground tree phenology and yield where: (a) is seasonal changes in root length per 0.58 m² vertical window area, and annual fruit yield (arrows indicate harvest times); (b) is seasonal changes in starch concentration of the rootstock and scion portions of the tree; (c) are periods of inflorescence development represented by the open bars, and anthesis represented by the closed bars; and (d) are periods of shoot growth. Root length, yield and starch data are mean values of five trees ± vertical SE bars.

There were strong seasonal variations in total measured root length of both rootstocks (Figs. 2 & 3). These appeared independent of soil temperatures at 450 mm depth which varied by 7.5°C between summer (23.5°C) and winter (16.0°C). Typically, two peaks of root growth occurred over a one year period; the first of the new season in spring and generally concomitant with spring flush, and the second beginning in late summer and peaking in winter immediately prior to anthesis (Figs. 2 & 3). The pattern was more pronounced in trees grafted to seedling 'Velvick' rootstocks and was not always apparent in trees growing on the cloned material. Similar bimodal periodicity for avocado root growth has been previously described by Whiley *et al.* (1988a) and Ploetz *et al.* (1992), although in both cases the extension of the second growth phase through winter to anthesis was not indicated. It is likely that roots observed in the surface mat technique used by Whiley *et al.* (1988a) suffered desiccation during the dry winter months giving the impression of growth cessation, while the young trees used by Ploetz *et al.* (1992) may not have developed root cycles typical of mature fruiting trees. The two-peak annual cycle has similarities with deciduous fruit crops (Head 1967; Rogers and Head 1969), however the major difference is extension of the second growth period of avocado roots into winter in this cool, mesic subtropical environment. With avocado major points of interest are alternation between shoot and root flush peaks; the prolonged winter root growth in deeper, warmer and moister soil zones; and the pronounced reduction in feeder root growth (die-off of feeder roots) during flowering and fruit set.

The bimodal periodicity observed in this study is likely due to competition between shoots and roots for photo-assimilates in this complex, much branched tree. In photosynthate translocation studies with avocado it was found that when leaves were exposed to ^{14}C during active shoot growth 43% was recovered in the new shoots while only 5% was recovered from roots. In contrast, when leaves were exposed during a period of shoot quiescence, 32% of the ^{14}C was recovered from the roots and only 5% from the most recent shoot flush (Whiley and Schaffer 1993).

The greatest root lengths were recorded during the first two years of the study when they reached ca. 14 m per 0.58 m² of window observation area for a month, and again in the fifth year when root length of the seedling 'Velvick' rootstock reached 25.8 m per 0.58 m² of window observation area. At other times root length was lower with maximum recordings from ca. 9 to 11 m for any one observation time. Root lengths during the first two years of the study may be due to either greater root activity at the peripheral zone of the tree's canopy, which was approximately aligned with the side of the rhizotrons 18 months after planting; or proportionally greater root growth in non-fruiting trees. The latter is supported by the root patterns determined for 'Hass' trees grafted to cloned 'Velvick' where during the 1991/92 season, trees carried ca. 44 kg of fruit and maximum root lengths measured were ca. 9 m (Fig. 2). In contrast, the 1992/93 crop was small (ca. 3 kg tree⁻¹) and the maximum root length at the soil-panel interface reached 11.6 m. Differences were not as clear with 'Hass' trees grafted to seedling 'Velvick' rootstocks though root growth on average during the fruiting years was greater than those trees on cloned rootstocks; 8.0 ± 0.3 m compared with 7.1 ± 0.4 m respectively (Figs. 2 & 3). Trees on both rootstocks showed strong root growth following spring shoot maturation in 1993 despite trees carrying a heavy crop. This is likely due to the vigorous shoot growth which was observed following anthesis. However, root growth during the late summer and winter was markedly suppressed, which is probably related to fruit lipid

accumulation (Kaiser and Wolstenholme 1994) and growth of fruit which occurs during this period.

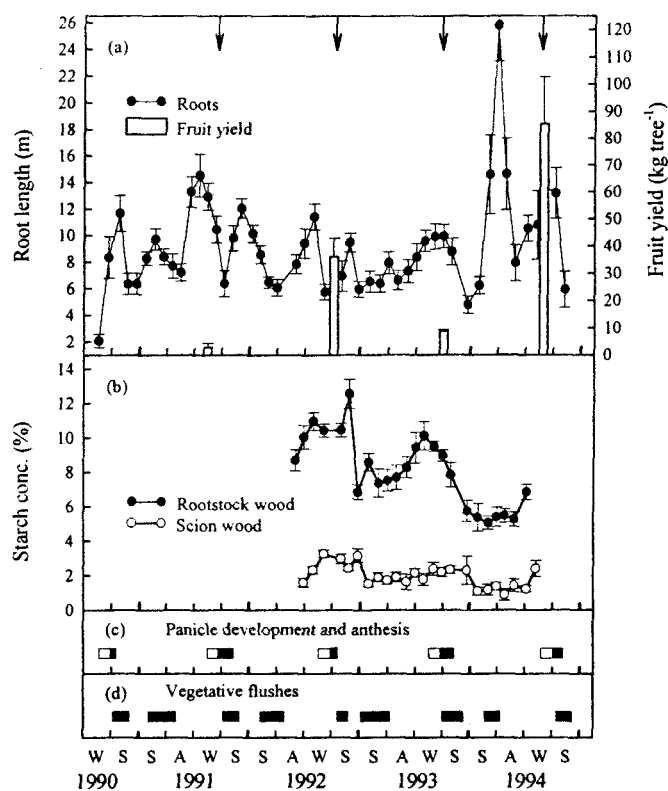


Figure 3 Root growth and starch cycling over a 4½ period in cv. Hass grafted to seedling 'Velvick' rootstock as they relate to above ground tree phenology and yield where: (a) is seasonal changes in root length per 0.58 m² vertical window area, and annual fruit yield (arrows indicate harvest time); (b) is seasonal changes in starch concentration of the rootstock and scion portions of the tree; (c) are periods of inflorescence development represented by the open bars, and anthesis represented by the closed bars; and (d) are periods of shoot growth. Root length, yield and starch data are mean values of five trees ± vertical SE bars.

The lower impact of fruiting on seedling rootstock may be due to the greater vigour of these trees. The effect of cropping on root growth of trees has been reported on many occasions and the outcomes have generally been consistent. Head (1969) found reduced periodicity and magnitude of new root growth in fruiting apple trees with the major summer growth peak eliminated in some years. Similarly, Ryhakov and Dzavakjanc (1967) and Dzhavakyants (1971) reported that cropping in apples reduced the number of root growth peaks from two in vegetative trees to one per season. Others finding adverse effects of cropping on root growth include Maggs (1963), Avery (1970), Cannell (1971) and Atkinson (1977). This is not surprising when considered in the context of the "priority sinks" philosophy. Here developing seeds (fruit) have a large "sink strength" or "mobilising ability" to attract photo-assimilates and are usually more competitive than other plant organs, of which roots are generally

acknowledged as among the weakest sinks of the plant (Cannell 1971; Chalmers and van den Ende 1975; Lenz 1979). For example, the proportion of the annual increment of dry mass allocated to the root system decreased from 20% in young peaches, to 1% in fruiting peach trees (Chalmers and van den Ende 1975).

There were seasonal changes in the starch content of major roots and the scion trunks of both scion/rootstock combinations (Figs 2 & 3). Accumulation occurred during the autumn and winter when shoots were quiescent with concentrations falling rapidly during or just after anthesis. However, it is very noticeable that the starch concentration in the large woody roots of the seedling 'Velvick' was always about double that in the cloned 'Velvick' rootstock. There was also a direct relationship between the root starch concentration of seedling 'Velvick' roots and root length (Fig. 4). This relationship would be expected as more photo-assimilates are translocated to the roots during relatively quiescent periods in the aerial portions of tree, thereby increasing the growth of roots, and remobilised to stronger aerial sinks at critical stages of phenological development, e.g. flowering, fruit set and seed growth.

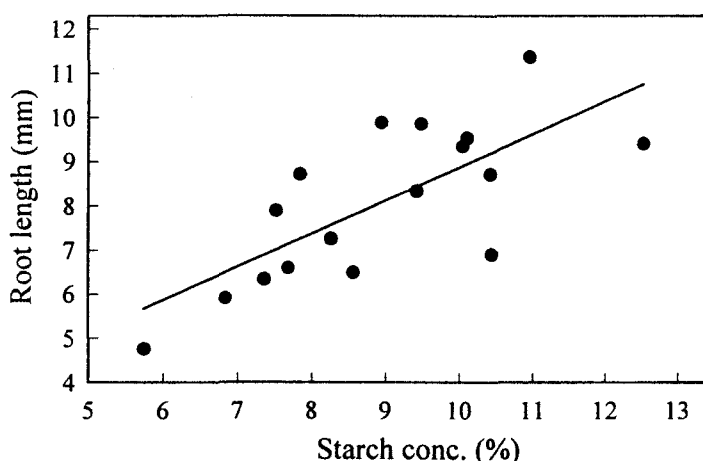


Figure 4 Relationship between starch concentration in the rootstock and root length measured at the soil-panel interface. The regression is represented by the equation $y = 1.37 + 0.75x$, $r^2 = 0.55^*$.

Differences in starch concentrations between the two rootstocks may be explained by mild incompatibility between the cloned 'Velvick' rootstock and the 'Hass' scion (Table 1). It is possible that the movement of translocate to roots was impeded due to phloem degeneration (Copes 1975) resulting in less root growth, particularly when trees had a substantial crop load, e.g. 1992 (Figs. 2 & 3). The outcome of less starch moving to the roots was a higher concentration maintained in the scion which was ca. 30% more than the concentrations measured in the 'Hass' scions on the seedling rootstocks.

The mild incompatibility and reduced vigour of the cloned 'Velvick' root system is most likely responsible for the smaller stature of these trees when compared with those on seedling 'Velvick' rootstock. When canopy measurements were taken in September 1992, ca. 30

months after planting, 'Hass' trees grafted to clonal or seedling 'Velvick' rootstocks had canopy volumes of $12.44 \pm 1.38 \text{ m}^3$ and $16.98 \pm 1.22 \text{ m}^3$, respectively. When the 1992 yield performance of trees on the two rootstocks was compared on a canopy volume basis, 'Hass' grafted to clonal 'Velvick' rootstocks produced $3.57 \pm 0.31 \text{ kg m}^{-3}$ of fruit which was significantly greater than the $2.12 \pm 0.42 \text{ kg m}^{-3}$ produced by trees grafted to seedling 'Velvick' rootstocks. These data are supported by a long-term rootstock experiment on the same site where 'Hass' grafted to clonal 'Velvick' rootstocks have continued to have the highest production efficiency on a canopy volume basis when compared with clonal 'Duke 7' and seedling 'Velvick' rootstocks (A.W. Whiley, unpublished data). In this case, mild incompatibility at the scion/rootstock interface and the resultant reduced tree vigour has been an effective horticultural tool in the repartitioning of assimilates to give higher fruit yields.

The central axis or primary inflorescence of avocado is usually terminated by a vegetative bud which at the finish of anthesis grows out into a new shoot (Chandler 1958). However, in some cases the inflorescence is terminated by a panicle sub-unit. The two types are known as either indeterminate or determinate compound inflorescences, respectively (Thorp *et al.* 1994). Compared to other major Mexican/Guatemalan race cultivars, 'Hass' produces a greater proportion of determinate inflorescences which in years of heavy cropping can become a problem due to exposed fruit becoming sunburnt. In their study Thorp *et al.* (1994) reported that in 37% of the floral shoots of 'Hass' the terminal meristem remained reproductive and gave rise to determinate compound inflorescences.

In this study fruit on both indeterminate and determinate inflorescences grew rapidly in length for the first 150 days after fruit set and thereafter the growth rate substantially diminished (Fig. 5). This latter stage of diminished growth coincides with rapid lipid accumulation in the fruit (Kaiser and Wolstenholme 1994). At 40 days after set, determinate fruit were already larger than those set on indeterminate inflorescences and during the first 150 days they maintained a higher growth rate (slope of curves). This growth advantage was still apparent at maturity where determinate fruit were ca. 18% longer than those set on indeterminate inflorescences.

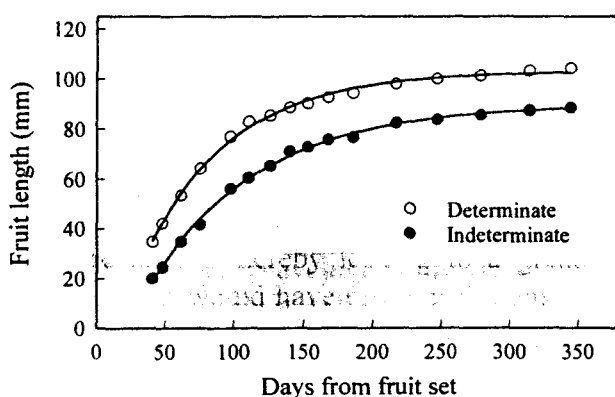


Figure 5 The growth of cv. Hass fruit on indeterminate and determinate terminals from 40 days after fruit set through until maturity. Growth was determined by measuring the increase in fruit length. The regression for determinate fruit is represented by the equation $y = 103.05 - 130.23(0.984^x)$, $r^2 = 0.99$; and the regression for indeterminate fruit is represented by the equation $y = 89.67 - 118.62(0.988^x)$, $r^2 = 0.99$. The curves are significantly different in placement and shape as judged by *t* tests ($P < 0.001$). Data points are mean values of fruit from three terminals on each of five trees.

The growth advantage of fruit on determinate shoots is thought to be due to spatial separation from shoots which develop concurrently with fruit set on indeterminate inflorescences. Using mid-bloom foliar sprays of paclobutrazol to suppress 'Hass' spring shoot growth from indeterminate inflorescences, Wolstenholme *et al.* (1990) reported increased fruit size when shoots matured. This resulted in larger fruit at maturity compared with fruit from the unsprayed control trees.

The yield data for 1992 and 1994 showed that the greatest percentage of fruit harvested from trees on either rootstock was from determinate shoots, > 80% for trees grafted to cloned 'Velvick' and > 60% for trees grafted to seedling 'Velvick' (Table 2). There were significant differences in the indeterminate/determinate yield ratios between rootstocks which was lowest for cloned 'Velvick' for the two years that data were collected.

Table 2 Effect of rootstock on the ratio of indeterminate/determinate fruit on cv. Hass. The ratios were calculated from the 1992 and 1994 crops which were "on" years for these trees. Data are mean values from five trees \pm standard errors; percentage determinate fruit are given in parenthesis.

Rootstocks	Indeterminate/determinate fruit ratio	
	1992	1994
Cloned 'Velvick'	0.22 \pm 0.06 (83.4)	0.17 \pm 0.01 (86.0)
Seedling 'Velvick'	0.91 \pm 0.33 (60.8)	0.48 \pm 0.05 (67.8)

Mechanisms for the production of determinate shoots have not been elucidated but the author has observed that trees infected with *Phytophthora cinnamomi* Rands, which causes Phytophthora root rot, usually have a higher percentage of determinate inflorescences, suggesting that root damage or stress (lack of vigour) is a primary cause. In this study trees grafted to clonal 'Velvick' rootstocks carried ca. 20% more of their crop on determinate inflorescences than trees on seedling rootstocks (Table 2). Of the physiological variables measured, the major difference between trees was in root starch concentrations. There is little doubt that roots play an important role in the regulation of flowering and promotion of bud development through the timely supply of growth regulators (Jackson 1993). It is suggested that the lower assimilate concentration in cloned compared with seedling 'Velvick' roots may have resulted in a reduced capacity of cloned roots to stimulate terminal vegetative buds in the inflorescences thereby leading to a greater proportion of determinate inflorescences. This mechanism would have ecological significance, in that trees in a cropping cycle with depleted reserves would enhance their ability to set and carry more fruit by reducing competition with indeterminate flowering shoots.

Pheno/physiological Models

Leaf starch concentrations of mature summer leaves increased rapidly from March reaching peak concentration in June/July (winter), when there was a sharp decline which coincided with inflorescence development and anthesis (Fig. 6a). The level declined again in November during the onset of leaf senescence. The leaf nitrogen concentration remained relatively stable from April until July, a period of extended quiescence in the canopy of the tree (Fig. 6a). However, there was a sharp decline during the growth of inflorescences. Leaf N concentrations showed recovery during anthesis but declined once more during fruit set and spring shoot growth. The leaf concentration flux of starch and nitrogen showed significant changes which could be related to critical stages of tree phenology. The fall in concentration of both products coincided with inflorescence development and it is likely that remobilisation occurred to support the proximal reproductive sink. The decline in leaf N concomitant with fruit set and shoot growth has similarly been reported in citrus where it was concluded that young vegetative flushes draw nitrogen from reserves in old leaves (Erner 1988).

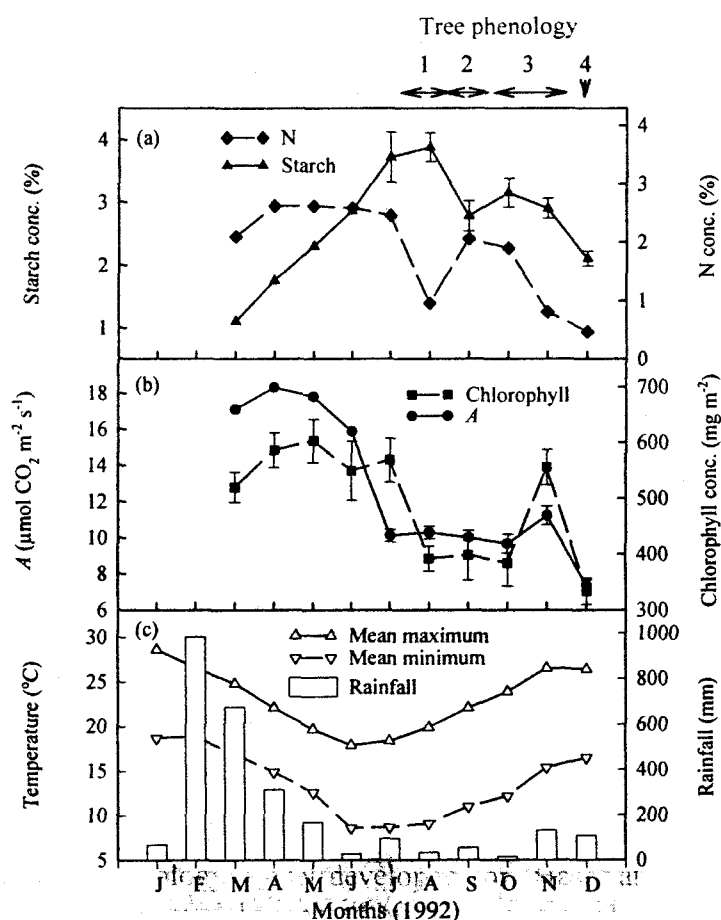


Figure 6 Seasonal changes in nitrogen, starch and chlorophyll concentrations and net CO₂ assimilation (*A*) of summer grown leaves of cv. Hass in relation to phenology (1 = inflorescence development; 2 = anthesis; 3 = fruit set and shoot growth; 4 = leaf senescence) and temperature where: (a) are mean 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.

Net CO₂ assimilation (A) of sunlit summer-flush leaves reached its highest rate in April (18.3 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and then slowly declined through to May (Fig. 6b). By June there was a rapid decline in A which remained at ca. 10.2 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ through to October. There was a small recovery in A by November followed by a rapid decline as leaves senesced. Except for a lag phase going into winter the pattern of chlorophyll concentrations in leaves substantially mirrored A . Levels increased from March to April but then remained stable through to July. There was a sharp decrease in August and concentrations remained low until October when there was a rapid increase through to November, then subsequently a fall as leaves senesced (Fig. 6b).

The autumn decline in A can be attributed to at least three factors. There was an increase in vapour pressure deficits (VPD) over the months that measurements were taken rising from < 1.0 kPa to ≈ 2.4 kPa. VPDs are known to affect A in most crops due to reduced stomatal conductance (g_s) (Schultze 1986). Bower *et al.* (1978) indirectly related lower A in avocado to an increase in VPD, i.e. they showed an inverse relationship between g_s and VPD. Over the duration of this study taking measurements before 1030 h reduced variation in VPD but nevertheless some effect may have occurred.

An increase in leaf starch levels was concomitant with the initial decline in A which may be the effect of end product feedback-inhibition. Schaffer *et al.* (1987) concluded that accumulation of leaf starch in avocado resulted in the inhibition of A . However, the sharp drop in July is more likely due to an inhibition of photosystem II activity brought on by exposure to low temperature stress (Smillie and Hetherington 1983). Smillie *et al.* (1988) reported that many tropical species develop photo-inhibition damage once temperatures fall below 12°C. In this case leaves had been exposed to mean minimum temperatures of $< 10^\circ\text{C}$ for one month prior to measuring the low A values (Fig. 6c). The winter fall in chlorophyll concentration is also more likely to be linked to temperature than to declining N concentrations. The one month lag in relation to the decline in A is consistent with photo-oxidation of chlorophyll, which develops after longer exposure to cold temperatures and an excess of absorbed light beyond that utilised in photosynthesis (van Hasselt 1974; Demmig-Adams and Adams III 1992). The partial recovery in both A and chlorophyll concentrations is consistent with the release from photo-inhibition conditions (Smillie *et al.* 1988) and did not occur until October when mean minimum temperatures rose above 12°C. However, this was at a time when leaf N concentrations were rapidly declining thereby restricting the full potential of A recovery (DeJong 1982; Syvertsen 1984). Furthermore, it is believed that there is strong competition between reproductive and vegetative sinks at this time for available photo-assimilates, either current or from stored sources (Biran 1979; Wolstenholme *et al.* 1990).

The phenology model developed for 'Hass' at Maleny (Fig. 7) has similarities to the earlier schematic model proposed by Whiley *et al.* (1988a) for 'Fuerte' (Fig. 2). The main differences between the two models are firstly the delay of phenological events in relation to the time dimension, e.g. anthesis for 'Fuerte' was early June to late September; for 'Hass' from early August until early October; and secondly the extended root growth through winter culminating in a sharp decline concomitant with inflorescence development and anthesis. The shift in the time frame of growth events illustrates the plasticity of the phenological response which is driven by genotypic/environmental interactions. For instance, 'Fuerte' is an early maturing

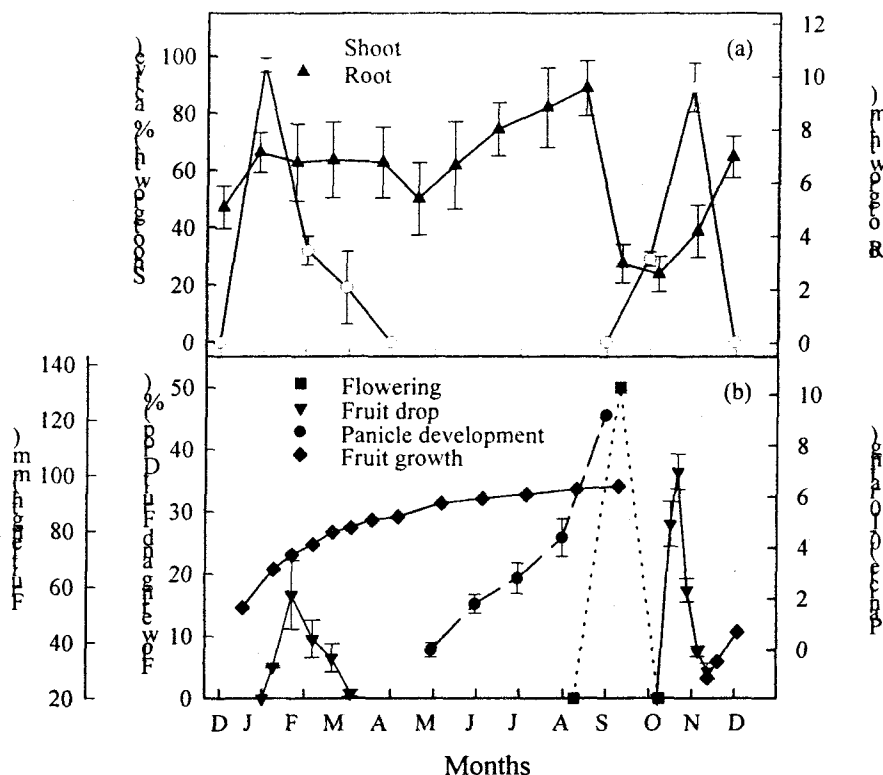


Figure 7 Phenology of cv. Hass on cloned 'Velvick' rootstock growing at Maleny, S.E. Queensland where: (a) is the seasonal relationship between shoot and root growth; and (b) is the relationship between floral development and fruiting. Data points are mean values from five trees \pm vertical SE bars which are obscured by symbols at some points.

cultivar and when studied was growing in a warm coastal environment compared with the later maturing 'Hass' growing in a cool, subtropical highland region. Modification by environmental factors may implement more significant changes to the model as shown by Kaiser and Wolstenholme (1994). In their studies with 'Hass' growing in the cool, mesic subtropical Natal midlands, one extended period of shoot growth was recorded over the spring and summer months in contrast to the bimodal periodicity reported for 'Fuerte' (Whiley *et al.* 1988a) and 'Hass' in this study (Fig. 7). Such changes require careful consideration of likely implications when research hypotheses or management strategies are being tested.

Differences in root growth patterns between the 'Fuerte' model (Whiley *et al.* 1988a) and 'Hass' (Fig. 7) can be explained by the different techniques used to collect the information. For 'Hass', studies were more quantitative and carried out from the surface to a depth of 820 mm thereby integrating results from a more representative zone of root activity than that used for 'Fuerte'. The extended period of root growth during summer through to mid-winter and the starch dynamics of scion/rootstock interactions have tree performance and management implications worthy of further research.

References

- Atkinson, D., 1974. Some observations on the distribution of root activity in apple trees. *Plant & Soil* 40, 333-42.
- Atkinson, D., 1977. Some observations on the root growth of young apple trees and their uptake of nutrients when grown in herbicide strips in grassed orchards. *Plant Sci.* 49, 459-71.
- Atkinson, D., 1978. The use of soil resources in high density planting systems. *Acta Hort.* 65, 79-89.
- Avery, D.J., 1970. Effects of fruiting on the growth of apple trees on four rootstock varieties. *New Phytol.* 69, 19-30.
- Banks, A., 1992. Growing avocados in Queensland, Department of Primary Industries, Brisbane. pp. 1-36.
- Berthelot, M.P.E., 1959. Letter to the editor. *Rep. Chem. Appl.* 1, 284.
- Biran, D., 1979. Fruitlet abscission and spring growth retardation - their influence on avocado productivity. Unpublished M.Sc. Thesis, The Hebrew University of Jerusalem, Israel, (in Hebrew).
- Cannell, M.G.R., 1971. Production and distribution of dry matter in trees of *Coffea arabica* L. in Kenya as affected by seasonal climatic differences and the presence of fruits. *Ann. Appl. Biol.* 67, 99-120.
- Chalmers, D.J. and van den Ende, 1975. Productivity of peach trees: factors affecting dry weight distribution during tree growth. *Ann. Bot.* 39, 423-32.
- Chandler, W.H., 1958. The avocado. In: *Evergreen Orchards*. Lea and Febiger, Philadelphia. pp. 205-28.
- Coffey, M.D., Guillemet, F., Schieber, E. and Zentmyer, G.A., 1988. *Persea schiedeana* and Martin Grande: the period from 1920 to 1975. *Calif. Avocado Soc. Yrbk.* 72, 107-120.
- Copes, D.L., 1975. Graft incompatibility in *Pinus contorta*. *Res. Note Pacif. NW Forest Range Exp. Sta.* PNW-260.
- da Graca, J.V. 1985. Sunblotch-associated reduction in fruit yield in both symptomatic and symptomless carrier trees. *S. Afr. Avocado Grower's Assoc. Yrbk.* 8, 59-60.
- Davenport, T.L. 1982. Avocado growth and development. *Proc. Fla State Hort. Soc.* 95, 92-6.
- DeJong, T.M., 1982. Leaf nitrogen content and CO₂ assimilation capacity in peach. *J. Amer. Soc. Hort. Sci.* 107, 955-9.
- Demmig-Adams, B. and Adams III, W.W., 1992. Photoprotection and other responses of plants to high light stress. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 43, 599-26.
- Dzhavakyants, Z.H.L., 1971. Growth changes in apple root systems (in Russian). *Uzbek Biol. Zh.* 6, 29-31. cited by Atkinson, D., 1985. The distribution and effectiveness of roots of tree crops. *Hort. Rev.* 2, 424-90.
- Erner, Y., 1988. Citrus fruit set: carbohydrate, hormone, and leaf mineral relationships. In: *Manipulation of Fruiting*. C.J. Wright (ed.). Butterworths, London. Pp. 233-2.
- Frankie, G.W., Baker, H.G., and Opler, P.A., 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62, 881-919.
- Frolich, E.F. and Platt, R.G., 1971-72. Use of the etiolation technique in rooting avocado cuttings. *Calif. Avocado Soc. Yrbk.* 55, 97-109.
- Hallé, F., Oldeman, R.A.A. and Tomlinson, P.B., 1978. Tropical Trees and Forests: an Architectural Analysis. Springer, Berlin. pp. 221-8.

- Head, G.C., 1967. Effects of seasonal changes in shoot growth on the amount of unsubscribered root on apple and plum trees. *J. Hort. Sci.* 42, 169-80.
- Head, G.C., 1967. Effects of seasonal changes in shoot growth on the amount of unsubscribered root on apple and plum trees. *J. Hort. Sci.* 42, 169-80.
- Issarakraisila, M and Considine, J.A., 1994. Effects of temperature on microsporogenesis and pollen viability in mango cv. Kensington. *Ann. Bot.* 73, 231-40.
- Jackson, M.B., 1993. Are plant hormones involved in root to shoot communication. *Adv. Bot. Res.* 19, 103-87.
- Janzen, D.H., 1971. Seed predation by animals. *Annu. Rev. Ecol. Syst.* 2, 465-92.
- Kaiser, C., and Wolstenholme, B.N., 1994. Aspects of delayed harvest of 'Hass' avocado (*Persea americana* Mill.) fruit in a cool subtropical climate. II. Fruit size, yield, phenology and whole-tree starch cycling. *J. Hort. Sci.* 69, 447-57.
- Kotzé, J.M., 1979. Phases of seasonal growth of the avocado tree. *S. Afr. Avocado Growers' Assoc. Res. Rpt.* 3, 14-6.
- Leakey, R.R.B., 1985. The capacity for vegetative propagation in trees. In: *Attributes of Trees as Crop Plants*. M.G.R. Cannell and J.E. Jackson (eds.). Institute of Terrestrial Ecology, England. pp. 110-33.
- Lenz, F. 1979. Fruit effects on photosynthesis, light- and dark-respiration. In: *Photosynthesis and Plant Development*. R. Marcelle, H. Clijsters and M. van Poucke (eds.). The Hague: Junk. pp. 271-81.
- Lieberman, D and Lieberman, M., 1984. The causes and consequences of synchronous flushing in a dry tropical forest. *Biotropica* 16, 193-201.
- Maggs, D.H., 1963. The reduction in growth of apple trees brought about by fruiting. *J. Hort. Sci.* 38, 119-28.
- McKenzie, M.A. and Wallace, H.S., 1954. The kjeldahl determination of nitrogen: a critical study of digestion conditions. Temperature, catalyst and oxidising agent. *Aust. J. Chem.* 7, 55-70.
- Ploetz, R.C., Ramos, J.L. and Parrado, J.L., 1992. Shoot and root growth phenology of grafted avocado. *Proc. Second World Avocado Congress* 1, 215-20.
- Possingham, J.V., 1986. Impact of physiological research on the productivity of tropical and subtropical fruit trees. *Acta Hort.* 175, 17-25.
- Proctor, J.T.A. and Creasey, L.L., 1971. Effect of supplementary light on anthocyanin synthesis in McIntosh apples. *J. Amer. Soc. Hort. Sci.* 96, 523-6.
- Rasmussen, T.S. and Henry, R.J., 1990. Starch determination in horticultural plant material by an enzymic colorimetric procedure. *J. Sci. Food Agric.* 52, 159-70.
- Rogers, W.S., 1934. Root studies IV. A method of observing root growth in the field; illustrated by observations in an irrigated apple orchard in British Columbia. *Rpt. East Malling Res. Sta. for 1933*. pp. 86-91.
- Rogers, W.S. and Head, G.C. 1969. Factors affecting the distribution and growth of roots of perennial woody species. In: *Root Growth*. W.J. Whittington (ed.). Butterworths, London.
- Ryhakov, A.A. and Dzavakjanc, Z.L., 1967. Root growth and development under irrigation (in Russian). *Sadovodstvo* 7, 34-5.
- Schaffer, B., Ramos, L., and Lara, S.P., 1987. Effect of fruit removal on net gas exchange of avocado leaves. *HortScience* 22, 925-7.

- Schultze, E.D., 1986. Carbon dioxide and water vapour exchange in response to drought in the atmosphere and in the soil. *Annu. Rev. Plant Physiol.* 37, 247-74.
- Sedgley, M. and Grant, J.R., 1983. Effect of low temperatures during flowering on floral cycle and pollen tube growth in nine avocado cultivars. *Scientia Hort.* 18, 207-13.
- Smillie, R.M. and Hetherington, S.E., 1983. Stress tolerance and stress-induced injury in crop plants measured by chlorophyll fluorescence *in vivo*. *Plant Physiol.* 72, 1043-50.
- Smillie, R.M., Hetherington, S.E., He, J., and Nott, R., 1988. Photoinhibition at chilling temperatures. *Aust. J. Plant Physiol.* 15, 207-22.
- Syvertsen, J.P., 1984. Light acclimation in citrus leaves. II. CO₂ assimilation and light, water, and nitrogen use efficiency. *J. Amer. Soc. Hort. Sci.* 109, 812-17.
- 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.
- Van Hasselt, P.R., 1974. Photo-oxidative damage to the ultrastructure of *Cucumis* chloroplasts during chilling. *Proc. K. Ned. Akad. Wet.* 77, 50-6. cited by Smillie *et al.*, 1988. *Aust. J. Plant Physiol.* 15, 207-22.
- Van Schaik, C.P., Terborgh, J.W. and Wright, S.J., 1993. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annu. Rev. Ecol. Syst.* 24, 353-77.
- Venning, F.D. and Lincoln, F.B., 1958. Development morphology of the vegetative axis of avocado (*Persea americana* L.) and its significance to spacing, pruning practices, and yields of the grove. *Proc. Fla. State Hort. Soc.* 71, 350-6.
- Verheij, E.W.M., 1986. Towards a classification of tropical tree fruits. *Acta Hort.* 175, 137-50.
- Whiley, A.W., Chapman, K.R. and Saranah, J.B., 1988b. Water loss by floral structures of avocado (*Persea americana* cv. Fuerte) during flowering. *Aust. J. Agric. Res.* 39, 457-67.
- Whiley, A.W. and Schaffer, B., 1993. ¹⁴C-Photosynthate partitioning in avocado trees as influenced by shoot development. *HortScience* 28, 850-2.
- Whiley, A.W., Saranah, J.B., Cull, B.W. and Pegg, K.G., 1988. Manage avocado tree growth cycles for productivity gains. *Queensland 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. 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. Yrbk* 10, 45-7.
- Wolstenholme, B.N., 1981. Root, shoot or fruit. *S. Afr. Avocado Growers' Yrbk.* 4, 27-9.
- 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, 315-27.
- Wolstenholme, B. N., 1990. Resource allocation and vegetative-reproductive competition: opportunities for manipulation in evergreen fruit trees. *Acta Hort.* 275, 451-60.
- Wright, S.J. and Cornejo, F.H., 1990. Seasonal drought and the timing of flowering and leaf fall in a neotropical forest. In: *Reproductive Ecology of Tropical Forest Plants*. K.S. Bawa and M. Hadley (eds.). Carnforth: UNESCO Parthenon, Paris. Pp. 49-61.

APPENDIX 1

Whiley, A.W., Sarahah, J.B. and Rasmussen, T.S. 1990. The relationship between carbohydrate levels and productivity in the avocado and impact of management practices, particularly time of harvest. *Talking Avocados*, May/June, 12.



The relationship between carbohydrate levels and productivity in the avocado and impact of management practices, particularly time of harvest.

A. W. Whiley, J. B. Saranah and T. S. Rasmussen, Queensland Dept of Primary Industries

This avocado research project funded by C.O.D. and H.R.D.C. is due to start in July 1990.

The avocado, an oil bearing fruit, has a high energy cost in comparison to sugar producing fruit (for example, apples and citrus). This results in a lower potential yield of fruit per hectare. However, average avocado production in Australia is only about 33% of the estimated potential yield of 32 t ha⁻¹.

Improvement in production efficiency is necessary for the avocado grower to remain competitive and to service the fledgling export markets that are developing. A mature avocado fruit does not ripen when on the tree. Growers commonly use this feature as a 'storage' procedure in the management of marketing their crop. Results from this practice are

often reflected in chronic biennial bearing or complete crop failure in the following year.

Successful marketing (both domestic and export) depends on stability of production so markets can be reliably supplied. Establishing criteria relating to the length of on-tree storage and yield loss in the following year would help in stabilizing production.

A direct relationship exists between the starch concentration in woody tissues of avocado trees before flowering and the fruit yield the following year. With citrus and mangoes, gibberellic acid concentrations in shoot tips are implicated in floral initiation. This research plans to study the effect of harvest date (fruit maturity) on the changing gibberellic acid and starch concentrations in avocado trees and their relationship to the following

years cropping performance. This will lead to the development of strategies that will help in stabilizing and maximising fruit yield.

Objectives

1. To study the impact of time of harvest on current and future yield of early (e.g. 'Fuerte') and late (e.g. 'Hass') maturing cultivars of avocados.
2. To relate the time of crop removal to its impact on reserve starch concentrations in the tree; to examine the feasibility of developing a 'predictive' threshold for future yield.
3. To investigate the role of plant growth regulators on flower initiation, particularly in the presence of late held fruit where flowering often fails.

To gain reliable data it will be necessary for this project to run for a minimum of 3 years.

Market Feedback: Asian Supermarkets? Why not?

Ewan Colquhoun Australian International Business Centre, Brisbane, Qld

Ross Garnaut (Ambassador to China 1985-88) tells us that never before in human history have living standards improved as fast and for so long as in parts of Asia over the past four decades. So, are there any implications for avocado growers in Australia? Does this rapid growth in Asian living standards offer us threats or opportunities? Why should we worry?

Take a casual walk among some of these now affluent urban customers. This will destroy any doubt in your mind.

Supermarket names like Daimaru, Sogo, Tokyu, Cold Storage and Park & Shop are just becoming the mass retailers of premium quality fresh produce from Hokkaido to Jakarta. At home, our own Coles Myer and DJs will feel the heat of Asian retail competition from later next year when the big Japanese retailer Daimura opens in central Melbourne. Others have plans for Sydney and Brisbane.

In the premium Asian supermarket chains you'll see discerning middle and upper income consumers buying Californian oranges, Japanese apples, dairy products from Europe, Australia and New Zealand, chilled chicken from Denmark, a kiwi fruit from Chile or Italy, and live, air-flown mudcrabs grown by a Japanese joint venture company in Thailand.

The first message is simple: global competition at the Asian daily-fresh retail outlets is well advanced. Our competition is not with Australian producers. It comes primarily from multinational overseas outfits who have sorted out their product distribution network and built culturally

sensitive marketing systems to deliver bulk fresh products across the globe. Cashed up Asian consumers are loving it, but can Australia's horticultural industries get together and grasp this supermarket opportunity before our southern hemisphere competitors lock up these growing markets? Chile and South Africa both have lower production costs than Australia, with quality control that is fast improving.

Sceptics may suggest "So what, only a fraction of Asia's 1600 million-odd shoppers buy from these western style supermarkets, the vast bulk (including those billion mainland Chinese) still buy daily from their 'wet' or street market. True enough, but their mountain of foreign cash reserves brings with it education, electricity, TV and refrigerators. Wet markets are being bulldozed all over urban Asia as consumers see how others in the West live. You don't need to make that daily trip to the street market to buy fresh produce when you have a refrigerator.

Consumer buying habits are changing and shopping preferences are being realigned. The well-to-do represent only a small rapidly growing percentage of some Asian populations, but quite massive numbers of sophisticated consumers in other more westernized centres, such as Hong Kong, Singapore, Seoul and all of Japan.

Price becomes less of a barrier to purchase as relative disposable income increases. Last week, single rock melons were selling for A\$25 in Daimaru, Singapore; apples for A\$6 each. Both products were grown

in Japan, where quality is king. As in the US and Western Europe, higher living standards are driving consumers to prefer produce that is fresh, of high quality and nutritious. Australian avocados have the potential to appeal to Asian consumers on all three grounds. Supermarket buyers and agents in Singapore are right now seeking our air shipments of quality avocados.

The second implication: the existing Australian avocado appears to meet the needs of new affluent Asian consumers, with scope for price movement upwards. But to ensure the needs of consumers are met and to keep out the low-priced Chilean competition, we need to add genuine value to our export avocados, through quality assurance and point-of-sale promotion.

"But why not concentrate on servicing the domestic market? There are significant markets for Australian grown avocados right here." Again that's partly true, but without the national grower/packer commitment to quality, the industry may well be faced with intense overseas competition from low cost, high quality products. The pineapple industry is already facing this prospect from the Philippines, with the mango industry currently being challenged in the off-season by the world's biggest producer, India.

So what's the result? Well, we don't need to worry if we are constantly aware of changing consumer preferences and market opportunities in Asia. Building solid business relationships with the Asian supermarket chains is our best approach to long-term market success.

APPENDIX 2

Whiley, A.W., Rasmussen, T.S. and Saranah, J.B. 1992. Effect of time of harvest on fruit size, yield and trunk starch concentrations of Fuerte avocados. *World Avocado Congress II Proceedings*, Orange, California (April 1991). 1, 155-9.

Effect of Time of Harvest on Fruit Size, Yield and Trunk Starch Concentrations of 'Fuerte' Avocados

Anthony W. Whiley and Jack B. Saranah

Maroochy Horticultural Research Station, P.O. Box 5083, SCMC, Nambour, Q4560, Australia

Trevor S. Rasmussen

Department of Primary Industries, Meiers Rd, Indooroopilly, Q4068, Australia

Abstract. Fruit from cv. 'Fuerte' avocado (*Persea americana* Mill) trees were harvested at different stages of maturity judged by flesh dry matter (DM). Treatments included strip-picking trees when fruit reached 21 (the minimum legal standard for avocados in Australia), 24 and 30% DM as well as two other treatments where 50% of the fruit was picked when they reached 21 and 24% DM, respectively, with the balance harvested from these trees at 30% DM. The treatments were applied to the same trees for 3 consecutive years. The seasonal flux of trunk starch concentration was monitored in each of the treatments and the data for the first year of the experiment are presented.

Strip-picking of the trees at 21% and 24% DM, and where 50% of the crop was harvested at 21% DM with the balance at 30% DM, produced about 3.6 t/ha more fruit annually (averaged over the three years) than from those trees harvested when fruit was more mature. The later harvesting of fruit, viz. the crop picked at 30% DM, resulted in pronounced biennial cropping over the 3 years studied. Mean fruit size was significantly greater from those trees where 50% of the fruit were previously harvested at 24% DM with the balance at 30% DM as well as where fruit were harvested after reaching 30% DM compared to fruit from trees which were strip-picked at 21 and 24% DM (about 345 vs. 304 g).

Trunk starch concentrations ranged between 4.5 to 6.3% during the time of active tree and fruit growth. In all treatments, except where the crop was left on the tree until 30% DM, the trunk starch concentration rose to about 7.7% in late winter prior to flowering. The treatment harvested late had a trunk starch concentration of 5.3%. During flowering and fruit set the flux of trunk starch concentrations was negatively correlated to the respective flowering and fruit retention performance of the treatments.

Biennial bearing in fruit tree crops is a persistent problem which by no means has been resolved. While many of the fundamental physiological principles extend over all fruit tree crops, the evergreen trees have a vastly different phenology compared to deciduous trees which creates specific problems in relation to flowering and fruiting. For instance, it is not uncommon for evergreen trees to be carrying fruit while flowering, e.g.,

'Valencia oranges', avocado. Low rates of photoassimilation can result in a greater dependence on reserve carbohydrate for cropping: avocado (Scholfield *et al.*, 1985; Hodgson and Cameron, 1935; mango (Chacko *et al.*, 1982; citrus (Goldschmidt and Colomb, 1982).

The avocado, rich in mono- and polyunsaturated fats (oil), has a high "energy cost" to produce a similar unit weight compared to sugar-producing

fruit (e.g. apples, citrus) and consequently lower yields per hectare must be expected (Wolstenholme 1986, 1987). However, average avocado production in subtropical Australia is only about 33% of the estimated potential sustainable yield of 32 tons per hectare. Production efficiency must be improved for the avocado grower to remain competitive and to successfully service domestic and export markets which depend on stability of production for reliable supply to consumers.

The avocado belongs to a unique group of species which do not ripen fruit which are attached to the tree. This feature is commonly used by growers as "on-tree-storage" in the management of marketing their crop. The consequences of this practice are often reflected in chronic biennial bearing or complete crop failure in the following year. This paper describes the impact of harvesting fruit at different stages of maturity on subsequent fruiting and the seasonal concentration flux of trunk starch in these trees.

Materials and Methods

Seven-year-old 'Fuerte' trees grafted to seedling Guatemalan race rootstock growing in a commercial orchard in southern Queensland (latitude 25°S) were used in the study. The trees were planted 6 x 9 m (150 trees/ha) and were irrigated with micro-sprinklers. Nutrition was programmed using leaf and soil analysis and scheduled as described by Whaley *et al.* (1988). Trees were sprayed at 3 to 4 week intervals during fruit development with copper fungicides and pesticides to control diseases and insect damage (Peterson and Inch, 1980; Fitzell, 1987). Fruit was harvested at various stages of maturity as judged by the percentage moisture in the flesh (Swartz, 1976). The five treatments chosen are described as follows:

1. All fruit harvested at 21% DM;

2. All fruit harvested at 24% DM;

3. 50% of fruit harvested at 21% DM and 50% harvested at 30% DM;

4. 50% of fruit harvested at 24% DM and 50% harvested at 30% DM; and

5. All fruit harvested at 30% DM.

Starch concentration was determined in wood samples collected from the tree trunks. The samples were collected at monthly intervals by drilling four 9 mm diameter cores of wood to the depth of 40 mm from the trunks. Samples were oven-dried to constant weight at 60C, milled to 100 mesh (Wiley Mill), and stored in airtight containers at -4.0C. Starch was analyzed using a two stage enzymic procedure to hydrolyze the starch to glucose which was then determined colorimetrically using a coupled-enzyme chromogen system (Rasmussen and Henry, 1990).

Results

There were no significant differences in yield between any of the treatments in the first year (1988) of the experiment confirming that the choice of trees was relatively uniform (Table 1). In the second year of the experiment, harvesting at the most advanced stage of maturity (30% DM) the previous year significantly ($P \leq 0.05$) reduced fruit yield by as much as 100 percent compared to some other treatments (Table 1). Fruit yield in the third year (1990) was not significantly different between treatments. The cumulative yield for the three years of the experiment gave significantly less fruit for the treatment harvested at 30% DM compared with the three treatments where fruit was harvested at the earliest stages of maturity (Table 1). Fruit size (pooled data for the three years) was significantly ($P \leq 0.05$) larger from those

Table 1. Annual and cumulative yield from trees harvested at different stages of fruit maturity (DM). Data are means from each of 6 trees. Means in columns not showing common letters are significantly different ($P \leq 0.05$).

DM at harvest	Yield (kg/tree)				Mean fruit size (g) (Pooled for 1988-90)
	1988	1989	1990	1988-90	
21% DM	127.2	147.4 a	168.4	442.9 a	302.1 c
24% DM	142.6	135.7 a	180.3	458.6 a	305.6 c
21% + 30% DM	152.5	131.1 a	171.5	455.2 a	328.0 b
24% + 30% DM	132.4	115.6 a	142.6	390.6 ab	347.6 a
30% DM	135.9	70.4 b	172.4	378.6 b	341.8 a

trees harvested at the most advanced stages of maturity (Table 1).

Trunk starch concentrations were variable from January until June without any significant differences between treatments. However by August, starch concentrations in all treatments with some or all fruit removed at 21 or 24% DM, had risen sharply and were significantly ($P \leq 0.05$) higher than the treatment where fruit were left until reaching 30% DM (Fig. 1). There were no significant differences in trunk starch concentrations in October but by December the treatment harvested at 21% DM was significantly ($P \leq 0.05$) lower than the treatment harvested at 30% DM (Fig. 1).

Discussion

Either complete harvest of fruit from trees when fruit reaches 21 to 24% DM or removal of 50% of the crop at 21 to 24% DM with the balance later, will maintain the greatest productivity in 'Fuerte' avocados. Fruit yields in the vicinity of 22.5 t/ha (averaged over 3 years) were recorded from trees managed in this manner. However, trees used for "on-tree-storage" of the crop until 30% DM was reached yielded 18.9 t/ha (averaged over 3 years), 3.6 t/ha less than earlier harvesting practices. For the period of the study there were no

real differences in fruit yield among those treatments where some or all fruit were removed by 24% DM suggesting a certain level of flexibility for the orchardist in handling his crop without an adverse impact on yield.

Prolonged "on-tree-storage" of 'Fuerte' fruit has demonstrated the ability of crop load to induce severe biennial bearing in trees (Table 1). The reduction in fruit yield from 20.4 t/ha (135.9 kg/tree) to 10.6 t/ha (70.4 kg/tree) and the subsequent recovery to 25.9 t/ha (172.4 kg/tree) in the third year, illustrates the severity of the biennial cycle that can be induced under environmental conditions favorable for production (Whiley and Winston, 1987). The impact of time of harvest on biennial cropping has similarly been reported for late maturing 'Valencia' oranges (Hilgeman *et al.*, 1967).

Reserve carbohydrate has been implicated with productivity of many tree crops (Monselise and Goldschmidt, 1982) and the relationship demonstrated for avocado growing in a "Mediterranean" type climate (Scholefield *et al.*, 1985). In the first year of our study (Fig. 1) trunk starch concentrations rose sharply immediately prior to anthesis (August-September) in those trees where at least 50% of the crop was removed by mid May. The low trunk starch concentration of the 30% DM harvest

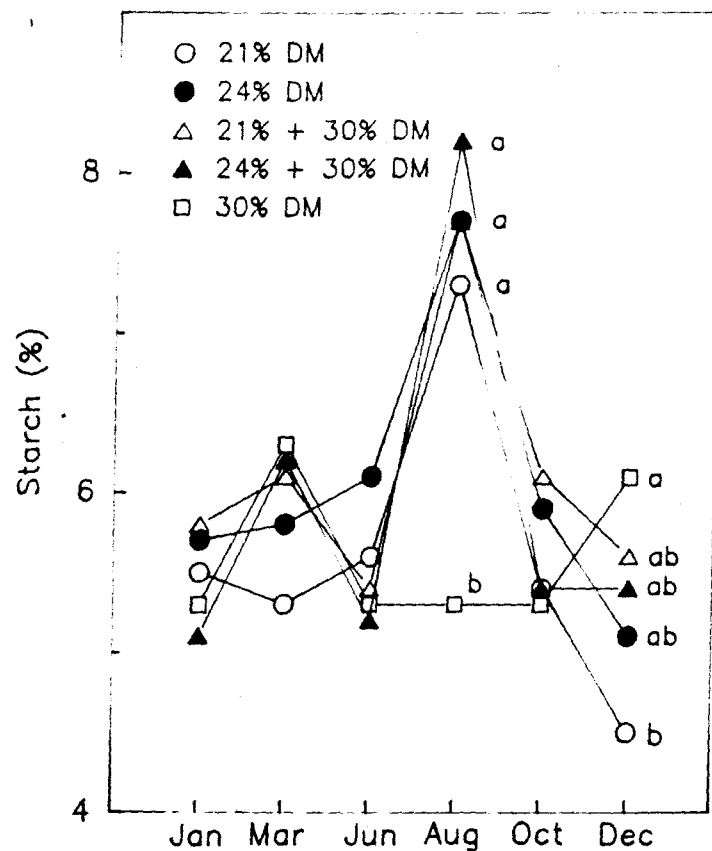


Fig. 1 Seasonal (1988) flux of trunk starch concentrations in cv. 'Fuerte' trees where fruit was harvested at different stages of maturity. Datum points are mean values from 6 trees. Points (vertically) not showing common letters are significantly different ($P \leq 0.05$).

treatment is directly correlated to the low yield (10.6 t/ha) in the following season. The low starch concentration of the 21% DM harvest treatment in December likewise may be attributed to the heavy flowering and fruit set (data not presented) recorded in these trees.

While our first year data produces some evidence of relationships between trunk starch concentrations and tree performance, the seasonal concentration flux (about 3-8%) is far short of the magnitude (about 2-17%) reported by Scholefield *et al.*, (1985). Furthermore, we have not been able to demonstrate a significant relationship in the following two years of the study. Recent investigations have demonstrated a greater magnitude of seasonal flux of starch concentrations in other organs (*viz.* roots, shoots and

leaves) and these will be a focus of future research.

Literature Cited

- Chacko, E.K., Y.T.N. Reddy, and T.V. Ananthanarayanan. 1982. Studies on the relationship between leaf number and area and fruit development in mango (*Mangifera indica* L.). *J. Hort. Sci.* 57:483-492.
- Fitzell, R.D. 1987. Epidemiology of anthracnose disease of avocados. *S. A. Avocado Growers' Assn. Yrbk.* 10:113-116.
- Goldschmidt, E.E., and Golomb, A. 1982. The carbohydrate balance of alternate-bearing citrus trees and significance of

- reserves for flowering and fruiting. *J. Amer. Soc. Hort. Sci.* 107:206-208.
- Hilgeman, R.H., J.A. Dunlap, and F.O. Sharp. 1967. Effect of time of harvest of 'Valencia' oranges in Arizona on fruit grade and size and yield, the following year. *Proc. Amer. Soc. Hort. Sci.* 90:103-109.
- Hodgson, R.W. and S.H. Cameron. 1935. Studies on the bearing behavior of the 'Fuerte' avocado variety. *Calif. Avocado Soc. Yrbk.* 1935:150-165.
- Monselesse, S.P., and E.E. Goldschmidt. 1982. Alternate bearing in fruit crops. *Hort. Rev.* 4:128-173.
- Peterson, R.A., and A.J. Inch. 1980. Control of anthracnose on avocados in Queensland. *Queensland J. of Agr. and Animal Sci.* 37:79-83.
- Rasmussen, T.S., and R.J. Henry. 1990. Starch determination in horticultural plant material by an enzymic-colorimetric procedure. *J. Sci. Food Agr.* 52:159-170.
- Scholefield, P.B., M. Sedgley, and D. McE. Alexander. 1985. Carbohydrate cycling in relation to shoot growth, floral initiation and development and yield in the avocado. *Scientia Hort.* 25:99-110.
- Swartz, D.H. 1976. Praktiese avokado-oliebepalings metode vir produsente. *Citrus and Subtrop. Fruit J.* 511:8-11, 14.
- Whiley, A.W., and E.C. Winston. 1987. Effect of temperature at flowering on varietal productivity in some avocado growing areas in Australia. *S. A. Avocado Growers' Assn. Yrbk.* 10:45-47.
- Whiley, A.W., J.B. Saranah, B.W. Cull, and K.G. Pegg. 1988. Manage avocado tree growth cycles for productivity gains. *Queensland Agr. J.* 114:29-36.
- 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. A. Avocado Growers' Assn. Yrbk.* 10:58-61.

APPENDIX 3

Whiley, A.W. and Saranah, J.B. 1992. Managing fruit harvest for sustainable yield. *Proceedings of the AAGF Conference '92 'Management into the future'*, Gold Coast (September 1992).

MANAGING FRUIT HARVEST FOR SUSTAINABLE YIELD

A.W. WHILEY and J.B.SARANAH

DPI, Maroochy Horticultural Research Station, PO Box 5083, SCMC, Nambour, 4560

INTRODUCTION

Agricultural systems harvest energy from sunlight and through the photosynthetic process, convert and store it in carbon-based consumable products. In horticultural systems these products result from direct packaging of photo-assimilates within the crop, e.g. fruit and vegetables. The success of these systems depends on their relative efficiency, level of technological development and how well they are managed.

Perennial fruit tree crops are complex systems as their cropping behaviour is influenced by both current and preceding events. Trees have the capacity to store photo-assimilates surplus to current needs and to remobilise these during critical periods of demand, e.g. flowering and fruit set. The avocado, rich in mono- and poly-unsaturated fats (oil), has a high 'energy cost' to produce fruit when compared with other species (e.g. apples, citrus, peaches, mangoes). It also has a unique feature of not ripening fruit while attached to the tree even though maturity has been reached. This latter characteristic is commonly used by producers as an "on-tree-storage" facility in the management of marketing their crop. The consequences of this practice are often reflected in chronic biennial bearing with little or no fruit production in alternate years. In recent times fruit size has become a more significant marketing factor with premium prices paid for specific packs. Research examining the impact of harvest time on subsequent fruit size and yield has progressed for a number of years and the preliminary results from these long-term investigations are discussed in this paper.

MATERIALS AND METHODS

Two locations were chosen for this research - one at Childers where 7-year-old 'Fuerte' trees were studied and the other at Maleny using 10-year-old 'Hass' trees. In each case trees were managed as per normal commercial practice. Nutrition was programmed using leaf and soil analysis and scheduled according to current recommendations. Trees were sprayed at 3-4 week intervals during fruit development with copper fungicides and pesticides to control diseases and insect damage. Fruit was harvested at various stages of maturity as judged by the percentage dry matter in the flesh. The five treatments chosen are described as follows:

1. All fruit harvested at 21% DM ('Fuerte') or 24% DM ('Hass')
2. All fruit harvested at 24% DM ('Fuerte') or 30% DM ('Hass')
3. 50% of fruit harvested at 21% DM ('Fuerte') or 24% DM ('Hass') and 50% harvested at 30% DM ('Fuerte') or 35% DM ('Hass')
4. 50% of fruit harvested at 24% DM ('Fuerte') or 30% DM ('Hass') and 50% harvested at 30% DM ('Fuerte') or 35% DM ('Hass')
5. All fruit harvested at 30% DM ('Fuerte') or 35% DM ('Hass')

RESULTS AND DISCUSSION

Yield and fruit size data from the 'Fuerte' trees has been collected over five years. Production on an annual basis shows the normal biennial fluctuations associated with tree fruit production (Figure 1a).

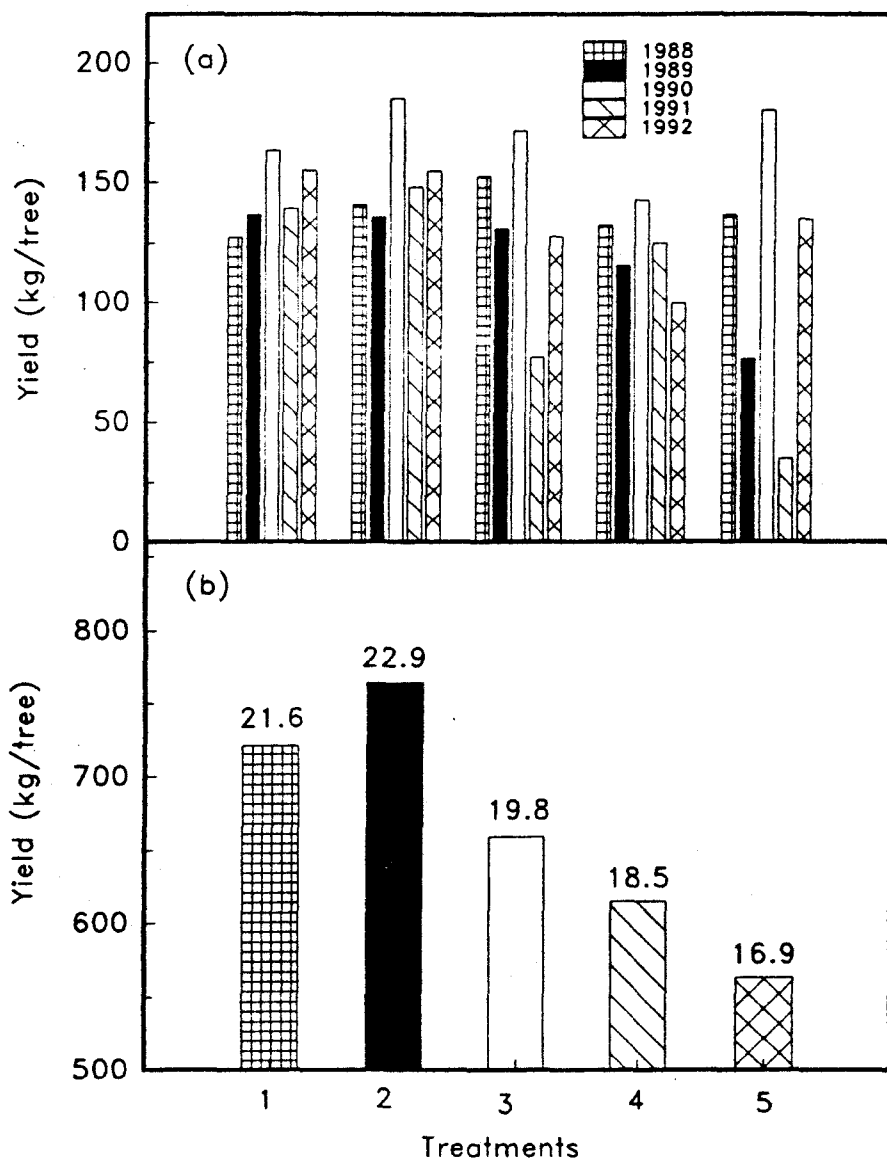


Figure 1. The effect of time of harvest on fruit yield of 'Fuerte' trees where (a) is the mean yield per tree and (b) is the cumulative yield for each treatment over the 5 years of the experiment. Column figures in (b) indicate the annual yield (t/ha) for each treatment. The treatments were: (1) all fruit harvested at 21% DM; (2) all fruit harvested at 24% DM; (3) 50% of fruit harvested at 21% DM and 50% harvested at 30% DM; (4) 50% of fruit harvested at 24% DM and 50% harvested at 30% DM; (5) all fruit harvested at 30% DM.

The strip picked treatments at 21 and 24% DM (treatments 1 & 2) have minimised the annual variability in yield. However, when fruit were held on the tree for longer periods (treatments 3, 4 and 5) the on/off cycle became more accentuated, reaching its greatest oscillation when fruit were hung until reaching 30% DM (Figure 1a). Fruit yield was highest in the two strip picked treatments at 21 & 24% DM with the annual average yield equivalent to about 22 and 23 t/ha respectively (Figure 1b). There was a marked drop off in yield when part or all of the crop was hung late, i.e. to fruit reaching 30% DM.

The early harvested strip picked treatments (Figure 2) gave the smallest fruit with size gains of up to about 15% when fruit was differentially harvested and hung later.

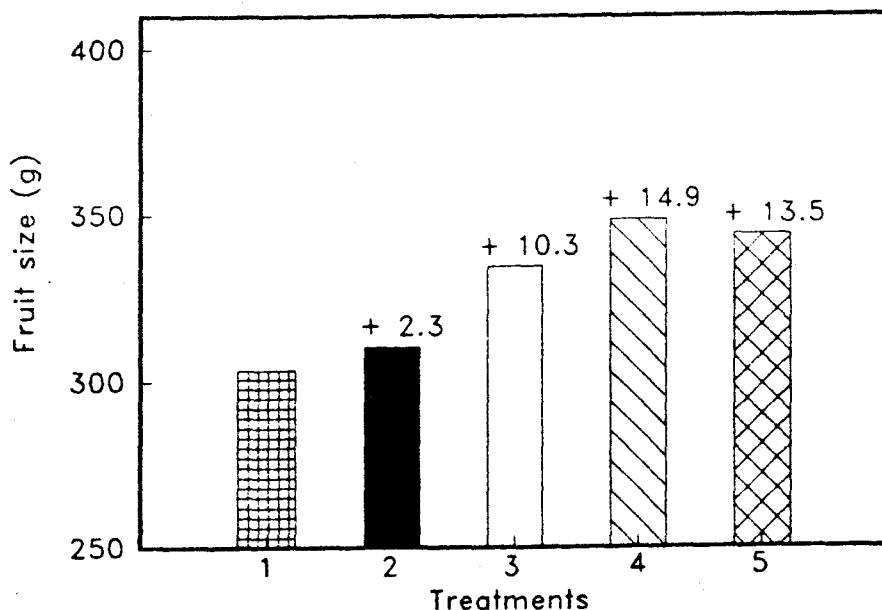


Figure 2. The effect of time of harvest on fruit size of 'Fuerte' trees. Columns indicate the mean fruit size from each treatment over the 3 years of the study. Column figures indicate the percent increase in size over the smallest fruit produced in treatment 1. The treatments were: (1) all fruit harvested at 21% DM; (2) all fruit harvested at 24% DM; (3) 50% of fruit harvested at 21% DM and 50% harvested at 30% DM; (4) 50% of fruit harvested at 24% DM and 50% harvested at 30% DM; (5) all fruit harvested at 30% DM.

The 'Hass' trees chosen for this research had been substantially damaged by hail the year prior to beginning the experiment and most of the fruit were lost in the spring. Consequently, in the first year of the experiment (1988) all trees had a heavy crop following a 'season of rest'. In this study none of the treatments were able to break the hail-induced biennial cropping cycle (Figure 3a). Crop load in the off-year was down by 60 to 90% of the yields from the two on-years (Figure 3a). Treatment 1, where all fruit were harvested at 24% DM, had the highest yield when pooled for the tree years of the study (Figure 3b). It produced an average yield equivalent to 22.4 t/ha for each of the three years of the experiment. Treatments 2, 3 & 4 all produced

an annual average yield equivalent to about 18 t/ha while treatment 5, where all fruit were hung late, produced the smallest crop at 15.8 t/ha per year.

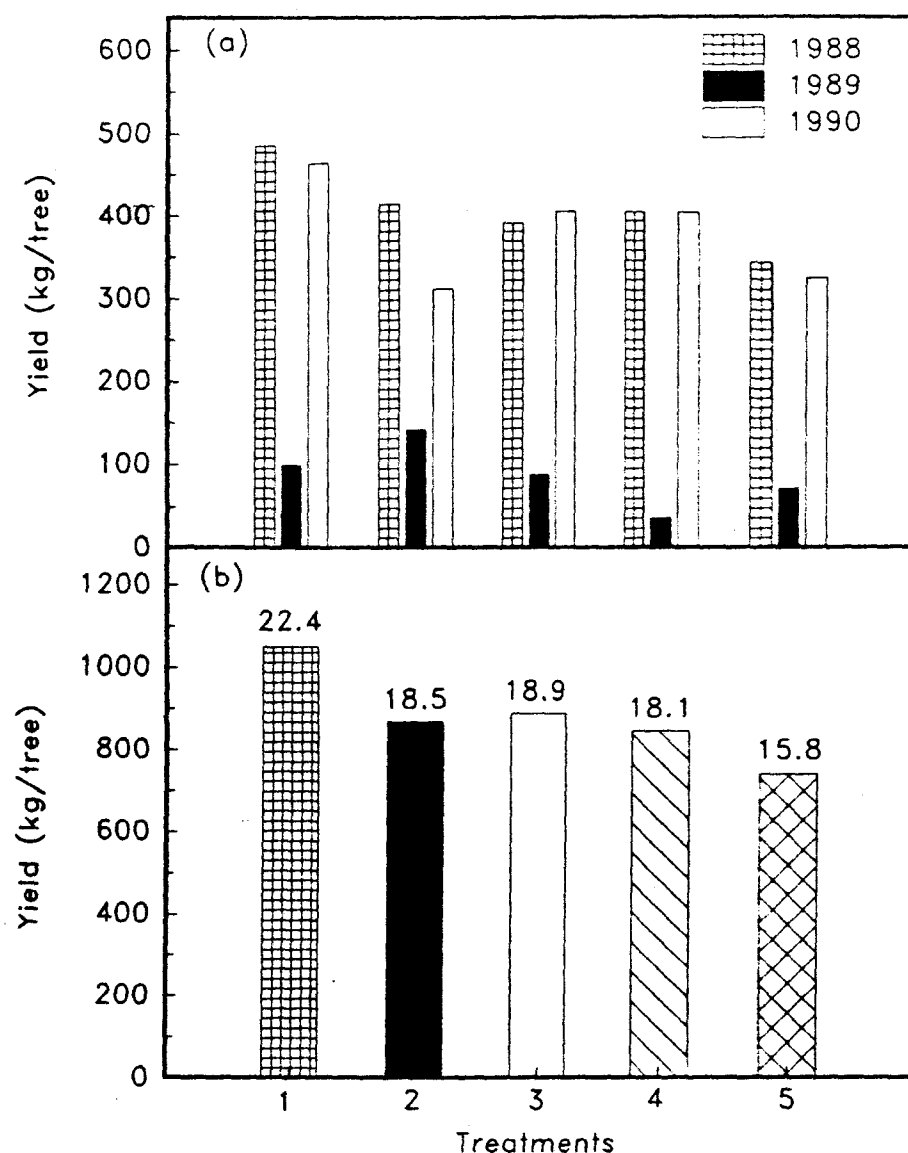


Figure 3. The effect of time of harvest on fruit yield on 'Hass' trees where (a) is the mean yield per tree ($n = 6$) and (b) is the cumulative yield for each treatment over the 3 years of the experiment. Column figures in (b) indicate the annual yield for each treatment in tonnes per hectare. The treatments were: (1) all fruit harvested at 24% DM; (2) all fruit harvested at 30% DM; (3) 50% of fruit harvested at 24% DM and 50% harvested at 35% DM; (4) 50% of fruit harvested at 30% DM and 50% harvested at 35% DM; (5) all fruit harvested at 35% DM.

With respect to fruit size (Figure 4), in general the longer the fruit was left on the tree the larger the size of the fruit when harvested.

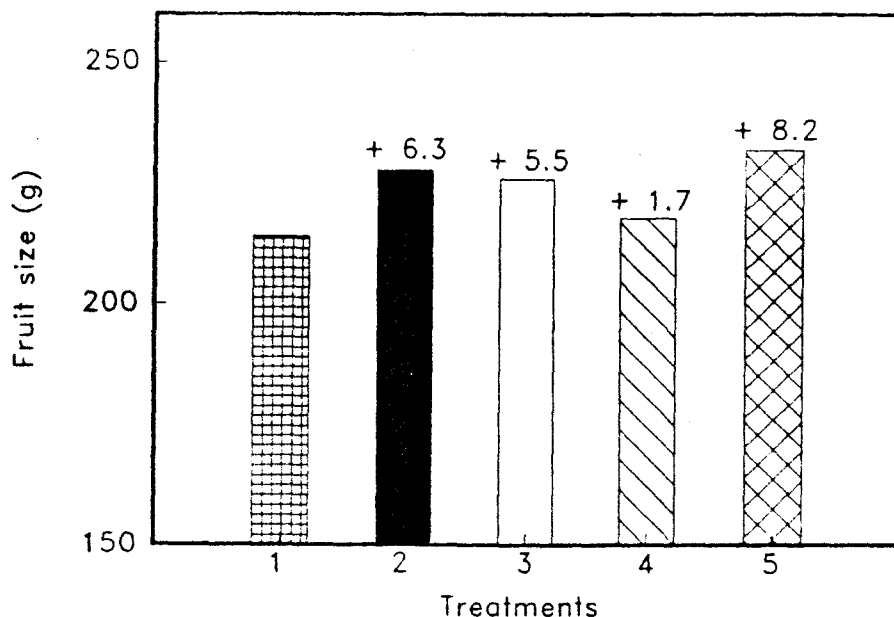


Figure 4. The effect of time of harvest on fruit size on 'Hass' trees. Columns indicate the mean fruit size from each treatment over the 3 years of the study. Column figures indicate the percent increase in size over the smallest fruit produced in treatment 1. The treatments were: (1) all fruit harvested at 24% DM; (2) all fruit harvested at 30% DM; (3) 50% of fruit harvested at 24% DM and 50% harvested at 35% DM; (4) 50% of fruit harvested at 30% DM and 50% harvested at 35% DM; (5) all fruit harvested at 35% DM.

CONCLUSIONS

Long-term yield and fruit size of avocados can be effected by the length of time the fruit is held on the tree after reaching commercial maturity. This result was expected as fruit will continue to accumulate oil (increase in dry matter) while attached to the tree thereby reducing resources available for the following crop. The research has shown that with 'Fuerte', the degree of biennial cropping can be strongly influenced by harvesting procedures. This is despite all fruit being harvested before the beginning of flowering. While the results with 'Hass' have not been as clear as those obtained with 'Fuerte', a similar trend has been measured with yield being depressed the longer fruit remained on the tree.

It is recognised that the strip pick treatments used in this research are not practical for many growers and indeed would probably lead to a chaotic market system if adopted across the industry. Differential harvesting with size picking beginning as soon as fruit reach legal maturity would appear to be the most practical method of harvesting minimising the effect of late hung crops on subsequent yield. In this type of harvesting 30-50% of the crop on each tree, selecting the largest fruit, should be harvested as soon as the fruit are mature. This requires the grower to harvest quickly

across each cultivar the first time over and then returning later to remove the balance of the crop. In some situations it may be convenient to only harvest those trees with heavy crops removing 50 to 70% of the fruit in the first pick with the remaining fruit being harvested later. Harvesting systems where the full crop is hung on the tree for extended periods after maturity has been reached should be avoided.

ACKNOWLEDGMENTS

Funding for the last two years of this research has been supplied by the QFVG and HRDC. The authors thank Mr and Mrs S. Gray and Mr and Mrs J. Dorrian for their support and access to their properties.

APPENDIX 4

Whiley, A.W., Rasmussen, T.S. and Saranah, J.B. 1995. Avocado crop prediction - usefulness and methods. *Proceedings of the AAGF Conference 1985 'The Way Ahead'*. Freemantle, May 1995.

AVOCADO CROP PREDICTION - USEFULNESS AND METHODS

A W Whiley¹, T S Rasmussen² and J B Saranah¹

¹ Maroochy Horticultural Research Station, DPI, PO Box 5083 SCMC, NAMBOUR 4560

² Agricultural Chemistry, Department of Primary Industries, Meiers Rd, INDOORROOPILLY 4068

Summary

Forward estimation of crop yield provides useful information with respect to planning farm expenditure and marketing strategies. There are several methods of making forward predictions for crop yield which include counting fruit across pre-determined transects of blocks and broadly estimating the crop load for every tree in each block of like varieties. Another technique to show potential is the measurement of trunk starch levels at the beginning of a new cropping cycle just prior to flowering. Provided some prior yield history is known an estimate of potential yield for Hass can be determined approximately 9-12 months before harvesting. Of course this does not allow for cyclones, droughts, floods, fires or any other 'acts of God' which may substantially reduce production at any stage between setting the crop and harvest. This paper discusses yield prediction, its methodology and usefulness to the avocado grower.

INTRODUCTION

The year to year variation in yield from fruit trees has been prolifically reported for most of the important crop species. It has been the domain of researchers for many years to study cropping irregularities and to develop management strategies to lessen the impact of annual yield variation. With temperate fruit crops the breeding of new, highly productive varieties, rootstocks to manage tree vigour and the development of sophisticated pruning techniques have all assisted in stabilising yield cycles. The reduction of annual variation in crop yield promotes relative ease of forecasting production well in advance of harvest thereby allowing ample time to organise storage, handling and marketing of fruit.

Subtropical and tropical evergreen fruit trees such as avocado, have not been researched as intensively or developed for as long as crops such as apple and peach and show considerable variation between annual yields and makes production forecasting more difficult. Variation is generally less in those areas where the crop is growing in climates close to that in which it evolved (eg the subtropical areas of Queensland and northern New South Wales). As there have been few serious attempts to forecast yield for avocado in Australia in the past it could be argued that there is little to be gained by developing crop prediction technology as we have survived quite adequately without these measures. However, we have largely been living with a situation in Australia where overall demand for avocados has exceeded supply to the extent that economic returns have been received by most growers despite the lack of planned marketing. In fact, prices have been sufficient to encourage another wave of planting of new trees in several districts from which the production is still to impact on the domestic market (see report by John Bolton in these Proceedings).

USEFULNESS

Growth in fruit industries must be accompanied by either more cost efficient production and/or the development and extension of markets if returns are to be sustained. To successfully achieve this, market intelligence, which includes forward estimates of the size of the current crop, is necessary and no successful fruit industry has been built and sustained without this type of information. For instance, after suffering successive years of depressed prices the Californian avocado industry developed a strategic plan to penetrate markets in the eastern states of the USA. This was built around forward crop estimates so that ample warning was available for the development of annual marketing plans. The usefulness of this information was soon realised and the Californian Avocado Commission now collects forward estimates of global production to assist with decisions on penetration of export markets (Europe and Japan).

The South African avocado industry is another which is dependant on accurate forward estimates of production. As 60% of the fruit is exported to Europe via sea freight, the industry needs an accurate estimate of crop well in advance so that shipping containers may be ordered from companies to carry the crop.

Another example of the usefulness of forward estimates is found with the New Zealand industry which supplies a niche market in Australia during January to March each year when Australian production is at its lowest. The maintenance of market prices to offset airfreight charges is dependent on regulating the volume sent across the Tasman and minimising the overlap with mainstream Australian production. Accurate crop forecasts are required to achieve this and historical events clearly emphasise this need. The under-estimation of the 1992 New Zealand avocado crop resulted in prolonged and heavy selling on Australian markets to the detriment of the Australian 'Shepard' growers. In retrospect this may not have been such a bad thing as it galvanised our 'Shepard' producers into a cohesive marketing group which has reclaimed market share for this early season variety.

CROP FORECASTING - HOW IS IT DONE?

Accurate estimates of crop yield are difficult to achieve without a significant input into collection and revaluation of the data as the season progresses. Due to the host of variables (both physiological and climatic) between flowering and fruit maturity, it is self evident that the accuracy of the estimate will improve the closer it is done to harvest. In fact, field results have shown that it is possible to estimate within $\pm 3\%$ of the actual crop if assessments are done within 2-3 weeks of harvesting a particular block (J Dorrian, pers. comm.). However, in most instances the strategic planning value of the information is greatest the further it occurs from the actual harvesting and marketing of the crop.

(i) *Yield prediction prior to flowering*

Recent research results with avocado have shown that it is the physiological condition of the tree as it approaches flowering that is a major predetermining factor influencing potential fruit set in any given season. Mature avocado trees have a biennial cropping trend which may be amplified or substantially reduced by management strategies in some districts (the effect of harvest time on subsequent yield of early and late maturing avocados growing in south-east Queensland has already been reported - Managing Fruit Harvest for Sustainable Yield, Proceedings of the AAGF

Conference 1992). Tree health with respect to *Phytophthora* root rot and nutrient status also contributes to flowering and fruit set performance. The effect of all of these variables is integrated into a common factor - the starch (carbohydrate) concentration in the tissues of the tree which reaches its highest level just before the beginning of flowering. It is this reserve level of energy stored in the tree that is drawn on to support the 'energy expensive' events of flowering and fruit set at a time when the foliage of the tree is weakened due to exposure to winter temperatures (and the accumulation of chloride in some districts).

Results from studies with 'Hass' in south-east Queensland have demonstrated that there is a relationship between the level of stored starch in the trunks of trees immediately prior to flowering and subsequent fruit yield. This relationship has been demonstrated in 12-year-old 'Hass' trees growing at Maleny which had developed a strong biennial bearing cycle (Figs. 1 & 2) and in 7-year-old 'Hass' trees growing at Childers (Figs. 3 & 4).

In those years when trees carried heavy crops (40 t/ha) starch concentrations in the trunks of 'Hass' trees at Maleny remained low prior to flowering and were followed by a subsequent low fruit yields (about 10 t/ha) (Fig. 1). From these data a relationship between trunk starch and yield can be estimated and predictions made with reasonable confidence in the outcome (Fig. 2). For instance, a trunk starch concentration of 5% predicts that these trees would produce 195 kg per tree (about 16 t/ha) while at 9% the same trees would yield 455 kg per tree (about 44 t/ha).

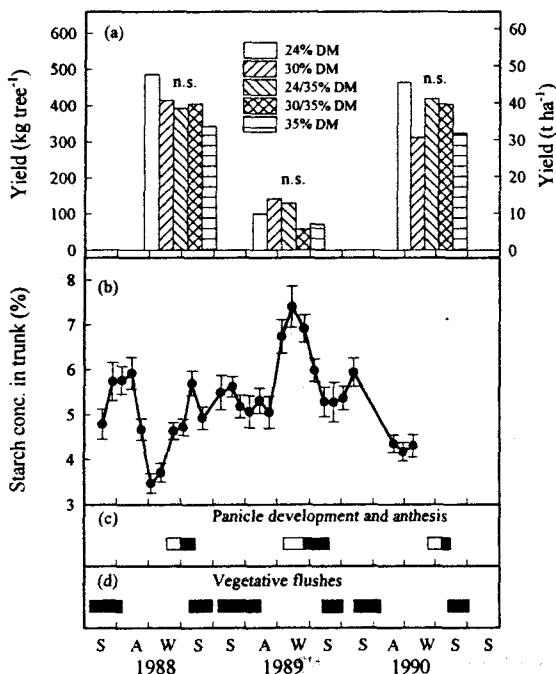


Fig. 1 The relationship between yield, seasonal starch concentration in trunks and tree phenology of cv. Hass at Maleny where (a) fruit was harvested at different stages of maturity as judged by dry matter (DM) from the 14.7 - 9.11.88, the 28.6 - 1.11.89 and the 18.7 - 7.11.90; (b) is the mean starch concentration of all treatments ($n = 30$ trees), vertical bars represent standard errors; (c) panicle development is represented by open horizontal bars, anthesis is represented by closed horizontal bars; (d) periods of vegetative growth are represented by closed horizontal bars.

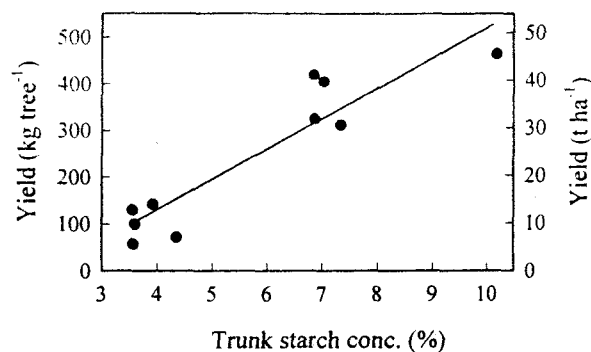


Fig 2 The relationship between the July trunk starch concentration and yield represented by the equation $y = 64.90x - 129.04$, $r = 0.93$, $P \leq 0.01$.

Prediction of yield from starch concentrations measured in 'Hass' shoots immediately prior to flowering was also possible. In trees growing at Childers seasonal variations in shoot starch levels ranged from about 1% through to near 14% (Fig. 3). There was a clear difference from treatments in the 1993 yields and the relationship between these yields and the shoot starch levels prior to flowering in spring 1992 is shown in Fig. 4. From this we can predict that when pre-flowering shoot starch concentrations are 8% subsequent yield would be 33 kg per tree (about 6 t/ha). By doubling the starch level to 16% expected yield from these same trees would be 152 kg per tree or about 30 t/ha.

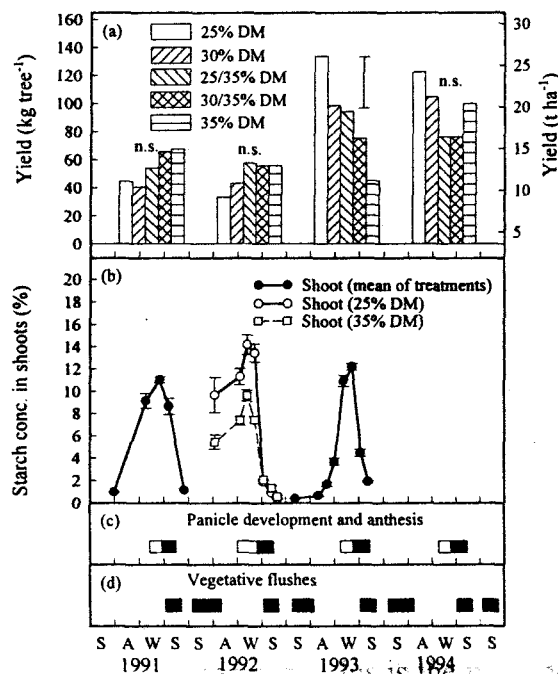


Fig. 3 Relationship between yield, seasonal starch concentration flux and tree phenology of cv. Hass at Childers where: (a) is yield of fruit which were harvested at different stages of maturity as judged by dry matter (DM), the vertical bar indicates LSD ($P \leq 0.05$); (b) is starch concentration of shoots of all treatments (\bullet , $n = 15$), or 25% DM (\circ , $n = 3$), or 35% DM (\square , $n = 3$), SEs are represented by vertical bars; (c) is periods of panicle growth represented by open horizontal bars, and periods of anthesis represented by closed horizontal bars; and (d) is periods of vegetative growth represented by horizontal closed bars.

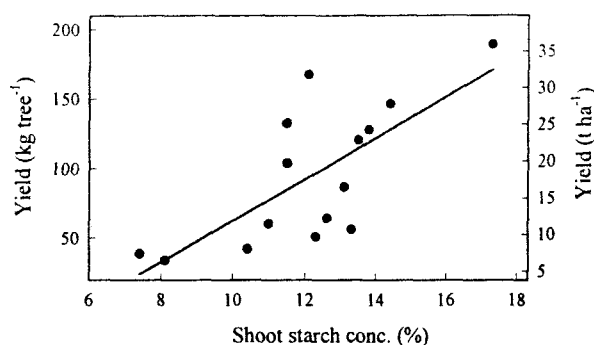


Fig. 4 Relationship between yield (1993) and July shoot starch concentration (1992) of cv. Hass growing at Childers. The regression is represented by the equation $y = 14.84x - 85.63$, $r^2 = 0.52^*$.

To get these predictions to work the planting density of the blocks being tested is required (for tonnes per ha calculations) and some prior yield history is also necessary. The technology offers a potential to develop an accurate forward yield prediction system which could be as easy to implement as the current leaf analysis system for nutrient application. However, further development and evaluation are necessary before widespread use could be implemented by industry.

(ii) Yield prediction at strategic stages of crop development

The number of estimates that are required between fruit set and harvest will vary depending on the experience of the operator, the production district and the occurrence of abnormal seasonal events (eg cyclones, heat waves etc) which promote excessive fruit loss. However, there are 3 periods between fruit set and harvesting at which crop estimation can be undertaken with some confidence that the data gathered will relate to the final yield: at spring flush maturity; at the completion of summer fruit drop; and 2-3 weeks prior to harvest.

(a) At spring flush maturity

Estimation of yield at this time has been done by counting a number of fruit in a specific sector of trees which have been identified across a transect in the orchard and then applying the appropriate mathematical model to the data. The system uses the following factors to arrive at its prediction:

- Yield capacity - this is the maximum yield recorded from trees in the block (depends on tree size).
- Average density of fruit set - determined by a defined measurement (counting) pattern across a block.
- Crop correction factor - the factor used to adjust for fruit drop which occurs between the time of estimation and harvest.

The data from these factors is calculated in the following manner to arrive at a predicted yield:

$PC = (Y_c \cdot D_f) C_f$ where Y_c = yield capacity; D_f = fruit set density and C_f = the crop correction factor which is less than 1.

For effective prediction using this system prior knowledge on yield capacity is required and the crop correction factor needs to be established as it will vary between cultivars and districts.

(b) At the completion of the summer fruit drop

Estimation of the crop at this point can be done either by using the process outlined for use at spring flush maturity or 2-3 weeks prior to harvest.

(c) At 2-3 weeks prior to harvest

Estimation at this point of time can be done very accurately but the information may not be as strategically important as there is little time to put marketing strategies in to place. One of the most accurate, but time consuming methods, is to evaluate every tree in each block. This can be done by estimating the crop load on each tree using a 0 to 10 rating scale where 0 is equal to nil fruit, five is considered an average crop load for the trees, say 5 trays, and 10 is a heavy crop load, say 10 trays. By individually scoring each tree, defining the average score and multiplying this by the number of trees in the block a estimate can be calculated. It is also possible to use this technique at earlier stages of the crop cycle but a crop correction factor would have to be introduced into the calculations to account for fruit drop between the time of estimation and harvest.

ACKNOWLEDGMENTS

The authors thank Spencer and Lyn Gray and John and Jay Dorrian for their support and cooperation in making their properties available for aspects of this research. Funding was supplied by the Queensland Department of Primary Industries, the Queensland Fruit and Vegetable Growers, the Australian Avocado Growers' Federation and the Horticultural Research and Development Corporation.

APPENDIX 5

Wolstenholme, B.N. and Whiley, A.W. 1995. Prospects for increasing 'Hass' fruit size - a southern hemisphere perspective. *Proceedings of the AAGF Conference 1985 'The Way Ahead'*. Freemantle, May 1995.

PROSPECTS FOR INCREASING HASS FRUIT SIZE - A SOUTHERN HEMISPHERE PERSPECTIVE

B Nigel Wolstenholme¹ and Anthony W Whiley²

¹ Department of Horticultural Science, University of Natal, Pietermaritzburg, South Africa

² Maroochy Horticultural Research Station, Nambour 4560, Australia

ABSTRACT

Even healthy 'Hass' avocado trees produce a proportion (5-20%) of fruit that is regarded as too small for profitable export marketing. In warm, dry growing conditions, the occurrence of small fruit in stressed and older trees may increase to 40%. The causes are in the first instance genetic, but are aggravated by certain soil, climatic and management factors. Possible partial solutions include cross-pollination, tree manipulation by plant growth regulators, summer girdling, strategic pruning, and late hanging but all have associated problems. An integrated, practical short-term solution is to improve root health and reduce tree stress through applying additional mulches of the correct type to the root zone. Enhanced root growth in well-aerated mulches is associated with increased cell division and delayed seed coat degradation in fruits. A preliminary trial in KwaZulu-Natal increased average fruit mass by 12%, number of fruits by 6%, and yield by 19%. Further studies are under way.

INTRODUCTION

The cultivar 'Hass', selected from a seedling tree in southern California (planted in the late 1920's and patented in 1935) has gradually eclipsed the standard 'Fuerte' which was California's main cultivar. It is now overwhelmingly the most important avocado cultivar in semi-arid subtropical, production areas of California, Chile and Israel, as well as most countries with warm subtropical summer rainfall climates. This is due mainly to the excellent internal fruit quality and higher yield potential of 'Hass' compared with its predecessor 'Fuerte'. Furthermore, 'Hass' is valued for its late fruit maturity (late winter through spring and even into summer, depending on climate), and consumers have mostly accepted its purple to black rind when ripe.

Nevertheless, 'Hass' does have certain drawbacks as a commercial cultivar. The most important is its potential to produce small fruit with low market acceptance. In South Africa, where 'Hass' is still not quite the most important export cultivar, up to 40% of the 'Hass' crop may fall into 'small fruit' counts. Exportable fruit is regarded as count 24 and less per standard 4kg (net) export carton (ie fruit 166 g or larger), with counts 14, 16 and 18 being regarded as ideal, and likely to fetch the highest prices on European markets (especially France, which takes \pm 60% of South Africa's current exports of 8 to 10 million cartons). Count 26 and higher constitutes small fruit (ie fruit of less than 154 g).

A series of workshops were held in South Africa in 1994 to determine industry problems and research priorities as a basis for funded projects for 1995. The 'horticultural problems' workshop identified small fruit size in 'Hass' as its main priority. It was estimated that a

satisfactory solution would have increased export earnings by R30 million, in an industry worth over R120 million in 1994, and in which over 60% of the crop is exported.

During the last 10 years 'Hass' has become the main variety grown in Australia where a strong market preference has developed for this cultivar. As in South Africa, the Australian industry is aware of the small fruit size problem with this variety where it is of particular significance in the warmer subtropical climates where avocados are produced, eg Bundaberg and the Atherton Tablelands. To date the Australian industry has not given this problem a high priority, even though it is causing concern to some of the major production areas. However, some preliminary research has been conducted into this problem with some promising results and further work is continuing on a limited scale.

This paper discusses research conducted in South Africa and Australia that has a bearing on the 'Hass' small fruit problem. Both long-term and shorter-term approaches are outlined. We draw both on our own research as well as that of colleagues throughout the world, but particularly on the problem as manifested in the warm to cool, high summer rainfall subtropics with deep red oxisol/krasnozem soils.

CAUSES OF SMALL FRUIT

Genetic Factors

In the final analysis, the small fruit problem is genetic. 'Hass' fruits are on average much smaller than 'Fuerte', 'Ryan', 'Sharwil' and most other major commercial varieties. Average fruit size is certainly influenced by management and by environment, but is ultimately determined by genes. There is of course a range of fruit size on any one tree, which reflects small differences related to position and other effects.

Self vs Cross-Pollination - possible Metaxenia Effects

Robbertse and Coetzer (1995) are testing the hypothesis that a contributing factor to 'Hass' small fruit is self-pollination. It is well-known that the avocado is a natural outbreeder (Bergh, 1969, 1986; Davenport, 1986), but with a 'fail-safe' mechanism assuring some fruit set from self-pollination. The relative merits of interplanting "A" and "B" type cultivars to enhance cross-pollination are still debated, with yield increases seemingly more likely in cooler climates and in "B" type flowerers.

Robbertse and Coetzer (1995) noted that pollen tube growth down the style was slower in self-pollinated as compared to cross-pollinated 'Hass'. Pollen tube growth is known to be slower at temperatures below 25/20°C (Sedgley and Annells, 1981), especially in "B" type flowerers such as 'Fuerte'. 'Hass' is an "A" type flowerer, less sensitive to cold temperatures at fruit set. Regularly heavy-bearing 'Fuerte' and 'Hass' (so-called A-rated trees) at Westfalia had a higher percentage of pistils with pollen tubes at flowering than consistently low bearers (so-called E-rated trees). It is possible that poor pollen tube growth in E trees is due to sunblotch viroid as all E trees tested were infected by this disease.

If cross-pollination leads to more robust embryos (seed) with the effects of the stronger seed growth being transmitted to the fruit flesh to increase fruit size, the rather rare phenomenon known as metaxenia, where fruit characteristics are attributed directly to the pollen parent, will have been discovered for avocado (it is well known in the date fruit).

Anatomy, Morphology and Kinetics of Fruit Growth

It is obvious that normal avocado fruit growth is dependent on a viable seed, which in turn requires pollen tube growth, fertilisation of the egg cell, and endosperm development. The underdeveloped fruits known as 'cukes' have been studied in detail by Blumenfeld and Gazit (1974), Tomer *et al.* (1980) and most recently by Steyn *et al.* (1993). All have shown that 'cukes' are usually not completely seedless - they contain a rudimentary embryo and endosperm and show some development of the micropylar portion of the outer integument. However, there is a missing layer of tissue called pachychalaza, which is the vascularised portion of the seed coat through which photosynthates, mineral nutrients and water are supplied to normal, developing seeds. It is not surprising therefore, that its absence leads to early seed abortion. In turn, the absence of a normal seed leads to very much less fruit development.

Casual observation suggests that there is a strong relationship between seed size and fruit size in avocado, although seed size does vary with cultivar and environment. Furthermore, as Blumenfeld and Gazit (1974) have shown, the seed coat (not strictly speaking a testa) which is thick, white and fleshy in young fruits, gradually becomes thinner as fruits grow. The vascular bundles permeating the fruit flesh (mainly mesocarp tissue) coalesce towards the base of the fruit, and enter the seed coat at the base of the seed in a single group. Therefore, once the seed coat becomes thin, brown and membranous, the seed is effectively cut off from the flesh and the potential for further growth of the fruit is reduced.

The role of the seed in avocado fruit growth is undoubtedly to supply the necessary plant growth hormones (first shown by Blumenfeld and Gazit, 1972) through the thick, fleshy seed coat and the seed endosperm (a nutritive tissue). Collectively, these create strong 'sinks' for photosynthates in the developing fruit. More recent studies by Cutting (1984) showed that just prior to seed maturity, relatively high levels of indoleacetic acid (an auxin) and the two cytokinins 2iP and IPA were found in the thick, fleshy seed coat, but declined rapidly to zero as it dried. Seed concentrations of IAA and 2iP exceeded those of the flesh in developing fruits. The concentration of abscisic acid rose throughout development.

Experience in South Africa has shown that consistently low-producing 'Fuerte' trees on Westfalia Estate (E-rated trees) produce many 'cukes'. Furthermore, 'cukes' develop from flowers that are female-sterile, (unable to produce viable seeds). These flowers are described as cryptically male-unisexual (with enhanced male function) by Steyn *et al.* (1993). This raises the question as to whether A-rated 'Fuerte' trees (consistently heavy bearers) may be cryptically female, i.e., 'Fuerte' may be cryptically dioecious; or whether the floral condition is a reflection of the tree's sunblotch viroid status.

Avocado fruit growth (based on length, width, volume or mass) follows a typical sigmoid curve (Schroeder, 1953; Valmayor, 1967). Cell division is most rapid in the early stages of

fruit growth, but Schroeder (1953) showed that it continues, albeit at a reduced rate, as long as fruits are firmly attached to the tree. Differences in fruit size, both within and between cultivars, appear to be due to cell number rather than cell size (Valmayor, 1967; Moore-Gordon *et al.*, 1995). Fruits develop stomates early on, with a maximum density of 50-70 mm⁻² after 3 weeks, giving 22,000 to 30,000 stomates per fruit. As fruits contain chlorophyll, they undergo photosynthesis and therefore contribute to their own carbon needs (Whiley and Schaffer, 1994). However, Whiley *et al.* (1992) showed that at all stages of fruit development, fruit photosynthesis was much less than fruit dark respiration. Nevertheless, this contribution of photosynthate may well be critical in the early stages of fruit growth contributing to cell division and growth.

The most detailed study of the kinetics of 'Hass' fruit growth is that of Zilkah and Klein (1987) in Israel. It is also known that temperature influences fruit shape, with more elongated fruits as temperatures become cooler, especially in cultivars such as 'Pinkerton' and to a lesser extent 'Fuerte'.

Climatic Factors

There is substantial evidence, although mainly anecdotal, that the 'Hass' small fruit problem is greater in warm as opposed to cool environments. This is certainly recognised in Israel, South Africa and Australia. Whiley and Schaffer (1994) note that 'Hass' fruit are 30% smaller in warm subtropical, coastal south-east Queensland compared with those from a cool, highland environment. Mean maximum/minimum temperatures for the four months preceding fruit maturity are 28.6/19.0°C at the warm site, and 21.4/13.6°C at the cool site. Larger crops were produced at the cool site, so crop load effects (high crops normally reduce fruit size) can be discounted in this example. These authors also note the much smaller fruit size of 'Hass' in Florida (31.5/24.4°C) as compared to cooler southern California. Part of the explanation may be that higher temperatures increase dark respiration of 'Hass' fruits ($Q_{10} \approx 2$), and this combined with the long development period of the fruit may lead to reduced assimilates for fruit growth (Blanke and Whiley, 1995).

Water relations are obviously vital in fruit growth, and water stress will induce temporary fruit shrinkage as water is withdrawn from the fruit (Schroeder and Wieland, 1956), especially young fruit. Water stress will accelerate both spring and summer fruit drop, with variable effects on fruit size. It also results in increased ring-neck symptoms on the fruit stalk, associated with premature seed coat death. For reasons explained earlier, this will reduce fruit size. Whiley *et al.* (1986) found a direct correlation between ring-neck and tree water deficit, the latter aggravated by *Phytophthora* root rot. Obviously, any loss of feeder roots will reduce water uptake. Whiley (1994) has drawn attention to a marked reduction in root activity during flowering and fruit set in spring, and the high water loss from inflorescences (Whiley *et al.*, 1988a). Similarly, temporary flooding and salinity will aggravate root loss and reduce root growth.

Poor Tree Condition / Tree Stress / Tree Age

Since medium to large fruit size requires maximisation of fruit (and seed) cell division, it stands to reason that any reduction in the resources for cell division will reduce average fruit size. The most important resources are promotive plant growth hormones (especially cytokinins); photoassimilates providing carbon skeletons; mineral nutrients from the soil; and water.

Growers and researchers agree that the 'Hass' small fruit problem is less severe in young, vigorous, healthy trees, and that it becomes greater as trees increase in size, age and complexity with an associated reduction in vigour. Crop load is a key factor here - younger trees have a more favourable leaf to fruit ratio, and expend proportionally less energy on growth and maintenance respiration. Older trees have a greater proportion of structural wood (heavy branches and trunks) to support in relation to their leaf area, and with reduced vigour may set too many fruits for their complement of photosynthetically efficient leaves. Tree phenological aspects also enter the picture, in so far as they affect vegetative/reproductive competition at critical phases, loss of root activity, and carbohydrate storage (Whiley *et al.*, 1988b; Whiley, 1994).

At the most recent SAAGA Research Symposium, Kremer-Köhne and Köhne (1995) summarised three years of data from Westfalia Estate relating to small fruit in 'Hass'. They found that the percentage of small fruit increased as tree condition (measured on the 0=healthy to 10=dead scale) deteriorated. Even for very healthy trees (0-1), every tree had 5 to 20% small fruit (count 26 or greater per 4kg export carton). This figure was virtually 100% when tree condition had deteriorated to a rating of 5 or 6. In 1991, tree condition was good and there was only \pm 10% small fruit in eight year old trees. Tree condition deteriorated slightly in 1992 due to drought and irrigation problems. In 1993, with tree condition rating 2, the small fruit proportion had increased to 25%.

PROSPECTS FOR INCREASING cv. HASS FRUIT SIZE

Large-Fruited 'Hass' Selections

An obvious but long-term approach is to find larger-fruited 'Hass' selections, or to use 'Hass' as a breeding parent in a dedicated breeding program. These approaches are being tried in Israel, California, and South Africa, *inter alia*. Five 'Hass' selections have been top-worked, starting in 1993, to existing trees at Westfalia Estate, and are being compared against standard 'Hass', with the first crop expected in the 1995 season. Inevitably, the Israeli and Californian breeding programs will supply most of the new genetic material, but it is pleasing to note that the ITSC avocado breeding program at Nelspruit, South Africa, which started in 1991 is progressing well.

Manipulation by Plant Growth Regulators

Competition between rapidly expanding spring flush leaves and setting fruitlets in indeterminate shoots has been shown to reduce fruit set in avocado (Biran, 1979; Blumenfeld *et*

al., 1983), especially in vigorous cultivars such as 'Fuerte'. This competition is most intensive in the 40 day period before new leaves change from sinks to sources of assimilates, during which trees depend on stored reserves and to a greater or lesser extent older, usually photoinhibited leaves (Whiley 1994). Furthermore, root activity is minimal at this critical period. Hence great stress is laid on managed nitrogen nutrition and irrigation, to meet the needs of the greatly expanded transpiration surface (mainly inflorescences) (Whiley *et al.*, 1988a), but also to control vegetative vigour (Whiley *et al.*, 1988b).

Other methods of controlling vigour at the critical fruit set period include shoot tip pinching (effective but impractical), and chemical pruning. Köhne and Kremer-Köhne (1987) showed the potential of the plant growth retardant paclobutrazol (Cultar®) on individual shoots. Further work on orchard trees using strategically timed foliar sprays (Wolstenholme *et al.*; 1990; Adato, 1990; Whiley *et al.*; 1991) showed that it is possible not only to increase fruit set by altering assimilate partitioning, but also, over a period of years, to increase yield substantially in 'Hass' avocado. Even more remarkably, this yield was accompanied by a \pm 20% increase in average fruit size of 'Hass', in spite of higher average yield. A pre-condition for consistency in this result is obviously excessive tree vigour - there is little point in attempting to control vigour with a growth retardant if vigour is not a problem!

Work with plant growth substance sprays continues (Whiley *et al.*, 1993). Paclobutrazol is not widely used as a foliar spray to fine tune fruit set or increase fruit size, probably because it requires a very good grower to use it effectively, it is relatively expensive and it is not registered in Australia for use on avocados. Furthermore, the "green movement" dictates caution in the use of persistent chemicals. There would appear to be scope for use of both auxin and gibberellin sprays, which can be effective in citriculture. The citrus example also suggests research on KNO_3 sprays and manipulation of the N:K ratio in leaves.

Girdling/Cincturing

Girdling is an ancient horticultural technique which is coming back into fashion, due both to the anti-chemical hysteria as well as our improving knowledge of tree manipulation. There are several reports of its effects in avocado orchards, usually to increase yield of selected branches on vigorous trees, for up to three years, but mostly with a decrease in fruit size and a loss of tree condition. It remains controversial but has, for example, been used to induce precocity in over-vigorous trees on 'Martin Grande' rootstock, and induce a heavy "death crop" on trees about to be thinned in high density orchards. Autumn girdling is most effective for these responses.

In citrus however, summer girdling can be used on two-thirds of the main branches in healthy, vigorous trees, to increase fruit size by 15% or more in that season. A 2.5mm girdle is carried out and repeated three weeks later in grapefruit and oranges. Autumn girdles improve yields but decrease fruit size (Cohen, 1982; 1984). Davie *et al* (1995) are conducting trials on summer girdling and cincturing of 'Hass' avocado in South Africa, with some promising results, but further research is necessary.

Cross Pollination

Following leads from Israeli research, Robbertse and Coetzer (1995) are testing cross-pollinators for 'Hass'. The objective is to find pollinators that give good pollen tube growth, and hopefully increased fruit size. To increase pollen exposure cross-pollinators will have to be found from the B-type flowerers with similarly timed floral phenology to 'Hass'. 'Bacon', 'Ettinger', 'Fuerte' and 'Sharwil' are the most likely candidates to fill this role.

Delayed Harvest / Selective Harvesting

In cooler areas, 'Hass' fruits can be stored on the tree for several months after reaching minimum legal maturity. This may have market advantages but may also initiate an alternate bearing cycle and reduce overall yield (Whiley, 1994). Several studies have shown that fruit size increases significantly with delayed harvest, although there is a practical limit as fruits will be in the final, slower phase of growth. Also, fruits are often small because of early seed coat abortion, after which there is reduced potential for increase in size, and very rapid softening after harvest.

Kaiser and Wolstenholme (1994) reported on delayed 'Hass' harvest from July to November at two sites in the Natal midlands. Fruit size increased on average by 1 count at the cooler site to 2 counts at the warmer site. At the warmer site, most fruit were count 18 (211-235g) in July and count 14 (266-305g) in November. In a cooler climate, equivalent figures were count 16 (236-265g) in August, and count 14 in November.

An Integrated Approach: Larger Fruits Through Improved Root Health

A research project started in 1993 by M.Sc. Agric. student C. Moore-Gordon, and supervised by Cutting and Wolstenholme, at Everdon Estates in the Natal midlands, South Africa, is testing the following integrated hypothesis on 'Hass' fruit size:-

The avocado evolved as a "litter feeder" in highland tropical and subtropical rainforests in Central America. It has a shallow, much branched feeder root system that requires a well aerated, well-drained litter/soil for healthy root growth. The roots efficiently intercept and recycle minerals released from decomposition of organic matter. A healthy tree becomes self-mulching; a tree lacking in vigour will have a poor natural mulch. Healthy roots, aided by additional mulching, will grow more during the two main root flushes recently redefined by Whiley (1994). Healthy roots will synthesise and translocate more cytokinins and gibberellins (and less abscisic acid and ethylene) through the xylem stream to aerial parts of the tree, including developing fruits. This will allow more cell division, especially early in the development of the fruit, and will also aid seed development - increasing the sink strength of individual fruits. In particular, seed coat longevity will be prolonged, lengthening the total growth period of the fruit flesh. Better water relations will reduce the incidence of "ringneck" symptoms, presumably by reducing concentrations of abscisic acid in fruit stalks. The overall result is reduced tree stress, more favourably balanced root: shoot: fruit interactions, and larger average fruit size. Mulching is therefore the key cultural treatment in this hypothesis.

Mulching - Pros and Cons

The work of Broadbent and Baker (1974), Nesbitt *et al.* (1979), Pegg & Whiley (1987) and many others has highlighted the benefits of mulching in the biological and later the integrated control of *Phytophthora* root rot. Recently, Turney and Menge (1994) have summarised this philosophy of creating "suppressive:" soils. However, mulching has other important benefits:

- Conservation of water - improved water relations
- Improved soil structure, porosity and aeration
- Reduction of weed growth
- Reduced ground water nitrate pollution
- Reduction of fertiliser bills through increased N, P, K, Ca, Mg and B in particular under a mulch
- Increased cation exchange capacity through humus
- Improved root growth
- Less fluctuation in soil temperature
- Less soil compaction

Mulching, therefore makes abundant sense for avocados, especially in stressful environments. However, the down-side is availability and cost, increased frost and fire hazard, and the necessity of tailoring timing and type of mulch to the phenological cycle and to nitrogen management in particular. Mulches must be carefully chosen, bearing C:N ratio and rapidity of breakdown in mind.

The Natal Mulching Trial

Healthy seven-year-old 'Hass' (in 1993) on clonal 'Duke 7' rootstock at Everdon Estate, Howick, a cool mesic mist belt area with about 1000 mm rainfall and irrigated with microjets, were used. Six trees had their natural leaf mulch regularly removed, and served as the unmulched controls. Six adjacent trees were each mulched in early winter 1993 with 1.5 m³ of composted pine bark, reinforced by natural litter drop. These trees also received fortnightly light applications of soluble calcium acetate. Further treatments, including a grass mulch were added in 1994, but are not discussed here. Root, shoot and fruit growth were regularly measured, and at maturity all fruits were graded, counted and weighed. Samples were taken regularly to study fruit and seed coat anatomy and xylem sap hormone concentrations.

(i) Results and Discussion (Moore-Gordon *et al.*, 1995)

Fruit growth measurements for length are presented in Fig. 1. Differences showed up after ± 4 weeks, and mulched fruits ended up significantly larger than fruits from unmulched trees, viz. 14.3 ± 2.3 mm longer.

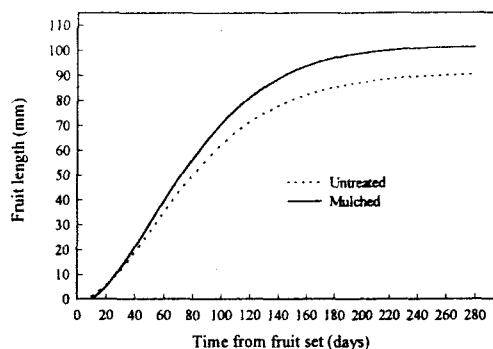


Fig. 1 Effect of mulching on fruit growth as measured by length in cv Hass avocado trees growing in a cool subtropical climate in KwaZulu-Natal, South Africa. The regression line for the untreated trees is represented by $y = 95.84 \exp\{-\exp(0.02252(x-48.29))\} - 7.07$ and for the mulched trees $y = 110.10 \exp[-\exp(0.02297(x-51.61))] - 8.16$. Redrawn with permission from Moore-Gordon *et al.*, 1995.

Cell counts showed significant differences in cell number (more cells in fruits from mulched trees), but not in average cell size (Fig. 2).

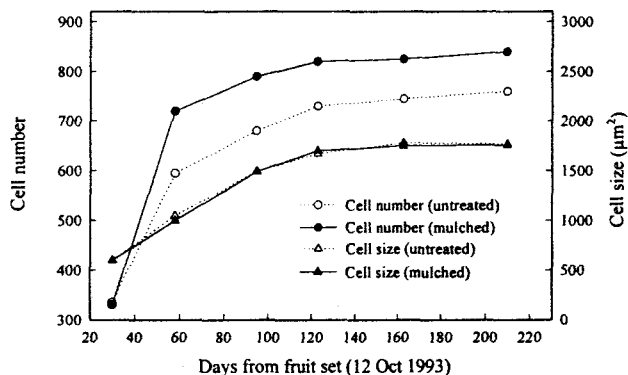


Fig. 2 Effect of mulching on cv. Hass fruit cell number and size during development. Trees were growing in a cool subtropical climate in KwaZulu-Natal, South Africa (Redrawn with permission from Moore-Gordon *et al.*, 1995).

Anatomical studies also indicated earlier breakdown and senescence of the seed coat in unmulched trees, i.e. prolongation of seed coat viability in mulched trees. Spot counts showed less ringneck in mulched as compared to unmulched trees. There was an earlier onset and greater levels of root activity throughout the 1993/94 season in mulched trees (Fig. 3).

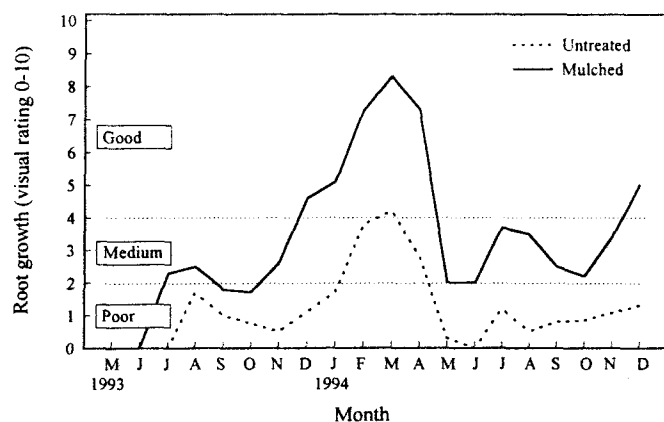


Fig. 3 Effect of mulching on seasonal root growth of cv. Hass avocado trees growing in a cool subtropical climate in KwaZulu- Natal, South Africa (Redrawn with permission from Moore-Gordon *et al.*, 1995).

At harvest, fruit from mulched trees were predominantly in count 18, and for this count and for counts 14, 16 and 20 out-yielded unmulched trees. Correspondingly, for counts 22, 24 and >26 (smaller fruits) the unmulched plots had more fruits (Fig. 4). The net effect was a distinct skewing of mulched plots towards the lesser counts (larger fruits).

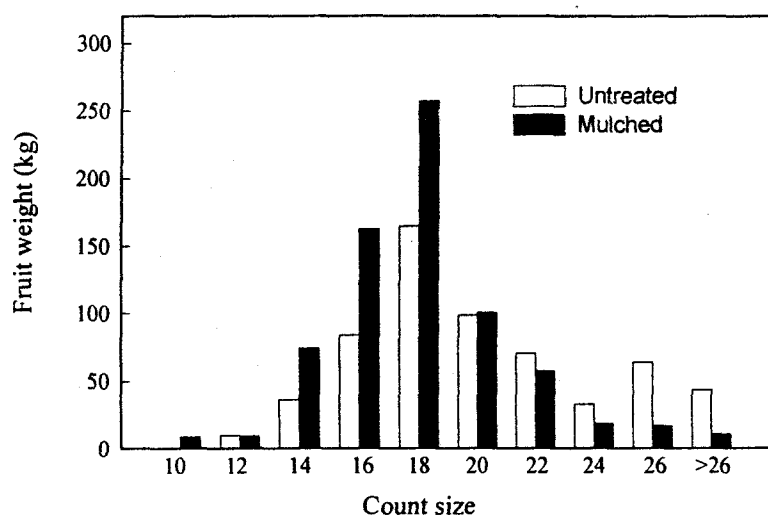


Fig. 4 Effect of mulching on the distribution of count size in cv. Hass avocado trees growing in a cool subtropical climate in KwaZulu-Natal, South Africa. Fruit size distribution at harvest was determined by fruit weight for each count (Redrawn with permission from Moore-Gordon *et al.*, 1995).

Table 1 summarises data on mean fruit mass, number of fruits, and yield. Fruit from untreated trees averaged 198 g while those from mulched trees averaged 221 g (12% heavier). The average number of fruits was 6% greater in mulched trees (509 vs 540 fruits per tree). Finally, yield per tree was 19% higher in mulched plots (101 kg vs 119 kg). Thus, even though mulched trees had higher yields with more fruits, the treatment still increased fruit size (Moore-Gordon *et al.*, 1995).

Table 1 Summary of effects of mulching on cv. Hass fruit weight, numbers of fruits per tree and yield. Data are mean values from six trees[†].

Treatments	Fruit size (g)	Fruit No./tree	Yield (kg/tree)
Untreated	198.0	509	100.8
Mulched	221.3	540	119.4
% Increase	+ 11.8	+ 6.1	+ 18.5

[†] (with permission of Moore-Gordon *et al.*, 1995)

The first full season's data have vindicated, at least superficially, most aspects of the hypothesis. Hormone measurements still have to be conducted, and tree stress is currently being monitored via advanced infrared thermometry. It is appreciated that pine bark is an unacceptably expensive mulch - it was used to establish a principle. The trial is being continued and expanded, and detailed studies on leaf dynamics and the mineral nutrient aspects of mulching (including boron nutrition) are being initiated. In another mulching trial on the same farm to investigate some aspects of fruit quality, all mulch treatments also improved fruit size in 'Fuerte' (Allwood and Wolstenholme, 1995).

CONCLUSIONS

Small fruit size in 'Hass' is a major problem and is greater in hotter, drier areas, in older trees, and whenever trees are stressed. It can also be a problem where trees are in the "on" year of an alternate bearing cycle. It is caused by reduced cell division in flesh and seed, and aggravated by premature seed coat abortion.

Physiology is less well understood, but plant growth hormone (promotive and inhibitory) effects are being investigated, and photoassimilate and mineral nutrient availability must be optimised. High dark respiration rates of fruits accentuated by higher mean temperatures in warmer areas may be a factor.

In the longer term, the solution is the selection of larger-fruited 'Hass' types. Short-term manipulations involving pinching of spring flush shoots, managed nutrition, growth regulator sprays, and summer girdling may ameliorate the problem, but the technologies are complex. Cross-pollination may also increase fruit size.

The most practical solution investigated to date involves improved root health through mulching (and of course *Phytophthora* root rot control). Properly regulated mulches appear to have the potential, through complex interactions affecting fruit growth anatomy and physiology, not only to increase fruit yield but also to increase the proportion of large and decrease the proportion of small fruits. The benefits of mulching on the sandy soils of Western Australia are probably even more profound.

ACKNOWLEDGMENTS

The authors acknowledge the contributors of a range of co-workers and grower co-operators. The senior author has cited results from several papers presented at the March, 1995 South African Avocado Growers' Association Research Symposium. Jonathan Cutting initiated the mulching trial at Everdon Estate before moving to New Zealand. Post-graduate students Clive Moore-Gordon and Martin Allwood at the University of Natal have supplied preliminary, up-to-the-minute results. Funding for some of the studies was supplied by the South African Avocado Growers' Association, the Australian Avocado Growers' Federation and the Horticultural Research and Development Corporation.

LITERATURE CITED

- Adato, A. 1990. Effects of paclobutrazol on avocado (*Persea americana* Mill.) cv. Fuerte. *Scientia Horticulturae* 45, 105-15.
- Allwood, M.E. and Wolstenholme, B.N. 1995. Modified atmosphere shock treatments and an orchard mulching trial for improving 'Fuerte' fruit quality. *South African Avocado Growers' Association Yearbook* 18, In Press.
- Bergh, B.O. 1986. *Persea americana*. In: *CRC Handbook of Flowering*. A.H. Halevy (ed.). CRC Press, Boca Raton.
- Blanke, M.M., and Whiley, A.W. 1995. Water relations and respiration of developing avocado fruit. *Journal of Plant Physiology* 145, 87-92.
- Blumenfeld, A. and Gazit, S. 1972. Gibberellin-like activity in the developing avocado fruit. *Physiologia Plantarum* 27, 116-20.
- Blumenfeld, A. and Gazit, S. 1974. Development of seeded and seedless avocado fruits. *Journal of the American Society of Horticultural Science* 99, 442-8.
- Blumenfeld, A., Gazit, S. and Argaman, E. 1983. Factors involved in avocado productivity. *Department of Subtropical Horticulture, Volcani Center, Israel, Special Publication* 222, 84-5.
- Biran, D., 1979. Fruitlet abscission and spring growth retardation - their influence on avocado productivity. Unpublished M.Sc. Thesis, The Hebrew University of Jerusalem, Israel, (in Hebrew).
- Broadbent, P. and Baker, K. 1974. Behaviour of *Phytophthora cinnamomi* in soils suppressive and conducive to root rot. *Australian Journal of Agricultural Research* 25, 121-37.
- Cohen, A. 1982. Recent developments in girdling of citrus trees. *Proceedings of the International Society of Citriculture*.
- Cohen, A. 1984. Citrus fruit enlargement by means of summer girdling. *Journal of Horticultural Science* 59, 119-25.

- Cutting, J.G.M. 1984. Optimization, validation and application of radioimmunoassays for plant growth substances in avocado (*Persea americana* Mill.) fruits. Unpublished PhD Thesis, University of Natal, Pietermaritzburg, South Africa.
- Davenport, T.L. 1986. Avocado flowering. *Horticultural Reviews* 8, 257-89.
- Davie, S.J., Stassen, P.J.C., van der Walt, M. and Snijder, B. 1995. Girdling avocado trees for improved fruit production. *South African Avocado Growers Yearbook* 18, In Press.
- Kaiser, C. and Wolstenholme, B.N. 1994. Aspects of delayed harvest of 'Hass' avocado (*Persea americana* Mill.) fruit in a cool subtropical climate. I. Fruit size, yield, phenology and whole-tree starch cycling. *Journal of Horticultural Science* 69, 447-57.
- Köhne, J.S. and Kremer-Köhne, S. 1987. Vegetative growth and fruit retention in avocado as affected by a new plant growth regulator (paclobutrazol). *South African Avocado Growers' Association Yearbook* 10, 64-6.
- Kremer-Köhne, S. and Köhne, J.S. 1995. Approaches to solving the small 'Hass' fruit problem - progress report. *South African Avocado Growers' Association Yearbook* 18, In Press.
- Moore-Gordon, C., Wolstenholme, B.N. and Levin, J. 1995. The effect of mulching on fruit growth and yield in 'Hass' avocado, with special reference to the small fruit problem. *South African Avocado Growers' Association Yearbook* 18, In Press.
- Nesbitt, H.J., Malajczuk, N. and Glenn, A.R., 1979. Effect of organic matter on the survival of *Phytophthora cinnamomi* Rands in soil. *Soil Biology and Biochemistry* 11, 133-6.
- Pegg, K.G. and Whiley, A.W. (1987). Phytophthora control in Australia. *South African Avocado Growers' Association Yearbook* 10, 94-6.
- Schroeder, C.A. 1953. Growth and development of the avocado fruit. *Proceedings of the American Society of Horticultural Science* 61, 103-9.
- Schroeder, C.A. and Wieland, P.A. 1956. Diurnal fluctuation in size of various parts of the avocado tree and fruit. *Proceedings of the American Society of Horticultural Science* 68, 253-8.
- Sedgley, M. and Annells, C.M. 1981. Flowering and fruit set response to temperature in the avocado cultivar 'Hass'. *Scientia Horticulturae* 14, 27-33.
- 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. *Sexual Plant Reproduction* 6, 87-97.
- Tomer, E., Gazit, S. and Eisentein, D. 1980. Seedless fruit in 'Fuerte' and 'Ettinger' avocado. *Journal of the American Society of Horticultural Science* 105, 341-6.
- Turney, J. and Menge, J. 1994. Root health: mulching to control root disease in avocado and citrus. *University of California, Riverside Circular CAS-94/2*.
- Valmayor, R.V. 1967. Cellular development of the avocado fruit - blossom to maturity. *Philippine Agriculture* L, 907-76.
- Whiley, 1994. Ecophysiological studies and tree manipulation for maximisation of yield potential in avocado (*Persea americana* Mill.). Unpublished PhD Thesis, University of Natal, South Africa.
- Whiley, A.W., Chapman, K.R. and Saranah, J.B. 1988a. Water loss by floral structures of avocado (*Persea americana* Mill.) cv. Fuerte during flowering. *Australian Journal of Agricultural Research* 39, 457-67.

- Whiley, A.W., Hofman, P.J., Smith, L.G., Saranah, J.B. and Meiburg, G.F. 1993. Enhancement of 'Hass' performance in warm climates. In: *Avocados, Focus on Fruit Seminar Booklet*, Maroochy Horticultural Research Station, pp 1-4.
- Whiley, A.W., Pegg, K.G., Saranah, J.B. and Forsberg, L.I. 1986. The control of Phytophthora root rot of avocado with fungicides and the effect of this disease on water relations, yield and ring neck. *Australian Journal of Experimental Agriculture* 26, 249-53.
- Whiley, A.W., Rasmussen, T.S. and Saranah, J.B. 1992. Effect of time of harvest on fruit size, yield and trunk starch concentrations of Fuerte avocados. *World Avocado Congress II Proceedings*, Orange, California (April 1991) 1, 155-9.
- Whiley, A.W. and Schaffer, B. 1994. Avocado, pp. 3-35. In: *CRC Handbook of Environmental Physiology of Fruit Crops* Vol. II. (Eds) B. Schaffer and P. C. Anderson, CRC Press Inc., Boca Raton, Florida.
- Whiley, A.W., Schaffer, B.S. and Lara, S.P. 1991. Carbon dioxide exchange of developing avocado (*Persea americana* Mill) fruit. *Tree Physiology* 11, 85-94.
- Whiley, A.W., Saranah, J.B., Cull, B.W. and Pegg, K.G. 1988b. Manage avocado tree growth cycles for productivity gains. *Queensland Agricultural Journal* 114, 29-36.
- Whiley, A.W., Saranah, J.S., Wolstenholme, B.N. and Rasmussen, T.S. 1991. Use of paclobutrazol sprays at mid-anthesis on fruit size and yield of avocado (*Persea americana* Mill.) cv Hass. *Journal of Horticultural Science* 66, 593-600.
- 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 Horticulturae* 41, 315-327.
- Zilkah, S. and Klein, I. 1987. Growth kinetics and determination of shape and size of small and large fruits of cultivar 'Hass' on the tree. *Scientia Horticulturae* 32, 195-202.

APPENDIX 6

Wolstenholme, B.N. and Whiley, A.W. 1995. Avocado productivity: strategies for balancing growth and cropping. *Proceedings of the World Avocado Congress III*. Tel Aviv, October 1995. Abstract submitted.

STRATEGIES FOR MAXIMISING AVOCADO PRODUCTIVITY - A REVIEW

B. Nigel Wolstenholme^{1*} and Anthony W. Whiley²

¹ Department of Horticultural Science, University of Natal, Pietermaritzburg 3209, South Africa

² Maroochy Horticultural Research Station, Department of Primary Industries Queensland, Nambour 4560, Australia

The extent of the avocado productivity problem varies regionally, with higher yield potential in the warm, humid subtropics as opposed to cooler, semi-arid areas. In the former, sustained yields of over 20 t ha⁻¹ have been achieved for both 'Fuerte' and 'Hass' in spite of greater tree vigour. More typical yields in cooler areas are 8-12 t ha⁻¹. A yield target with current germplasm of 30 t ha⁻¹ in the subtropics still appears realistic for large plantings over several years.

Accepting that the problem is genetic, and that both evolutionary history and the "energy expensive" fruit are constraints, the long-term solution obviously lies in a concerted breeding and selection effort. This applies to both scion and rootstock, with equal cognisance to yield, fruit quality, horticultural characters such as semi-dwarf growth habit and tree complexity, and resistance to *Phytophthora* root rot. The latter remains a priority in spite of excellent control by trunk injection of phosphonates, which has reduced the impact of a major limitation to production.

The recently refined pheno-physiological growth model of Whiley sheds new light on productivity constraints. Fruit set can be limited not only by temperature and moisture stress, but also by lost photo-assimilation efficiency of leaves during winter and early spring, possibly aggravated by the precipitous attrition of feeder roots towards the end of flowering. Management of shoot vigour is a key component to balanced shoot, root and fruit relationships for optimised productivity and fruit quality. Increasing evidence of cross-pollination benefits needs to be quantified and integrated into applied management strategies. Productivity also requires optimisation of light interception, bearing surface and canopy bearing volume through the life of the orchard. High density plantings (200-400+ trees ha⁻¹) followed by timely orchard thinnings at the onset of crowding have been successfully applied in the absence of sustainable tree size control options. Guidelines from deciduous orchards are discussed for possible relevance to avocado.

APPENDIX 7

Whiley, A.W., Saranah, J.B. and Wolstenholme, B.N. 1995. Pheno/physiological modeling in avocado - An aid to research planning. *Proceedings of the World Avocado Congress III*. Tel Aviv, October 1995. Abstract submitted.

PHENO-PHYSIOLOGICAL MODELLING IN AVOCADO - AN AID IN RESEARCH PLANNING

Anthony W. Whiley^{1*}, B. Nigel Wolstenholme² and Jack B. Saranah¹

¹ Maroochy Horticultural Research Station, Department of Primary Industries Queensland, Nambour 4560, Australia

² Department of Horticultural Science, University of Natal, Pietermaritzburg 3209, South Africa

A revised and expanded pheno-physiological model has been developed for cv. Hass growing in a cool, humid subtropical climate in south-east Queensland. The model quantifies and incorporates the seasonal growth activities of reproductive and vegetative components of the tree and defines temporal relationships between root, shoot, flowering and fruit development. The model also details seasonal changes in leaf nitrogen, starch and chlorophyll concentrations and records changes in the photo-assimilation efficiency of leaves from summer through to spring. It identifies, in well managed trees in a mesic soil and aerial environment, prolonged second flush root growth through winter, followed by feeder root attrition associated with flowering. It also shows a marked decline in the photo-assimilate efficiency of over-wintered leaves due to photo-inhibition, photo-oxidation of chlorophyll and nitrogen depletion, with implications for fruit set and retention.

The pheno-physiological model has assisted in the development of disease prevention strategies and limitations to production have been identified. Studies based on this information have been implemented and successful outcomes achieved. These are discussed in relation to a whole-tree approach to research and development of avocado in subtropical regions.