

Delayed harvest effects on yield, fruit size and starch cycling in avocado (*Persea americana* Mill.) in subtropical environments. II. The late-maturing cv. Hass

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Abstract

Effects of early and delayed harvest were investigated in 'Hass' avocado, at Childers, a warm subtropical site (over 4 years), and at Maleny, a cool, mesic subtropical site (over 3 years) in 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 (Maleny), 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. Pre-flowering starch concentrations in shoots (Childers) or trunks (Maleny) were directly correlated to the following seasons' yield.

Keywords: Avocado; Fruit size; 'Hass'; Starch cycling; Yield

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1. Introduction

'Hass' has become the most important cultivar grown by those countries with mild Mediterranean or subtropical climates. It is a late maturing cultivar and is 'stored' on the tree for varying periods after reaching minimum physiological maturity to take advantage of market opportunities, especially in cooler growing areas. Later maturity in cooler areas is also due to later flowering and fruit set. Delayed harvest of 'Hass', which is normally picked during winter in the warm subtropics, may result in the tree simultaneously carrying mature fruit while flowering and setting the next season's crop. For example, where 'Hass' is grown in cooler climates, e.g. California, Israel, southern Australia and New Zealand, it is a normal event for trees to simultaneously carry two crops for a period of time — mature fruit from the previous season as well as current season's fruit.

Carbohydrate (starch) accumulation in woody tissues of fruit trees and its subsequent recycling during periods of peak assimilate demand have been documented for several species (Jones et al., 1964; Hilgeman et al., 1967; Grochowska, 1973; Jones et al., 1975; Goldschmidt and Golomb, 1982). In general, the accumulation of high concentrations of starch in woody tissues during the quiescent period prior to flowering, results in high fruit yields while the failure to accumulate starch reserves prior to flowering, inevitably due to heavy cropping, most often ends in crop failure.

Chandler (1958) noted that avocado trees growing in a mild Mediterranean climate, store greater amounts of reserve carbohydrates than typical evergreen fruit trees, and the dynamics of starch concentration fluxes more closely resembled the amplitude and patterns of deciduous fruit trees. This observation is supported by the results of Scholefield et al. (1985) who reported that with 'Fuerte' trees growing in southern Australia, trunk starch concentrations reached about 18% during winter and fell to about 3% by late summer. Furthermore, maximum trunk starch concentration showed considerable annual variation with high levels of accumulation and subsequent high yield being followed by low accumulation and low yields.

As dry matter (lipids) of avocado fruit continues to increase while fruit remain on the tree it is expected that delayed harvesting would reduce the available 'energy' from stored sources for the following years crop. Intuitively, one might also expect the impact of delayed harvest to be greater in the late-maturing 'Hass' than the early maturing 'Fuerte', if cropping is primarily dependent on adequate carbohydrate reserves. Kaiser and Wolstenholme (1994) in a similar but shorter term experiment on 'Hass' in South Africa, were unable to demonstrate any adverse effect on yield in a very cool, mesic subtropical environment, but their experiment was compromised by unforeseen factors. In Part I (Whiley et al., 1996a), we presented the first long-term quantitative evidence of reduced yield and initiation of alternate bearing from prolonged on-tree storage for the early maturing cv. Fuerte.

Fruit size in avocados is also an important component of yield as premium prices are often paid for larger fruit. Fruits of cv. Hass are at best medium-sized, but with a proportion of the crop being too small for profitable marketing (Lahav and Adato, 1990; Köhne, 1991; Cutting, 1993; Wolstenholme and Whiley, 1995). Delayed harvest has the potential to bring about small but commercially significant increases in fruit size (Kaiser

and Wolstenholme, 1994) due to the potential for continued cell division in avocado fruits attached to the tree (Schroeder, 1952; Valmayor, 1967).

In this paper we report on the effect of early and delayed harvest, of all or part of the crop, on longer-term yield, regularity of bearing, fruit size and starch cycling in the late-maturing cv. Hass grown in two contrasting environments in summer rainfall subtropical areas of Australia.

2. Materials and methods

The research was carried out in commercial 'Hass' avocado orchards located at Childers (latitude 25°S, altitude 40 m), a warm subtropical mildly stressful environment and with a mean annual summer maximum rainfall of ca. 900 mm; and at Maleny (latitude 26.5°S, altitude 520 m), a cool subtropical mesic low-stress environment with a very high annual rainfall (summer predominant) of ca. 2000 mm. Both localities are situated in the coastal belt of S.E. Queensland within 50 km of the coast, and experience high summer humidity (> 60%). The experiments were conducted over seven seasons, from 1988 to 1990 at Maleny and from 1991 to 1994 at Childers.

The climate at Childers is considered marginally too warm for 'Hass', with small fruit at maturity a significant commercial problem. This cultivar is much more suited for production in the cool, mesic subtropical climate of Maleny. At Childers, 7-year-old 'Hass' (in 1990) trees grafted to seedling Guatemalan rootstock spaced at 8 × 6 m (208 ha⁻¹), were chosen while at Maleny 10-year-old 'Hass' trees (in 1987) grafted to seedling 'Velvick' spaced at 12 × 8 m (104 ha⁻¹) 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. (1988) and Banks (1992). Irrigation at Childers was by under-tree sprinklers (two per tree each delivering 14 l h⁻¹) and was scheduled with tensiometers to supplement rainfall (annual average of 900 mm) while at Maleny trees relied solely on the very high rainfall (annual average of 2000 mm) and the deep krasnozem soil with high clay and organic matter content with good water storage ability.

Procedures for maturity indexing of fruit, monitoring tree phenology and sampling and analysis of starch are described by Whiley et al. (1996a). Harvesting treatments used for the experiments were:

1. All fruit harvested at 25% dry matter (25%) (early harvest);
2. All fruit harvested at 30% dry matter (30%) (early harvest);
3. Half of the fruit harvested at 25% and half at 35% dry matter (25/35%) (intermediate harvest);
4. Half of the fruit harvested at 30% and half at 35% dry matter (30/35%) (intermediate harvest); and
5. All fruit harvested at 35% dry matter (35%) (late harvest); these maturities being typical of normal commercial practice in Australia.

Data were analysed by ANOVA, with covariance analysis to separate the effect of yield on fruit size. Where applicable, the relationship between trunk starch concentration

in July (mid-winter) and subsequent yield was established using linear regression analysis (TableCurve™, Jandel Scientific, CA, USA).

3. Results

3.1. 'Hass' at Childers

'Hass' fruit at Childers reached 24% dry matter from mid- to late May (late autumn) over the duration of the study (Table 1). From mid- to late July, fruit had accumulated 30% dry matter with 35% dry matter being reached from late August to mid-September (early spring). All fruit were harvested within $\pm 1\%$ of the target dry matter for the respective treatments. Some fruit were therefore tree-stored for up to 3 1/2 months.

There was an increase in crop load from the start to the finish of the study, particularly in the last 2 years of the experiment (Fig. 1a). However, fruit yield was lower than expected in 1992 due to the damaging 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% out-yielded those in which harvest was delayed until 35%. In this case, carry-over effects from the storm may have enhanced the magnitude of treatment effects thereby precipitating a conclusive result. Treatment yields ranged between 9.4 and 27.8 t ha⁻¹ in 1993.

There were no significant differences in fruit size between any of the treatments in each of the four years of the study (Table 2). 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.

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% treatments (Fig. 1b). Starch levels for the 30%, 25/35% and 30/35% treatments in 1992 fell between concentrations for the 25% and 35% treatments and were not significantly different (data not presented). Starch concentrations in the shoots followed similar seasonal patterns for the first 3 years of the study when they were measured. Levels were initially low at the completion of summer

Table 1

Maturity of cv. Hass fruit at Childers indicated by flesh dry matter at the different times of harvest in 1991 to 1994. Data are 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 (%)
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

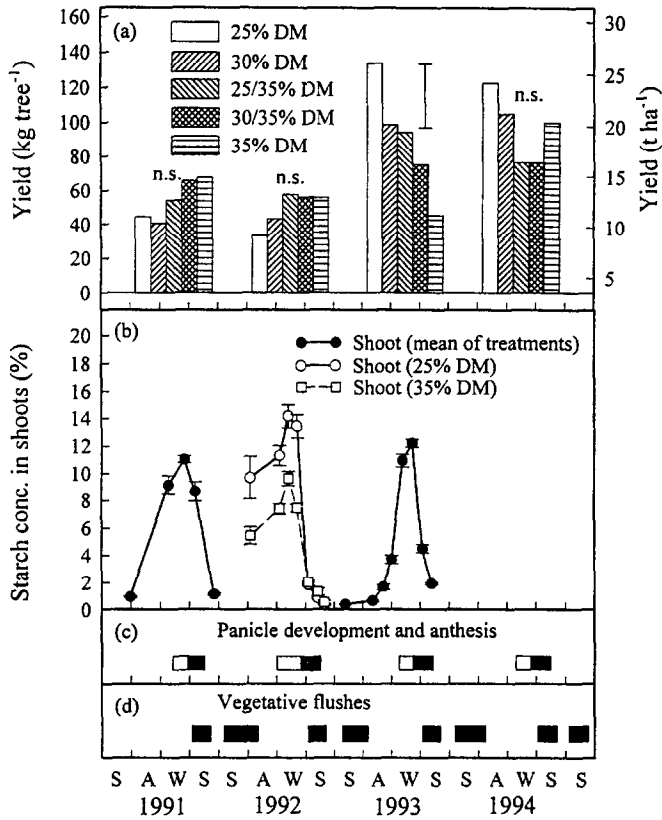


Fig. 1. Relationship between yield, seasonal starch concentration flux and tree phenology of cv. Hass at Childers where: (a) is yield of fruit which were harvested at different stages of maturity as judged by dry matter (DM), the vertical bar indicates LSD ($P \leq 0.05$); (b) is starch concentration of shoots of all treatments (●, $n = 15$), or 25% DM (○, $n = 3$), or 35% DM (□, $n = 3$), 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.

Table 2

Effect of time of harvest on fruit size of cv. Hass growing at Childers. Data are mean of six 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

Time of harvest (fresh % DM)	Fruit size (g)			
	1991	1992	1993	1994
25%	172.9 (179.8)	169.1 (164.8)	230.2 (203.8)	188.9 (183.8)
30%	178.6 (188.3)	146.5 (144.7)	239.6 (241.5)	194.0 (195.2)
25/35%	186.2 (186.4)	160.3 (163.0)	244.8 (240.4)	192.5 (195.5)
30/35%	185.4 (177.6)	162.7 (164.6)	236.4 (242.5)	192.8 (195.8)
35%	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

** Regression coefficient is significant at $P \leq 0.01$.

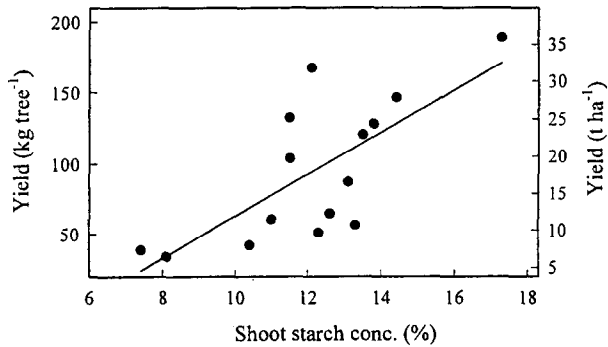


Fig. 2. Relationship between yield (1993) and July shoot starch concentration (1992) of cv. Hass growing at Childers. The regression is represented by the equation $y = 14.84x - 85.63$, $r^2 = 0.52^*$.

shoot growth but increased rapidly as shoots entered a period of quiescence and peaked prior to flowering (Fig. 1). Concentrations declined rapidly during flowering and spring shoot growth.

Shoot growth occurred during two periods over each cropping cycle; a relatively short period of activity in 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 ceased by mid-March (Fig. 1d).

The light crop due to storm damage and the different harvesting times of fruit are 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 May 1992) 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. 2).

While there were no significant differences in cumulative fruit yield until the 4th year of the study, the combined yield of the first and second years was higher for treatments which were harvested late (Fig. 3). This was most likely 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 (3 years) this trend was changing, slightly favouring the earlier harvested fruit and after 4 years, trees harvested at 25% dry matter cumulatively produced more fruit than other treatments (Fig. 3).

With respect to the sustainability of production there was little impact made on yield by any of the treatments during the first 2 years of the study (Fig. 4). This in part may be due to the severe 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 treatments with split

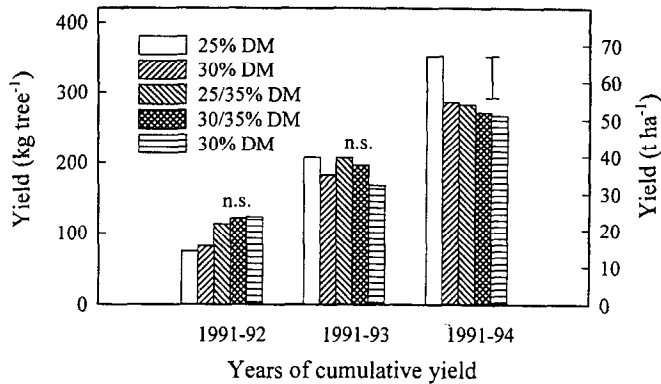


Fig. 3. Effect of time of harvest, based on fruit dry matter (DM), on the cumulative yield of cv. Hass avocado trees at Childers over 4 consecutive years. Columns are mean values of six trees for each treatment and vertical bar represents LSD ($P \leq 0.05$) determined by ANOVA.

harvests at 25/35% and 30/35%. However, for those trees where all fruit were harvested at 35% there was a reduction in the 1993 yield compared with 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 (Whiley et al., 1996a).

3.2. ‘Hass’ at Maleny

At Maleny, the cooler site, fruit reached 25% dry matter from late June to mid-July (mid-winter); 30% from early August to late September; and 35% in early November (late spring) (Table 3). 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.

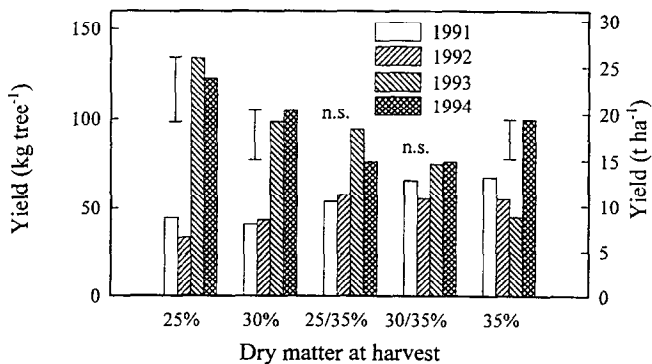


Fig. 4. Effect of time of harvest, as judged by fruit dry matter (DM), on the sustainability of yield of cv. Hass at Childers. Columns represent mean values of six trees for each treatment and vertical bars LSDs ($P \leq 0.05$) determined by ANOVA.

Table 3

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 3 years of the study (Fig. 5a). 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

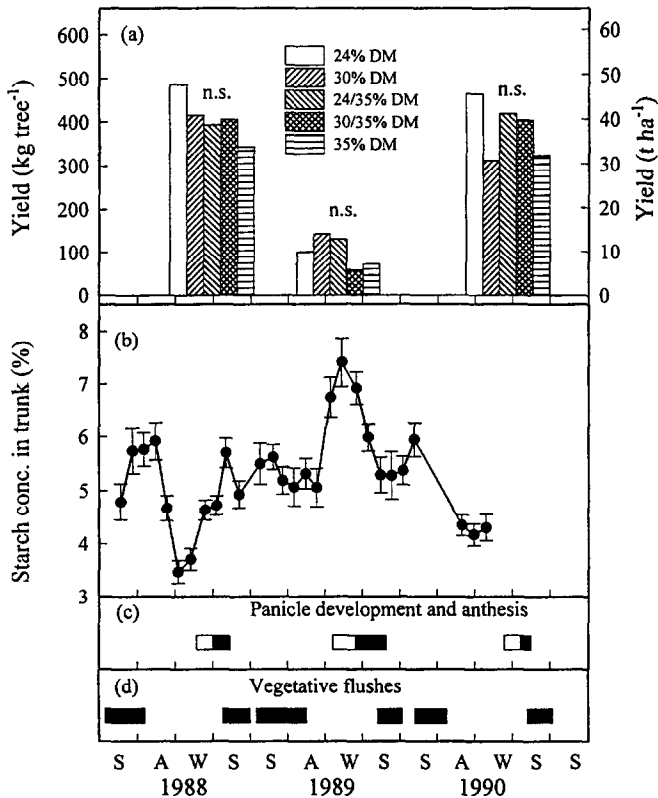


Fig. 5. Relationship between yield, seasonal starch concentration flux and tree phenology at Maleny where: (a) yield of fruit which was harvested at different stages of maturity as judged by dry matter (DM); (b) is starch concentration ($n = 30$), of trunk wood for all treatments, SEs are represented 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.

39.2 and 37.0 t ha⁻¹, respectively) and low yield (equivalent to 9.6 t ha⁻¹) in the second year.

As there were no significant differences in trunk starch concentrations between treatments throughout the 3 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 and 1990) or during flowering (1989) (Fig. 5b and c). Starch concentrations of trunk wood tended to be relatively stable during shoot growth and were in the vicinity of 5 to 6% (Fig. 5b and d). 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 (Fig. 5a and b).

Panicle emergence began in mid- to late July each year with anthesis mainly during September and extending into October (Fig. 5c). The flowering intensity was noticeably greater and extended for longer in the spring of the off-year compared with that when the trees carried heavy crops. Shoot growth occurred in two major flushes over each crop cycle (Fig. 5d). 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 concentrations in July 1988 and 1989 were directly related to the yields in 1989 and 1990, respectively (Fig. 6). 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.

The effect of harvest time on fruit size is reported in Table 4. 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

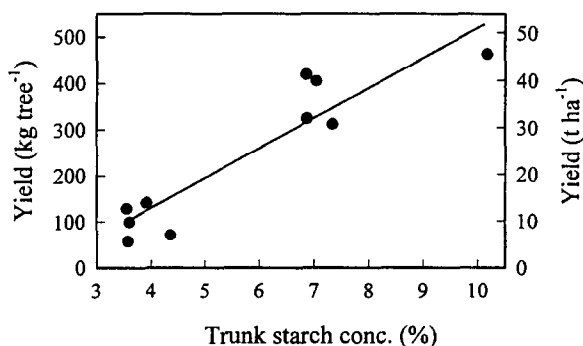


Fig. 6. Relationship between July trunk starch concentration and next season's yield of cv. Hass growing at Maleny. The regression is represented by the equation $y = 64.90x - 129.04$, $r^2 = 0.86$ ($P \leq 0.01$).

Table 4

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

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

* Regression coefficient is significant at $P \leq 0.05$.

harvest. This increase in fruit size was achieved without any significant reduction in fruit yield, either in the 1989 or 1990.

4. Discussion

4.1. Yield and fruit size

Avocado yields are strongly influenced by the interaction of fruit load and duration of the crop on the tree. With early (Whiley et al., 1996a) and late maturing cultivars growing at Childers, removal of fruit within reasonable time of reaching physiological maturity maintained yield performance over a number of seasons. However, a prolonged delay in harvesting 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 (Whiley et al., 1996a).

The development of the alternate bearing pattern at Childers was delayed with 'Hass', as yields were relatively low across all treatments over the first 2 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 cyclone in 1992. Nevertheless, in the final 2 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 are likely

to increase the 'cost of fruiting' at Childers through increased respiratory losses (Blanke and Whiley, 1995) thereby limiting photo-assimilates for fruit growth and subsequent production.

'Hass' trees at Maleny were in a hail-induced biennial bearing cycle when treatments began 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 for avocados (Wolstenholme, 1986; Wolstenholme, 1987). It was associated with depletion of trunk starch content as the crop matured during winter, which supports 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 bearing cycle, and it appears that more rigorous manipulation 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 7 months after anthesis. Similarly, El-Zeftawi and Thornton (1975) showed that stripping fruit from 'Valencia' trees within 4 months of setting their first commercial crop, moderated alternate bearing for 6 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 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 when trees were over-loaded with fruit. Kaiser and Wolstenholme (1994), who graded the entire crop of all trees, found larger 'Hass' fruit when harvesting was delayed. Their result is consistent with continuation of cell division while 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 2 and 4). At Childers the mean fruit size over the 4 years of the study was 195.0 ± 6.5 g while for the 3 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.

4.2. Seasonal starch cycling

Starch concentrations in either the trunk or shoots of trees were a better indicator of crop performance for 'Hass' than for 'Fuerte'. 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 late-maturing 'Hass' (ca. 14%) than early-maturing 'Fuerte' (ca. 7%) (Whiley et al., 1996a). The reasons for this are not clear but may be associated with magnitude and temporal differences in phenology. 'Fuerte' (Whiley et al., 1996a) showed more vegetative vigour than 'Hass' and flushed longer during summer. 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 (Whiley, 1994) and this combination of sinks together with decreased CO₂ assimilation efficiency during the winter, may have caused the lower peak concentrations.

The reduced yields from late harvesting and from 'off' years 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 reduced flowering are beyond the scope of data presented, but may 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 (Whiley et al., 1996b) clearly show suppression of root growth during the autumn/winter period, a time of floral induction in avocado (Davenport, 1982; Whiley et al., 1988), when trees carry heavy crop loads. Poor root growth and consequently reduced cytokinin supply may well be a factor contributing to the

diminished flowering observed in trees where delayed harvesting reduced the subsequent yield.

It is also pertinent to note that average 'Hass' yields (t ha^{-1}) at Childers (a sub-optimal site) were lower than at Maleny, a close to ideal site for this cultivar. Equally, industry experience is that there is little meaningful difference in yield (t ha^{-1}) between the late-maturing 'Hass' and the early-maturing 'Fuerte', when both are grown in environmental optimal areas ('Fuerte' at Childers, 'Hass' at Maleny). In contrast, when 'Fuerte' is grown in cold subtropical and Mediterranean climates its yield performance is poor ($< 10 \text{ t ha}^{-1}$), and this is the main reason for its eclipse by 'Hass' in most of the subtropics. Although reliable yield data for tropical (West Indian race), very early maturing avocados are scarce, there is correspondingly no evidence that they out-yield later-maturing subtropical cultivars.

5. 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 criterion with respect to sustainability of productivity on an annual 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, whereas markedly delayed harvesting of fruit precipitated strong alternate cropping patterns. Early harvesting of 'Hass' where biennial bearing was already entrenched, did not release the tree from this cropping pattern and more extreme practices such as fruit thinning or pruning are likely to be needed to moderate the cycle. Indeed, where storm damage effectively removed crop load 5 months after fruit set, cropping patterns were modified in cv. Fuerte (Whiley et al., 1996a). In both cultivars the starch concentration flux closely followed changes in phenological events and generally peaked in winter during an extended quiescent period. Although heavy fruiting depressed winter starch levels which resulted in reduced yield, production is more likely to be constrained by other environmental, resource and management limitations at critical phenological stages.

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References

- Banks, A., 1992. Growing avocados in Queensland. Department of Primary Industries, Brisbane, 36 pp.
- 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. *Plant Cell*, 5: 1147–1155.
- Bernier, G., Kinet, J.M. and Sachs, R.M., 1981. *The Physiology of Flowering*, Vol. II. CRC Press, Boca Raton, FL.
- Blanke, M.M. and Whiley, A.W., 1995. Bioenergetics and water relations of developing avocado fruit. *J. Plant Physiol.*, 145: 87–92.
- Cameron, S.H. and Borst, G., 1938. Starch in the avocado tree. *Proc. Am. Soc. Hort. Sci.*, 36: 255–258.
- Chandler, W.H., 1958. The avocado. In: *Evergreen Orchards*. 2nd edn. Lea and Febiger, Philadelphia, PA, pp. 205–228.
- 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: 282–285.
- Cutting, J.G.M., 1993. The cytokinin complex as related to small fruit in 'Hass' avocado. *S. Afr. Avocado Growers' Assoc. Yrbk*, 16: 20–21.
- Davenport, T.L., 1982. Avocado growth and development. *Proc. Fla State Hort. Soc.*, 95: 92–96.
- 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: 219–226.
- 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. 273–276.
- 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. Am. Soc. Hort. Sci.*, 107: 206–208.
- 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: 347–356.
- 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. Am. Soc. Hort. Sci.*, 90: 111–116.
- Jones, W.W., Embleton, T.W. and Coggins, 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., 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: 441–449.
- Jones, W.W., Embleton, T.W., Steinacker, M.L. and Cree, C.B., 1964. The effect of time of fruit harvest on fruiting and carbohydrate supply in the Valencia orange. *Proc. Am. Soc. Hort. Sci.*, 84: 152–157.
- 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: 447–457.
- 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.
- Rodrigues, J. and Ryan, G.F., 1960. The influence of season and temperature on carbohydrates in avocado shoots. *Proc. Am. Soc. Hort. Sci.*, 76: 253–261.
- 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. *Scient. Hort.*, 25: 99–110.
- Schroeder, C.A., 1952. Floral development, sporogenesis, and embryology in the avocado, (*Persea americana*). *Bot. Gaz.*, 113: 270–278.
- 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. *Scient. Hort.*, 2: 399–403.
- Sparks, D., 1975. The alternate fruit bearing problem in pecans. 65th Annu. Proc. Northern Nut Growers' Assoc. 1974, pp. 145–158.

- Valmayor, R.V., 1967. Cellular development of the avocado fruit — blossom to maturity. *Philippine Agricult.*, L: 907–976.
- Whiley, A.W., 1994. Ecophysiological studies and tree manipulation for maximisation of yield potential in avocado (*Persea americana* Mill.). Unpublished PhD Thesis, University of Natal, Pietermaritzburg, South Africa, 174pp.
- 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, CA, pp. 155–159.
- Whiley, A.W., Rasmussen, T.S., Saranah, J.B. and Wolstenholme, B.N., 1996a. Delayed harvest effects on yield, fruit size and starch cycling in avocado (*Persea americana* Mill.) in two subtropical environments. I. The early-maturing cv. Fuerte. *Scientia. Hortic.*, 66 (1996) 23–34.
- 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., 1996b. Verification and quantification of a growth model for avocado (*Persea americana* Mill.). I. Root and Rootstock Components. *J. Hort. Sci.*, in press.
- Williams, M.W. and Edgerton, L.J., 1974. Biennial bearing of apple trees. *Proc. XIX Intern. Hortic. Congr. Warsaw*, 3: 343–352.
- Wolstenholme, B.N., 1986. Energy costs of fruiting as a yield-limiting factor with special reference to avocado. *Acta Hort.*, 175: 121–126.
- Wolstenholme, B.N., 1987. Theoretical and applied aspects of avocado yield as affected by energy budgets and carbon partitioning. *S. Afr. Avocado Growers' Assoc. Yrbk.*, 10: 58–61.
- Wolstenholme, B.N. and Whiley, A.W. 1995. Prospects for increasing Hass fruit size — A southern hemisphere perspective. *Aust. Avocado Growers' Federation Conf.*, Fremantle, Australia, 30 April–3 May, pp. 89–102.