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Delayed harvest effects on yield, fruit size and starch cycling in avocado (*Persea americana* Mill.) in subtropical environments. I. the early-maturing cv. Fuerte

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Abstract

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 of fruit at 21 and 24% flesh dry matter (DM) resulted in highest cumulative and average yield (21.5 t ha^{-1} $year^{-1}$). A harvest delay of ca. 2 months, until flesh DM reached 30%, reduced average annual yield by 26% and initiated an alternate bearing cycle. Early harvest of half the crop and late harvest of the remainder did not significantly reduce yield. Wood starch concentrations from trunks and bearing shoots fluctuated seasonally but could not be related to harvest treatment. Harvesting late led to significantly larger fruit in three of the six seasons.

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

1. 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

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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 for growth and reproduction. Avocados have the capacity to store significant quantities of minerals and carbohydrates which are largely re-cycled 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 a substantial 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; Wolstenholme, 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 abiotic environmental variables such as temperature (particularly in relation to critical phenological events), humidity, wind and storms, light and nutrient supply (Proctor and Creasey, 1971; Sedgley and Annells, 1981; Whiley and Winston, 1987; Issarakraisila and Considine, 1994; Crane et al., 1994, Whiley, 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 physiological maturity (Eaks, 1980; Kaiser and Wolstenholme, 1994), this practice undoubtedly will have some impact on the total carbon economy of the tree. While currently there are no published reports on the long-term effect of delayed harvest of avocado on subsequent productivity, the consequences have been reported for 'Valencia' orange. This fruit may also be 'stored' on trees in cool areas for up to 8 months after commercial maturity has been reached, with several months overlap of successive crops. Extended 'on-tree-storage' of 'Valencia' orange results in 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).

The two most important avocado cultivars grown in Australia and in most of the subtropics are the early maturing 'Fuerte' and the late maturing 'Hass'. We report on the effect of delayed harvesting of these two cultivars at two localities. Part I deals with cv. Fuerte at Childers, and Part II with cv. Hass at both Childers and Maleny in S.E. Queensland.

2. Materials and methods

The 'Fuerte' experiment was located at Childers (latitude 25°S, altitude 40 m) in S.E. Queensland, which has a warm, subtropical climate well suited to this cultivar. The study extended over six consecutive seasons from 1988 until 1993 inclusive. The 7-year-old trees (in 1988) were on seedling Guatemalan rootstock and spaced 9 × 7 m (143 trees ha^{-1}) in a deep, well-drained krasnozem soil. Fertilisation and pest and disease control were according to recommendations of Whiley et al. (1988) and Banks (1992). Each tree was irrigated by two under-tree sprinklers (each delivering 14 l h^{-1}) scheduled with tensiometers to supplement the mean annual rainfall of ca. 900 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 (DM) 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% DM (Brown, 1984) though commercially 'Hass' is generally harvested when it reaches 23 to 25% DM. In many instances fruit is stored on trees for market opportunities, so that pulp DM may exceed 30 to 35% when harvested. Thus treatments selected spanned those of normal commercial practice and for 'Fuerte' were:

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

Treatments were applied to single-tree plots and replicated six times in a randomised block design. To determine the correct stage of maturity for harvesting, random fruit samples were periodically collected for pulp DM determination. In addition, pulp DM percentage of five fruit from each tree was measured at harvest to establish the actual maturity of fruit from each treatment at harvest.

Tree phenology was detailed by recording the date of floral bud-break and development of the inflorescence, the duration of anthesis, and the periods of active shoot growth. Wood samples from trunks and the most recently produced shoots were collected for starch analysis at 1–2 month intervals depending on growth activity within the tree. Wood samples from trunks 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. Shoot samples were obtained by the removal of approximately 6 cm of terminal growth from 10 randomly selected, non-fruiting, mature-summer grown shoots with leaves being discarded. Samples were placed in a cool, insulated box for transport back to the laboratory and within 3 h of collection, were dried at 60°C to constant mass in a convection oven. Dried samples were ground at 100 mesh in a Udy Mill (Udy Corporation, USA) and stored in airtight containers. 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 were analysed by ANOVA, and covariance analysis was used to separate the effect of yield on fruit size.

3. Results

Depending on the year, fruit flesh reached 21% DM between late March and mid-April (autumn); 24% DM between late April to mid-May, and 30% DM from late May to mid-June (early winter) (Table 1). All fruit over the duration of the study were harvested within ±1% of the target DM for the respective treatments.

3.1. Yield

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 probably due to pre-conditioning of the trees following the application of treatments over a number of years and the exceptionally high yields of late-harvest trees the previous year.

After the second year of the study treatments began to affect the cumulative yield of trees (Fig. 2). Treatments with the earliest harvest times, viz. 21%, 24% and 21/30%, had significantly higher yields than where fruit was allowed to hang until 30%. The yield increment increased with time, though the earliest harvested treatments never significantly out-yielded the split harvests at 21/30% or 24/30%: i.e. split harvests did not prejudice cumulative yields over the six seasons. Mean yields over six seasons were 21.5 t ha^{-1} for the two early harvests, 18.8 t ha^{-1} for the split harvests and 15.9 t ha^{-1} for the late harvest. Late harvesting therefore reduced mean annual yield by 5.6 t ha^{-1}, or by 26% when compared with early harvesting ($P \leq 0.05$ judged on a cumulative basis).

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

Table 1
Maturity of cv. Fuerte fruit at Childers indicated by flesh dry matter at the different times of harvest in 1988 to 1993. Data are means ± SE of five fruit from trees 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 ± 0.3	06.05.88	24.6 ± 0.4	17.06.88	31.1 ± 0.3
28.03.89	21.1 ± 0.2	26.04.89	24.9 ± 0.5	08.06.89	29.8 ± 0.4
24.04.90	21.4 ± 0.3	15.05.90	25.4 ± 0.4	19.06.90	29.7 ± 0.3
11.04.91	21.7 ± 0.1	09.05.91	24.8 ± 0.2	21.05.91	30.4 ± 0.4
09.04.92	21.2 ± 0.2	29.04.92	24.6 ± 0.2	18.06.92	30.6 ± 0.3
14.04.93	21.7 ± 0.2	04.05.93	25.7 ± 0.6	24.05.93	30.0 ± 0.5

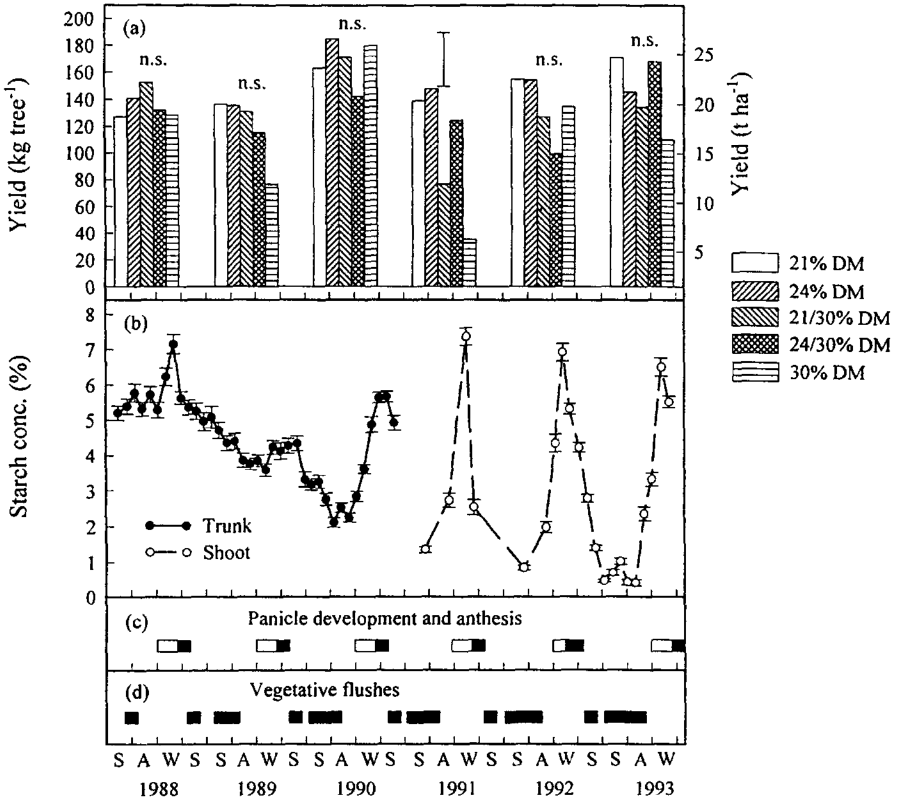

Fig. 1. Relationship between yield, seasonal starch concentration flux and tree phenology of cv. Fuerte over six seasons at Childers where: (a) is yield of fruit which were harvested at different stages of maturity as judged by dry matter (DM), vertical bar indicates LSD ($P \leq 0.05$); (b) is the mean 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.

absence of bias in the experimental population (Fig. 1a). The continued early harvesting of fruit at 21 and 24% DM for 6 years resulted in cropping patterns with insignificant ($P \leq 0.05$) annual variation, and limited to fluxes which probably reflected environmental conditions at critical periods of development (Fig. 3). In contrast, delayed harvesting of either half or all of the crop, resulted in the development of an alternate bearing cycle in which the amplitude increased with time. Examination of the data show that the cycle was atypical from 1992 to 1993 where yields for the 21/30% and 30% DM treatment were almost identical (Fig. 3). This may be explained by a cyclonic tropical storm in February 1992 when a significant portion of the crop was blown off trees when fruit was about 60% grown. This effectively acted as an unscheduled, very early harvest across all treatments allowing a similar sized crop to be carried the following year.

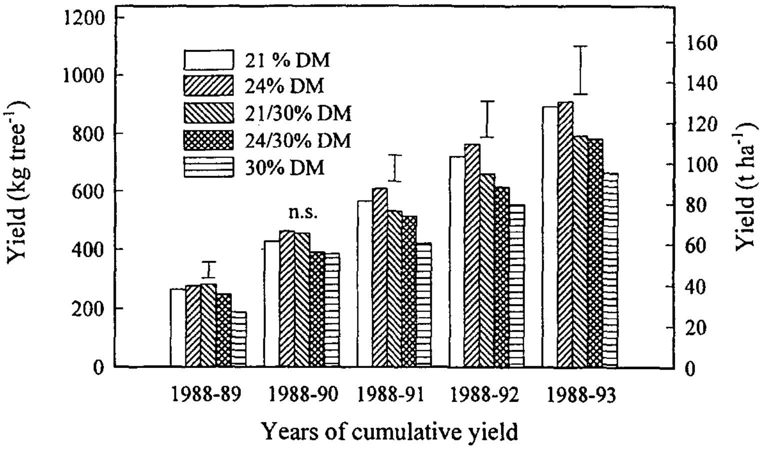

Fig. 2. Effect of time of harvest, based on fruit dry matter (DM), on the cumulative yield of cv. Fuerte avocado trees at Childers over six consecutive years. Columns are treatment means ($n = 6$) and vertical bars indicate LSDs ($P \leq 0.05$).

3.2. Fruit size

Mean fruit size was dependent on the time of harvest although significant differences were not apparent in all years (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. For example, in 3 years out of six, fruit size of the 21/30% and 30% treatments was significantly larger than in the 21% treatment.

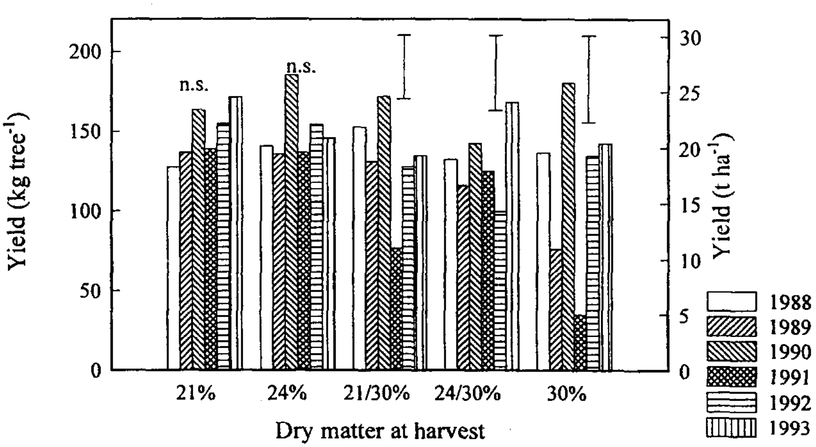

Fig. 3. Effect of time of harvest on the sustainability of yield of cv. Fuerte avocado trees at Childers over six consecutive years. Columns are mean values ($n = 6$) and vertical bars indicate LSDs ($P \leq 0.05$).

Table 2

Effect of time of harvest on fruit size of cv. Fuerte at Childers. Data are mean tree values ($n = 6$) of treatments 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. Values in columns not sharing a common letter are significantly different ($P \leq 0.05$) as determined by ANOVA

Time of harvest (flesh % DM)	Fruit mass (g)					
	1988	1989	1990	1991	1992	1993
1. 21% DM	269.3 (276.4)c	306.6 (308.5)c	318.9 (320.5)a	339.4 (325.9)a	309.3 (318.4)b	290.9 (294.3)a
2. 24% DM	309.5 (309.5)b	313.6 (315.2)abc	312.3 (307.2)a	338.2 (321.2)a	313.0 (302.8)b	321.8 (320.1)a
3. 21/30% DM	343.9 (343.9)a	331.2 (332.4)ab	329.3 (328.3)a	330.6 (341.6)a	343.6 (347.1)a	334.4 (328.3)a
4. 24/30% DM	340.2 (340.2)a	357.9 (357.5)a	340.6 (348.5)a	351.8 (343.9)a	320.2 (337.6)ab	314.3 (315.8)a
5. 30% DM	339.8 (339.8)a	343.0 (338.7)ab	327.2 (323.7)a	344.8 (367.3)a	345.5 (345.2)a	335.8 (338.7)a
Regression coefficient	−0.784 **	0.102	−0.305	−0.394 **	−0.505	−0.372

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

3.3. Starch cycling

Trunk and shoot starch concentrations have been pooled as there were no significant differences between treatments. The concentration flux of trunk wood starch over 3 years was in the order of 5% (from ca. 2 to 7%) (Fig. 1b). Starch levels peaked during each winter and declined during and immediately after flowering. The lowest trunk starch concentrations were during the summer and autumn of 1990 when trees were carrying their heaviest crop (Fig. 1a and b). 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 more defined seasonal pattern (Fig. 1b). Peak starch concentrations accumulated during the autumn/winter period when shoot growth had ceased and trees were in a relatively quiescent phase (Fig. 1b, c and d). During the flowering and spring flush periods shoot starch levels dropped rapidly to < 1% by the end of spring.

3.4. Phenology

Panicle development and flowering occurred over a 16 week period with panicle growth beginning in June and flowering completed by the end of September in each year of the investigation (Fig. 1c). 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.

4. Discussion

4.1. Yield and fruit size

Results have shown that avocado yields are strongly influenced by the interaction of fruit load and the duration of post-maturity storage of the crop on the tree. With 'Fuerte', an early season cultivar growing under good management at Childers, harvesting within a reasonable time of reaching minimum commercial maturity (21 to 24% flesh DM) maintained high commercial yields with minimal fluctuation over the six seasons. However, more delayed harvesting caused a strong alternate bearing cycle to develop starting in the second season, i.e. evident in the 1989 crop. Only a tropical cyclone, which blew a substantial portion of the crop from the trees in February 1992, broke the regular cyclic yield pattern. In general, cumulative yields were highest in the 21% and 24% DM treatments, which were significantly better than the 30% DM treatment. Split harvests gave intermediate yields, though not significantly different from the early-strip or late harvest treatments. Early, selective harvest of the largest fruits (50% of the crop), allowing remaining fruit to be stored on-tree for another 3 to 4 weeks, will therefore not prejudice overall yield or initiate alternate bearing in well-managed orchards. This practice facilitates greater efficiency of limited farm resources and allows increased flexibility with respect to marketing opportunities.

Picking date is reported to have affected yield in other fruit crops. Apple fruits were picked over an 8 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., 1964).

There was a trend of increased fruit size with delayed harvest, although results were not significant in all seasons. 'Fuerte' fruit size (mass) increased by ca. 8 to 18% with later harvested treatments. However, these gains must be balanced against lower yields, as small fruits are generally not a commercial problem with cv. Fuerte in well-managed orchards. Studies on some other fruits have reported increased fruit size with delayed harvest, e.g. 'Bramley Seedling' apples (Williams et al., 1980). Avocado fruits could be expected to increase in size more than other fruits, due to the continued cell division as long as the fruits remain firmly attached to the tree (Schroeder, 1952; Valmayor, 1967). This effect is likely to be greater in fruit in which seed coats do not abort prematurely (Blumenfeld and Gazit, 1974; Steyn et al., 1993; Wolstenholme and Whiley, 1995).

4.2. 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 of 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 with levels when trees have cropped heavily. The 3 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 our 6 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 lower dependence on reserve carbohydrate of 'Fuerte' trees to maintain yield in subtropical summer rainfall climates. It is suggested that carbohydrates from current photo-assimilation play a proportionally greater role in cropping than in cooler regions. Observations at Childers indicated the trees retained most summer-grown leaves 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 leaves 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. Thus avocado trees in such stressful environments were semi-deciduous, and this was reflected in starch concentration fluxes more typical of deciduous trees.

5. Conclusions

It is concluded, in an area conductive to high yields of 'Fuerte', that early harvesting of half the crop at a fruit flesh DM of 21 to 24%, permits regular annual bearing in well-managed orchards. However, a harvest delay until 30% flesh DM (an additional ±2 months tree storage under the conditions of the study) reduced average yield significantly and initiated an alternate bearing cycle. Although both trunk and shoot wood starch levels followed seasonal concentration fluxes related to phenological events (especially the latter), there were no significant differences between treatments. However, it appears that accumulated starch is important in supporting flowering when concentrations in the tree rapidly decline; but not so critical for fruit retention and early growth by which time starch levels are very low. Late harvest led to significant fruit size increases in three of the six seasons. The economic benefits of delayed harvest, if any, therefore need to be carefully evaluated against the loss of management control implicit in reduced yield and the onset of alternate bearing in 'Fuerte' trees.

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References

Banks, A., 1992. Growing avocados in Queensland, Department of Primary Industries, Brisbane, 36 pp.

Blumenfeld, A. and Gazit, S., 1974. Development of seeded and seedless avocado fruits. J. Am. Soc. Hort. Sci., 99: 442–448.

Brown, B.I., 1984. Market maturity indices and sensory properties of avocados grown in Queensland. Food Technol. Aust., 37: 474–476.

Cameron, S.H. and Borst, G., 1938. Starch in the avocado tree. Proc. Am. Soc. Hort. Sci., 36: 255–258.

Cameron, S.H., Mueller, R.T. and Wallace, A., 1952. Nutrient composition and seasonal losses of avocado trees. Calif. Avocado Soc. Yrbk, 36: 201–209.

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: 483–492.

Crane, J.H., Balerdi, C., Campbell, R. and Goldweber, S., 1994. Managing fruit orchards to minimize hurricane damage. Hort. Technol., 4: 21–27.

Davis, J.T. and Sparks, D., 1974. Assimilation and translocation patterns of carbon-14 in the shoot of fruiting pecan trees. J. Am. Soc. Hort. Sci., 99: 468–480.

Dickson, R.E., 1991. Assimilate distribution and storage. In: A.S. Raghavendra (Editor). Physiology of Trees. Wiley, New York, 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. Am. Soc. Hort. Sci., 105: 744–747.

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.

Issarakraisila, M. and Considine, J.A., 1994. Effects of temperature on microsporogenesis and pollen viability in mango cv. Kensington. Ann. Bot., 73: 231–240.

Jones, W.W. and Cree, C.B., 1954. Effect of time of harvest on yield, size and grade of Valencia oranges. Proc. Am. Soc. Hort. Sci., 64: 139–145.

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., 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.

Lee, S.K., 1981a. Methods for percent oil analysis of avocado fruit. Calif. Avocado Soc. Yrbk, 65: 133–141.

Lee, S.K., 1981b. A review and background of the avocado maturity standard. Calif. Avocado Soc. Yrbk, 65: 101–109.

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. Am. Soc. Hort. Sci., 108: 390–394.

Monselise, S.P. and Goldschmidt, E.E., 1982 Alternate bearing in fruit trees. Hort. Rev., 4: 128–173.

Proctor, J.T.A. and Creasey, L.L., 1971. Effect of supplementary light on anthocyanin synthesis in McIntosh apples. J. Am. Soc. Hort. Sci., 96: 523–526.

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: 525–534.

Rasmussen, T.S. and Henry, R.J., 1990. Starch determination in horticultural plant material by an enzymic colorimetric procedure. J. Sci. Food Agric., 52: 159–170.

Schaffer, B. and Baranowski, R.M., 1986. Sample size estimates for avocado yield experiments. J. Am. Soc. Hort. Sci., 111: 985–987.

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. Sci. Hortic., 25: 99–110.

Schroeder, C.A., 1952. Floral development, sporogenesis and embryology in the avocado *Persea americana*. Bot. Gaz., 113: 270–278.

Sedgley, M. and Annells, C.M., 1981. Flowering and fruit-set response to temperature in the avocado cultivar 'Hass'. Sci. Hortic., 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. Sex. Plant Reprod., 6: 87–97.

Swarts, D.H., 1976. 'n Praktiese avokado-oliebepalingsmetode vir produsente. Citrus and Subtropical Fruit J., 511: 8–14.

Swarts, D.H., 1978. Use of microwaves to determine maturity of avocados. Citrograph, 63: 325–326.

Valmayor, R.V., 1967. Cellular development of the avocado fruit — blossom to maturity. Philippine Agric., 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, 174 pp.

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. Agric., 26: 249–253.

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: 45–47.

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: 359–362.

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 applies 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. Proc. Aust. Avocado Growers Federation Conf., Fremantle, Australia, 30 April–3 May, pp. 89–102.