PRELIMINARY RESULTS ON THE INFLUENCE OF LATE HANGING OF HASS AVOCADOS (*PERSEA AMERICANA* MILL) ON TREE PERFORMANCE

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ABSTRACT

A study of the phenological and some of the physiological impacts of 'late hanging' of mature Hass avocado fruit in the Natal midlands (RSA), at a cool and warm site was carried out during 1989 and 1990. Effects of fruiting were inconsistent, but the general trend was that trees harvested before flowering tended to result in earlier flowering, a more prolific first (spring) growth flush, and higher wood and bark starch concentrations than those harvested after flowering. While this experiment should be considered as a preliminary investigation towards ongoing research in this field, it appears that producers should limit Hass fruit on tree storage in this region to September to ensure balanced (low risk) cropping for maximum long term returns. Further, if producers in the Natal midlands intend to harvest fruit later than September in future, it may be necessary for them to consider thinning fruit early in the season after set, depending on the crop load; the profitability of which will depend implicitly on market dictum. Selective harvesting is also implied.

INTRODUCTION

Until now the export market has largely determined the economic viability of the South African avocado producer. In 1989 the net on tree value of fruit sold on the export market amounted to between R1 614 ton^{-1} (air freight) and R2 015 ton^{-1} (sea freight), while that for the domestic market only amounted to between R289 ton^{-1} (local market) and R550 ton^{-1} (under grade). Since the export industry relies on its reputable ability to reliably produce fruit of superior quality, only fruit of a certain standard is exported. At present an estimated 78% of fruit from a production average of 51 ha^{-1} is suitable for export. This resulted in an income to the industry of R55 million in 1989. By increasing the fruit export percentage to 85% and the average yield to 7,5 t ha^{-1}, the industry stands to approximately double its income. Clearly the present economic value of the avocado crop is determined by its yield and quality (Toerien, 1989).

At present this export incentive is promoted by the weak Rand compared to most foreign Western currencies. However, in view of the relatively high inflation rate in South Africa and the high fixed costs associated with avocado production, it would appear that the profitability of exporting fruit will be severely affected by an appreciation in the value of the Rand (Toerien, 1989). Further there is the ever present possibility of stronger

competition from other exporting countries, with a possible saturation of the overseas market.

Considerable scope still remains to exploit the local South African domestic market more thoroughly. Here market prices show a distinct seasonal variation, with lowest prices in autumn and winter; rising prices through spring and peak prices in summer. This trend exhibits a typical supply and demand function. At present there is a very distinct price advantage available to the producer who markets fruit from October to January.

Characteristically different cultivars are marketed throughout the season. Typically, Fuerte fruit usually dominate the early local market (April, May and June), followed by mid-season Edranol fruit, while the tail end of the season is filled by Hass (July onwards) and Ryan (October).

Due to its more southerly latitude and the moderating influences of the Drakensberg, the sea, high rainfall and high humidity, cultivars grown in the Natal midlands generally flower and are harvested later than their counterparts in the Transvaal. Hence, by marketing typically late maturing cultivars such as Hass and Ryan, the Natal producer has the obvious advantage towards realising the October to January price advantage on the local market, as well as helping to increase market volume in the second half of the export season, *viz* July through September.

One alternative that is currently being considered is on-tree storage or 'late hanging' of fruit. This involves picking fruit after their optimum picking date. However, since, apart from socio-political inferences, the success of agriculture depends intrinsically on risk minimisation as well as profit maximisation, the long term effects of late hanging have not as yet been determined. The aim of the experiment presented in this paper was to study the phenological and some aspects of the physiological impact of 'late hanging' of mature Hass avocado fruit in the Natal midlands (RSA) for four months past the region's optimal picking date (legal maturity between July and August). A similar trial is presently in progress in SE Queensland, Australia (Whiley, pers comm) [1].

Flowering of Hass avocado trees peaks during September in inland Natal. Unless the trees are harvested before this time, they set fruit while the previous season's crop is still on the tree. Consequently, the trees will be required to maintain a double fruit load until harvesting or natural abscission takes place. Since these fruit are known to accumulate oil with development to as much as 15 to 30% of total fresh mass, it is expected that 'on tree storage' of mature fruit will exert a continuing demand for assimilate supply, with pronounced effects on tree phenology and subsequent productivity.

While most of the avocado fruit grown in the RSA is eaten, the option also remains to process blemished fruit for their oil content which is reputed to be of very high quality in the cosmetic industry. Clearly the more oil the grower can produce and sell from his crop, the higher his immediate returns are likely to be (Human, 1987). These in turn are likely to be intimately linked to the length of time the fruit is left on the tree.

Over the history of improvement in genetic yield potential of annual field crops, the partitioning of photosynthetic products between economic yield and the rest of the plant

has been of primary importance, even though selection was not directly towards that end (Donald & Hamblin, 1976).

As agricultural yield (the economic end-product) is not necessarily synonymous with the biological yield (total biomass), the concept of an 'efficiency index' was proposed by Beaven in 1914 (Donald & Hamblin, 1976). Donald (1962) expressed this, using the term 'harvest index' (HI) for annual cereal crops, which is defined as the ratio of economic yield to total biomass production. By definition HI has a value less than unity, or between 0% to 55% for most annual cereal crops when expressed as a percentage. The equivalent ratio for perennial crops is the harvest increment (H Incr), defined by Cannell (1985) as the increment opportioned to the harvestable part over one year or longer. For mature fruit trees H Incr is surprisingly large and may exceed 60%.

The avocado fruit is a typically high energy fruit which stores a considerable amount of oil in the edible flesh (mesocarp + endocarp) and carbohydrate in the seed. Because of this high energy cost of reproduction, it has been suggested that the H Incr and hence the yield potential of the avocado tree is limited to considerably lower levels than other fleshy starch and sugar storing fruit types such as apples, bananas, grapefruit, grapes or oranges (Wolstenholme, 1986).

What are considered as low yields for healthy avocado orchards (5 t ha^{-1}) appear to be a problem worldwide, compared to other fleshy fruit types. This problem appears exacerbated through irregular bearing and tree decline. These often result from the competitive interactions that occur between vegetative and reproductive growth (Wolstenholme & Whiley, 1990; Wolstenholme, Whiley & Saranah, 1990).

Since ± 90% of a plant's dry matter is the result of photosynthesis, yield manipulation is likely to be intimately linked to changes in partitioning of photo-assimilate between harvested and non-harvested portions of the crop (Gifford, Thorne, Hitz & Giaquinta, 1984; Daie, 1985). Also, while not contributing as directly to biomass gain, partitioning of root-assimilated mineral ions influences crop productivity, firstly, by determining biomass production through effects on leaf growth; and secondly, by direct action on processes governing photo assimilate partitioning, such as membrane transport and cellular metabolism.

METHODS AND MATERIALS

Using well managed five to six-year-old (Hass scion grafted onto Duke 7 rootstock) trees, two random block design field experiments were set out during late February 1989, one at a warm site (Cooling farm, Wartburg, Natal, RSA) and the other at a relatively cooler site (Everdon farm, Howick, Natal, RSA). Five treatments, replicated six times, involving differential fruit harvest from the end of July through August, September, October, and November were imposed on the above-mentioned design. Where comparisons between years was required, the design was modified to a split-plot design where the main effects were year and treatment. Data were collected over 20 months, between the beginning of 1989 and the end of 1990, and analysed according to general randomised block design procedures; under the assumption that the experimental errors were random, independently and normally distributed about zero

mean and with common variance (Rayner, 1976). Where comparisons between 1989 and 1990 were required, the experimental design was extended to a split-plot design where the main effects were year and treatments (i.e. month of harvest). The null hypotheses to these were tested by way' of computer generated F-tests. Data were transformed where the distribution of the experimental errors deviated from normality and, since sample sizes were equal, significance of treatment differences at the 5% (P ≤ 0,05) and 1% P ≤ 0,01) levels were calculated using the principle of least significant differences (LSDs).

Fruit size distributions for each treatment were assessed from the percentage of fruit harvested per tree falling into each of a number of classifications. Fruit size was determined gravimetrically and classified on the basis of fruit number marketed in a box: count 24 and smaller = 170 g and below; count 22 = 171 to 190g; count 20 = 191 to 210 g; count 18 = 211 to 235 g; count 16 = 236 to 265 g; count 14 = 266 to 305 g; count 12= 306 to 365 g; and count 10 = 366 to 450 g. Total yield per tree was calculated by adding the products of: fruit number in each size class and their respective class centres.

Eight count 16 fruit from each replication were sampled from each of the respective treatments. These fruit were peeled, the flesh (mesocarp + endocarp) and pips were separated. The flesh and pip tissues were finely diced and homogenised separately, after which 500 g sub-samples were taken, freeze-dried and stored frozen for later analysis. Fruit moisture contents were recorded. Subsequently the flesh and pip tissues were analysed for lipid, gross energy, and starch concentrations (Graham, 1991).

Phenological events were studied and recorded for each treatment throughout the duration of the trial. Newspaper mats (~ 1 m^2 x 0,05 m thick) were placed under the natural leafy mulch below each tree, so as to monitor root flushing in a similar manner to that described by Whiley *et al* (1988). Shoot flushing was rated visually on a scale of 1 to 10 on a monthly basis while flowering was rated similarly but on a weekly basis (Graham, 1991).

Bark and stem wood samples were collected on a monthly basis throughout the duration of the trial. Bark was sampled by cutting three to five small squares (~ 1,5 cm^2) using a sharp budding knife from the main branches and around the graft union of the trunk. Wood samples were taken by drilling three to five shallow holes (approximately 2 to 3 cm deep) into the trunk and main branches using a Makita 6072D® battery operated drill. Samples were packed in ice in the field and dried at 90°C for 1 hr and then at 70°C for 3C hr, upon returning to the laboratory. The dried bark and wood samples were stored frozen before analysis for starch concentration in batches of 360 (Graham, 1991)

RESULTS AND DISCUSSION

Fruit yield and size distributions

Yield tree[-1] did not differ significantly in response to duration of fruit hanging at either Everdon or Cooling farms during 1989 or 1990, despite continued fruit growth (Table 1; Figure 1). The data from Table 1 and Figure 1 clearly exhibit a continued fruit growth with later hanging, in a similar manner to that described by Schroeder (1953) and

Robertson (1971); where fruit size at any one time was most likely to have been a function of its growth rate and stage of development from pollination and fruit-set. The lack of significance between the yields harvested in the different months can most likely be attributed to high 'tree to tree' variability which, on Everdon .farm, was considerably more variable during 1990 compared to 1989. The general trend, however, was a decreased yield in response to later hanging on Everdon farm, due to a smaller number of fruit harvested with later hanging; while on Cooling farm yield generally increased with later hanging. Note that the yields harvested (Table 1) clearly indicate the presence of an alternate bearing cycle on both farms. A yield of ca 70 kg tree^{-1} was recorded on both Cooling and Everdon farms in 1989, representing a 'heavy' year, while less than this yield was recorded in 1990, representing a 'light' year. On Cooling farm in 1989 the increases in larger fruit, notably counts 18, 16 and 14, were associated with corresponding decreases in the proportion of smaller fruit, notably count 24 and smaller, while intermediate sized fruit occupied a fairly constant proportion of the total fruit yield tree~^{1} at any one time, reflecting a constant gradual transition from small to large fruit as the season progressed. Similarly on Everdon farm general increases in larger fruit, notably counts 16,14,12 and 10 were associated mainly with decreases in count 18 fruits, while counts 22 and 24 appeared to occupy the transitory pool. Interestingly the fruit growth rates, while not actually measured, appeared to be greatest after flowering in September (Figure 1), coinciding with the spring flush. This can probably be attributed to the effects of change in climate associated with the onset of spring and possibly also a stimulative effect from the new actively growing flower and shoot apices.

On the whole fruit from Cooling farm (warm site) were considerably smaller than those from Everdon farm (cool site) in the same year (compare Table 1A with 1B and Figure 1A with 1C). Hass fruit are renowned for exhibiting what has been termed a 'small fruit problem' in warm areas. This appears to have been the case here. Many more ($P \leq 0,05$) fruit were set on trees growing on cooling farm compared to those from Everdon farm over the same period. This probably resulted in a total assimilate demand for growth and especially respiration (possibly elevated further by the warmer environment) that was greater than the genetic potential of trees at Cooling farm. Thus the amount of available assimilate per reproductive unit was probably lower in these trees compared to Everdon farm, and probably explains why fruit from the former did not grow to the same extent as those from the latter. Thus the prevalence of a 'small fruit problem' in warm areas might indicate that either Hass trees generally set more fruit in these environments than in similar cooler environments, resulting in reduced growth to the extent that they are considered small by industry standards; or that the supply of assimilates is impeded relative to cooler areas. The authors are of the opinion that both of these factors might contribute to the problem but do not rule out the possibility that some heat labile PGR in the fruit may also be a limiting factor. Of pertinence with this respect is that Whiley (pers comm)[1] has obtained evidence of higher fruit respiration rates in the early stages of Hass avocado fruit development compared to that of the larger Fuerte, which are indubitably likely to be influenced by higher temperatures.

TABLE 1 Changes in the mean (n = 6) fruit size distribution and fruit mass harvested (kg) tree^{-1} with later hanging on: Cooling farm (warm site) in A (1989); and Everdon farm (cool site) in B (1989) and C (1990)

A

Count	Jul (5%) (1%)	Aug (5%) (1%)	Sep (5%) (1%)	Oct (5%) (1%)	Nov (5%) (1%)
10	0,00 (a)(a)	0,00 (a)(a)	0,00 (a)(a)	0,00 (a)(a)	0,00 (a)(a)
12	0,00 (a)(a)	0,00 (a)(a)	0,00 (a)(a)	0,00 (a)(a)	0,00 (a)(a)
14	0,00 (b)(b)	0,0 (b)(b)	0,0 (b)(b)	1,33 (a)(a)	1,41 (a)(a)
16	0,00 (c)(c)	0,88 (b)(a)	1,11 (b)(a)	4,50 (a)(a)	5,06 (a)(a)
18	1,06 (c)(c)	7,74 (b)(b)	7,11 (b)(b)	17,81 (a)(a)	24,6 (a)(a)
20	3,51 (b)(b)	12,2 (a)(a)	13,4 (a)(a)	11,5 (a)(a)	14,9 (a)(a)
22	11,7 (a)(a)	13,5 (a)(a)	14,3 (a)(a)	15,7 (a)(a)	15,2 (a)(a)
≤24	83,7 (a)(a)	65,7 (b)(a)	64,1 (b)(a)	49,2 (c)(d)	38,9 (c)(b)
YIELD	76,26 (a)(a)	75,0 (a)(a)	76,23 (a)(a)	79,89 (a)(a)	82,46 (a)(a)

B

% Count	Jul (5%)(1%)	Aug (5%)(1%)	Sep (5%)(1%)	Oct (5%)(1%)	Nov (5%)(1%)
10	0,00 (c)(c)	0,06 (b)(b)	0,0 (c)(c)	0,11 (b)(b)	2,72 (b)(b)
12	2,09 (b)(b)	2,07 (b)(b)	2,18 (b)(b)	3,46 (b)(b)	17,0 (a)(a)
14	19,8 (a)(b)	10,3 (c)(c)	8,80 (c)(c)	28,5 (a)(ab)	34,0 (a)(a)
16	21,8 (a)(b)	15,8 (c)(c)	16,1 (c)(c)	29,1 (a)(a)	24,2 (a)(ab)
18	29,5 (a)(a)	40,0 (a)(a)	35,5 (a)(a)	16,4 (b)(b)	12,0 (b)(b)
20	4,90 (ab)(b)	9,40 (a)(a)	16,1 (a)(a)	5,60 (ab)(b)	3,70 (b)(b)
22	10,7 (a)(a)	10,98 (a)(a)	11,2 (a)(a)	7,06 (ab)(a)	3,64 (b)(b)
≤24	11,8 (a)(a)	11,4 (a)(a)	10,2 (a)(a)	9,79 (a)(a)	2,74 (a)(b)
YIELD	72,54 (a)(a)	66,34 (a)(a)	57,38 (ab)(a)	48,23 (b)(a)	71,85 (a)(a)

C

% Count	Jul (5%)(1%)	Aug (5%)(1%)	Sep (5%)(1%)	Oct (5%)(1%)
10	2,70 (b)(b)	2,20 (b)(b)	6,90 (ab)(ab)	18,0 (a)(a)
12	21,6 (b)(b)	30,7 (ab)(ab)	32,8 (ab)(ab)	33,7 (a)(a)
14	27,4 (a)(a)	30,6 (a)(a)	26,8 (a)(a)	26,2 (a)(a)
16	15,9 (a)(a)	12,9 (ab)(a)	7,00 (b)(a)	13,8 (ab)(a)
18	11,3 (ab)(a)	13,3 (a)(a)	9,50 (ab)(a)	4,00 (a)(b)
20	4,70 (a)(a)	4,21 (ab)(a)	2,93 (ab)(a)	0,58 (b)(a)
22	7,30 (a)(a)	4,10 (a)(a)	6,50 (a)(a)	0,30 (a)(a)
≤24	9,10 (a)(a)	2,00 (a)(a)	7,60 (a)(a)	3,50 (a)(a)
YIELD	44,88 (a)(a)	33,39 (a)(a)	28,64 (a)(a)	29,65 (a)(a)

Note treatments in rows (ie harvest date from the end of July to the end of November) with symbols in common are not significant at the 5% (P ≤ 0,05) and 1% (P ≤ 0,01) levels.

Slabbert (pers comm)[2] has noted that of the different sized fruit harvested, the sale of count 16 and 14 fruit realises the greatest net profit on overseas markets. With respect to this, Table 1B and Figure 1C suggest that the optimum time to have harvested the 1989 fruit on Everdon farm was at the end of October. In contrast, significantly (P ≤ 0,05) fewer fruit were set to maturity on Everdon farm during 1990 than in 1989, which appears to have facilitated a more rapid fruit growth rate in the former, possibly due to a greater assimilate availability in the light of the smaller overall fruit demand; resulting in a considerably greater proportion of large fruit (> count 14) earlier on in the season. Thus from Table 1C and Figure 1D, it would appear that the optimum time to have (economically) picked Everdon farm fruit in 1990 was in July, since the proportion of count 10 and 12 fruit generally increased from this date onwards at the expense of the more profitable counts 16 and 14. Since fruit were generally small throughout the season on Cooling farm, the best time to have picked these fruit was most likely as late in the season as was possible — from a purely size related profit point of view.

Depending on the time of fruit maturity, this evidence suggests that cyclical picking on Everdon farm might have been of most benefit from October onwards in the 'heavy' year of 1989 and from some time before July onwards in the 'light' year of 1990; while on Cooling farm fruit thinning early on in the season might have been more beneficial.

On the assumption that the poorer fruit-set in 1989 following the 'heavy' crop set the previous year was associated with a physiological tree status reflecting depleted assimilate reserves and not an environmental influence limiting fruit-set; the authors propose that fruit thinning and cyclical picking, employed to maintain an as yet to be determined optimum leaf : fruit ratio (like that suggested by Fishler, Goldschmidt & Monselise (1983) in their work on citrus), might be essential to future optimisation of avocado yields for best long term profitability. Research into this is lacking on avocados and is likely to be cultivar, tree age and site specific.
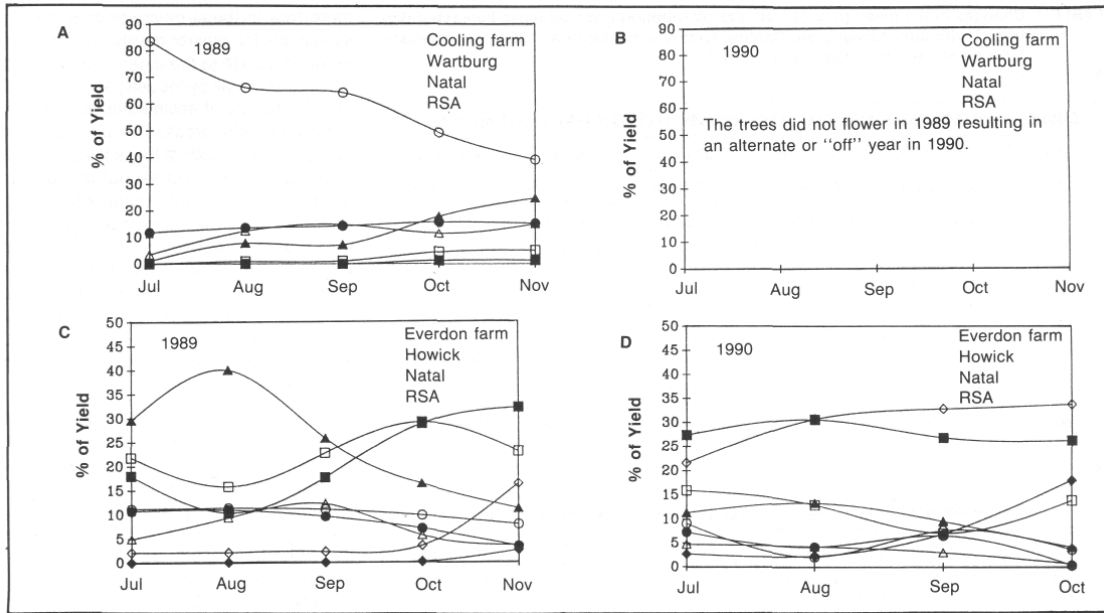
Fig 1 Changes in the mean (n = 6) fruit size distribution tree^{-1} with later hanging on Cooling farm (warm site) in: (A) 1989 and (B) 1990, and on Everdon farm (cool site) in: (C) 1989 and (D) 1990, where: ○————○ = % count 24 and smaller fruit (≦ 170 g); ●————● = % count 22 fruit (171 to 190 g); △————△ = % count 20 fruit (191 to 210 g); ▲————▲ = % count 18 (211 to 235 g); □————□ = % count 16 fruit (236 to 265 g); ■————■ = % count 14 fruit (266 to 305 g); ◇————◇ = % count 12 (306 to 365 g) and ◆————◆ = % count 10 fruit (366 to 450 g) of the mean (n = 6) number fruit harvested tree^{-1}.
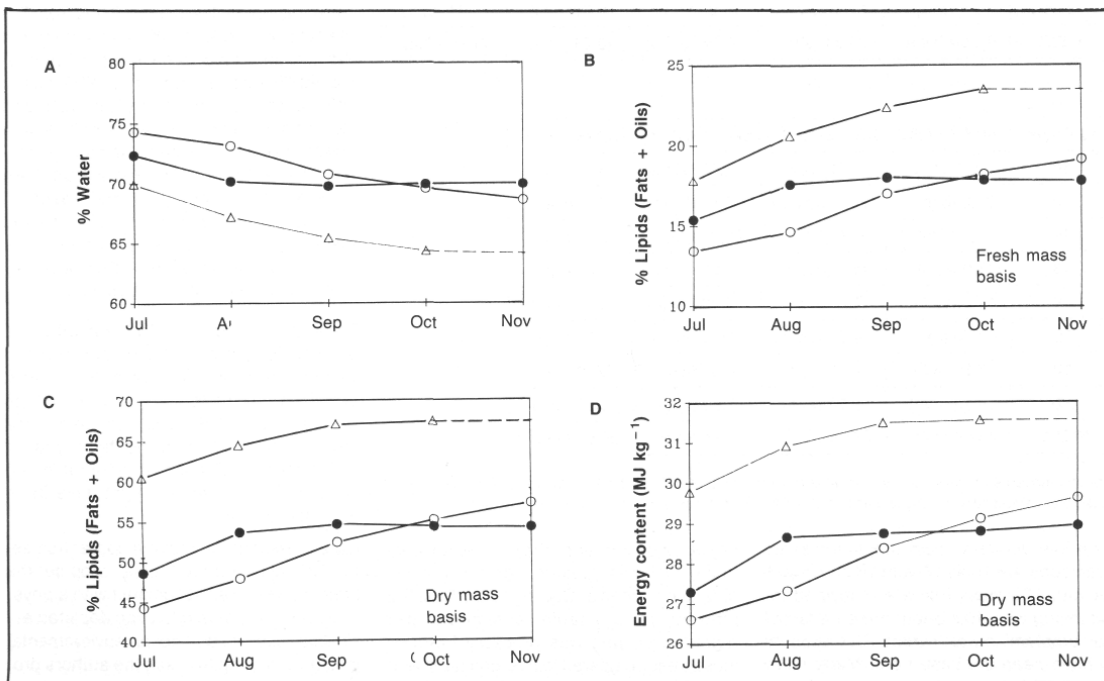

Fig 2 Changes in the: (A) Water, (B) Lipid on a fresh mass basis (FM), (C) Lipid on a dry mass basis (DM) and (D) Energy (DM) content of Hass avocados with later hanging on Cooling farm (○————○) and Everdon farm (●————●) in 1989, and Everdon farm in 1990 (△————△).
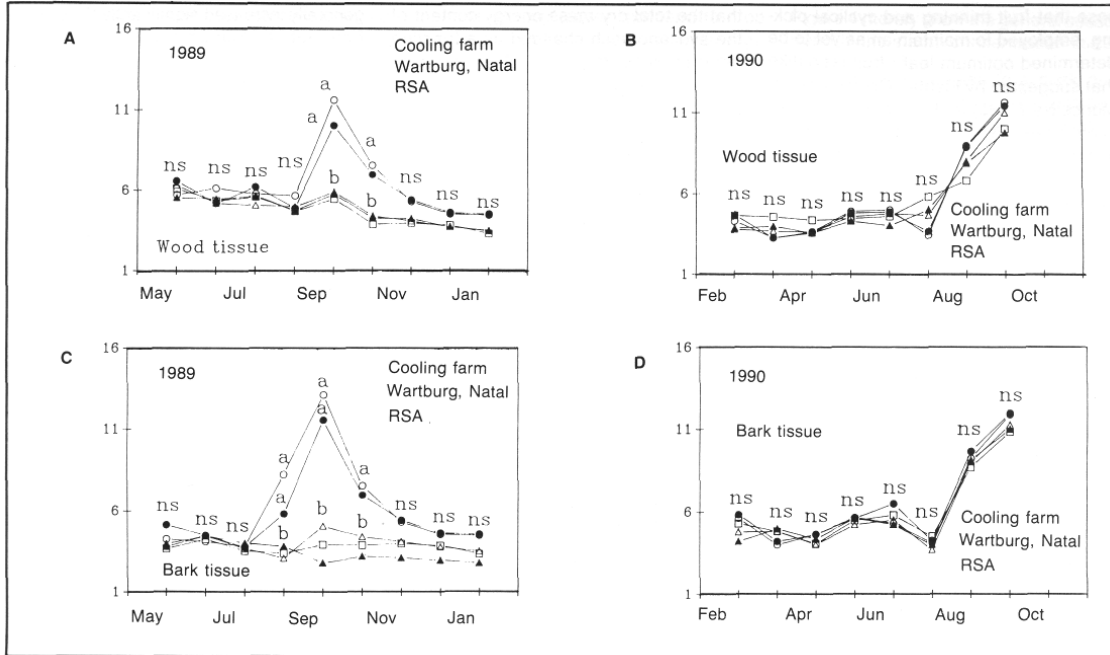
Fig 3 Seasonal changes in starch concentration of Cooling farm (warm site): trunk and main branch wood tissue in (A) 1989 and (B) 1990, and bark tissue in (C) 1989 and (D) 1990, in response sequentially later fruit harvesting from the end of July (○_____○) through August (●_____●), September (△_____△) and October (▲_____▲), and November (□_____□).
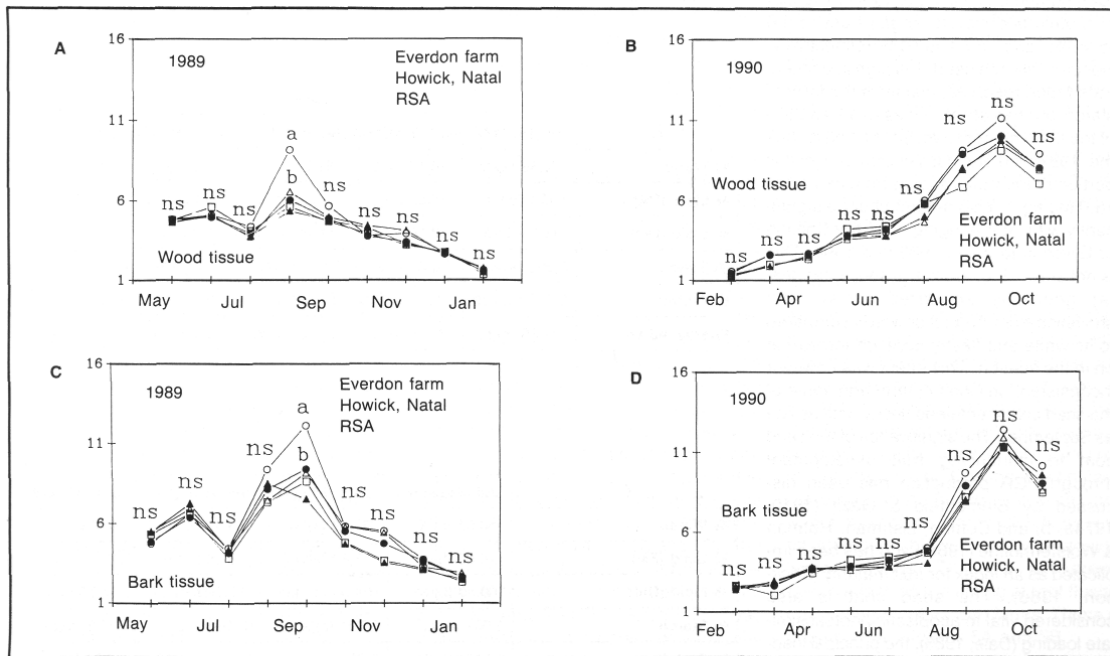

Fig 4 Seasonal changes in starch concentration of Everdon farm (warm site): trunk and main branch wood tissue in (A) 1989 and (B) 1990, and bark tissue in (C) 1989 and (D) 1990, in response sequentially later fruit harvesting from the end of July (○_____○) through August (●_____●), September (△_____△) and October (▲_____▲), and November (□_____□).

Fruit energy content

A study into changes in the reproductive energy cost of fruiting, associated with sequentially later hanging, is clearly vital to orchard management in the light of the depressive effects of fruiting on vegetative growth, particularly root proliferation (Cannell, 1971a; b; Chalmers & Van den Ende, 1975; Cannell, 1985; Wolstenholme, 1990), and the implications this might have on long term yields, keeping in mind the potentially devastating problems of tree physiological dieback and decline.

There were no obvious consistent differences in seed lipid, protein or starch concentrations, on a dry mass basis (DM), between seasons or between Cooling and Everdon farms. Seed lipid concentration (DM) ranged from *ca* 1,5 to 1,8% while that of protein and starch ranged from *ca* 3,0 to 4,4%, and *ca* 54 to 61% respectively. Hence, while the seed was high in concentrated food reserves, mainly in the form of starch and can constitute as much as 25% of the fresh mass of avocados (Wolstenholme, 1987), the dry mass energy cost of this portion of the fruit, ranging from *ca* 17,4 to 18,0 MJ kg^{-1}, also did not change significantly with later hanging on either Cooling or Everdon farms in 1989 and 1990. This is not surprising, since the seed coat (testa) generally appeared brown and shrivelled from August onwards compared to its white and fleshy appearance earlier on in the season. This effect was however inconsistent on Cooling farm and some of the seed coats remained fleshy until as late as September. The significance of the seed coat in influencing fruit development through PGR production has been discussed by Blumenfeld & Gazit (1970; 1974a; b) and Cutting, Lishman, Hofman & Wolstenholme (1986); and has been implicated as an index for fruit maturity (Erickson, 1966).The seed coat is also considered vital to apoplastic photoassimilate loading (Daie, 1985), the principal loading mechanism in dicot reproductive tissues. Hence the shrivelling of the testa clearly indicates a termination of the assimilate demand by the seed.

From Table 2 and Figure 2, it is apparent that the total dry mass energy content of the avocado flesh changed as a function more of oil content than either starch or protein contents with later hanging, in a similar manner to the data presented by Pearson (1975). Fruit from Cooling farm generally increased significantly in oil content from 13,47% in July to 19,18% November (Table 2A and Figure 2), while water content dropped from 74,3% to 68,6% over a similar period of time. Such an increase in the reproductive energy cost of fruiting with later hanging is very likely to be at the expense of new leaf growth, essential to sustaining the following season's crop, and to flowering and fruit drop the following season. In contrast, the oil content of fruit growing on Everdon farm generally increased significantly (P ≤ 0,05) from July to August and then tended to plateau, or only increase slightly, as the season progressed (Table 2B and 2C and Figure 2). Further, as with fruit size, the oil content was significantly greater (P ≤ 0,5) during 1990 than 1989 on Everdon farm (Table 2B and 2C and Figure 2). This might also be attributed to a greater assimilate availability due to the lower yield in the I former, and highlights the importance of leaf: fruit ratios in crop manipulation. In this case more fruit could probably have been carried on the tree while containing a lower relative energy content. As at Cooling farm, flesh starch concentration, which varied from 3,0 to 3,9 in 1989 and 3,5 to 3,7 in 1990, was not significantly affected by late hanging. Protein contents tended to be higher on Everdon farm than at Cooling farm in

1989, and while there also were significant differences between months harvested, these are not easy to explain. One possible explanation is that, since protein concentration was calculated indirectly from nitrogen concentration using a conversion constant of 6,25, differences in protein concentration between Cooling and Everdon farm might merely reflect differences in nitrogen availability to the fruits. The different patterns in oil accumulation between Cooling and Everdon farms (Figure 2) could possibly be due to temperature induced differences in the amounts of oleic acid formed (Eaks, 1990). Alternatively they could be explained by differences in the amounts of fruit-set, where the assimilate supply fruit $^{-1}$ for lipid synthesis early on in the season on Cooling farm could have been less than on Everdon farm, due to a greater overall assimilate demand due to the larger crop-set in the former, further influenced by a later seed activity and greater respiration losses due to a higher temperatures. Interestingly, while the total lipid fatty acid composition was not analysed, there did however appear to be more satured (hard) fat left in the laboratory receptacles after lipid extraction from Cooling farm fruit than Everdon farm fruit. This warrants further research in the light of the consumer preference for "cholesterol free" oils (Pierce, 1959).

TABLE 2 Constitution of Hass avocado flesh with later hanging in terms of water, lipid on a fresh mass (FM), lipid on a dry mass basis (DM), starch (DM) and protein (DM) contents on: A: Cooling farm in 1989; B: Everdon farm 1989 and C: 1990

A	Jul (5%)(1%)	Aug (5%)(1%)	Sep (5%)(1%)	Oct (5%)(1%)	Nov (5%)(1%)
% Water	74,33 (a)(a)	73,12 (a)(a)	70,74 (b)(a)	69,54 (c)(b)	68,62(d)(c)
% Lipid (FM)	9,671 (d)(c)	10,88 (c)(b)	13,26 (b)(a)	14,46 (a)(a)	15,38 (a)(a)
% Lipid (DM)	45,03 (d)(c)	49,03 (c)(b)	53,62 (b)(a)	55,73 (a)(a)	56,25 (a)(a)
% Starch	2,517 (a)(a)	2,713 (a)(a)	3,010 (a)(a)	2,727 (a)(a)	2,902 (a)(a)
% Protein	3,520 (a)(a)	3,355 (b)(a)	3,890 (a)(a)	3,503 (a)(a)	3,300 (b)(a)
Energy MJ kg^{-1}	26,62 (e)(d)	27,33 (d)(d)	28,44 (c)(c)	28,98 (b)(a)	29,63 (a)(a)

B	Jul (5%)(1%)	Aug (5%)(1%)	Sep (5%)(1%)	Oct (5%)(1%)	Nov (5%)(1%)
% Water	72,39 (a)(a)	70,17 (b)(b)	69,75 (b)(b)	69,91 (b)(b)	69,95 (b)(b)
% Lipid (FM)	9,671 (b)(b)	10,88 (a)(a)	13,26 (a)(a)	14,56 (a)(a)	15,38 (a)(a)
% Lipid (DM)	48,65 (b)(b)	53,80 (a)(a)	56,23 (a)(a)	53,12 (a)(a)	55,61 (a)(a)
% Starch	2,995 (a)(a)	3,230 (a)(a)	3,872 (a)(a)	3,720 (a)(a)	3,531 (a)(a)
% Protein	3,506 (db)(db)	4,625 (ab)(ab)	3,544 (b)(b)	4,531 (ab)	4,810 (a)(a)
Energy MJ kg^{-1}	27,30 (b)(b)	28,78 (a)(a)	28,68 (a)(a)	28,70 (a)(a)	28,94 (a)(a)

C	Jul (5%)(1%)	Aug (5%)(1)	Sep (5%)(1%)	Oct (5%)(1%)
% Water	69,95 (a)(a)	67,18 (a)(a)	65,42 (ab)(a)	64,32 (b)(a)
% Lipid (FM)	14,05 (b)(a)	16,82 (ab)(a)	18,58 (a)(a)	19,68 (a)(a)
% Lipid (DM)	60,50 (b)(a)	64,50 (ab)(a)	67,00(a)(a)	67,35 (a)(a)
% Starch	3,501 (a)(a)	3,721 (a)(a)	3,689 (a)(a)	3,578 (a)(a)
% Protein	3,518 (a)(a)	3,624 (a)(a)	3,512 (a)(a)	3,630 (a)(a)
Energy MJ kg^{-1}	29,79 (b)(a)	30,93 (ab)(a)	31,49 (a)(a)	31,54 (a)(a)

Note rows (ie harvest date from the end of July to the end of November) with symbols in common are not significant at the 5% (P ≤ 0,05) and 1% (P ≤ 0,01) levels.

Bark and wood starch contents

Figures 3 and 4 shows the changes in starch concentration of trunk bark and trunk and main branch wood samples for Cooling and Everdon farms respectively over the duration of the experiment. On both farms, fluctuations in the bark concentration appeared to change in a very similar pattern to that of the stem wood, but tended to be

of greater amplitude. Of interest was the general conspicuous decrease in the starch concentration of both of these tissues between July and August, followed by a relatively larger increase between August and September. The former coincided with flower bud development in spring, while the latter coincided with flowering and old leaf fall. The extent of the increase over the flowering period appeared to be influenced significantly by the presence of fruit and the demand for assimilates by such fruit during 1989. Such a response to fruiting was not distinguishable in 1990. The starch concentration peaks observed in September (Figures 3 and 4) might well be attributed to a greater overall assimilate income than expenditure over this period (notably when vegetative growth is most inactive, conditions for photosynthesis are good and remobilisation of assimilates from older senescing leaves that tend to drop during this period is likely to be strong), resulting in a greater surplus of assimilates available for storage in the trunk. On Cooling farm in September 1989 (Figure 3), starch concentrations were significantly higher ($P \leq 0,05$) in trees where the fruit was harvested before the flowering period, i.e. at the end of July and August respectively, compared to those where the fruit was still to be harvested. No significant difference was observed, however, between the two pre-flowering treatments at the 5% level. On Everdon farm in September 1989 (Figure 4), a significant increase in the starch concentrations of barks and stem wood occurred in trees under the first harvest treatment, i.e. end of July, compared to the rest. Unlike Cooling farm, there was no significant difference between the August and later three harvest times. This is possibly due a more prominent effect of the increase in energy content of the fruit harvested between July and August (Figure 2) on the supply of assimilates to the bark and wood of the former compared to the latter.

The lack of such a response in September 1990 on Cooling farm (Figure 3) was most probably due to the absence of fruit on the trees during this period, *as* a result of the total absence of flowering during spring in 1989. Of interest is that the influence of fruiting in 1989 on bark and stem wood concentration was apparently not carried over to 1990. The inevitable conclusion is that the extra assimilate stored in the earlier harvested trees was utilised by the tree's vegetative components. Assuming this to be the case, it is uncertain whether more went towards growth and maintenance of assimilatory organs such as leaves and roots or to the carbon cost of construction of trunk and main branches. This is likely to depend on the assimilate demand by the various organs at the time of its availability; where demand may be interpreted as a function of the respective organs' size and activity (Ho, 1988). There was also no similar response to later fruit hanging in the starch concentrations of bark and stem wood tissues of trees from Everdon farm in September 1990 (Figure 4). However, the situation here differs from that of Cooling farm, since in this case fruit was set in 1990 even though the extent of this was only a half to two-thirds that of the previous year (compare Tables 1B and 1C). The lack of significant starch differences between the tissues of trees under the various treatments from Everdon farm in 1990 is due mainly to the greater tree variability observed over this period. This was increased by the necessity for a reduction in sample replication in 1990 to avoid further damaging trees that had started to express symptoms of tree decline and physiological dieback. Hence the graphs depicted in

Figure 4 merely show the general seasonal trend in the starch concentration in 1990.

Following the increase to a peak during flowering in September, there was generally a marked reduction in starch concentration in both bark and stem wood tissues at the onset of the first (spring) leaf flush and fruit-set period. This remained low for most of the season and only started to increase again markedly at the onset of winter, in a similar manner to that described by Scholefield, Sedgley, & Alexander (1985).

On the whole, starch concentrations were higher in trees on Cooling farm (warm site) than Everdon farm (cool site). This may be attributed to the smaller storage space associated with the smaller overall size of the Cooling farm trees compared to the Everdon farm trees, and to the lesser vegetative activity on the Cooling farm trees. The fact that the starch concentration decreased over the summer period, indicates that the fruit and leaf components of the trees exhibited a greater overall sink strength than the bark and stem wood tissue components respectively; in a similar manner to that described by Cannel! (1985).

Phenological events

Except for root growth, no differences in the timing of events on a broad scale were observed between the trees growing at Cooling and Everdon farms. On a smaller time scale, however, there were significant responses (P ≤ 0,05) to the treatments in leaf flushing and flowering. These also tended to differ between 1989 and 1990. General preliminary phenological models for Cooling and Everdon farms are presented graphically in Figures 5A and 5B respectively.

Root flushing

No differences in root flushing in response to the treatments were observed on either Cooling or Everdon farms, due to sporadic root emergence into the mulch layer; unlike that of Whiley, Saranah, Cull & Pegg (1988), where root growth into the mulch layer was prolific. Further, while sporadic, root emergence on Cooling was limited to the cooler south facing side of the trees where most of the leafy mulch layer resided, after being blown there by seasonal afternoon winds. This did not prevent observations on the timing of root flushing on Cooling and Everdon farms. These are presented in Figures 5A and 5B.

Flowering and leaf flushing

On Cooling farm in 1989 no flowers were initiated. No significant differences between treatments were observed in the first (spring) and second (summer) leaf flushes, due to 'wild', highly variable flushing patterns. This was attributed to root infection with *Phytophthora cinnamomi,* probably exacerbated by the previous relatively heavy crop. Leaves from these flushes were sparse and appeared chlorotic, abnormally small and elongated in appearance. There was a trend, however, towards more prolific flushing in trees subjected to the first three treatments compared to the latter two (i.e. July, August and September vs. October and November harvesting dates).
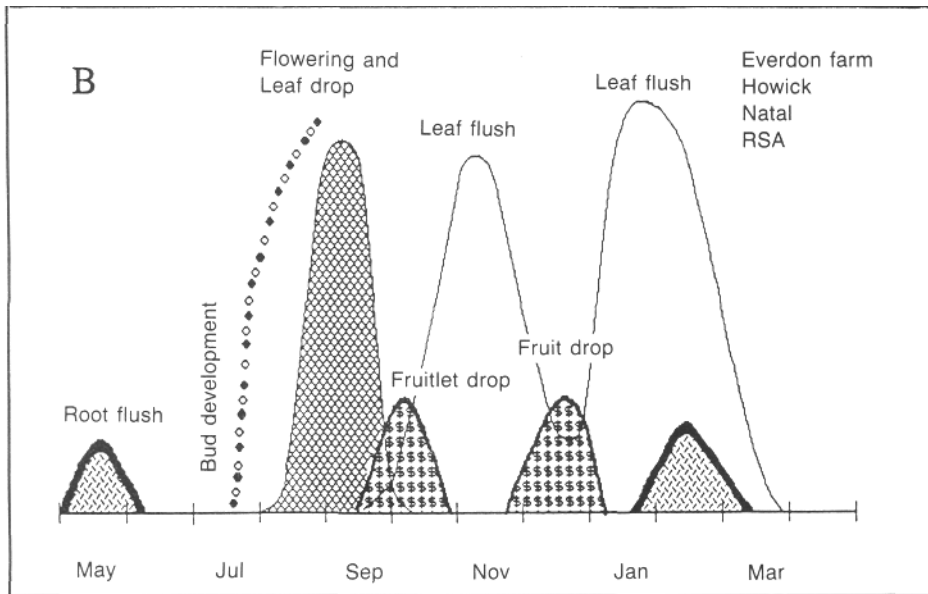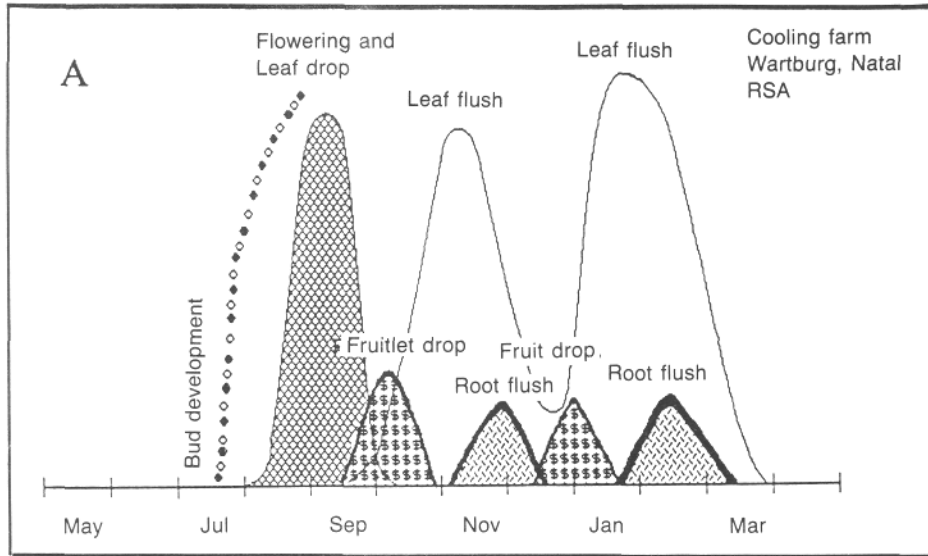
Fig 5 Hass avocado trees on (A) Cooling farm (warm site) and (B) Everdon farm (cool site).
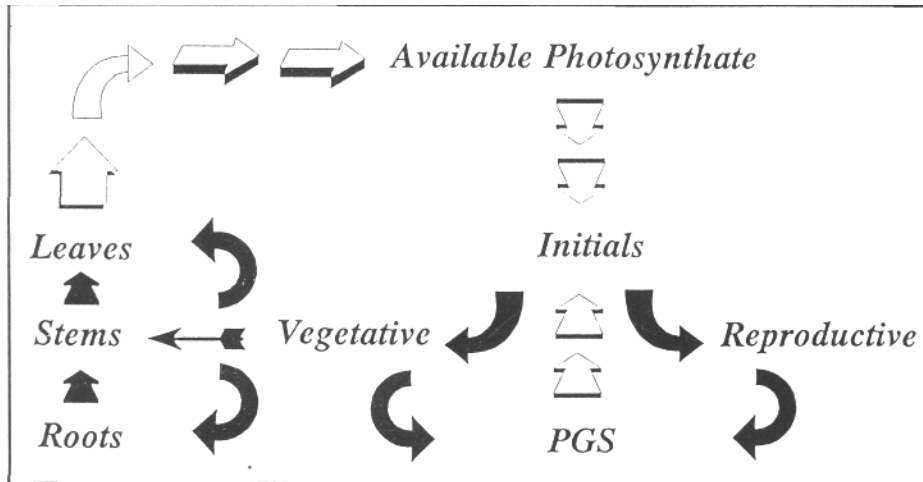
Fig 6 Diagram to illustrate a possible interaction between available photosynthate, PGSs and plant organ development.

On Cooling farm in 1990, however, the trees appeared to have responded^ very well to trunk injection with Aliette Ca® (20 to 30% phosphorous acid), by producing two dense flushes, the first coinciding with the latter stages of flowering towards the end of September and the second starting towards the end of December, with large healthy leaves. Flowering, distributed fairly uniformly around the trees (± 80% of all vegetative terminals), commenced one to two weeks earlier ($P \leq 0,05$) in trees subjected to the first three treatments compared to the rest (i.e. July, August and September vs. October and November harvesting dates) at the beginning of September. However, no differences were noted in the intensity of flowering or the extent or time of commencement of either the first (spring) or second (summer) leaf flushes.

On Everdon farm in 1989 the first (spring) leaf flush commenced three to four weeks after flowering, which commenced early in September and terminated towards the end of that month. No significant differences in flowering were observed between treatments and flowering (± 60% of vegetative terminals) was distributed fairly uniformly around the tree but appeared to predominate in the lower and middle parts. The first (spring) leaf flush however commenced one to two weeks earlier in trees subjected to the first two treatments than the rest (i.e. July, August vs. September, October, November). No significant differences were observed between treatments in the second (summer) leaf flush, which commenced towards the end of December.

On Everdon farm in 1990 the first (spring) leaf flush commenced together with the latter stages of flowering towards the end of September. However, no significant differences were observed in the commencement date of either flowering or leaf flushing. Further, no significant differences were observed between treatments in the second (summer) leaf flush which, like 1989, also commenced towards the end of December. Here flowering and leaf flushing was very variable exhibiting responses to the interactive effects of the treatments set, soil depth (possibly confounded by *Phytophthora cinnamomi)* and tree yield; which varied between Individual trees both within and between blocks. While inconsistent, leaf flushing appeared more prolific in trees

subjected to the first three treatments compared to the rest (i.e. July, August and September vs. October and November harvesting dates). Flowering during 1990 (± 60% of vegetative terminals) was largely restricted to the warmer, sunny, north facing side of the trees, predominating in the middle and top parts. This can most likely be attributed to effects of overcrowding, possibly initiated the previous year. The initially double spaced orchards were thinned early in 1990, after which the remaining trees grew vigorously. This did not affect the experimental design however, as this was taken into consideration while planning the experiment.

Of significance here is that in 1989, Ever-don trees initiated both vegetative and floral axes despite the apparently lower bark and stem wood starch concentrations compared to that of Cooling farm, where no flower initials were set after the heavy crop in 1989. Clearly some other factor apart from the starch level in the trees' main limbs must have induced the lack of flowering on Cooling farm in 1989. The authors propose that the lack of flowering on Cooling farm was elicited either by an excess of some phytohormonal (PGR) influence emanating from the previous season's fruit crop (Luckwill, Weaver & McMillan, 1969), or alternatively by a deficiency of some other shoot or root produced or controlled PGR; due to the known depressive effects of heavy fruiting on such vegetative terminals. The latter particularly may have been exacerbated by the presence of *Phytophthora cinnamomi* on Cooling farm. Further since nitrogen assimilation is an energy dependent process that would depend on the availability of carbohydrates in roots (Losecher, McCamant & Keller, 1990), a reduction in root activity due to *Phytophthora cinnamomi* and possibly exacerbated by heavy fruiting might well be implicated in inducing PGR imbalances in the plant. This is qualified by the fact that avocado roots have been shown to have a greater capacity for nitrogen reduction and amino acid synthesis, both precursors to protein synthesis, than in leaves (Lovatt & Cheng, 1990). The presence of a heavy crop also appeared to delay the emergence of the first (spring) flush. In 1989 the leaf flush occurred as long as three to four weeks after flowering on Everdon farm and even later during the year on Cooling farm. However in 1990 the first (spring) leaf flush coincided with the latter stages of flowering on both these farms. The authors suggest that this might be associated with the fruit number carried per tree, which was greater on Cooling farm than on Everdon farm in 1989. Further more fruits were carried per tree in 1989 than in 1990 on Everdon farm.

Active new leaf growth might also be necessary for flower initiation, since leaf removal in pecan trees (which also produce an energy demanding fruit crop) has been shown to prevent flowering the following season, while not necessarily depleting the carbohydrate reserves of the defoliated branches (Worley, 1979). In this experiment, the precarious absence of flowering on the shaded side of the Everdon trees in 1990 due to possible overcrowding; and the shift from an evenly distributed flowering in 1989 to a predominantly higher position in 1990 might also suggest a similar response of leaf activity. The differences in flower position between 1989 and 1990 reflect changes in apical dominance, with the more vigorous vertical growth in 1990 possibly associated with the considerably smaller crop load compared to the previous year. Other possibilities that could also be considered with this respect is a necessity for light and water for flower induction, as influenced by growth of young leaves. Under this pretext it is not surprising that the trees on Cooling farm did not set flowers in 1989 since the leaves were considerably stunted and distorted for most of that year.

CONCLUSIONS

The data gathered from Cooling and Everdon farm in 1989 and 1990 suggest that increasing the crop load in terms of fruit number per tree is likely to result in increasingly later fruit maturity, increasingly slower rates of fruit growth and increasingly smaller energy contents per fruit. Further, fruit from trees bearing relatively lighter crops in terms of fruit number per tree generally grew faster than those on more heavily bearing trees. Hence it is likely that fruit on trees in a 'heavy year' generally require a longer time on the tree to reach the count 16 and count 14 size classifications than those from trees in a 'light year'. This has an important management implication. It suggests that in order to cash in on the observation by Slabbert (pers comm), that count 16 and count 14 fruit are the most profitable counts on the export market, the producer should start cyclical picking much later in the season on heavily bearing trees than on light bearing trees. However, whether a heavy crop in terms of fruit number set per tree is generally more energy demanding from the trees than a relatively lighter crop that is more energy expensive fruit was not clear, since bark and wood starch concentrations of the trunk and main branches of the trees in this experiment did not indicate as much. It must be remembered that these effects may take several seasons to manifest themselves more fully, and this trial has only run for a short time.

One of the major problems encountered in this experiment was a high 'tree to tree' variability, despite the implied uniformity of clonal trees. Treatment replication should be increased substantially in future research of this kind. While not significant at the 5% level due to high tree variability, yield per tree on a mass basis generally tended to decrease due to a general decline in fruit number, despite increased fruit growth, with later hanging on Everdon farm. In contrast, on Cooling farm there was a fairly constant fruit number per tree throughout the duration of the experiment in 1989, and yields tended to increase as the season progressed, most probably due to increased fruit growth. Hence the short-term effect of late hanging on fruit yield per tree was inconsistent between the two farms. What the true short term effect of sequentially later hanging on fruit mass harvested per tree is, and if indeed there is a difference between cool and warm sites in this regard, is yet to be determined, and the trial needs to run for a further two seasons to investigate this.

This experiment indicated differences in the pattern of oil accumulation in fruit between Cooling (warm site) and Everdon (cool site) farms as the season progressed. On Everdon farm, irrespective of the fruit load and energy status at the commencement of harvesting, the oil content of the fruit generally increased significantly from July to August and September, after which it plateaued. While the lipid content of the fruit was not characterised in terms of fatty acid content, the authors surmise that such a pattern in oil accumulation is attributed mostly to an oleic acid content, the synthesis of which probably terminated between the end of August and September, since a similar pattern was observed by Eaks (1990). On Cooling farm, however, there was a more linear increase in fruit oil content with later hanging. This is the more commonly observed pattern of avocado oil accumulation, as observed in the warmer areas of South Africa. The authors conclude that the different patterns of oil accumulation between Cooling and Everdon farms could possibly be due to temperature induced differences in the amount of oleic acid formed; or alternatively to differences in assimilate availability per

fruit. Interestingly the authors observed solid (saturated) fat as well as oils in the laboratory receptacles after lipid extraction of fruit from Cooling farm fruit but only oils in the Everdon farm fruit extracts. This warrants further research in light of the consumer preference for "cholesterol free" oils (Pierce, 1959). A further, as yet unsubstantiated, implication is that the reduced saturated fat in the Everdon farm fruit could be connected with cold tolerance of such fruit with respect to maintaining membrane integrity.

The greater sink strength that reproductive tissues possess over vegetative tissues is well established in the literature, although the extent and mechanisms of PGR production and action between the different plant organs is less certain. Here the effects of fruiting, as exercised through sequentially later hanging, on tree phenology were inconsistent but the general trend was that harvesting trees before flowering generally tended to result in earlier return flowering and a more prolific first (spring) leaf flush. This implies that the earlier harvested trees were embellished with a greater photosynthetic area soon after flowering than later harvested trees (indirectly resulting in an extended photosynthetic season in the former) and hence were likely to maintain a higher overall level of productivity the following year.

The authors are of the opinion that the phenological patterns observed in this experiment can be explained by the axiom that the induction of meristematic initials sets the potential for development of reproductive (particularly flowering and fruiting) or vegetative (particularly leaf proliferation and fine root replacement) organs *via* growth dependent PGR production, and that assimilate level inter-organ sink competition only influence the extent of their development *after* induction (Figure 6). This implies interdependence between the balance of PGRs produced by the different plant organs with respect to their initiation the following year, the amount of assimilate available for their growth after initiation, and their respective sink strengths.

Clearly under this pretence, the success of this experiment amounts to optimising monetary returns from fruiting, as determined by market dictum, by optimising the balance between the vegetative and reproductive hormonal influences on the tree, while also optimising assimilate partitioning between the different organs.

While this experiment should be regarded as a preliminary investigation to ongoing research in this field, the authors believe that for the present —

    (i)   in view of the marked increase in energy cost of fruiting observed from July to September;

    (ii)   as well as the more prolific leaf flushing and earlier flowering associated with trees harvested before flowering;

    (iii)   together with the implications that these have on return fruiting;

producers in climates similar to those in this study should limit fruit hanging to the month of September (when flowering takes place). This would ensure balanced (low risk) cropping for maximum long term yield. Further, the authors believe that if producers intend to harvest their fruit later than September, it might be necessary to consider fruit thinning early on in the season after fruit-set, depending on crop load. The profitability of this will inevitably depend on the net gains attained from the later marketing. By implication also, *selective* harvesting of larger fruits earlier in the season would be

advantageous.

The authors are confident that the potential to improve return on investment, above that presently attained by the avocado industry as a whole, exists in lieu of exercising the practical implications of the axiom discussed earlier in connection with phenological cycling and the fact that sink enhanced photosynthesis has been implicated in the avocado. However, the authors are of the firm opinion that the key to this involves future research on the manipulation of fruit-set, to establish a set of cultivar, tree age and site specific leaf area per fruit norms that optimise productivity.

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REFERENCES

BLUMENFELD, A & GAZIT, S, 1970. The role of the seed coat in fruit growth and maturation. *Calif Avocado Soc Yrb,* 54, 100 - 104.

BLUMENFELD, A & GAZIT, S, 197a. Cytokinin activity in avocado seeds during fruit development. *Plant Physiol,* 46, 331.

BLUMENFELD, A & GAZIT, S, 1974b. Development of seeded and seedless avocado fruits. *J Amer Soc Hort Sci,* 99, 442 - 446.

CANNELL, M G R, 1971a. Effects of fruiting, defoliation and ring-barking on the accumulation and distribution of dry matter in *Coffea arabica* L in Kenya. *Expl Agric,* 7, 63 - 74.

CANNELL, M G R, 1971b. 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.

CANNEL, M G R, 1985. Dry matter partitioning in tree crops. In: *Attributes of trees as crop plants,* ed. Cannell, M G R, & Jackson, JE Institute of Terrestrial Econology, pp 160 - 193.

CHALMERS, D J & Van Den Ende, B, 1975. Productivity of peach trees: factors affecting dry-weight distribution during tree growth. *Ann Bot,* 39, 423 - 432.

CUTTING, J G, LISHMAN, A W, HOFMAN, P J & WOLSTENHOLME, B N, 1986. Plant growth substance trends in developing avocado fruit as determined by radioimmunoassay. *Acta Hort,* 175, 285 - 289.

DAIE, J, 1985. Carbohydrate partitioning and metabolism in crops. *Hort Rev,* 7, 69 - 107.

DALE, J E, & MILTHORPE, F L, 1983. General features of the product of growth of leaves. In: *The growth and functioning of leaves,* ed: Dale, J E & Milthorpe, F L Cambridge Univ Press, UK.

DONALD, C M, 1962. In search of yield. *J Aust Ins Agric Sci,* 28, 171 - 178. (Cited by Gifford, Thorne, Hitz & Giaquinta, 1984).

DONALD, C M, & HAMBLIN, J H, 1976. The biological yield and harvest index of cereals as agronomic and plant breeding criteria. *Adv Agron,* 28, 361 - 405.

EAKS, 1,1990. Change in the fatty acid composition of avocado fruit during ontogeny, cold storage and ripening. *Acta Hort,* 269, 141 - 157.

ERICKSON, L C, 1966. Seed coat thickness: a guide to avocado maturity. *Calif Citrogr,*

51, 260.

FISHLER, M, GOLDSCHMIDT, E E, & MONSE-LISE, S P, 1983. Leaf area and fruit size on girdled grapefruit branches. *J Am Soc Hort Sci,* 108, 218 - 221.

GEIGER, D R, & GIAQUINTA, R T, 1982. Trans-location of photosynthates. In: *Photosynthesis: CO_2 assimilation and plant productivity,* Govindjee, Academic Press, New York, pp 345 - 386.

GIFFORD, R M, THORNE, J H, HITZ, W & GIAQUINTA, R T, 1984. Crop productivity and photoassimilate partitioning. *Science,* 225, 801 - 807.

GRAHAM, A D N, 1991. General procedures and techniques. In: *Starch and energy aspects of fruiting and delayed harvest in 'Hass' avocado [Persea americana* Mill]. MSc. Dissertation, University of Natal, P O Box 375, Natal, RSA.

HO, L C, 1988. Metabolism and compartmentation of imported sugars in sink organs in relation to sink strength. *Ann Rev Plant Physiol Plant Molec Biol,* 39, 355 - 378.

HUMAN, T P, 1987. Oil as a byproduct of the avocado. *S A Avocado Growers' Assoc Yrb,* 10, 61 - 64.

KOTZÉ, J M, 1989. Opening address of the 12th SAAGA research symposium. *S A Avocado Growers' Assoc Yrb,* 12, 5 - 7.

LOESCHER, W H, McCAMANT, T & KELLER, J D, 1990. Carbohydrate reserves, translo-cation, and storage in woody plant roots. *HortScience* 28, 274 - 281.

LOVATT, C J & CHENG, A H, 1990. Comparison of some aspects of nitrogen metabolism of avocado with citrus. *Acta Hort* 275, 489 - 495.

LUCKWILL, L C, WEAVER, P & McMILLAN, 1969. Gibberellins and other growth hormones in apple seeds. *J Hort Sci,* 44, 413 - 424.

PATRICK, J W, 1988. Assimilate partitioning in relation to crop productivity. *Hort Science* 23, 33 - 40.

PEARSON, D, 1975. Seasonal English market variation in the composition of South African and Israeli avocados. *J Sci Food Agr* 26, 207 - 213.

PIERCE, H P, 1959. The nutritional value of the avocado. *California Avocado Soc Yrb* 43, 83 - 85.

ROBERTSON, B L, 1971. Fruit growth of the 'Fuerte' avocado. *Leaflet No. 58* Subtrop Fruit Series No 10. Pretoria: Dept Of Agric Tech Serv.

SCHAFER, B, RAMOS, L & LARA, S P, 1987. Effect of fruit removal on the net gas exchange of avocado leaves. *HortScience* 22, 925 - 927.

SCHOFIELD, P B, SEDGLEY, M & ALEXANDER, D M E, 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, 1953. Growth and development of the Fuerte avocado fruit. *Proc Am Soc Yrb* 61, 103 - 107.

TOERIEN, J C, 1989. Aspects of the economy of avocado production in South Africa. *S A Avocado Growers' Assoc Yrb* 12, 7 - 10.

WHILEY, A W, SARANAH, J B, CULL, B W & PEGG, K G, 1988. Manage avocado tree growth cycles for productivity gains. *Queensland Agric J* 114, 457 - 467.

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. *Proceedings of the World*

Avocado Congress, Pretoria, S A Avocado Growers' Assoc Yrb 10, 58 - 61.

WOLSTENHOLME, B N, 1990. Resource allocation and the vegetative-reproductive competition: opportunities for manipulation in evergreen fruit trees. *Acta Hort* 275, 451 - 460.

WOLSTENHOME, B N & WHILEY, A W, 1990. Prospects for vegetative-reproductive growth manipulation in avocado trees. S *A Avocado Growers' Assoc Yrb* 13, 21 - 24.

WOLSTENHOLME, B N, WHILEY, A W & SARANAH, J B, 1990. Manipulating vegetative: reproductive growth in avocado (*Persea Americana* Mill) with paclarbutrazol foliar sprays. *Scientia Hort* 41**,** 315 - 327.

WORLEY, R E, 1979. Fall, defoliation date and seasonal carbohydrate concentrations of pecan wood tissue. *J Am Soc Hort Sci* 104, 195 - 199.