5. Influence of shoot age on floral development and early fruit set in 'Hass' avocado.

5.1 Summary.

Floral bud development, early fruit set, bud size, leaf nitrogen and shoot starch content were investigated in shoots of different ages to determine whether shoot age influences fruit set in avocado. Growth, floral bud development and early fruit set were compared on spring, summer and autumn (youngest) flush shoots of 'Hass' avocado. In branching systems with three growth flushes, more flowers were produced and more fruit set on autumn and summer, than on spring flush shoots. Leaf nitrogen accumulation and floral development occurred later on autumn than on summer shoots, but leaf number, dry and fresh weights, starch content of wood, mean floral status at anthesis, anthesis date and number of fruit set one month post-anthesis, were similar. However, fruit set was reduced on late-formed autumn shoots. When branches were pruned such that only spring or summer shoots were present, there was no difference between the floral status of the two classes. The results suggest that shoot age does not influence the ability of a shoot to flower and set fruit, provided the shoot is located at the canopy periphery at the time of floral initiation and has sufficient vigour to produce new shoot growth in spring.

5.2 Introduction.

In seasonal climates, avocado trees produce one reproductive (spring) and usually one or two vegetative (summer and autumn) growth cycles over an annual growing period. Flowers are initiated in late autumn on the terminal shoot modules on their respective growth axes. Floral buds may initiate on shoots from the previous spring, summer or autumn flush, as not all shoots extend during each growth flush. Floral shoots, therefore, may be classified according to the flush on which they develop. Factors such as climate, irrigation and pruning, will affect the number of shoots in each age class by influencing the frequency of production of growth flushes and the number of shoots which extend during a flush (Gregoriou and Kumar, 1982; Scholefield et al., 1985; Kalmar and Lahav, 1977; Lahav and Kalmar, 1977; and Smoyer et al., 1951).

Avocado leaves function at their physiological optimum from shortly after full leaf expansion until at least 70-98 days after bud break (Schaffer et al., 1991). Leaves on shoots in the spring age class, however, may be up to 200 days old when flowers are initiated in late autumn. Leaf age may therefore be important to floral development on these shoots, especially on trees with severe leaf necrosis due to salt-laden irrigation water (Ayers et al., 1951; Downton, 1978). Leaf nutrients (Koo and Young, 1977; Bar, Lahav and Kalmar, 1987), and carbohydrate status (Rodrigues and Ryan, 1960; Whiley et al., 1991) of shoots from different age classes have been studied, but floral development on these shoots has not been measured. Inoue and Takahashi (1990) found increased fruit numbers on summer compared with spring flush shoots on 'Bacon', 'Fuerte' and 'Zutano', in an area with only two major flushes per year.

In this study, floral development and early fruit set are compared on floral shoots from the spring, summer and autumn age classes of 'Hass' avocado trees. Leaf nitrogen and shoot starch content during shoot formation, floral development and at early fruit set are also monitored.

5.3 Materials and methods.

5.3.1 Plant material.

Avocado trees (cv 'Hass') used in this research were growing on a commercial property in South Australia (35.12 S., 138.32 E.). All trees were 6 years old in 1989, the first year of observation, and had been flowering for at least three years. Timing of major flushes of vegetative growth were recorded from September (spring) 1989 until December 1991.

5.3.2 Shoot age treatments.

In May 1990 (autumn), summer and autumn flush shoots were labelled. All shoots were of similar length, and were selected from the northern aspect of canopy perimeters, 1-2 m above ground level. The summer and autumn shoots were randomly allocated to groups which were harvested in June (winter), September (early spring) or December (summer) 1990. Shoot length, leaf number, and area and node number of buds were recorded. Bud cross-section area (A) was determined from maximum (L) and minimum (B) diameters using the formula for the area of an ellipse (A = LB x 0.7854). Node number per bud was estimated by counting all leaf primordia, bud scales and bud-scale scars.

Buds were observed with a Phillips SEM505 scanning electron microscope or dissected under a light microscope and the development of each axillary meristem was classified according to stages 1 - 9 previously described (section 4.4.2). All shoots were divided into stems, leaves, and apical and axillary buds. Stem length together with fresh weights of stems, leaves and buds were recorded. All material was frozen in liquid nitrogen and freeze-dried before re-weighing. Stems and leaves were stored at -20°C and starch content (% dry weight) of stems was determined in a 0.05 g sample of finely ground tissue, using an enzymic-colorimetric procedure with a heat-stable α-amylase (Termamyl 120 L) and amyloglucosidase to hydrolyse the starch to glucose (Rasmussen and Henry, 1990). The glucose produced was measured colorimetrically using a coupled glucose/peroxidase reaction. Nitrogen content (% dry weight) was determined in a 1 g sample of ground leaf tissue using standard Kjeldahl procedures with a Kjeltec Auto 1030 analyzer. The number of new shoots was counted on summer and autumn shoots during anthesis (October). Their floral status was recorded using the following scale: F1 = no inflorescences, F2 = < 4 axillary inflorescences, F3 = 4 or more axillary inflorescences, and F4 = terminal bud floral. Early fruit set was recorded approximately one month after anthesis.

Individual annual growth modules containing spring, summer and autumn shoots were also labelled in autumn. The number of new shoots, floral status and early fruit set on these modules was recorded in the following spring for shoots in terminal positions on their respective axes.

5.3.3 Pruning treatments.

Annual growth modules with spring, summer and autumn shoots were pruned in autumn to leave spring or summer shoots as the terminal shoot modules. In the following spring, the numbers of emergent shoots and their floral status and early fruit set were recorded.

5.3.4 Late-formed shoots.

In May 1991 (late autumn), 12 pairs of the earliest-formed summer flush shoots and 12 pairs of the latest-formed autumn flush shoots were identified. Shoot pairs were selected to have similar lengths, leaf number and area, and were sited at similar positions in the same tree. One shoot from each pair was harvested immediately and shoot length, leaf number and area recorded. Leaf area was determined with a Paton Electronic Planimeter. Bud area, node number and floral development of apical and axillary buds were also determined. The second shoot in each pair was left intact, and date of bud break and anthesis, number of new shoots, their floral status, and fruit set one month after anthesis was recorded.

5.3.5 Statistical analyses.

Pooled- and separate-variance t-tests were used to compare two independent means. Analysis of variance was performed when three or more means were compared, and Duncan's multiple range test used to separate means when differences were statistically significant ($P < 0.05$).

5.4 Results.

In 1989/90 and 1990/91 flowering occurred in October (spring), followed by major vegetative growth flushes in November/December (spring), January/February (summer) and April/May (autumn).

5.4.1 Shoot age treatments.

For shoots labelled in autumn 1990, summer flush shoots were approximately 3 months older than autumn flush shoots. No significant differences were recorded between the length of these shoots at each sampling date, with an overall mean of 89.7 ± 3.5 mm.

In winter and early spring, leaf number and their fresh and dry weights were the same on summer and autumn flush shoots (Table 5.1). In winter, leaf nitrogen content was higher in summer than in autumn flush shoots; in spring the difference was not significant. Starch content, and fresh and dry weights of wood tended to be higher in autumn than in summer flush shoots (Table 5.2). Starch content was lowest in shoots collected in winter, but was the same in shoots collected in spring and summer, before and after flowering.

Fresh and dry weight of buds increased between winter and spring, but no significant differences were found between buds on summer and autumn shoots. Apical and axillary buds increased in size (cross-sectional area and node number) between winter and spring (Table 5.3). Apical buds were larger on summer than on autumn flush shoots in winter, but this difference was not apparent at bud break in spring. No significant differences were recorded in axillary bud size between shoot types.

The number of floral nodes in a bud was determined as the number of nodes with discernible inflorescence primordia (stages 3 to 9, section 4.4.2). Buds on summer shoots tended to have more floral nodes and more advanced floral development than buds on autumn shoots (Table 5.4) but the difference was not significant. Timing of major phenological events, from bud break onwards, did not differ between summer and autumn flush shoots. Bud break occurred on 6 September. Ten percent of flowers had reached anthesis by 18 October, and 90 % had reached anthesis by 7 November.

Levels of bud break were similar on the summer and autumn flush shoots, producing the same number of new axillary shoots in spring (3.6 ± 0.5 and 3.9 ± 0.4, respectively; $P < 0.05$). These new shoots (compound inflorescences) were mostly indeterminate. Fruit set one month post-anthesis (10 December) was the same for summer and autumn shoots (1.3 ± 0.4 and 0.9 ± 0.2, respectively; $P < 0.05$).

Levels of bud break were also similar on spring, summer and autumn shoots in terminal positions on the same annual growth module (Table 5.5). Mean floral status of shoots decreased with shoot age, however, and more fruit set on summer and autumn, than on spring shoots.

5.4.2 Pruning treatments.

Pruned shoots had increased numbers of buds which burst compared with the unpruned shoots from the same age class, but the resulting growth was mainly vegetative with few flowers and practically no fruit set. No significant differences were found between pruned spring and summer shoots ($P < 0.01$). Mean shoot numbers were 2.3 ± 0.08 and 2.5 ± 0.11; and mean floral status 1.3 ± 0.06 and 1.3 ± 0.11 for pruned spring and summer shoots, respectively.

5.4.3 Late-formed shoots.

At the time of selection in May, early summer flush shoots were longer, their leaves larger and their apical and axillary buds had more nodes, than the selected late autumn flush shoots. All apical and many axillary buds on summer flush shoots contained floral nodes; whereas no floral development was observed at this time on autumn flush shoots. Nevertheless, mean floral status at anthesis and dates of anthesis were the same for each shoot type. Bud break levels were higher on summer than on autumn shoots in 1991, producing twice as many spring shoots (5.9 ± 0.7 and 2.8 ± 0.6, respectively). Relative proportions of vegetative and reproductive shoots were not affected, so there were more flowers on summer than on autumn flush shoots. More fruit set on early summer compared with late-forming autumn flush shoots (1.7 ± 0.7 and 0.4 ± 0.2, respectively).

5.5 Discussion.

This study has demonstrated a variable relationship between shoot age and the ability of an avocado shoot to flower and set fruit. No difference in floral development or fruit set was observed between summer and autumn shoots with similar vigour and aspects in the tree canopy. However, less fruit set on spring than on summer and autumn flush shoots, and on late-formed autumn than on summer shoots. Shoots were placed in the spring age class because they had not resumed growth in later growth flushes. They were relatively few, weak growing and located deeper in the canopy than shoots from summer and autumn age classes. This lack of vigour and probable low level of intercepted light may have led to reduced fruit set (Jackson, 1980), which may also explain the observation of Inoue and Takahashi (1990) that less fruit set on spring than on summer avocado shoots. In this region in Japan with only two growth flushes per year, the summer shoots would have been located at the canopy periphery, terminal to the spring shoots. Late-formed autumn shoots on the canopy periphery showed reduced fruit set in this study. These shoots also were very weak growing, possibly due to the cooler autumn temperatures during their growth, and they produced relatively few shoots in the subsequent spring flush. Mean floral status of the spring flush was not reduced, rather it was the number of new shoots formed which led to reduced flower numbers and fruit set. Node initiation within buds was delayed on late-formed autumn shoots. Possibly buds have to reach a critical stage of development before they can extend as new shoots.

Adequate carbohydrate (starch) and leaf nitrogen reserves are required to sustain flowering and high fruit yields in avocado (Scholefield et al., 1985; Embleton et al., 1959). It was therefore of interest to compare accumulation of these reserves with floral development in different aged shoots. As with deciduous trees, leaf nitrogen and shoot starch content appeared to quickly equilibrate between age classes with little shoot autonomy (Oliveira and Priestley, 1988; Sprugel et al., 1991). In winter, nitrogen content was low in autumn flush shoots, but otherwise was similar to values reported elsewhere for avocados (Bar et al., 1987; Embleton et al., 1959; Koo and Young, 1977). Shoot starch contents did not differ between newly-formed shoots in each age class, but increased between winter and spring during floral development in apical and axillary buds. Overall, starch levels were similar to those reported by Scholefield et al. (1985).

In trees with multiple growth flushes, stimulating increased production of summer or autumn flush shoots would reduce mean leaf age. This may improve average leaf health, with likely benefits to assimilate production. Scholefield et al. (1985) suggested that "new" summer leaves may be more important to productivity of avocado than leaves from the spring flush. A similar situation has been demonstrated with single flush deciduous fruit trees, except that here carbohydrate reserves, and hence fruit yields in the following season, were increased by extending the functional life of leaves (Oliveira and Priestley, 1988). While it is not suggested that growth stimulation is a viable option for vigorously growing avocado trees, used cautiously it may have application in arid regions, with trees on dwarfing rootstocks, or with more compact, high yielding cultivars such as 'Gwen' (Bergh and Martin, 1988). Changing tree design to improve light penetration to shaded, unproductive shoots deep in the canopy may be a more suitable approach. However, maintaining good light penetration would be difficult due to the multiple flushing habit of avocados. Clearly this growth habit is not in keeping with the horticultural requirements of compact growth and high fruiting ability. Its modification is a major challenge in increasing avocado productivity.

Table 5.1 Number, fresh and dry weight (g) and nitrogen content (% dry weight) of leaves (mean ± s.e.) on 15 summer and autumn flush shoots of 'Hass' avocado in winter (June) and early spring (September).

Shoot formed:	Summer	Autumn	Summer	Autumn
Observations:	Winter		early Spring	
No. of leaves	8.0 ± 0.5	8.2 ± 0.5 NS[1]	7.5 ± 0.5	8.2 ± 0.5 NS
Fresh weight	16.7 ± 0.8	15.4 ± 0.9 NS	15.6 ± 0.8	18.3 ± 1.7 NS
Dry weight	7.3 ± 0.4	6.4 ± 1.2 NS	7.5 ± 0.6	8.3 ± 0.7 NS
Nitrogen	1.9 ± 0.02	1.7 ± 0.07 **	1.9 ± 0.05	1.8 ± 0.03 NS

[1] Paired t-test carried out for each variate (NS = not significant, ** = $P < 0.01$).

Table 5.2 Fresh and dry weight (g), and starch content (% dry weight) of wood (mean ± s.e.) on 15 summer and autumn flush shoots of 'Hass' avocado in winter (June), early spring (September), and summer (December) at early fruit set one month post-anthesis.

Shoot formed:	Summer	Autumn	Summer	Autumn
Observations:	Winter		early Spring	
Fresh weight	5.0 ± 0.4	5.5 ± 0.9 NS[1]	5.1 ± 0.4	7.5 ± 0.5 *
Dry weight	1.4 ± 0.1	1.4 ± 0.3 NS	1.8 ± 0.2	2.3 ± 0.2 NS
Starch	5.8 ± 0.1	6.2 ± 0.2 NS	8.5 ± 0.2	8.9 ± 0.2 NS

Shoot formed:	Summer	Autumn
Observations:	Summer	
Fresh weight	3.2 ± 0.4	5.1 ± 1.1 NS
Dry weight	0.8 ± 0.1	1.3 ± 0.3 NS
Starch	8.1 ± 0.4	8.9 ± 0.6 NS

[1] Paired t-test carried out for each variate (NS = not significant, * = $P < 0.05$).

Table 5.3 Bud area (mm^2 ± s.e.) and node number (mean ± s.e.) of apical buds and the first five axillary buds below these on 15 summer and 11 autumn flush shoots of avocado in winter (June) and in early spring (September) at bud break.

Shoot formed:	Summer	Autumn		Summer	Autumn	
Observations:	Winter			early Spring		
Bud area						
Apical bud	22.5 ± 1.6	16.7 ± 1.7	*[1]	49.1 ± 4.1	45.9 ± 7.3	NS
Axillary buds						
1	8.1 ± 1.9	4.4 ± 0.8	NS	8.5 ± 2.3	9.1 ± 1.7	NS
2	7.3 ± 1.6	5.4 ± 0.7	NS	10.6 ± 1.6	13.1 ± 2.7	NS
3	7.0 ± 1.1	6.7 ± 0.9	NS	10.0 ± 2.2	17.8 ± 4.5	NS
4	6.9 ± 1.2	6.4 ± 0.8	NS	8.1 ± 2.4	13.3 ± 3.2	NS
5	5.7 ± 0.7	5.7 ± 0.8	NS	6.6 ± 1.5	11.5 ± 3.3	NS
Node number						
Apical bud	20.9 ± 0.6	17.3 ± 0.9	**	23.4 ± 0.9	23.0 ± 0.9	NS
Axillary buds						
1	13.5 ± 1.1	11.8 ± 0.7	NS	14.7 ± 1.5	15.1 ± 0.8	NS
2	13.1 ± 1.2	13.5 ± 0.6	NS	17.2 ± 1.1	17.0 ± 1.4	NS
3	13.3 ± 1.2	13.5 ± 0.8	NS	16.1 ± 1.1	17.8 ± 1.2	NS
4	13.6 ± 1.0	13.0 ± 0.7	NS	14.1 ± 1.1	16.1 ± 1.4	NS
5	12.0 ± 0.9	12.5 ± 0.7	NS	14.5 ± 1.1	16.0 ± 1.4	NS

[1] Paired t-test carried out for each variate (NS = not significant, * = $P < 0.05$; ** = $P < 0.01$).

Table 5.4 Number of floral nodes and maximum stage of floral development (mean ± s.e.) in apical buds and the first five axillary buds below these on 15 summer and 11 autumn flush shoots of 'Hass' avocado in winter (June) and in early spring (September) at bud break.

Shoot formed:	Summer	Autumn	Summer	Autumn
Observations:	Winter		early Spring	
Number of floral nodes[1]				
Apical bud	5.4 ± 0.7	3.6 ± 0.9	8.5 ± 0.8	7.1 ± 1.3
Axillary buds				
1	1.1 ± 0.6	0.5 ± 0.5	3.3 ± 0.9	2.7 ± 0.9
2	1.3 ± 0.6	0.7 ± 0.5	4.3 ± 0.7	4.2 ± 1.1
3	1.1 ± 0.6	1.2 ± 0.7	3.5 ± 0.7	4.4 ± 1.3
4	1.1 ± 0.6	0.6 ± 0.5	2.4 ± 0.8	3.1 ± 1.2
5	0.9 ± 0.6	0.1 ± 0.1	2.3 ± 0.8	1.9 ± 1.1
Maximum stage of floral development[1]				
Apical bud	4.1 ± 0.4	3.1 ± 0.8	7.3 ± 0.5	6.7 ± 1.0
Axillary buds				
1	0.9 ± 0.5	0.3 ± 0.3	3.7 ± 0.9	3.0 ± 0.9
2	1.4 ± 0.6	0.8 ± 0.4	5.1 ± 0.8	4.6 ± 1.0
3	1.1 ± 0.5	0.9 ± 0.5	4.1 ± 0.9	4.4 ± 1.2
4	1.1 ± 0.5	0.5 ± 0.4	2.6 ± 0.9	3.1 ± 1.1
5	0.7 ± 0.5	0.3 ± 0.3	2.7 ± 0.9	1.7 ± 0.9

[1] 1 = meristem formation, 2 = first bract primordia, 3 = bract primordia extend over meristem, 4 = bract primordia tomentose, 5 = bud elongates, 6 = first branch primordia, 7 = first flower primordia, 8 = axis extends, 9 = flower primordia visible. Commitment to floral development occurs at Stage 3.

T-tests, with buds on summer and autumn flush shoots as pairs, performed for all sampling dates and bud locations, found no significant differences ($P < 0.05$).

Table 5.5 Shoot number, floral status and early fruit set (mean ± s.e.) in late spring on shoots from the previous spring, summer and autumn growth flushes in 'Hass' avocado.

Shoot formed (n)	No. of spring shoots	Mean floral status[1]	Fruit set
Spring (43)	2.7 ± 0.08	1.0 ± 0.02 a[2]	0.2 ± 0.06 a
Summer (38)	3.0 ± 0.12	1.8 ± 0.23 b	0.8 ± 0.18 b
Autumn (66)	2.7 ± 0.09	3.1 ± 0.27 c	1.0 ± 0.17 b

[1] Floral status: 1 = no inflorescences; 2 = < 4 axillary inflorescences; 3 = 4 or more axillary inflorescences; 4 = terminal bud floral.

[2] Mean separation down columns by Duncan's multiple range test (P = 0.05).