6. Manipulation of shoot growth patterns in relation to early fruit set in 'Hass' avocado.

6.1 Summary.

Shoot tipping and pruning, rootstocks and plant growth regulator applications were evaluated for their potential to change canopy structure and improve productivity of 'Hass' avocado. Tipping and pruning were successful in limiting the length of the primary shoot axis and increasing axillary branching, without influencing total fruit set. Trees on the rootstock 'Velvick' had greater vigour with a higher ratio of sylleptic to proleptic shoots than trees on 'Hass' rootstock. The growth inhibitor Cultar (paclobutrazol) reduced shoot length and leaf size, but had no effect on the number of shoots or on fruit set. The auxin inhibitor TIBA (2,3,5-triiodobenzoic acid) stimulated axillary shoot growth without effect on fruit set. Cytolin (6-benzyladenine and gibberellins$_{4+7}$) increased sylleptic axillary shoot growth and subsequent fruit set, but the timing of application was critical. Manipulation of sylleptic shoot growth may provide the key to improving tree form and productivity in avocado.

6.2 Introduction.

Manipulation of tree growth via pruning, rootstock and plant growth regulator application is fundamental to yield optimisation. Such practises are well understood with temperate tree fruit crops that have a clear distinction between periods of dormancy and active growth (Mika, 1986; Marini and Barden, 1987; Rom and Carlson, 1987; Miller, 1988; Davis and Curry, 1991). In contrast, very little is known regarding yield control in tropical and subtropical tree fruits, such as avocado, which have diffuse rhythmic patterns of reproductive and vegetative growth, and produce two shoot types, proleptic and sylleptic (Hallé et al., 1978; Wheaton, 1980). Both forms of shoot growth are found in avocado (Venning and Lincoln, 1958). Avocado cultivars may have predominantly sylleptic shoot growth, as in 'Gwen' and 'Reed', or predominantly proleptic, as in 'Sharwil', whereas Hass' has an even balance of both shoot types (Chapter 4). In this chapter, the effects of shoot tipping and pruning, rootstocks and a range of plant growth regulator treatments, on shoot growth and productivity are examined with 'Hass'.

6.3 Materials and methods.

6.3.1 Plant material.

Avocado trees (cv 'Hass') were growing in commercial orchards in South Australia and Queensland. In these regions, trees have one reproductive (spring) and one or two vegetative (summer and autumn) growth flushes per year. Flowers are initiated in autumn on shoots in terminal positions on their respective axes (Scholefield et al., 1985).

6.3.2 Shoot tipping and pruning.

The trees for this experiment were growing on a commercial property in McLaren Vale, South Australia (35.12 S., 138.32 E.). All trees were 7 years old and grafted onto 'Zutano' seedling rootstocks. Five treatments, including a control, were applied to the summer flush in early autumn just prior to floral initiation (Scholefield et al., 1985). Five shoot modules containing spring and summer flush shoots were labelled on each of 15 trees, from canopy perimeters 1-2 m above ground level. Shoot tipping treatments removed apical buds from either the primary growth axis, axillary shoots or both (Table 6.1). The pruning treatment removed the whole axillary summer flush, so that only spring flush shoots remained in terminal positions on axes. Number and length of shoots was recorded at the end of the autumn flush, and early fruit set on the subsequent spring flush was recorded approximately one month after anthesis.

6.3.3 Rootstock.

Six 'Hass' trees growing in Maleny, Queensland (26.51 S., 152.51 E.) were studied. All trees were 4 years old, and grafted on 'Hass' (x3) or 'Velvick' (x3) seedling rootstocks. Two limbs from two trees and one limb from one tree, i.e. five per rootstock, were selected and the lengths of primary growth axes of terminal annual growth flushes measured. Numbers of nodes and proleptic and sylleptic axillary shoots on these axes were also recorded, as was the total number of shoots comprising the annual growth module. Fruit set was erratic on these relatively young trees and was not recorded.

6.3.4 Plant growth regulators.

Treatments were applied to seven year old 'Hass' trees growing at McLaren Vale or at Waikerie (34.11 S., 139.59 E.), South Australia. Chemicals used were Cultar (paclobutrazol, 8 ml/l), Cytolin (6-benzyladenine + gibberellins$_{4+7}$, 25 ml/l) and TIBA (2,3,5-triiodobenzoic acid, 0.5 g/l). Control shoots were sprayed with water. The surfactant Agral (0.05 %) was added to each solution. Growth substances were dissolved in water except TIBA which was dissolved in sodium bicarbonate (0.1 g/l). Shoots were sprayed to run-off, using approximately 750 ml per shoot. Excess solution was collected in a plastic shield which also prevented spray drift onto neighbouring shoots. Solutions were applied to spring flush shoots at the end of shoot extension (November), to summer flush shoots at the end of shoot extension (February), to autumn flush shoots during shoot extension (April), to autumn flush shoots following shoot extension (June), and to autumn flush shoots at floral bud break in spring (August). A different group of shoots and trees were used at each treatment date.

All treatments were applied to shoots forming the primary growth axes of terminal growth flushes, and each treatment was applied once on 12 or 13 trees. Regular observations were made of the current or subsequent growth flush to determine shoot lengths at flush maturity, as determined by the absence of red colouration in young leaves. Number of axillary shoots, and leaf length and width, were also recorded. Shoot numbers and lengths of primary axes in the subsequent spring flush were measured, and early fruit set determined.

6.3.5 Statistical analysis.

Paired t-tests were used to compare two independent means. Analysis of variance was performed when three or more means were compared.

6.4 Results.

6.4.1 Shoot tipping and pruning.

Autumn growth in control shoots occurred from apical and subapical buds on both primary and axillary growth axes. Autumn growth on pruned or tipped shoots occurred from axillary buds subjacent to the cut. On control shoots, the total length of the primary autumn flush was greater than for axillary flush shoots (Table 6.1). Autumn regrowth from a subapical bud on tipped primary shoots was less than that on untipped shoots. The primary autumn flush shoot was stimulated if it was left intact and axillary shoots were pruned, but not if axillary shoots were tipped. Autumn growth on axillary shoots that had been tipped or pruned was less than that on untreated shoots, except when the primary axis had also been tipped. The same number of proleptic axillary shoots formed during the autumn flush in each treatment (1.1 ± 0.1, P = 0.238), and no sylleptic shoots formed in the treatments that reduced shoot growth. When primary shoot growth was stimulated by pruning axillary shoots, sylleptic shoots resulted, but the difference between pruned and unpruned shoots was not statistically significant (2.5 ± 0.7 and 1.4 ± 0.6 respectively, P = 0.22).

The total number of fruit set in spring was unaffected by treatment (4.4 ± 0.4, P = 0.6097). More fruit set on the axillary than on the primary shoots, except when the axillary shoots were pruned (Table 6.1).

6.4.2 Rootstock.

Primary axes were longer in trees on 'Velvick' compared with 'Hass' rootstock, while node number was unaffected (Table 6.2). Total numbers of shoots on primary and axillary axes were the same with both rootstocks. More proleptic than sylleptic shoots developed on primary axes on 'Hass' rootstock, but this pattern was reversed on 'Velvick' rootstock.

6.4.3 Plant growth regulators.

When spring flush shoots at the end of shoot extension were sprayed with Cultar, the primary axis of the subsequent summer shoot growth was shorter than on unsprayed shoots (Table 6.3). Similar numbers of new shoots were recorded on sprayed and unsprayed shoots at this time. No effect on primary shoot length or number of axillary shoots was recorded when Cultar was applied to autumn shoots during shoot extension, although leaves were smaller on sprayed than on unsprayed shoots. No carryover effect from this treatment, or from Cultar applications at any other time of year, was recorded in the length of the primary axis, the number of shoots, leaf dimensions or early fruit set on the subsequent spring growth flush. When Cytolin was applied at the end of extension of the spring flush, the main axis of the subsequent summer flush was longer, and more axillary shoots formed on sprayed than on unsprayed shoots (Table 6.4). The extra axillary shoots were sylleptic. Leaves were smaller on sprayed than on unsprayed shoots (length 104.6 ± 3.6 and 134.8 ± 6.6 mm, width 41.3 ± 2.7 and 67.7 ± 3.9 mm respectively; $P < 0.001$). No autumn flush developed on the sprayed shoots, but the increased axillary shoots on the summer flush resulted in more shoots and more fruit set in the subsequent spring growth flush (Table 6.4). Cytolin caused immediate resumption of growth when applied to summer flush shoots at the end of shoot extension. Final length of the subsequent autumn flush was 158 ± 14.9 mm, and produced, on average, 4.0 ± 0.7 sylleptic and 0.8 ± 0.3 proleptic axillary shoots. In the subsequent spring flush main growth axes were shorter on sprayed than on unsprayed shoots (72 ± 5.1 and 103 ± 5.1 mm, respectively; $P < 0.001$), and axillary shoot number, leaf dimensions and fruit set were the same. Final shoot length was increased after Cytolin application to extending autumn flush shoots, but treatment at this time did not increase axillary shoot number (Table 6.4), or leaf dimensions. Fewer shoots formed in the next spring flush, which were mostly vegetative, so that no fruit set on the sprayed branches. A small increase in primary shoot length of the subsequent spring flush was recorded as a result of Cytolin applications to autumn shoots at floral bud break in spring, but there was no effect on the number of new shoots, leaf dimensions or on fruit set.

TIBA applications affected shoot development only when applied to actively growing shoots in autumn (April). The chemical caused premature leaf-drop, and more shoots formed during the subsequent spring growth flush on sprayed than on unsprayed shoots (6.9 ± 1.2 and 4.5 ± 0.4 respectively, $P < 0.05$). There was no effect on fruit set or on leaf dimensions.

6.5 Discussion.

This study has shown that there is considerable potential for the use of Cytolin to manipulate shoot growth and increase fruit set in avocado, but timing of application is critical. Increased sylleptic shoot number led to increased fruit set in the following year when Cytolin was applied in late spring, before extension of the summer flush. Treatment at this time prolonged the summer flush and prevented the formation of an autumn flush. A basic shift in flowering habit resulted, such that inflorescences were located individually on numerous short leafy axillary shoots, rather than at the end of single primary growth axes. This growth pattern led to significantly higher fruit set. Applied to young trees, Cytolin may increase the number of potential fruiting points and may bring trees into production more quickly than those trees with few axillary branches (Köhne, 1986). Similar methods are well established in temperate fruit industries such as apple, to increase branch production (Miller, 1988; Quinlan and Tobutt, 1990).

It is well established that axillary shoot growth is controlled by the ratio of auxins to cytokinins, with relatively high levels of cytokinins acting to release buds from inhibition (Sachs and Thimann, 1964; Smigocki and Owens, 1989; Tamas, 1987). Cytolin contains the cytokinin-like compound 6-benzyladenine (BA) and the gibberellins$_{4+7}$ (GA_{4+7}). When we applied Cytolin, the BA apparently altered the auxin:cytokinin ratio and released axillary buds from inhibition, while the GA_{4+7} most likely acted on internode extension during the post-release phase (Tamas, 1987). The stage of bud and shoot development at the time of Cytolin application influenced the growth response in this study and could be traced to meristem activity. Cytolin applied at bud break, when there was active node initiation in buds (Chapter 5), caused only a small increase in shoot length and no change in shoot number. When Cytolin was applied at the end of shoot extension, when apical and axillary meristems in buds were quiescent, a large increase in shoot length and number was recorded. It would seem that meristems were sensitive to the action of BA only when they were quiescent, and internodes were most sensitive to GA_{4+7} when they were not extending. Cytolin had no effect on the number of nodes in the bud, neither did it stimulate activity of latent axillary buds. This latter observation is consistent with results from temperate fruit trees (Miller, 1988).

Growth suppression in avocados, following foliar application of Cultar to spring flush shoots from bud break to flush maturity, has been reported by several authors (Adato, 1990; Köhne and Kremer-Köhne, 1987 and 1990; Whiley et al., 1991; Wolstenholme et al., 1990). This study gave a similar result, but no effects were observed when the same concentrations were applied at the end of summer and autumn growth flushes. This was probably a combined effect of shoot age at the time of application, and the interval between time of application and subsequent extension growth, that may be overcome with different application techniques. Application via soil drenches or trunk injections are effective at all stages of development, indicating increased persistence in the plant or soil using these methods (Köhne and Kremer-Köhne, 1990; Whiley et al., 1991). Cultar is generally thought to increase fruit yields by reducing the dominance of vegetative growth (Davis et al., 1988). No effect on fruit set following Cultar application to individual shoots was observed in this study. Köhne and Kremer-Köhne (1987) reported increased fruit set on branches sprayed with Cultar, but this was a difference between a total of 3 and 1 fruit on 19 branches. Single applications of Cultar to whole trees have been shown to increase, decrease or have no effect on fruit yields (Adato, 1990; Köhne and Kremer-Köhne, 1990; Wolstenholme et al., 1990; Whiley et al., 1991). Cumulative yield is generally increased, however, following repeat applications in successive years. These data suggest that conditions prevailing in whole trees rather than in individual shoots are more important to fruit retention. McCarty et al. (1971) reported increased axillary growth on young potted avocado plants sprayed with TIBA. These were seedlings growing in controlled conditions, and may have responded to lower concentrations than the field grown, fruiting plants used here.

Pruning methods employed in temperate fruit industries to improve tree structure generally stimulate vigorous unfruitful growth when applied to evergreen trees from tropical regions. Light pruning, which redistributes growth, is generally the preferred option for these trees, and is recommended for avocado (Bergh and Martin, 1988; Bertin, 1976; Montgomery, 1955). This study is the first to provide detailed analysis of such growth redistribution in avocado. It was demonstrated that changes in growth patterns were achieved by limiting primary extension and stimulating axillary shoot growth, with no deleterious effects on fruit set.

Changes in shoot length in this study were mainly due to increased internode length as node numbers were generally unchanged by treatment, and were similar to those reported in Chapter 5. Apart from internode length, the number of sylleptic shoots formed was the growth response most affected by treatment. Increased sylleptic shoot number was observed when shoots were sprayed with Cytolin, and there was a similar trend following pruning, and in trees growing on 'Velvick' rootstocks. 'Velvick' is an important Australian rootstock for avocados, typically producing vigorous trees (Whiley et al., 1990). Increased sylleptic shoot growth appeared to be a consequence of this vigorous growth. A similar association has been identified in other tree species where the greater the shoot extension rate, the greater the likelihood of sylleptic axillary growth (p. 46., Hallé et al., 1978). Syllepsis, however, is not exclusively associated with rapid shoot growth. 'Gwen' (Bergh and Martin, 1988) and 'Reed' are both highly productive, compact, upright cultivars of avocado which have predominantly sylleptic shoots. Perhaps this growth form should become an important goal of future breeding programmes with avocado. Hormone metabolizing genes, such as those which control axillary bud growth by inhibiting auxin or stimulating cytokinin synthesis, play important roles in plant morphogenesis (Klee and Estelle, 1991). Molecular genetic techniques, therefore, may provide a more permanent means of increasing sylleptic shoot growth than exogenous plant growth regulator applications. Whichever approach is taken, manipulating tree structure by increasing sylleptic shoot growth would appear to have good potential for improving yield efficiency in tropical fruit trees such as avocado.

Table 6.1 Length (mm ± s.e.) of autumn flush shoots and early fruit set (± s.e.) in spring, on 'Hass' avocado shoots tipped or pruned in early autumn just prior to floral initiation.

	Terminal shoot on primary axis	Axillary shoots	Terminal flush on primary axis	Axillary flush shoots
			Total length of autumn shoots	
Control	X	X	193 ± 66	46 ± 22
Tipped	T	X	80 ± 29	59 ± 26
Tipped	T	T	60 ± 30	72 ± 39
Tipped	X	T	133 ± 61	11 ± 7
Pruned	X	P	300 ± 82	2 ± 1
	F. prob.		0.138	0.017
			No. fruit set	
Control	X	X	1.9 ± 0.7	3.7 ± 1.1
Tipped	T	X	2.1 ± 0.8	3.0 ± 0.8
Tipped	T	T	1.1 ± 0.6	2.5 ± 0.8
Tipped	X	T	0.5 ± 0.3	3.6 ± 0.9
Pruned	X	P	2.7 ± 0.9	0.8 ± 0.3
	F. prob.		0.200	0.089

X = intact, T = apical bud removed, P = whole shoot removed.

Table 6.2 Length, number of nodes and axillary shoot growth on the primary growth axes (n = 5) of 'Hass' avocado trees growing on 'Hass' or 'Velvick' seedling rootstock.

	Rootstock		
	'Hass'	'Velvick'	T-test[1]
Length (mm)	1330	2122	**
No. of nodes	57.4	69.8	NS
Axillary shoots on primary axis			
No. of sylleptic shoots	7.8	13.4	NS
No. of proleptic shoots	12.6	6.4	**
Total	20.4	19.8	NS
No. of shoots on primary and axillary axes	64.0	76.8	NS

[1] Levels of significance: NS = not significant, ** = $P < 0.01$.

Table 6.3 Effects of Cultar (8 ml/l) applied to shoots of 'Hass' avocado.

	Control	Cultar	T-test[1]
Applied to spring flush at end of shoot extension (November)			
Effects on subsequent summer flush (V):			
length of primary axis (mm)	78	49	***
no. of shoots	1.1	0.8	NS
Applied to autumn flush during shoot extension (April)			
Effects on current autumn flush (V):			
length of primary axis (mm)	52	55	NS
no. of shoots	1.1	0.7	NS
leaf length (mm)	111.2	88.8	**
width	60.6	48.5	**
Effects on subsequent spring flush (R):			
length of primary axis (mm)	135	120	NS
no. of shoots	4.5	5.6	NS
no. fruit set	1.7	1.7	NS

[1] Level of significance: NS = not significant; ** = $P < 0.01$; *** = $P < 0.001$.

V = vegetative flush; R = reproductive flush

Table 6.4 Effects of Cytolin (25 ml/l) applied to shoots of 'Hass' avocado.

	Control	Cytolin	T-test[1]
Applied to autumn flush at bud break (August)			
Effects on subsequent spring flush (R):			
length of primary axis (mm)	121	138	*
no. of shoots	6.8	6.4	NS
no. fruit set	1.8	1.7	NS
Applied to spring flush at end of shoot extension (November)			
Effects on subsequent summer flush (V):			
length of primary axis (mm)	78	312	***
no. of shoots	1.1	8.6	***
Effects on subsequent spring flush (R):			
no. of shoots	2.6	11.3	***
no. fruit set	0.2	2.8	***
Applied to autumn flush during shoot extension (April)			
Effects on current autumn flush (V):			
length of primary axis (mm)	52	135	***
no. of shoots	1.1	0.7	NS
Effects on subsequent spring flush (R):			
length of primary axis (mm)	135	124	NS
no. of shoots	4.5	1.3	***
no. fruit set	1.7	0	

[1] Level of significance: NS = not significant; * = $P < 0.05$; *** = $P < 0.001$.

V = vegetative flush; R = reproductive flush