Short Communication

Manipulation of shoot growth patterns in relation to early fruit set in 'Hass' avocado (*Persea americana* Mill.)

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Abstract

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 proleptic 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.

Key words: Avocado; *Persea*; Plant growth regulators; Prolepsis; Pruning; Rootstock; Shoot growth; Syllepsis

Abbreviations: TIBA = 2,3,5-triiodobenzoic acid

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; Rom and Carlson, 1987; Miller, 1988). In contrast, very little is known about yield control in tropical and subtropical tree fruits, such as avocado, which have diffuse rhythmic patterns of reproductive and vegetative growth, and produce two

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axillary shoot types, proleptic and sylleptic (Venning and Lincoln, 1958; Hallé et al., 1978). Proleptic shoots develop only after a period of dormancy as a resting axillary bud. They have a zone of bud-scale scars at their base, and they are the dominant form of growth in temperate fruit trees. Sylleptic shoots do not undergo a dormant period as a resting bud, but develop from meristems initiated in axillary positions in apical or axillary buds. They have a bulbous base with no bud-scale scars, and their growth is contemporaneous with extension of the parent axis. Both forms of shoot growth are found in avocado (Thorp and Sedgley, 1993; Thorp et al., 1993). In this study, the effects of shoot tipping and pruning, rootstocks and a range of plant growth regulator treatments, on shoot growth and productivity are examined with the cultivar 'Hass' growing in Australia. Here, avocado trees typically produce one reproductive (spring) and one or two vegetative (summer and autumn) growth flushes each year, with flowers being initiated in autumn on shoots in terminal positions on their respective axes (Scholefield et al., 1985). A shoot (module) is a unit of extension developed in a single growth flush from a bud or bud primordium (Thorp and Sedgley, 1993).

Materials and methods

Plant growth regulators. – Treatments were applied to 7 year old 'Hass' trees on 'Zutano' seedling rootstocks, growing at McLaren Vale (35.12 S., 138.32 E.) or at Waikerie (34.11 S., 139.59 E.), South Australia. 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. Treatments were applied during five seasons, with different groups of shoots and trees being used at each treatment date. Chemicals used were Cultar (paclobutrazol, 8 ml l^{-1}), Cytolin (6-benzyladenine+gibberellins$_{4+7}$, 25 ml l^{-1}) and TIBA (2,3,5-triiodobenzoic acid, 0.5 g l^{-1}). 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^{-1}). Shoots were sprayed to run-off, using approximately 75 ml per shoot. Excess solution was collected in a plastic shield which also prevented spray drift onto neighbouring shoots. Solutions were applied as follows: (1) to spring flush shoots at the end of shoot extension in spring (November); (2) to summer flush shoots at the end of shoot extension in summer (February); (3) to autumn flush shoots during shoot extension in autumn (April); (4) to autumn flush shoots following shoot extension in winter (June); (5) to autumn flush shoots at floral bud break in spring (August). 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.

Shoot tipping and pruning. – The trees for this experiment were grown on a commercial property in McLaren Vale, South Australia. All trees were 7 years old and grafted onto 'Zutano' seedling rootstocks. Five treatments 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. 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 1 month after anthesis.

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' (three) or 'Velvick' (three) seedling rootstocks. Limbs with a basal diameter of more than 35 mm were identified. Five of these limbs 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.

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

Results

Plant growth regulators. – When spring flush shoots that had just completed shoot extension were sprayed with Cultar, the primary axis of the subsequent summer shoot growth was shorter than on unsprayed shoots (Table 1). 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 2). The extra axillary shoots formed on the summer flush were sylleptic. Leaves were smaller on

Table 1
Effects of Cultar (8 ml^{-1}) 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)[2]			
Length of primary axis (mm)	78.0	49.0	***
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)	52.0	55.0	NS
No. of shoots	1.1	0.7	NS
Leaf length (mm)	111.2	88.8	**
Leaf width (mm)	60.6	48.5	**
Effects on subsequent spring flush (R)			
Length of primary axis (mm)	135.0	120.0	NS
No. of shoots	4.5	5.6	NS
No. fruit set	1.7	1.7	NS

[1]Level of significance: NS, not significant; ** $= P < 0.01$; *** $= P < 0.001$.
[2]V, vegetative flush; R, reproductive flush.

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 number of sylleptic axillary shoots on the summer flush resulted in more shoots and more fruit set in the subsequent spring growth flush (Table 2). Cytolin caused immediate resumption of growth when applied to summer flush shoots at the end of shoot extension in February. No similar autumn flush occurred on the unsprayed shoots. However, the main axis of the autumn flush on the sprayed shoots was longer and had more axillary sylleptic shoots than did unsprayed autumn flush shoots selected in April. In the subsequent spring flush, main growth axes on the shoots selected in February, were shorter on sprayed than on unsprayed shoots, 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, 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. There was no effect of Cytolin application at other times of year.

TIBA applications affected shoot development only when applied to actively growing shoots in autumn (April; data not presented). The chemical

Table 2
Effects of Cytolin (25 ml^{-1}) applied to shoots of 'Hass' avocado

	Control	Cytolin	T-test[1]
Applied to spring flush at end of shoot extension (November)			
Effects on subsequent summer flush (V)[2]			
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 summer flush at end of shoot extension (February)			
Effects on subsequent autumn flush (V)			
Length of primary axis (mm)	0.0	158	
No. of shoots	0.0	4.8	
Effects on subsequent spring flush (R)			
Length of primary axis (mm)	72.0	103	***
No. of shoots	7.1	6.1	NS
No. fruit set	0.8	0.6	NS
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	
Applied to autumn flush at floral 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

[1]Level of significance: NS, not significant; $* = P < 0.05$; $*** = P < 0.001$.
[2]V, vegetative flush; R, reproductive flush.

caused premature leaf-drop, and more proleptic axillary 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.

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 3). Autumn regrowth from a subapical bud on tipped primary shoots was less than that on untipped shoots.

Table 3
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[1]	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	T	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

[1]X, intact; T, apical bud removed; P, whole shoot removed.

Table 4
Length, number of nodes and axillary shoot growth on the primary growth axes ($n = 5$) of 'Hass' avocado trees growign on 'Hass' or 'Velvick' seedling rootstock

	Rootstock		T-test[1]
	'Hass'	'Velvick'	
Length (mm)	1330	2122	**
No. of modes	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	60.4	76.8	NS

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

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 3).

Rootstock. – Primary axes were longer in trees on 'Velvick' compared with 'Hass' rootstock, while node number was unaffected (Table 4). 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, while more sylleptic than proleptic shoots developed on 'Velvick'.

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. Cytolin sprays increased sylleptic shoot number, but only when applied to shoots that had just completed shoot extension. At this stage of shoot growth, apical buds are quiescent and there is a pause in node initiation (Thorp et al., 1993). New nodes are initiated in apical buds during bud break and shoot extension, and Cytolin sprays at these times had no effect on sylleptic shoot growth.

Increased sylleptic shoot number led to increased fruit set in the following year when Cytolin was applied in late spring to shoots that had just completed shoot extension, i.e. 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 so bring trees into production more quickly than those trees with few axillary branches (Köhne, 1986). Similar methods to increase branch production are well established in temperate fruit industries such as apple (Miller, 1988; Quinlan and Tobutt, 1990).

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 (Köhne and Kremer-Köhne, 1987, 1990; Adato, 1990; Wolstenholme et al., 1990; Whiley et al., 1991). 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, e.g. soil drenches or trunk injections (Köhne and Kremer-Köhne, 1990; Whiley et al., 1991). No effect on fruit set following Cultar application to individual shoots was observed in this study. In previous studies, single applications of Cultar to avocado trees or branches have resulted in variable effects on fruit yields (Köhne and Kremer-Köhne, 1987, 1990; Adato, 1990; Wolstenholme et al., 1990; Whiley et al., 1991), probably because conditions prevailing in whole trees rather than in individual shoots are 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 (Montgomery, 1955; Bertin, 1976; Bergh and Martin, 1988). This study has demonstrated that such growth redistribution in avocado is achieved by limiting primary extension and stimulating growth of axillary axes, with no deleterious effects on fruit set.

Changes in shoot length in this study were mainly caused by increased internode length as node numbers were generally unchanged by treatment. 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). 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 (Hallé et al., 1978). High rates of syllepsis without excessive shoot vigour occur in the highly productive avocado cultivars 'Gwen' and 'Reed' (Thorp and Sedgley, 1993). Both cultivars have a compact growth habit which means more trees can be planted per hectare. Thus, a high rate of syllepsis, occurring independent of shoot vigour, should be an important selection criteria in future avocado breeding programs, especially as it is a trait which could be selected for in relatively young plants. A high rate of syllepsis is generally associated with weak proleptic axillary shoot growth (Thorp and Sedgley, 1993). This character may also be a useful selection criteria. 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.

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