PUTATIVE TIMING OF IRREVERSIBLE COMMITMENT TO FLOWERING OF 'HASS' AVOCADO TREES IN THE WESTERN BAY OF PLENTY

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ABSTRACT

An important event in the growth cycle of avocado trees is the development of flower buds. To help overcome alternate bearing the ability to manipulate flowering would be desirable. To change the timing and intensity of flowering it is essential to know when the new buds are irreversibly committed to flowering. Flower bud initiation in New Zealand is considered to occur in April or May but research in California and Mexico would indicate flower buds are initiated earlier. Avocado flowers form on terminal shoots or the tips of axillary growth shoots and develop earlier and faster at the shoot tip than down the shoot. To determine the timing of irreversible commitment to flowering of 'Hass' avocado trees, spring initiated shoots were defoliated and the development of shoots followed. The effect on the timing of the irreversible commitment to flowering of removing the shoot tips on promoting new vegetative shoots was also investigated. The defoliation treatments in mid-April were identified as the time of irreversible commitment to flowering in agreement with the timing of irreversible commitment to flowering in California and Mexico. The presence of floral shoots at low levels at all treatment dates indicates that the transition from vegetative to reproductive shoots is occurring in January to March, earlier than previously thought in April/May. The timing of floral initiation varied from orchard to orchard by as much as six weeks and may be related to the cropping history where the earliest floral initiation was on Orchards 2 and 3 that had not set fruit in the prior year. The time of floral initiation on individual orchard needs to be determined so that the timing of management activities can be adjusted to be most effective. The removal of the shoot tip reduced the percentage of axillary buds that developed into flower buds to low levels at all defoliation treatment times. About half of the flowering and vegetative growth on an avocado shoot develops from apical buds with the two to three axillary buds closest to the shoot tip contributing about 40% of the flowering and vegetative shoots. Removing the shoot tip appeared to have inhibited the development of floral shoots. Light pruning of shoot tips in April may be useful for promoting additional shoot growth.

Keywords: *shoots, floral initiation, apical buds, axillary buds*

INTRODUCTION

A major problem for avocado growers in the Western Bay of Plenty is alternate bearing where there are inconsistent crops from year to year. To overcome alternate bearing there must be sufficient numbers of flowers to set a good crop from year to year. An important event in the growth cycle of avocado trees is the development of flower buds from vegetative buds that would otherwise produce shoots. Alternate bearing is typically characterised by differences in flowering intensity in "on" and "off" cropping years (Salazar-Garcia *et al*., 1998; Scora *et al.*, 2002). As well as less shoot growth in an "on" cropping year fewer flower buds are developed on shoots than in an "off" cropping year (Salazar-Garcia and Lovatt, 1999). Hass avocado trees typically flower in spring (September/October) in the Western Bay of Plenty when climactic conditions, principally temperature, can be very variable. To help overcome the alternate bearing of avocado trees in the Western Bay of Plenty the ability to manipulate flowering would be desirable. Such manipulation would include delaying the bloom to when climactic conditions are considered to be more favourable

and shortening of a long flowering period to avoid excessive reserve depletion or competition with developing shoots (Thorp *et al*., 1994). As a first step in considering possible methods for changing the timing and intensity of flowering it is essential to know when the new buds are irreversibly committed to flowering.

The earliest event in the development of flowers is inflorescence initiation that has been considered to occur over two to three months and that flower development to open flowers takes at least another two to three months (Schroeder, 1951). This would explain why it is possible to have flowers opening in winter with flower initiation potentially occurring in April or May (Cutting and Dixon, 2004). Salazar-Garcia *et al.* (1998) described 11 stages of flower development that could be used to visually determine the stage of inflorescence development. In California, the transition of vegetative buds to floral buds on summer initiated shoots has been reported to occur in September to October (Salazar-Garcia *et al*., 1998). This is similar to Nayarit, Mexico, where mid-October was identified as the date when irreversible commitment to flowering occurred (Salazar-Garcia *et al*., 2006). These dates are about 4 to 7 months prior to bloom in California and Mexico. The months of September and October in California and Mexico roughly correspond to March and April in New Zealand. Flower bud initiation, in New Zealand, is considered to occur in April or May (Cutting and Dixon, 2004) but the research in California and Mexico would indicate flower buds are initiated slightly earlier. Using a visual assessment of flower bud development flower initiation while reduced in the "on" year still occurred at the same time as in an "off" year (Salazar-Garcia *et al*., 1998). Although September to mid-October was viewed as the time of irreversible commitment to flowering the transition of vegetative buds to flower buds was considered to start at the end of July through August (January to February in New Zealand) that was earlier than previously thought (Salazar-Garcia *et al*., 1998). If flower bud initiation in New Zealand is earlier this may require some aspects of fertilizer programmes to be altered and would affect the timing of possible plant growth regulator treatments (Salazar-Garcia and Lovatt, 1998; 1999) that may delay or advance flowering.

Avocado shoots have a structure that is typical of many plants in that at the extreme tip of the shoot is a special region of cells that form new leaves or flowers (Scora *et al.*, 2002). The bud at the tip of the shoot is commonly called the apical bud. When a leaf has formed below the apical bud there are also axillary buds formed. The axillary buds can form new shoots or flowers in a similar way to the tip of the shoot. The apical bud has a strong influence on axillary buds on a shoot where they remain inactive while the shoot tip grows (Taiz and Zeiger, 1998). Removal of the apical bud often then allows the other buds on the shoot to become active and grow a new vegetative shoot or develop into a flower bud (Taiz and Zeiger, 1998). Avocado flowers form primarily on terminal shoots or the axillary growth shoots (Thorp *et al.*, 1993). Flower buds develop earlier and faster at the shoot tip than down the shoot on axilllary buds with the second bud down from the shoot tip being more advanced than the third bud down (Thorp *et al.*, 1994). Removing the shoot tip in an "on" cropping year may be useful to promote additional vegetative shoot growth giving a better balance between flowering and vegetative shoots. This may help to even out fruit set from year to year.

To determine the timing of irreversible commitment to flowering of Hass avocado trees in the Western Bay of Plenty, New Zealand spring initiated shoots were defoliated and the development of shoots followed. The effect on the timing of the irreversible commitment to flowering of removing the shoot tips on promoting new vegetative shoots was also investigated.

MATERIALS AND METHODS

Spring shoots initiated in 2005 from three avocado orchards in the Western Bay of Plenty (37°S, 176°E), New Zealand were used to identify the time of irreversible bud commitment to flowering. Within each orchard 15 trees were selected where

on each tree 28 spring initiated shoots from indeterminate inflorescences were tagged for later leaf stripping. Leaves were stripped off the shoots at two weekly intervals starting on the 11/1/2006 each of seven times with a final stripping time of the 27/4/2006. At each leaf stripping time four shoots per tree, 2 on the north side and 2 on the south side, were randomly selected and stripped of leaves down to the twelfth leaf from the shoot tip. Half of the shoots also had the shoot tip removed at the time the leaves were removed. The apical bud and between 2 to 3 additional buds close to the apical bud were removed. On each orchard at each time there was a total of 30 shoots with intact shoot tips and 30 shoots with the shoot tip removed that were stripped of their leaves. The shoots selected were of similar length and thickness and were between 1.5 to 2.5m height. The shoots were between 150 to 200mm length on the north side of the tree and 50 to 100 mm length on the south side of the tree and were about 10mm in diameter. The trees selected in Orchard 1 had a regular cropping history and were carrying a moderate crop (12-15 t/ha) and had a good fruit set in the spring of 2005. The trees in Orchard 2 were in an "off" year following a heavy crop (>25 t/ha) and had no fruit set in the spring of 2005. The trees in Orchard 3 had not carried a crop for two years previously and failed to set a crop in the spring of 2005. The trees in each of these orchards set a heavy crop (>25 t/ha) in the spring of 2006.

The shoots from each treatment were assessed for the type of growth produced by apical and axillary buds (floral buds, vegetative shoots and inactive buds). The number of dead or the amount of shoot die back, if present, was also recorded. The length of any shoot produced was measured and recorded and considered evidence that the bud was not irreversibly committed to flowering. The shoots were assessed on 31/7/2006 on Orchard 1 and on the 4/8/2006 for Orchards 2 and 3, about 5-6 weeks before flower bud break in September. Buds were considered to be floral if they had a shape that conformed to at least stage 5 buds as described by Salazar-Garcia *et al.* (1998).

The data from the type of growth produced from treated shoots was expressed as percentages and were transformed by square root or arcsine of the square root before One-Way Analysis of Variance using MINITAB version 13.31.

RESULTS

Apical buds

The type of growth that developed from the apical buds was affected by the date of treatment on shoots (Table 1). The proportion of floral shoots, although present at most treatment dates, was not significantly different between defoliation dates until April (Table 1). Vegetative growth decreased with each treatment date and had become low (<7%) by the mid-March treatment date. The proportion of inactive buds varied with each treatment date and was lowest when the proportion of floral or vegetative shoots was greatest (Table 1). A small number of shot tips died back after the defoliation treatment (Table 1). The number of

Table 1. Type of growth by apical buds from spring initiated shoot flush of 'Hass' avocado trees where the shoot was defoliated at different dates and evaluated at 31 July 2006 to 4 August 2006.

	Type of growth (%)			
Defoliation date	**Floral**	**Vegetative**	**Inactive**	**Dead**
11/1/2006	4.5a[1]	54.6a	36.4a	4.5
23/1-31/1/2006	6.7a	44.5a	40.0a	8.8
9/2-13/2/2006	10.2a	22.7b	59.1bc	8.0
2/3-3/3/2006	10.0a	17.8b	66.6c	5.6
9/3-10/3/2006	12.2a	4.4c	75.6c	7.8
21/3-29/3/2006	15.5a	6.7bc	71.1c	6.7
19/4-27/4/2006	40.0b	3.3c	52.3ab	4.4

[1]*Means followed by the same letter within a column are not different according to a One-Way Analysis of Variance using a Tukey's family error rate of 5%.*

dead shoots was not significantly different between treatment dates. Based on the response of spring flush shoots to the defoliation treatments applied the mid-April treatments were identified as the time when most of the apical buds (shoot tips) became irreversibly committed to flowering.

Shoot tip removal

The proportion of floral shoots was affected by the removal of the shoot tip where the percentage of axillary buds on tipped shoots that developed into flower buds remained low at all defoliation treatment times (Table 2). By the April treatment

Table 2. Type of growth by axillary buds from spring initiated shoot flush of 'Hass' avocado trees where the apical bud was removed and defoliated to the twelfth leaf from the shoot tip at different dates and evaluated at 31 July 2006 to 4 August 2006.

		Type of growth (%)							
Defoliation Date	**Bud**	**Floral**		**Vegetative**		**Inactive**		**Dead**	
2006		**I[1]**	**T[2]**	**I**	**T**	**I**	**T**	**I**	**T**
11 Jan[3]	1	4.6		54.5a[4]		36.4a		4.5	
	2	1.1	1.2	22.6b	54.5a	71.6b	26.0a	4.7	18.3a
	3	0.0	1.2	11.5b	43.0ab	88.5bc	44.5a	0.0	11.3ab
	4	0.0	2.3	9.0b	29.5bc	90.0c	63.5b	1.0	4.7b
	5	1.1	0.0	6.9b	13.5c	90.9c	84.0c	1.1	2.5c
23-31 Jan	1	6.7a		44.5a		40.0a		8.8ab	
	2	2.2ab	0.0	31.1a	27.8a	53.4a	60.0a	13.3b	12.2a
	3	1.1ab	4.4	11.1b	33.3a	87.8b	61.1a	0.0a	1.2b
	4	0.0b	2.2	3.3b	16.7b	96.7b	81.1b	0.0a	0.0b
	5	0.0b	0.0	3.3b	10.0b	96.7b	90.0b	0.0a	0.0b
9-13 Feb	1	10.2a		22.7a		59.1a		8.0a	
	2	1.1b	9.1a	3.4b	8.0	89.8b	76.1a	5.7ab	6.8a
	3	0.0b	3.3ab	1.1b	10.0	98.9b	86.7ab	0.0b	0.0b
	4	0.0b	1.1b	1.1b	6.7	98.9b	92.2b	0.0b	0.0b
	5	0.0b	1.1b	0.0b	2.2	100.0b	96.7b	0.0b	0.0b
2-3 Mar	1	10.0a		17.8a		66.7a		5.5a	
	2	3.3ab	5.6	0.0b	14.5a	96.7b	76.7a	0.0b	3.2
	3	4.4ab	7.8	0.0b	5.5ab	94.5b	86.7ab	1.1ab	0.0
	4	3.3ab	1.1	0.0b	3.3b	96.7b	95.6bc	0.0b	0.0
	5	0.0b	1.1	0.0b	0.0b	100.0b	98.9c	0.0b	0.0
9-10 Mar	1	12.2a		4.4		75.6a		7.8a	
	2	1.1b	5.6	1.1	5.6a	91.1b	81.1a	6.7ab	7.7a
	3	2.2b	6.7	2.2	2.2ab	95.6b	90.0ab	0.0b	1.1b
	4	2.2b	5.6	0.0	0.0b	97.8b	94.4b	0.0b	0.0b
	5	0.0b	6.7	1.1	0.0b	98.9b	93.3b	0.0b	0.0b
21-29 Mar	1	15.6a		6.7a		71.1a		6.6a	
	2	3.3b	5.6	0.0b	2.2	91.2b	87.8a	5.5ab	4.4a
	3	3.3b	1.1	0.0b	2.2	96.7b	96.7b	0.0b	0.0b
	4	2.2b	2.2	0.0b	0.0	97.8b	97.8b	0.0b	0.0b
	5	2.2b	1.1	0.0b	0.0	97.8b	98.9b	0.0b	0.0b
19-27 Apr	1	40.0a		3.3a		52.2a		4.5	
	2	15.6b	6.7	0.0b	1.1	81.1b	90.0	3.3	2.2
	3	13.3b	6.7	0.0b	0.0	86.7b	93.3	0.0	0.0
	4	12.2b	4.4	0.0b	0.0	87.8b	95.6	0.0	0.0
	5	7.8b	4.4	0.0b	0.0	92.2b	95.6	0.0	0.0

[1]Intact shoot; [2]Shoot tip removed; [3]Jan = January, Feb = February, Mar = March, Apr = April; [4]Means followed by the same letter within a column are not different according to a One-Way Analysis of Variance using a Tukey's family error rate of 5%.

date the axillary buds on intact shoots had a significant proportion of floral shoots developed compared to the tipped shoots where floral bud development was not significantly different to previous treatment dates (Table 2). The proportion of vegetative shoots for tipped shoots on the 11 January treatment was greater in general than for the intact shoots. The apical buds developed a similar percentage of vegetative shoots to the second bud of tipped shoots while the third bud of tipped shoots developed a greater percentage of vegetative shoots than bud three on intact shoots (Table 2). There was a similar pattern of vegetative shoot development with bud number on the 23 to 31 January treatments. By February and March the tipped shoots while having more buds, in general, develop into shoots further down the stem did not produce as many vegetative shoots as the intact shoots from the apical bud (Table 2).

Shoots that were tipped died back by one to three buds more frequently than the intact shoots when defoliated in January (Table 2). Removing the shoot tip from February onwards did not increase the number of dead shoots over that of intact shoots.

Differences between orchards

The date of treatment and orchard where the treatment was applied affected the type of growth from the apical buds. There was considerable variability between orchards in the timing of shoot development following the defoliation treatment. Some floral buds were present at the earliest treatment dates on trees in Orchards 2 and 3 but were not present on trees in Orchard 1 (Table 3). There was a greater proportion of floral shoots in Orchard 3 than Orchards 2 and 1. The timing of floral shoots and cessation of vegetative shoots in response to defoliation varied between orchards. There was a significant decrease in vegetative shoots in the March treatments on Orchards 1 and 2 and in the February treatment on Orchard 3 (Table 3). This decrease was before there was a significant increase in floral shoots in April. Orchard 1 had not developed significant amounts of floral shoots by April whereas Orchard 3 had about two-thirds of apical buds as floral shoots at the same time. This was also matched by the timing of the decrease in vegetative shoots generally occurring earliest in Orchard 3 and the latest in Orchard 1 (Table 3).

Table 3. Type of growth by apical buds from spring initiated shoot flush of 'Hass' avocado trees defoliated at different dates and evaluated at 31 July 2006 to 4 August 2006.

Orchard 1		**Type of growth (%)**		
Date of defoliation	**Floral**	**Vegetative**	**Inactive**	**Dead**
11/1/2006	0.0	76.7a[1]	16.7a	6.6
23/1/2006	0.0	60.0a	36.7ab	3.3
9/2/2006	3.3	50.0a	43.4ab	3.3
2/3/2006	3.3	46.7ac	46.7ab	3.3
9/3/2006	13.3	13.3b	63.4b	10.0
21/3/2006	3.3	16.7bc	66.7b	13.3
27/4/2006	13.3	3.3b	73.4b	10.0
Orchard 2	**Type of growth (%)**			
Date of defoliation	**Floral**	**Vegetative**	**Inactive**	**Dead**
11/1/2006	10.0a	50.0a	36.7a	3.3
31/1/2006	13.4a	43.3a	43.3a	0.0
13/2/2006	3.6a	7.1b	89.3bc	0.0
3/3/2006	16.7a	6.7b	73.3b	3.3
10/3/2006	0.0a	0.0b	93.3c	6.7
22/3/2006	13.3a	3.3b	83.4bc	0.0
19/4/2006	40.0b	3.3b	56.7a	0.0
Orchard 3		**Type of growth (%)**		
Date of defoliation	**Floral**	**Vegetative**	**Inactive**	**Dead**
11/1/2006	3.6a	35.7a	57.1ab	3.6
26/1/2006	6.7a	30.0ab	40.0ab	23.3
10/2/2006	24.0a	10.0bc	46.0ab	20.0
3/3/2006	10.0a	0.0c	80.0b	10.0
10/3/2006	23.3a	0.0c	70.0b	6.7
29/3/2006	30.0a	0.0c	63.3ab	6.7
26/4/2006	66.7b	3.3c	26.7a	3.3

[1]*Means followed by the same letter within a column are not different according to a One-Way Analysis of Variance using a Tukey's family error rate of 5%.*

DISCUSSION

Spring initiated vegetative shoots on Hass avocado trees in the Western Bay of Plenty were irreversibly committed to flowering by mid-April. This observation is in agreement with the timing of irreversible commitment to flowering in California and Mexico (Salazar-Garcia *et al.*, 1998; Salazar-Garcia *et al.*, 1999). This study also confirms that apical buds do not need a clear period of dormancy before initiation of reproductive growth (Salazar-Garcia *et al.*, 1998). The presence of floral shoots at low levels at all treatment dates may indicate that the transition from vegetative to reproductive shoots is occurring earlier in January to March. The identification of floral shoots was at a relatively late stage in development, Stage 5, rather than after full commitment to reproductive growth had occurred at Stage 3 (Salazar-Garcia *et al.,* 1998). Stage 3 floral shoots have an appearance that is similar to vegetative shoots that can only be determined by microscopic examination. We speculate that based on previous research (Salazar-Garcia *et al.*, 1998) and the large decrease in the proportion of vegetative shoots that development in response to treatment that the transition to Stage 3 had occurred by mid-March. Floral initiation in the Western Bay of Plenty is therefore likely to be occurring in March earlier than previously thought in April/May (Cutting and Dixon, 2004).

Using the above criteria, the initiation of floral shoots to Stage 3 was different on trees in each orchard. In Orchard 1 floral shoot initiation occurred in April, Orchard 2 early February and Orchard 3 early March (Table 3). The different time for floral initiation between orchards may be related to the cropping history where the earliest floral initiation was on Orchards 2 and 3 that had not set fruit in the prior year. This finding contrasts with the conclusion that crop load did not affect the production of floral shoots (Salazar-Garcia *et al.*, 2006).Therefore, we consider that factors associated with individual orchards have an influence on the initiation of floral shoots. Should the timing of floral initiation differ between orchards then the same orchard management activity designed to influence floral initiation at the same time over a number of orchards will not always work as expected. Care, therefore, needs to be taken to identify, for each orchard, the time of floral initiation so that the timing of management activities can be adjusted to be most effective.

A key factor involved in the timing of flower initiation is believed to be exposure to cool temperatures where the development of inflorescences, in California, was correlated with night temperatures of 15°C (Salazar-Garcia *et al.*, 1998). Temperature has been used to induce or inhibit floral initiation (Salazar-Garcia *et al.*, 1999). Four weeks of temperatures below 15°C and short day length promoted flower initiation in Fuerte and Hass avocado trees (Buttrose and Alexander, 1978). Temperatures above 20°C inhibit flower initiation (Buttrose and Alexander, 1978). Hass avocado trees under a day temperature of 15-18°C and night temperature of 10-13°C for four or eight weeks induced about the same number of flowers while trees under a day temperature of 24°C and night temperature of 19°C did not flower (Nevin and Lovatt, 1989). The number of chilling days where the minimum temperature was below 19°C required for apical buds to become irreversibly committed to flowering, in Mexico, was between 24 to 31 days (Salazar-Garcia *et al.*, 2006). Given that the initiation of floral shoots on Hass avocado trees in New Zealand occurs at a similar time to those in California and Mexico it is reasonable to expect that a similar duration of exposure to cool temperatures as in Mexico, would also predict the timing of floral shoot initiation. Monitoring temperatures over the course of a year could be used to identify when the vegetative shoots were transitioning from vegetative to floral shoots.

The results of this study show that about half of the flowering and vegetative growth on an avocado develops from apical buds. The two to three axillary buds closest to the shoot tip contribute about 40% of the flowering and vegetative shoots. There was a clear dominance by the apical bud in development of shoots over axillary buds and that the further away from the shoot tip the fewer buds that developed into flowers or shoots. Removing

the shoot tip overcame some of the dominance of the shoot tip on adjacent axillary buds where they developed into vegetative shoots. The first bud below the shoot tip developed about as many vegetative shoots as intact apical buds. Buds further down a shoot with the apical bud removed produced more vegetative shoots than the equivalent buds on shoots without the tip removed. The promotion of additional vegetative shoot development in tipped shoots was limited to January and February after which tipped shoots had about the same vegetative shoots as intact shoots. Interestingly, the tipped shoots developed low numbers of floral shoots and never developed floral shoots to the same level as intact shoots. Removing the shoot tip appeared to have inhibited the development of floral shoots. This response may be useful to avocado growers when a reduction in the number of flowers is desired and vegetative growth needs to be promoted. Light pruning of shoot tips in April may potentially be useful on the spring flush that grew in an "on" cropping year to promote additional shoot growth.

It is unknown what the influence of the apical bud has on the development of floral shoots and why it may be specific to a particular time of year. Apical buds are known on other plants to influence growth and development through changes in hormone levels (Taiz and Zeiger, 1998). Recent research in California has suggested that floral intensity is influenced by fruit drop, carbohydrate concentrations and plant hormone ratios in buds (Lovatt, 2007 California Avocado Commission Mid-Year report). This study would suggest there may be inhibitory or promotional factors associated with apical buds that could be advancing or delaying flowering and explain the orchard to orchard differences in the timing of transition to floral shoots.

CONCLUSIONS

Apical buds on shoot tips are usually irreversibly committed to flowering by mid April and may be in transition to flowers during February and March. The timing of floral initiation varies from orchard to orchard by as much as six weeks. Therefore orchard management activities designed to assist floral shoot development need to be applied at a time specific for each orchard. Flowers develop mostly on shoot tips which when removed promote new vegetative shoots to grow on other buds but only before the inactive buds are in transition from vegetative shoots to floral shoots in February.

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ACKNOWLEDGEMENTS

The AIC wishes to thank Jack and Bette Crozier, Ron and Chris Bailey and Mitsuo and Mayumi Nagae for the use of their trees.