Management and Physiology

Developing Field Strategies to Correct Alternate Bearing

Carol Lovatt UC Riverside

Jess Ruiz - Irvine Company

Project overview

In alternate bearing 'Hass' avocado orchards, yield is reduced below the potential of the orchard and grower income is significantly reduced during off-crop years. The goal of this research is to increase grower profitability by clarifying whether treatments that increase summer and/or fall shoot growth can be used to increase floral intensity the following spring and, thus, yield by establishing which buds (apical or axillary), if any, on which shoot flush (spring, summer or fall) of on-crop trees remain floral and for how long. This information is essential to learn whether future PGR treatments can be designed to increase return bloom or whether only fruit thinning strategies will work and how they should be employed, i.e., which shoots should have fruit removed and the deadline before which fruit thinning must occur.

Spring flush branches with and without fruit on on-crop trees were tagged. On-crop refers to trees that had a heavy bloom in the current spring and set a heavy on crop of fruit that develop during the current summer and fall through next spring to be harvested later the next year. The following treatments were applied to sets of 20 trees each, five each apical and axillary buds were collected from spring, summer and fall flushes from 5 of 15 trees in a rotating pattern each month from July to February to have enough buds for the 8 months; the remaining five trees with no buds removed were evaluated for the number of summer and fall shoots they produced and for the contribution of each flush to return bloom in spring: (1) all young developing fruit of the on crop removed in July, (2) trees with setting fruit removed in July but with the mature fruit of a heavy crop from the previous year left through October, (3) trees with mature fruit removed in July but setting on-crop fruit left through October, (4) control trees setting a heavy on-crop and (5) control trees setting a light off-crop. Treatments were arranged in randomized complete block design.

Results

Bloom was evaluated during the first two weeks of April. The results are summarized in Tables 1 through 4. The bloom data presented in Table 1 confirm the lack of importance of the spring shoots to return bloom the following year. The data also reveal the limited contribution of spring flush shoots to the number of vegetative shoots and inactive buds during bloom the following spring.

By comparing Table 2 with Table 3, it is clear that summer flush shoots are the primary contributor of inflorescences during the following spring bloom. Spring bloom 2008 had an uncharacteristically high number of determinate inflorescences produced by the summer shoots. For off-crop control trees and trees with no fruit and on-crop trees with the crop removed by August or September, the number of determinate inflorescences was greater than the number of indeterminate inflorescences. This was to

our advantage because it provided additional information about apical versus axillary buds and the importance of spring, summer and fall shoots to return bloom. Removing fruit from on-crop trees progressively later than September reduced the number of determinate floral shoots and total inflorescences with a concomitant increase in inactive buds and vegetative shoots. It is clear that the highly productive determinate inflorescences develop predominantly from axillary buds on summer flush shoots.

The entry labeled "mature fruit only" represents trees used to determine the effect of the mature fruit on return bloom. For these trees the setting 2007 off crop was removed but the mature 2006 on crop was left on the trees through October to mimic a late harvested on-crop orchard. The mature fruit significantly reduced the number of inflorescences that developed the following spring on summer shoots (Table 2), but not fall shoots (Table 3). Thus, carrying mature fruit past July significantly reduces the floral intensity of the return bloom and, in particular, reduces the number of highly productive determinate inflorescences.

The data for fall shoots presented in Table 3 reveals several interesting facts: (*i*) fall shoots contribute significantly fewer indeterminate and determinate inflorescences and, thus, fewer total inflorescences to return bloom than summer shoots; (*ii*) mature fruit, which were removed in October, reduced the number of inflorescences produced by summer flush shoots but did not reduce the number of inflorescences contributed by fall shoots to return bloom; and (*iii*) removal of young developing (current crop) fruit after October reduced flowering and increased the number of vegetative shoots produced by fall shoots during the next spring bloom, with only a slight increase in the number of inactive buds on fall shoots during spring bloom compared to on-cop trees with no fruit removed.

Thus, axillary buds on the summer flush shoots and apical and axillary buds on the fall flush shoots are the buds most influenced by the presence of young or mature fruit (crop load). When fruit are not removed, they contribute significantly to the number of vegetative shoots and inactive buds during spring bloom the following year.

Summary of the mechanisms and underlying physiology by which the young developing oncrop influences flowering and yield the next year

1. The developing on crop reduces floral shoot development, increases vegetative shoot development and the number of inactive buds.

2. The contribution of shoot flushes to return bloom is summer > fall > spring.

3. Early fruit removal increases floral shoot development, but fruit must be removed before mid-September for the number of determinate inflorescences to increase; fruit removal in October and after reduces floral shoot number and increases vegetative shoot number. Harvest your mature crop before mid-September, if possible harvest earlier. Fruit thinning by size picking will help increase return bloom.

4. Mature fruit have only a slightly stronger effect than young fruit on spring and summer flush shoots; young fruit have a stronger effect on fall flush shoots

5. Axillary buds on summer shoots are floral, the on crop inhibits the development of summer shoots and greatly reduces return bloom; axillary buds on fall shoots are predominantly vegetative and contribute vegetative shoots in spring.

6. The on crop inhibits spring bud break.

7. Fruit export hormones that inhibit the growth of buds producing the summer and fall shoots by correlative inhibition (bud auxin > cytokinin) and that also inhibit bud break in spring, (bud abscisic acid

> cytokinin) with inhibition greatest in axillary buds of summer flush shoots > axillary buds of fall flush shoots.

Take home message

Summer flush shoots are the key to having a good return bloom and a good return crop when the trees have set and are developing a heavy on crop. Both setting and mature fruit inhibit not only the development of these shoots to reduce the number of sites on which to bear inflorescences the next spring, but are also inhibit bud break of axillary buds in spring on the reduced number of summer and fall shoots that do develop, further reducing the floral intensity of the return bloom. Carrying mature fruit past July is significantly reduces return bloom and, in particular, the number of highly productive determinate inflorescences. The summer vegetative shoot flush must be stimulated to grow to increase return bloom in the spring following the setting of a heavy on crop to increase return yield and prevent an off-crop. Promoting fall shoot development will do little to increase floral intensity the spring following an on-crop year. In addition to the need to increase the number of summer flush shoots to increase return bloom and yield, spring bud break needs to be increased. Two PGR treatments will be required during the on-crop year to overcome these effects of the on-crop - a summer (July-August) auxin transport inhibitor and/or cytokinin or GA_3 spray and a spring cytokinin or GA_3 spray. Testing the efficacy these treatments to overcome alternate bearing is the final step in the research.

Benefits of the research to the industry (includes achievements and future prospects)

The results of this research identified the mechanism and underlying physiology by which the current crop influences floral intensity and, hence, yield the following year. The results dictate adoption of management strategies (fruit removal, early harvest, pruning, PGR treatments) that promote summer shoot growth and, thus, increase floral shoot bud break in spring. Elucidation of the hormone physiology underlying the inhibitory effects of the fruit on bud break in summer and spring enables us to design PGR strategies to overcome the inhibitory effect of the fruit produced hormones. Thus, the final step in our study of alternate bearing is demonstrating the efficacy of PGR treatments to increase summer shoot growth and spring bud break in order to increase floral intensity and yield following an on-crop year. We already have preliminary results, obtained though our research project "PGR Strategies to Increase Yield of the 'Hass' avocado", that GA₃ (100 mg/L) applied in July and a cytokinin with or without GA₃ applied in February increase bud break of summer (sylleptic) vegetative shoots and spring floral shoots, respectively. With adequate funding, we can complete the final step in four years and provide growers with a treatment(s) to even out alternate bearing. Alternate bearing is a recurring problem resulting from adverse climatic conditions, e.g. freeze, high temperatures, etc., a strategy that can be used in such cases to mitigate alternate bearing will contribute significantly to grower profitability.

To enhance my ability to conduct research on behalf of the avocado growers of California, I wrote and submitted, with an Israeli colleague, a BARD grant in September 2008 and I wrote and submitted an IR-4 proposal in October 2008 to continue research with GA₃. To date I personally have obtained \$257,218 in funding from the CDFA-FREP program to conduct research optimizing fertilization of the 'Hass' avocado and an additional \$245,000 from the CDFA-FREP in collaboration with Dr. Richard Rosecrance, CSU-Chico, and Dr. Ben Faber, UCCE-Ventura and Santa Barbara, for the avocado tree dissection research to determine up-take and partitioning of soil nutrients in response to crop load and for the development of a demand driven web-based fertilization program. Further, Dr. Rosecrance was awarded partial matching funds from CSU for the two collaborative projects. Thus, I have played a key role in brining over half a million dollars from outside CAC to avocado research for improving fertilization and, hence, productivity and grower profitability.

_		Inflorescences	Vegetative		
_	Total	Indeterminate	Determinate	shoots	Inactive buds
		Aı	/erage no./8 sho	ots per tree	
No Fruit	1.40	0.00	1.40	0.20	2.20
Off Crop Control	0.00	0.00	0.00	0.00	3.40
Mature Fruit					
Only	0.00	0.00	0.00	0.00	2.80
ON Crop					
Control	0.20	0.20	0.00	0.00	0.60
Fruit Removed					
August	0.00	0.00	0.00	0.40	1.80
September	0.00	0.00	0.00	0.00	1.40
October	0.20	0.20	0.00	0.00	1.20
November	0.20	0.20	0.00	0.20	2.80
December	0.00	0.00	0.00	0.00	1.60
<i>P</i> -value	0.5267	0.6211	0.4551	0.6137	0.2852

Table 1. Effect of the crop set in 2007 on the contribution of spring 2007 shoots to bloom 2008.

 P-Value
 0.5267
 0.6211
 0.4551
 0.6137
 0.2852

 ²Means followed by different letters within a vertical column are significantly different by Fisher's Protected LSD test, P=0.05.

Table 2. Effect of the crop set in 2007 on the contribution of summer 2007 shoots to bloom 2008.

		Inflorescences	Vegetative		
	Total	Indeterminate	Determinate	shoots	Inactive buds
		Aι	/erage no./8 sho	ots per tree	
No Fruit	11.60 abc	4.60	7.00 abc	1.20 c	25.60 bc
Off Crop Control	18.00 a	5.00	13.00 a	0.20 c	24.40 c
Mature Fruit					
Only	5.20 c	3.00	2.20 bc	3.20 c	26.80 bc
ON Crop					
Control	8.80 abc	4.00	4.80 abc	5.00 bc	36.20 ab
Fruit Removed					
August	19.00 a	6.60	12.40 a	0.80 c	21.60 c
September	16.20 ab	6.20	10.00 ab	1.40 c	25.00 c
October	8.60 abc	7.00	1.60 bc	2.20 c	30.20 abc
November	6.40 bc	5.20	1.20 bc	9.00 ab	31.40 abc
December	2.40 c	2.40	0.00 c	11.60 a	38.00 a
<i>P</i> -value	0.0248	0.3344	0.0409	0.0016	0.0494

²Means followed by different letters within a vertical column are significantly different by Fisher's Protected LSD test, P=0.05.

		Inflorescences	6	Vegetative	
	Total	Indeterminate	Determinate	shoots	Inactive buds
		Av	erage no./8 sho	ots per tree	
No Fruit	5.80 a	3.40 ab	2.40	2.60	12.20 ab
Off Crop Control	5.60 ab	3.40 ab	2.20	2.20	12.40 a
Mature Fruit					
Only	4.40 abc	4.00 a	0.40	3.40	11.00 abc
ON Crop					
Control	1.40 cd	0.80 c	0.60	0.40	2.60 d
Fruit Removed					
August	3.20 abcd	2.00 abc	1.20	0.00	3.00 d
September	4.20 abc	2.00 abc	2.20	0.20	3.40 cd
October	1.40 cd	1.20 bc	0.20	1.40	5.40 abcd
November	1.80 bcd	1.80 abc	0.00	3.20	4.00 cd
December	0.00 d	0.00 c	0.00	2.60	4.60 bcd
P-value	0.0377	0.0560	0.2942	0.7430	0.0403

Table 3. Effect of the crop set in 2007 on the contribution of fall 2007 shoots to bloom 2008.

^zMeans followed by different letters within a vertical column are significantly different by Fisher's Protected LSD test, *P*=0.05.

Table 4. Effect of the crop set in 2007 on the contribution of spring, summer and fall (total) 2007 shoots on bloom 2008.

		Inflorescences	Vegetative		
_	Total	Indeterminate	Determinate	shoots	Inactive buds
		Av	/erage no./8 sho	ots per tree	
No Fruit	18.80 abc	8.00	10.80 abc	4.00 bc	40.00
Off Crop Control	23.60 a	8.40	15.20 a	2.40 c	40.20
Mature Fruit					
Only	9.60 bcd	7.00	2.60 bc	6.60 abc	40.60
ON Crop					
Control	10.40 bcd	5.00	5.40 abc	5.40 abc	39.40
Fruit Removed					
August	22.20 a	8.60	13.60 a	1.20 c	26.40
September	20.40 ab	9.40	11.00 ab	1.60 c	29.80
October	10.20 bcd	8.40	1.80 bc	3.60 bc	36.80
November	8.40 cd	7.20	1.20 bc	12.40 ab	38.20
December	2.40 d	2.40	0.00 c	14.20 a	44.20
P-value	0.0051	0.1097	0.0374	0.0528	0.2285

²Means followed by different letters within a vertical column are significantly different by Fisher's Protected LSD test, *P*=0.05.

UNIVERSITY OF CALIFORNIA, RIVERSIDE

Department of Botany and Plant Sciences

Alternate Bearing of the 'Hass' Avocado and the Role of Sylleptic and Proleptic Shoots

Carol J. Lovatt Department of Botany and Plant Sciences, University of California, Riverside, CA 92521-0124.

Introduction – In alternate bearing 'Hass' avocado orchards, yield and grower income are significantly reduced below the potential of the orchard during off-crop years. The goal of this research is (1) to determine the mechanism and underlying physiology by which young developing fruit influence floral intensity the following spring and (2) to use this knowledge to reduce the severity of alternate bearing and increase grower profitability. To achieve this goal we investigated the following mechanisms: (1) the on crop inhibits summer and fall shoot development (Aug.-Oct.), decreasing the number of nodes on which to bear flowers; (2) the on crop inhibits the transition of vegetative buds to reproductive buds, resulting in more vegetative shoots and fewer floral shoots (Aug.); and (3) the on crop inhibits spring bud break (Feb.-Mar.) and underlying physiology: (1) competition for carbohydrate, nitrogen and other nutrients; (2) fruit produce a growth-inhibiting hormone; and (3) fruit reduce the availability of a growth-promoting hormone.

Avocado trees produce two shoot types. Proleptic shoots develop from lateral buds that have gone through a dormant period and, thus, produce bud scale scars when they begin to grow in spring. Sylleptic shoots develop from lateral meristems that develop *de novo* on a primary shoot as it develops from spring through fall. Proleptic shoots have limited branching, whereas sylleptic shoots increase canopy complexity. Greater complexity means more sites on which to bear inflorescences and fruit. In prior research, foliar-applied 6-benzyladenine plus gibberellic acid₄₋₇ increased sylleptic shoots number (64% and 300% in two separate experiments), decreased proleptic shoot number (38% and 46%, respectively), and increased the proportion of sylleptic shoots from 16.67% to 50% of the canopy. The goal is to achieve increased syllepsis in a commercial 'Hass' orchard, concomitant increased yield, and reduced alternate bearing.

Alternate Bearing — Results from our alternate bearing research provide the following information about (1) the effect of the current year's (setting) young developing fruit on return bloom the following spring and (2) the additional effect of mature fruit from the previous year (Table 1). Refer to the poster entitled "Hass' Avocado Tree Phenology" to relate fruit development and fruit removal dates to stages of vegetative and reproductive development.

• A high number of young developing fruit (on-crop) inhibits floral shoot development the following spring, promotes vegetative shoot development and increases the number of inactive buds. That inactive buds are floral buds was confirmed by removing the fruit from on-crop trees. This increased floral shoot number and reduced the number of vegetative shoots and inactive buds. Note that shoots with and without fruit on on-crop trees behave similarly during return bloom, demonstrating the strong whole tree effect of fruit in contrast to an effect localized only to branches bearing fruit.

• The contribution of spring, summer and fall flush shoots to the number of floral shoots that develop during return bloom is summer > fall > spring. The importance of summer and fall flush shoots to return bloom was confirmed by removing these shoots from off-crop trees that would flower intensely the following spring. Trees with fall shoots removed produced a low inflorescence number and yield equal to the low return bloom and yield produced by trees carrying an on crop. Off-crop trees having both summer and fall shoots removed produced almost no inflorescences and only 0.5 kg fruit per tree the following year. The results provide strong evidence of the importance of summer and fall vegetative shoots to return bloom and yield.

• The earlier fruit are removed, the more significant the increase in the number of indeterminate, determinate and total inflorescences that develop the following spring. To increase total inflorescence number to that of off-crop trees and greater than that of on-crop trees, fruit must be removed before mid-September. Only fruit removal in August and September increases the number of determinate inflorescences is high when fruit removal is early (before Sept.) or fruit number (crop load) is extremely low. Fruit removal in October or later, progressively increases the number of vegetative shoots in the return bloom to a high value equaling on-crop trees.

• Mature fruit have a slightly stronger negative effect on the number of inflorescences produced by spring and summer flush shoots than younger developing fruit. In contrast, mature fruit have a less negative effect than young developing fruit on the number of inflorescences contributed by fall flush shoots to bloom the following spring. As a result the effect of mature and young developing fruit on the total number of inflorescences in the return bloom is similar.

Axillary (lateral) buds on summer flush shoots and apical buds on fall flush shoots are the most affected by the presence of fruit (crop load).

• Shoot apical buds, but not root apices, from off-crop and on-crop trees have the anticipated differences in available starch by December. Fruit removal monthly from July through December increases starch concentrations in shoot apical buds, but not root apices, equal to off-crop trees and greater than on-crop trees. There were no differences in starch concentrations in shoot apical buds from on- or off-crop trees from July through September when crop load has its greatest effect on summer and fall shoot growth.

• The positive effect of an August application of TIBA, an IAA (auxin) transport inhibitor, in stimulating summer and fall shoot growth confirms that carbohydrate is not limiting to summer or fall shoot growth and not the physiological basis for inhibition of summer and fall shoot growth by fruit. The positive effect of TIBA is consistent with inhibition of summer and fall shoot growth by correlative inhibition – a high IAA to cytokinin ratio. Fruit removal increases the cytokinin concentration of the buds, but had no affect on IAA. Whereas we could increase the number of summer and fall shoots with TIBA, they only produced vegetative or inactive buds in spring. The presence of the crop past November significantly reduces floral shoot development and increases the number of vegetative shoots and inactive buds on summer shoots. Early results suggest that floral buds are inhibited in spring by a high ABA to cytokinin ratio. Progressively later fruit removal from February through April reduces floral shoot number, but not vegetative shoot number.

•Two PGR treatments will be required during the on-crop year and every year if mature fruit are not harvested before July-August to mitigate alternate bearing: in summer - TIBA and/or cytokinin or GA₃ and in spring - cytokinin or GA₃. Optimal application rates and times need to be determined.

	All Shoots				Spring shoots			Summer shoots			Fall shoots		
	Inflorescences	Vegetative	Inactive buds	Inflorescences	Vegetative	Inactive buds	Inflorescences	Vegetative	Inactive buds	Inflorescences	Vegetative	Inactive buds	
						Average no.	shoots/tree					·	
No Fruit	18.80 abc	4.00 bc	40.00	1.40	0.20	2.20	11.60 abc	1.20 c	25.60 bc	5.80 a	2.60	12.20 ab	
Off Crop Control	23.60 a	2.40 c	40.20	0.00	0.00	3.40	18.00 a	0.20 c	24.40 c	5.60 ab	2.20	12.40 a	
Mature Fruit Only	9.60 bcd	6.60 abc	40.60	0.00	0.00	2.80	5.20 c	3.20 c	26.80 bc	4.40 abc	3.40	11.00 abc	
ON Crop Control	10.40 bcd	5.40 abc	39.40	0.20	0.00	0.60	8.80 abc	5.00 bc	36.20 ab	1.40 cd	0.40	2.60 d	
ON Crop Removed													
August	22.20 a	1.20 c	26.40	0.00	0.40	1.80	19.00 a	0.80 c	21.60 c	3.20 abcd	0.00	3.00 d	
September	20.40 ab	1.60 c	29.80	0.00	0.00	1.40	16.20 ab	1.40 c	25.00 c	4.20 abc	0.20	3.40 cd	
October	10.20 bcd	3.60 bc	36.80	0.20	0.00	1.20	8.60 abc	2.20 c	30.20 abc	1.40 cd	1.40	5.40 abco	
November	8.40 cd	12.40 ab	38.20	0.20	0.20	2.80	6.40 bc	9.00 ab	31.40 abc	1.80 bcd	3.20	4.00 cd	
December	2.40 d	14.20 a	44.20	0.00	0.00	1.60	2.40 c	11.60 a	38.00 a	0.00 d	2.60	4.60 bcd	
P-value	0.0051	0.0528	0.2285	0.5267	0.6137	0.2852	0.0248	0.0016	0.0494	0.0377	0.7430	0.0403	

Sylleptic and Proleptic Shoots - The

results of this research confirmed that 'Hass' avocado trees in California are strongly proleptic. Repeated measure analysis for the 3 years of research demonstrated that foliar-application of GA₃ (100 mg/L) in July consistently increased summer and fall sylleptic shoot growth (Data not shown). In spring following the on-crop years, GA₃ increased the number of vegetative shoots borne on sylleptic shoots produced by the summer flush, resulting in the off-crop. In spring following the off-crop years, GA₃ applied in July increased the number of inflorescences (predominantly determinate) borne on proleptic shoots produced by the summer flush underwent dormancy) resulting in the on-crop (Table 2). The effect of this increased complexity on yield and alternate bearing will be determined with the harvests of 2007 and 2008.

Treatment (mg/L)	Proleptic shoots				Sylleptic shoot				All shoots			
	Spring	Summer	Fall	Total	Spring	Summer	Fall	Total	Spring	Summer	Fall	Tota
	No.of Inflorescences/four shoots											
July application												
GA ₃ (100)	0.00	15.25 a	1.50	16.75	0.00	0.00	0.00	0.00	0.00	15.25 a	1.50 bc	16.75
Туру (50)	1.75	3.00 b	3.25	8.00	0.00	0.50	0.00	0.50	1.75	3.50 b	3.25 ab	8.50
Туру (250)	0.33	3.78 b	2.11	6.22	0.00	0.11	0.22	0.33	0.33	3.89 b	2.33 abc	6.56
January application												
GA ₃ (100)	0.88	4.13 b	1.63	6.63	0.00	0.25	0.50	0.75	0.88	4.38 b	2.13 abc	7.38
Туру (50)	0.00	7.50 b	0.50	8.00	0.00	0.17	0.17	0.33	0.00	7.67 b	0.67 c	8.33
Control	0.00	3.83 b	3.17	7.00	0.00	0.00	0.83	0.83	0.00	3.83 b	4.00 a	7.83
P-value	0.4810	0.0040	0.1817	0.1158	-	0.7840	0.5207	0.9365	0.4810	0.0068	0.0689	0.172

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