

## **Eliminating Alternate Bearing of the 'Hass' Avocado**

### **Continuing Project: Year 4 of 4**

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### **Benefit to the Industry**

This research addresses the objective of the California avocado industry to develop and implement research programs that lead to increased grower profitability.

Production data reported by R. Brokaw (Brokaw Nursery Inc, 2002) and from the California Avocado Commission website clearly depict 2- to 3-year on-off cycles for industry production over the last 14 years. Moreover, yield data from our numerous research orchards clearly demonstrate that alternate bearing is a problem to a significant number of growers. The alternate bearing index ( $ABI = \text{year 1 yield} - \text{year 2 yield} \div \text{year 1 yield} + \text{year 2 yield}$ ) for California avocado orchards ranges from 0.57 to 0.92. Thus, every other year, grower income is significantly reduced below the orchard's potential. Lower yields over the past years of 5,700 lbs./acre (Arpaia, 1998) have reduced the ABI, but reduced yields are not an acceptable solution to alternate bearing. Alternate bearing is initiated by climatic conditions (freeze damage, high temperatures during fruit set) that result in the loss of flowers or fruit and an off-crop year. This is typically followed by an on-crop year, unless additional time is required for the trees to recover. Conversely, climatic conditions that are optimal for flowering and fruit set such that thinning fails to take place result in an on-crop that is followed by an off-crop. Holding fruit to increase fruit dry matter and oil content significantly increases the alternate bearing index (Whiley, 1994). Once initiated, alternate bearing becomes entrained by endogenous factors within the tree. Salazar-Garcia et al. (1998) demonstrated that avocado trees carrying a heavy on-year crop produce vegetative shoots at the expense of floral shoots (inflorescences). Conversely, trees carrying a light off-year crop produce floral shoots at the expense of vegetative shoots. The reciprocity between floral vs. vegetative shoot development for on-crop vs. off-crop trees is a clear indication that endogenous PGRs are playing a more important role in alternate bearing in the 'Hass' avocado than carbohydrate availability which would have resulted in a reduction in both vegetative and floral shoot development when trees were carrying a heavy on-crop vs. a light off-year crop. What remains to be determined is (1) whether reduced flowering in spring for on-crop trees is due to inhibition of vegetative shoot production and thus a lack of shoots to bear the inflorescences in the spring or (2) to simple inhibition of inflorescence development on an adequate number of vegetative branches and (3) the PGR(s) responsible for the inhibition of vegetative shoot growth or inflorescence development, as the case proves to be. Preliminary results suggested that it is the inhibition of vegetative shoot growth in summer-fall when trees are carrying a heavy on-crop that results in reduced flowering the following spring (Paz-Vega, 1997). Supplying a double dose of N in mid-April (anthesis, fruit set and initiation of the spring vegetative flush) significantly reduced alternate bearing for the 4 years of the study presumably by increasing vegetative shoot growth (Lovatt, 2001). However, export of compounds from the

developing fruit that inhibit the transition of vegetative shoot apices to floral meristems can not be ruled out (Paz-Vega, 1997). The goals of our research were to define the mechanism by which alternate bearing becomes entrained in the 'Hass' avocado, identify the physiology underlying the mechanism and devise and test strategies to eliminate alternate bearing.

### **Objectives**

The specific objectives of our research were: (1) to determine the mechanism by which the heavy on-crop reduces flowering the next spring, resulting in an off-crop; (2) to determine whether fruit export an inhibitory hormone during a period related to the reduction in return bloom identified by the results of objective 1; (3) to determine if the heavy on-crop (*a*) results in the accumulation in the buds of an inhibitory compound (e.g., ABA or IAA) exported from the fruit (and/or loss in cytokinins or other growth promoting hormone in the buds) and/or (*b*) reduces allocation of carbohydrates, N or other nutrient resources to buds and shoots proximal to developing fruit; (4) to determine if the heavy on-crop reduces allocation of carbohydrates, N or other resources causing a loss in root-produced hormones, particularly cytokinins, that contributes to reduced floral intensity the next spring; and (5) to develop a cost-effective strategy to correct alternate bearing and increase cumulative yield of valuable large size fruit.

### **Experimental Plan and Design**

A commercial orchard exhibiting strong alternate bearing with sufficient trees having a heavy on-year and light off-year bloom in a given year was selected for this research and approved by the PRC. The orchard, located in Irvine, CA, was 7 years old at the start of the research. The 'Hass' scions are on Mexican seedling rootstocks. To meet objective 1 we set up the following treatments: **1)** 10 trees with a low crop harvested in June 2003 followed by heavy crop harvested in March 2004 – on-crop control trees; **2)** 10 trees with a heavy crop harvested in June 2003 followed by a low crop harvested in March 2004 – off-crop control trees; **3)** 10 trees with a low harvest in 2003 (high fruit set in spring 2003) with all the setting fruit removed during harvest of the mature fruit in June 2003 – on-crop trees converted to putative off-crop trees to contrast the effect of the presence and absence of fruit early in the season; and **4)** 10 trees with high crop harvested in June 2003 and low crop harvested in March 2004, of these trees 5 had all summer and fall vegetative shoot growth removed and 5 trees had only the fall vegetative shoot growth removed to test the hypothesis that reduced summer and fall vegetative shoot growth reduces return bloom. For the trees in treatments 1 to 4, four 1-m long branches with fruit and four 1-m long branches without fruit were tagged. The amount of summer and fall vegetative shoot growth was determined. For those spring shoots that produced no summer or fall vegetative growth, apical buds were collected and analyzed to determine whether or not the buds had transitioned from vegetative to reproductive. At spring bloom 2004 the number of indeterminate and determinate floral shoots, vegetative shoots and inactive buds were counted and the age (spring, summer or fall 2003) of the shoot producing each was determined. **5)** For 10 trees that produced an off-crop harvested in June 2003 and an on-crop harvested in March 2004, we selected 5 shoots with fruit set in 2003 and 5 shoots with fruit removed in July of 2003. The shoots were tagged at the point of attachment of the fruit to the shoot. In-depth data were being taken on these shoots to determine the effects of fruit set on determinate vs. indeterminate floral shoots, shoot vigor, nearness of the fruit to the shoot apex and effect of pruning on the number of

determinate or indeterminate floral shoots, vegetative shoots and inactive buds produced during spring bloom 2004. All shoots were evaluated through spring bloom 2005 to see the effect of the alternate half of the alternate bearing cycle on summer and fall vegetative shoot growth and return bloom, vegetative shoot growth and inactive buds and the composition of the bloom in 2005 (determinate vs. indeterminate) and the age of the shoots producing them (spring, summer or fall 2004 shoots). **6)** Using a separate set of 10 on-crop trees, we attempted to remove fruit each month, starting in July 2003, from 10 shoots and leave 10 shoots with fruit for comparison. Due to high fruit abscission rates, this did not work; so we set up another experiment and removed all the fruit from three trees each month from June through January. For comparison there are 10 on-crop trees and 10 off-crop trees. For each set of trees, four 1-m long branches with fruit and four 1-m long branches without fruit were tagged. The amount of summer and fall vegetative shoot growth was determined. At spring bloom 2005 the number of indeterminate and determinate floral shoots, vegetative shoots and inactive buds was counted and the age (spring, summer or fall 2004) of the shoot producing each was recorded. This set of trees enabled us to determine the critical period during which the fruit exerts its effect on return bloom. For these trees, samples of shoot apices and the subtending shoot tissue and root apices and the subtending root tissue were collected at the time of fruit removal and at specific times after fruit removal and analyzed for plant growth regulators, carbohydrate (starch), N and other nutrients to determine the effect of crop load on each factor. Fruit were also collected at the time of removal to determine if they are exporting an inhibitory compound that is accumulating in the buds.

In year 3, we began testing treatments to overcome inhibition of the growth of the summer-fall flush. We are conducting this research in the Irvine orchard that we are using for the alternate bearing research, so that we can treat trees with known cropping histories. The trees in this experiment were all carrying a heavy on-crop to fully test the ability of the treatments to increase the number and length of summer-fall shoots produced. We tested the theory that the cytokinins 6-BA or CPPU, GA<sub>3</sub> or the auxin-transport inhibitor (triiodobenzoic acid, TIBA) will stimulate summer and fall shoot growth and return bloom and yield by injecting the PGRs into the trunks of 'Hass' avocado trees at the start of the summer flush or at the start of the fall flush.

In year 3, we also initiated another fruit removal experiment to determine the effect of fruit in spring (fruit removal in February, March and May) on bud break and the development of indeterminate and determinate floral shoots, vegetative shoots and resting buds. Shoot apical buds and root apices were collected from on- and off-crop trees just before fruit removal and 2 and 4 weeks after fruit removal for quantification of endogenous concentrations of hormones, starch, glucose, nitrogen compounds and nutrients. Fruit were collected monthly and the concentrations of hormones exported from the fruit quantified.

### **Summary**

The results of our research provide convincing evidence that the presence of a high number of fruit in an on-crop year inhibits floral shoot development the following spring, but promotes vegetative shoot development and increases the number of inactive buds (Table 1). Since the number of inactive buds increases when the number of floral shoots decreases, it is likely that inactive buds are floral buds. This interpretation of the effect of the heavy on-crop was confirmed by removing all fruit from on-crop trees in June, which resulted in a significant

increase in the number of indeterminate floral shoots and in a significantly reduced number of vegetative shoots and inactive buds (Table 1). It should be noted that shoots with and without fruit on on-crop trees behaved identically during return bloom. This establishes the strong whole tree effect of the crop in contrast to an effect localized only to branches bearing fruit.

To determine the importance of the spring, summer and fall vegetative shoot flushes to return bloom and yield, we quantified the contribution of each flush on on-crop trees (+ fruit) and off-crop trees (- fruit) to return bloom (Table 2). The contribution of the summer-fall flush to the number of floral shoots that develop during return bloom is much greater (5- and 2.5-fold, respectively) than the contribution of the spring flush shoots for on-crop and off-crop trees (Table 2). This second set of data confirms that the heavy on-crop reduces floral shoot number with concomitant increase in vegetative shoot development and increase in the number of inactive buds. It is of interest that the only determinate inflorescences that developed did so on the spring flush shoots of branches with fruit on on-crop trees. To confirm the importance of the summer and fall flushes to the floral intensity of the return bloom, these shoots were removed from off-crop trees that should have flowered intensely the following spring. Trees with just their 2003 fall shoots removed produced a flower number similar to that of on-crop trees but those with their 2003 summer and fall shoots removed produced almost no flowers during the return bloom in spring 2004. Off-crop trees with only fall shoots removed yielded 6.4 kg of fruit per tree in 2005, which was similar to the return yield of on-crop trees (5.5 kg/tree) but significantly less than the return yield of off-crop trees without the summer or fall shoots removed (16.1 kg/tree). Trees with both summer and fall shoots removed produced only 0.5 kg fruit per tree in 2005, which was significantly less than the return crop produced by on-crop trees. The results provide strong evidence of the importance of summer and fall vegetative shoot growth to return bloom and yield.

In year 2 of the study, fruit (setting in 2004) were removed from trees each month beginning early in fruit development (i.e., June) through January. We then quantified the effect of on- and off-crop load and fruit removal on the contribution of the 2004 spring, summer and fall shoots to return bloom 2005 (Tables 3-7). Note that the data presented here are the average number per shoot per tree and that the contribution of summer and fall shoots that developed directly from old wood are not included. This makes the values presented much lower than the numbers presented in my oral presentations. The combined contribution of spring, summer and fall flush shoots to return bloom is reported in Table 3. Off-crop trees produced significantly more floral shoots to the return bloom than on-crop trees (Table 3). However, the significant difference was due to a greater number of determinate inflorescences rather than indeterminate floral shoots. The earlier fruit were removed, the more significant the increase in the number of indeterminate, determinate and total inflorescences that developed the following spring (Table 3). To increase total inflorescence number to a value equal to that of the off-crop trees and greater than that of on-crop trees, fruit had to be removed no later than mid-September. With the exception of June fruit removal, vegetative shoot number increased with later fruit removal and equaled the number of vegetative shoots produced by on-crop trees if fruit were removed in mid-November or later (Table 3). There was no effect of crop load or fruit removal on the number of inactive buds when the data for the spring, summer and fall flushes were pooled.

Analyses of the contribution for each flush revealed the following information: For spring flush shoots, crop load and fruit removal influenced the contribution of determinate inflorescences, but not indeterminate floral shoots (Table 4). Only fruit removal in August and September increased the number of determinate inflorescences to a number greater than that of on-crop trees. Spring flush shoots exhibited reciprocity between floral versus vegetative shoot development, with the number of inactive buds tending to increase when floral shoot number decreased.

The number of inflorescences contributed by the summer-fall flush to return bloom was greater than that of the spring flush shoots (compare Tables 4 and 5). Fruit removal increased the number of summer flushes that developed on the spring flush shoots, resulting in an increase in the number of indeterminate and determinate floral shoots contributed by summer-fall flush shoots, with earlier fruit removal having a more positive effect (Table 5). The reciprocal effect on the number vegetative shoots and inactive buds was evident but not statistically significant. Comparison of Tables 6 and 7 reveals the significantly greater contribution of the summer flush shoots to return bloom compared to the fall flush shoots. This is due to the development of a greater number of summer versus fall flush shoots. For fall flush shoots, fruit removal influenced the number of determinate inflorescences to a greater degree than indeterminate floral shoots (Table 7). The number of determinate inflorescences was quite high this year in this orchard (just under 30%).

In addition, we quantified the effects of these treatments on the concentrations of starch, arginine, proline and hormones in shoot apical buds and root apices. The carbohydrate and N-metabolite status of buds and roots was analyzed 2 and 4 months after fruit removal (Table 8). The starch concentrations of buds increased with time from August to February. Bud starch concentrations also increased with time after fruit removal and were always greater than those of on-crop trees (with the exception of August when all trees sampled had the same starch concentrations). Starch concentrations of buds from trees with fruit removed were only greater than those of off-crop trees in September. In February, the buds of all trees were sampled for starch concentration. Apical buds from on-crop trees had significantly lower starch concentrations than all other trees (Table 8). Buds from off-crop trees had high concentrations of starch equal to those of trees with fruit removed in July, August, September, October, November and December. No treatment increased bud starch content to a value greater than that of the off-crop trees. Two treatments resulted in buds with less starch than the off-crop trees, but more than the buds of the on-crop trees: fruit removal in June and January. Bud starch concentration was significantly positively correlated with inflorescence number and significantly inversely related to both the number of vegetative shoots and inactive buds (Data not shown).

Root starch concentration increased with time from August to February but not as dramatically as in buds (Table 9). In general, 2 months after fruit removal, the starch concentration of root apices was increased to a value greater than that of on-crop trees, but the difference did not always persist. In February, the roots of all trees were sampled and analyzed for carbohydrate concentration. There were no significant differences in the starch concentration of the root apices despite very big differences in crop load and time of fruit removal (Table 9).

In general, crop load and fruit removal had no effect on the arginine concentration of apical buds (Table 10). The one exception was that, in September, arginine concentration was significantly

greater in the apical buds of on-crop trees than off-crop trees or trees with fruit removed in July. The significance of this is unknown at this time, but it is of interest that in September root apices showed the reverse, being highest in trees with fruit removed in July and lowest for on-crop trees (Table 11). By February, trees with fruit removed late in the season (Nov.-Jan.) had higher arginine concentrations in their root apices than on-crop trees and trees with fruit removed in June through September.

Crop load and fruit removal had no effect on the proline concentration of shoot apical buds (Table 12) or root apices (Table 13).

Fruit removal in June resulted in a significant increase in the number of summer-fall flush shoots that developed. These shoots in turn contributed significantly to the number of inflorescences in the return bloom. In response to fruit removal, shoot apical buds had a lower amount of IAA and a greater amount of IPA relative to buds from on- and off-crop trees (Table 14). There were no differences in the hormone concentrations of root apices (Table 15). The results are consistent with correlative inhibition (high IAA relative to IPA) of the buds that should produce the summer-fall flush. Fruit removal shifts the ratio such that IPA is greater than IAA, releasing the buds from inhibition and allowing the summer-fall flush to develop. The fact that there is no difference in the hormone concentrations of the shoot apical buds from on- and off-crop trees is consistent with the fact that there was no significant difference in the number of summer-fall flush shoots produced by on- and off-crop trees, whereas there were differences in the number of inflorescences produced by the summer-fall shoots. Whereas we now understand the mechanism controlling the number of summer-fall shoots that develop, we do not completely understand the mechanism controlling the reciprocity between inflorescence development and vegetative shoot and inactive bud number.

To better understand the effect of crop load on return bloom, we removed fruit that set in 2005 just before the return bloom in February and March 2006. The data presented in Tables 16 through 20 are expressed as an average for the spring 2005 shoot per tree. On-crop trees produced significantly fewer indeterminate, determinate and total floral shoots than off-crop trees, but significantly more vegetative shoots (Table 16). Removing fruit from on-crop trees in February or March had no effect on flowering but significantly increased the number of vegetative shoots that developed compared to both on- and off-crop trees (February fruit removal) or off-crop trees (March fruit removal). March fruit removal also increased the number of inactive buds (Table 16).

Crop load and fruit removal had no effect on the number of inflorescences, vegetative shoots or inactive buds produced by spring flush shoots (Table 17). In Table 18 as anticipated, off-crop trees produced more summer-fall shoots and, thus, more indeterminate, determinate and total floral shoots than on-crop trees. Fruit removal in February or March could not influence the number of summer-fall shoots that developed and our fruit removal trees (on-crop trees until the fruit were removed) had the same number of summer and fall shoots as the on-crop control trees. Fruit removal did not affect inflorescence number. For off-crop trees, the majority of inflorescences in the return bloom developed on summer flush shoots (Table 19) compared to fall flush shoots (Table 20), which contributed more inflorescences than spring flush shoots (Table 17). The summer shoots were also the source of the increased number of vegetative

shoots and inactive buds that occurred in response to fruit removal (Compare tables 17, 19 and 20).

The starch concentrations of shoot apical buds of on-crop trees increased from February 15 to March 15, but were always lower than those of off-crop trees and fruit removal had no effect on starch concentration in shoot apical buds (Table 21). In contrast, the glucose concentration of the shoot apical buds was greater for on-crop-trees. Fruit removal tended to reduce the glucose concentration from that of on-crop trees to that of off-crop trees 2 weeks after the fruit were removed. The opposing effect of crop load on bud glucose versus sucrose concentration is not clear.

In years 3 and 4, trees were trunk injected with PGRs to increase the amount of summer and fall shoots that developed. However, successful treatments that increased summer-fall shoot number only increased the number of vegetative shoots (August application of TIBA) or inactive buds (September application of GA<sub>3</sub>) that occurred during the following spring bloom (data not shown). The summer flush shoots were the source of the vegetative shoots and inactive buds during return bloom.

This year we completed the anatomical analysis of apical buds to determine if compounds exported from the developing fruit inhibit the transition of vegetative shoot apical meristems to floral meristems. The results provided clear evidence that the shoot apical meristems from summer shoots bearing fruit transitioned from vegetative to reproductive. This result is consistent with accumulation of hormones in the buds preventing them from undergoing bud break. There was a strong negative relationship between the duration of exposure of buds to fruit and inflorescence number during return bloom in the order less floral shoots and more inactive buds for spring shoots than summer-fall shoots. Interestingly, there was only a weak positive effect of duration of exposure of fruit on vegetative shoot development during return bloom for spring flush shoots, but a strong positive relationship for summer-fall shoots. The effect of duration of exposure to fruit on resting buds was positive but weak for both spring and summer-fall shoots. The results suggest that the presence of fruit after some point in time does cause some percentage of the summer shoots to be vegetative, whereas the remaining buds remain floral but inactive. This year, we will trunk inject trees with PGRs in spring to stimulate growth of the inactive floral buds.

***Take home message.*** The heavy on-crop increases the number of inactive buds. This is reflected in the reduced number of summer-fall shoots that develop on on-crop trees or when fruit removal is delayed to November or later. In addition, a percentage of floral buds on spring and summer shoots transition to floral buds but remain inactive during return bloom. Shoot apical buds, but not root apices from off-crop and on-crop trees have the anticipated differences in available starch. Fruit removal monthly from July through December increased the starch concentrations of shoot apical buds, but not root apices, to a level equal to that of off-crop trees and greater than that of on-crop trees. However, the positive effect of TIBA in stimulating summer-fall shoot growth suggests that carbohydrate is not limiting to summer-fall shoot growth, but that the accumulation of auxin and even more strongly the lack of cytokinin in the buds is the cause of their inability to grow (correlative inhibition). Whereas we could increase the number of summer-fall shoots, they only produced vegetative or inactive buds in spring. The presence of

fruit past November significantly reduces floral shoot development and increases the number of vegetative shoots and inactive buds on summer shoots. The results of the spring hormone analyses will identify which, if any, hormones are exported by the fruit and which, if any, are accumulating or failing to accumulate in the buds in spring. This provides needed information for designing strategies to release these buds from inhibition to increase return bloom following the setting and development of an on-crop.

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Table 1. Effect of the crop set in 2003 on spring 2004 bloom.

Treatment	Branch	Yield 2004 <i>Kg/tree</i>	Inflorescence		Vegetative shoot	Inactive buds
			Indeterminate	Determinate		
			----- % -----			
On-crop trees	+ fruit	36.82 a	15.71 b <sup>z</sup>	0.70	61.47 a	22.11 a
	- fruit		15.79 b	0.00	61.80 a	22.41 a
Off-crop trees	- fruit	1.95 b	29.77 b	0.00	64.97 a	5.26 b
Fruit removed in June	- fruit	2.68 b	71.14 a	0.44	23.58 b	4.92 b

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Tukey HSD test,  $P=0.05$ .

Table 2. Effect of the presence or absence of fruit (fruit set in 2003) on branches of on-crop and off-crop trees, respectively, on spring bloom 2004 borne on spring and summer-fall 2003 shoots.

Treatment	Inflorescence		Vegetative shoot	Inactive buds
	Indeterminate	Determinate		
			----- % -----	
Total shoots				
+ fruit	25.00	1.39	53.29	24.30
- fruit	64.20	0.00	32.33	3.46
Spring shoots				
+ fruit	4.17	1.39	16.67	8.33
- fruit	18.00	0.00	4.00	0.80
Summer-fall shoots				
+ fruit	20.83	0.00	32.62	15.97
- fruit	46.20	0.00	28.33	2.66

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Tukey HSD test,  $P=0.05$ .

Table 3. Effect of the crop set in 2004 on bloom 2005 borne on spring, summer and fall 2004 shoots.

	Inflorescences			Vegetative shoots	Inactive buds
	Indeterminate	Determinate	Total		
----- Average no./shoot per tree -----					
On-crop trees	1.17 bc <sup>z</sup>	0.49 cd	1.67 bc	1.43 a	0.41
Off-crop trees	1.22 bc	3.23 ab	4.45 a	0.35 abcd	0.12
Fruit removed					
June	3.30 a	2.73 ab	6.03 a	0.46 abcd	0.37
July	2.98 a	3.20 ab	6.17 a	0.29 bcd	0.19
August	1.74 abc	4.21 a	5.95 a	0.26 bcd	0.08
September	2.58 ab	3.35 ab	5.93 a	0.21 cd	0.06
October	1.79 abc	2.05 bc	3.84 ab	0.16 d	0.20
November	1.84 abc	1.72 bcd	3.56 abc	0.73 abcd	0.32
December	0.87 c	0.08 d	0.95 c	1.36 ab	0.42
January	1.31 bc	0.30 cd	1.60 bc	1.27 abc	0.43
<i>P</i> -value	0.0512	0.0009	0.0016	0.0585	0.1227

<sup>z</sup>Means 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 2004 on spring bloom 2005 borne on spring 2004 shoots.

	Inflorescences			Vegetative shoots	Inactive buds
	Indeterminate	Determinate	Total		
	----- Average no./shoot per tree -----				
On-crop trees	0.29	0.13 cd <sup>z</sup>	0.41 cd	0.42 ab	0.32 a
Off-crop trees	0.21	0.88 ab	1.09 abcd	0.07 c	0.08 b
Fruit removed					
June	0.71	0.69 abcd	1.40 ab	0.32 abc	0.26 ab
July	0.59	0.71 abc	1.30 abc	0.15 c	0.12 ab
August	0.43	1.27 a	1.69 a	0.17 bc	0.06 b
September	0.67	1.15 ab	1.82 a	0.11 c	0.05 b
October	0.57	0.58 bcd	1.15 abcd	0.08 c	0.16 ab
November	0.82	0.67 abcd	1.48 a	0.21 bc	0.15 ab
December	0.46	0.07 d	0.52 bcd	0.56 a	0.22 ab
January	0.20	0.07 d	0.27 d	0.24 bc	0.26 ab
<i>P</i> -value	0.1785	0.0033	0.0145	0.0079	0.0789

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Fisher's Protected LSD test,  $P=0.05$ .

Table 5. Effect of the crop set in 2004 on spring bloom 2005 borne on summer and fall 2004 shoots.

	Inflorescences			Vegetative shoots	Inactive buds
	Indeterminate	Determinate	Total		
	----- Average no./shoot per tree -----				
On-crop trees	0.89 cd <sup>z</sup>	0.37 cd	1.25 cd	1.01	0.09
Off-crop trees	1.01 bcd	2.35 ab	3.37 abc	0.28	0.05
Fruit removed					
June	2.59 a	2.05 ab	4.63 a	0.14	0.11
July	2.39 ab	2.49 ab	4.88 a	0.14	0.07
August	1.31 abcd	2.95 a	4.25 ab	0.10	0.02
September	1.92 abc	2.20 ab	4.12 ab	0.10	0.01
October	1.22 abcd	1.48 bc	2.70 abcd	0.08	0.04
November	1.02 bcd	1.06 bcd	2.08 bcd	0.52	0.17
December	0.41 d	0.02 d	0.43 d	0.80	0.20
January	1.11 bcd	0.23 cd	1.34 cd	1.03	0.18
<i>P</i> -value	0.0995	0.0017	0.0051	0.1610	0.3661

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Fisher's Protected LSD test,  $P=0.05$ .

Table 6. Effect of the crop set in 2004 on spring bloom 2005 borne on summer 2004 shoots.

	Summer	Inflorescences			Vegetative shoots	Inactive buds
		Indeterminate	Determinate	Total		
----- <i>Average no./shoot per tree</i> -----						
On-crop trees	1.49 bc <sup>z</sup>	0.80	0.35 cd	1.15 de	0.84	0.09
Off-crop trees	1.73 bc	0.93	2.23 ab	3.16 abcd	0.25	0.05
Fruit removed						
June	2.64 a	2.48	2.05 ab	4.53 a	0.14	0.11
July	2.26 ab	2.13	2.30 ab	4.42 a	0.14	0.07
August	1.50 bc	1.02	2.62 a	3.63 ab	0.10	0.02
September	1.41 c	1.67	1.70 ab	3.36 abc	0.09	0.01
October	1.42 c	1.18	1.48 abc	2.65 abcd	0.06	0.03
November	1.50 bc	0.94	1.06 bcd	1.99 bcde	0.41	0.17
December	1.13 c	0.40	0.02 d	0.41 e	0.73	0.20
January	1.75 bc	1.10	0.23 cd	1.33 cde	0.76	0.17
<i>P</i> -value	0.0450	0.1132	0.0014	0.0058	0.1442	0.3483

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Fisher's Protected LSD test,  $P=0.05$ .

Table 7. Effect of the crop set in 2004 on spring bloom 2005 borne on fall 2004 shoots.

	Fall	Inflorescences			Vegetative shoots	Inactive buds
		Indeterminate	Determinate	Total		
----- <i>Average no./shoot per tree</i> -----						
On-crop trees	0.15	0.08	0.02 b <sup>z</sup>	0.11	0.17	0.00
Off-crop trees	0.10	0.09	0.12 b	0.21	0.03	0.00
Fruit removed						
June	0.04	0.11	0.00 b	0.11	0.00	0.00
July	0.15	0.27	0.19 ab	0.46	0.00	0.00
August	0.29	0.29	0.33 ab	0.62	0.00	0.00
September	0.23	0.25	0.51 a	0.76	0.01	0.00
October	0.06	0.05	0.00 b	0.05	0.02	0.02
November	0.13	0.09	0.00 b	0.09	0.11	0.00
December	0.08	0.02	0.00 b	0.02	0.08	0.00
January	0.20	0.01	0.00 b	0.01	0.27	0.01
<i>P</i> -value	0.4504	0.4210	0.1045	0.1178	0.4679	0.2245

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Fisher's Protected LSD test,  $P=0.05$ .

Table 8. Effect of the crop set in 2004 on the starch concentration (mg/g dry weight) of shoot apical buds.

	Aug. 2004	Sept. 2004	Oct. 2004	Nov. 2004	Dec. 2004	Feb. 2005
On-crop trees	5.78 a <sup>z</sup>	4.83 c	5.13 b	13.34 b	19.12 b	45.46 e
Off-crop trees	6.40 a	6.32 b	5.89 ab	26.28 ab	49.40 ab	115.19 ab
Fruit removed						
June	4.80 b	–	6.27 a	–	–	86.26 cd
July	–	8.24 a	–	21.20 b	–	106.18 abc
August	–	–	6.48 a	–	75.61 a	97.92 abcd
September	–	–	–	40.89 a	–	94.41 bcd
October	–	–	–	–	–	104.82 abc
November	–	–	–	–	–	122.62 a
December	–	–	–	–	–	101.86 abcd
January	–	–	–	–	–	76.59 d
<i>P</i> -value	0.0105	<0.0001	0.0674	0.0144	0.0273	<0.0001

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Fisher's Protected LSD test, *P*=0.05.

Table 9. Effect of the crop set in 2004 on the starch concentration (mg/g dry weight) of root apices.

	Aug. 2004	Sept. 2004	Oct. 2004	Nov. 2004	Dec. 2004	Feb. 2005
On-crop trees	4.63 a <sup>z</sup>	5.93	5.45 b	7.31 b	6.73 b	27.47 <sup>z</sup>
Off-crop trees	6.54 a	7.46	6.34 b	11.19 b	13.05 a	30.38
Fruit removed						
June	6.15 a	–	6.46 b	–	–	37.42
July	–	11.13	–	11.13 b	–	55.57
August	–	–	9.63 a	–	16.37 a	31.80
September	–	–	–	20.37 a	–	27.62
October	–	–	–	–	–	48.89
November	–	–	–	–	–	23.06
December	–	–	–	–	–	28.04
January	–	–	–	–	–	43.74
<i>P</i> -value	0.0834	0.1219	0.0448	0.0003	0.0083	0.22130

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Fisher's Protected LSD test, *P*=0.05.

Table 10. Effect of the crop set in 2004 on the arginine concentration (mg/g dry weight) of shoot apical buds.

	Aug. 2004	Sept. 2004	Oct. 2004	Nov. 2004	Dec. 2004	Feb. 2005
On-crop trees	23.74	24.76 a <sup>z</sup>	21.47	22.90	22.66	21.69
Off-crop trees	22.85	21.79 b	18.84	23.68	22.41	24.99
Fruit removed						
June	25.62	–	19.10	–	–	20.47
July	–	20.35 b	–	23.75	–	22.45
August	–	–	21.23	–	24.38	21.63
September	–	–	–	24.13	–	22.33
October	–	–	–	–	–	21.37
November	–	–	–	–	–	19.33
December	–	–	–	–	–	21.86
January	–	–	–	–	–	21.66
<i>P</i> -value	0.5850	0.0153	0.0734	0.6185	0.4754	0.1546

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Fisher's Protected LSD test, *P*=0.05.

Table 11. Effect of the crop set in 2004 on the arginine concentration (mg/g dry weight) of root apices.

	Aug. 2004	Sept. 2004	Oct. 2004	Nov. 2004	Dec. 2004	Feb. 2005
On-crop trees	22.90	27.85 b <sup>z</sup>	26.01	20.30	30.56	24.32 b
Off-crop trees	24.89	30.43 ab	26.59	23.45	28.09	29.20 ab
Fruit removed						
June	20.10		23.13			24.93 b
July		31.76 a		27.95		23.60 b
August			28.44		31.59	24.52 b
September				31.87		24.79 b
October	–	–	–	–	–	29.26 ab
November	–	–	–	–	–	31.90 a
December	–	–	–	–	–	31.22 a
January	–	–	–	–	–	34.88 a
<i>P</i> -value	0.6975	0.0472	0.4598	0.2479	0.8096	0.0093

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Fisher's Protected LSD test, *P*=0.05.

Table 12. Effect of the crop set in 2004 on the proline concentration (mg/g dry weight) of shoot apical buds.

	Aug. 2004	Sept. 2004	Oct. 2004	Nov. 2004	Dec. 2004	Feb. 2005
On-crop trees	16.57	11.79	13.51	14.52	15.67	13.54
Off-crop trees	16.32	11.38	13.22	15.53	15.54	15.88
Fruit removed						
June	15.98	–	15.46	–	–	12.84
July	–	10.24	–	16.83	–	14.73
August	–	–	12.63	–	16.42	14.88
September	–	–	–	15.02	–	16.67
October	–	–	–	–	–	15.21
November	–	–	–	–	–	12.99
December	–	–	–	–	–	14.37
January	–	–	–	–	–	14.40
<i>P</i> -value	0.9390	0.2995	0.5626	0.3458	0.8079	0.3532

Table 13. Effect of the crop set in 2004 on the proline concentration (mg/g dry weight) of root apices.

	Aug. 2004	Sept. 2004	Oct. 2004	Nov. 2004	Dec. 2004	Feb. 2005
On-crop trees	12.81	15.24	16.41	14.46	19.46	17.13
Off-crop trees	14.71	15.98	15.78	20.20	17.43	17.95
Fruit removed						
June	4.70		15.11			15.82
July		16.15		19.66		16.30
August			19.55		23.94	15.91
September				18.36		14.10
October	–	–	–	–	–	19.23
November	–	–	–	–	–	15.98
December	–	–	–	–	–	15.68
January	–	–	–	–	–	17.75
<i>P</i> -value	0.1988	0.8301	0.3541	0.5361	0.4330	0.9489

Table 14. Effect of the crop set in 2004 on IAA, ABA and IPA concentrations in ‘Hass’ avocado apical buds in August 2004.

	IAA	ABA	IPA
	----- <i>ng·g<sup>-1</sup> dry wt apical buds</i> -----		
On-crop trees	39.94 ab <sup>z</sup>	101.26	13.24 b
Fruit removed (June)	23.42 b	67.85	55.23 a
Off-crop trees	60.01 a	101.11	14.93 b
<i>P</i> -value	0.0767	0.4689	<0.0001

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Fisher’s Protected LSD test, *P*=0.05.

Table 15. Effect of the crop set in 2004 on IAA, ABA and IPA concentrations in ‘Hass’ avocado root apices in August 2004.

	IAA	ABA	IPA
	----- <i>ng·g<sup>-1</sup> dry wt root apices</i> -----		
On-crop trees	253.22	67.46	96.12
Fruit removed (June)	266.11	73.79	74.92
Off-crop trees	179.39	52.78	63.71
<i>P</i> -value	0.2876	0.5593	0.1846

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Fisher’s Protected LSD test, *P*=0.05.

Table 16. Effect of the crop set in 2005 on spring bloom 2006 borne on spring, summer and fall 2005 shoots.

	Inflorescences			Vegetative shoots	Inactive buds
	Indeterminate	Determinate	Total		
	----- <i>Average no./spring shoot per tree</i> -----				
On-crop trees	0.6 b	0.0 b	0.6 b	0.5 b	0.4 b
Off-crop trees	5.0 a	2.0 a	6.9 a	0.1 c	0.2 b
Fruit removed					
February	0.2 b	0.0 b	0.2 b	0.9 a	0.3 b
March	0.2 b	0.0 b	0.2 b	0.5 ab	0.9 a
<i>P</i> -value	<0.0001	<0.0001	<0.0001	0.0011	0.0065

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Fisher’s Protected LSD test, *P*=0.05.

Table 17. Effect of the crop set in 2005 on spring bloom 2006 borne on spring 2005 shoots.

	Inflorescences			Vegetative shoots	Inactive buds
	Indeterminate	Determinate	Total		
	----- <i>Average no./spring shoot per tree</i> -----				
On-crop trees	0.2	0.0	0.2	0.2	0.1
Off-crop trees	0.1	0.3	0.3	0.0	0.0
Fruit removed					
February	0.1	0.0	0.1	0.2	0.1
March	0.0	0.0	0.0	0.0	0.1
<i>P</i> -value	0.1737	0.3060	0.3355	0.1635	0.5093

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Fisher’s Protected LSD test, *P*=0.05.

Table 18. Effect of the crops set in 2005 on spring bloom 2006 borne on summer and fall 2005 shoots.

	Summer+fall	Inflorescences			Vegetative shoots	Inactive buds
		Indeterminate	Determinate	Total		
----- Average no./spring shoot per tree -----						
On-crop trees	1.0 b <sup>z</sup>	0.4 b	0.0 b	0.4 b	0.3 bc	0.3 b
Off-crop trees	4.2 a	4.9 a	1.7 a	6.6 a	0.1 c	0.2 b
Fruit removed						
February	1.3 b	0.1 b	0.0 b	0.1 b	0.7 a	0.2 b
March	1.5 b	0.2 b	0.0 b	0.2 b	0.5 ab	0.8 a
<i>P</i> -value	<0.0001	<0.0001	<0.0001	<0.0001	0.0031	0.0062

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Fisher's Protected LSD test, *P*=0.05.

Table 19. Effect of the crop set in 2005 on spring bloom 2006 borne on summer 2005 shoots.

	Summer	Inflorescences			Vegetative shoots	Inactive buds
		Indeterminate	Determinate	Total		
----- Average no./spring shoot per tree -----						
On-crop trees	0.8 b <sup>z</sup>	0.3 b	0.0 b	0.3 b	0.2 bc	0.2 b
Off-crop trees	2.5 a	2.9 a	0.9 a	3.8 a	0.0 c	0.1 b
Fruit removed						
February	1.1 b	0.1 b	0.0 b	0.1 b	0.6 a	0.2 b
March	1.5 b	0.2 b	0.0 b	0.2 b	0.4 ab	0.8 a
<i>P</i> -value	<0.0001	<0.0001	0.0015	<0.0001	0.0035	0.0022

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Fisher's Protected LSD test, *P*=0.05.

Table 20. Effect of the crop set in 2005 on spring bloom 2006 borne on fall 2005 shoots.

	Fall	Inflorescences			Vegetative shoots	Inactive buds
		Indeterminate	Determinate	Total		
----- <i>Average no./shoot per tree</i> -----						
On-crop trees	0.2 b <sup>z</sup>	0.1 b	0.0 b	0.1 b	0.1	0.0
Off-crop trees	1.7 a	2.0 a	0.8 a	2.8 a	0.1	0.1
Fruit removed						
February	0.2 b	0.0 b	0.0 b	0.0 b	0.1	0.0
March	0.1 b	0.0 b	0.0 b	0.0 b	0.1	0.0
<i>P</i> -value	0.0013	0.0005	0.0421	0.0017	0.8389	0.4193

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Fisher's Protected LSD test, *P*=0.05.

Table 21. Effect of the crop set in 2005 on the glucose and starch concentration of shoot apical buds.

	15 Feb. 2006		1 Mar. 2006		15 Mar. 2006	
	Glucose	Starch	Glucose	Starch	Glucose	Starch
----- <i>mg/g dry weight</i> -----						
On-crop trees	5.40 a <sup>z</sup>	15.05 b <sup>z</sup>	3.44 a	58.74 b	5.54 a	88.06 b
Off-crop trees	2.22 b	129.64 a	1.60 b	156.03 a	1.54 b	158.13 a
Fruit removed						
1 February	2.81 b	13.69 b	2.46 ab	68.33 b	–	–
1 March	–	–	3.62 a	54.40 b	2.07 b	79.40 b
<i>P</i> -value	<0.0001	<0.0001	0.0099	0.0004	0.0002	0.0068

<sup>z</sup>Means followed by different letters within a vertical column are significantly different by Fisher's Protected LSD test, *P*=0.05.