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Eliminating Alternate Bearing of the 'Hass' Avocado

Continuing Project: Year 3 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.

Annual production data for the last 14 years clearly depict 2- to 3-year on-off cycles for the California avocado industry (Brokaw Nursery Inc., 2002; California Avocado Commission, www.avocado.org). The alternate bearing index [ABI = (year 1 yield – year 2 yield) ÷ (year 1 yield + year 2 yield)] for our numerous research orchards ranges from 0.57 to 0.92 (Lovatt, 1997). By this calculation, every other year grower income is significantly reduced below the orchard's potential. ABIs of this magnitude mean that growers are producing ~ 60% to 90% less fruit the year following an on-crop. Lower yields (5,700 lbs./a) in the 1990's (Arpaia, 1998) reduced ABI, but reduced yields are not an acceptable solution to alternate bearing. Moreover, it is only a matter of time before climatic conditions initiate alternate bearing in avocado growing areas entraining trees again in on-off cycles. Alternate bearing is initiated by climatic conditions (freeze damage, high temperatures, drought) causing flower or fruit abscission which result in an off-crop year that is followed 1, 2 or 3 years later by an on-crop year, depending on how long it takes for the trees to recover. Conversely, climatic conditions that are optimal for flowering and fruit set such that crop thinning fails to take place result in an on-crop that is followed by an off-crop. Once initiated, alternate bearing becomes entrained through the effect of crop load on endogenous tree factors that ultimately impact floral intensity (Salazar-García et al., 1998). Thus, there is a recurring need for a corrective strategy that does not reduce yield, but the mechanism and the underlying physiological basis by which yield one year affects yield the next year remain unknown for avocado. The cultural practice of harvesting late to increase fruit dry matter and oil content or to wait for a higher market price exacerbates alternate bearing (Whiley, 1994); whereas early harvest (not possible in many areas or years if fruit do not meet legal maturity) or fruit removal by pruning or chemical or hand fruit thinning in an on-crop year reduce the severity of alternate bearing, but they all reduce yield. The proposed research will define the mechanism by which alternate bearing becomes entrained in 'Hass' avocado and identify the physiology underlying the mechanism and devise and test strategies to eliminate alternate bearing.

Salazar-García et al. (1998) and Salazar-Garcia and Lovatt (2000) demonstrated that avocado trees carrying a heavy on-crop produced vegetative shoots at the expense of floral shoots (inflorescences). Conversely, trees carrying a light off-crop produced floral shoots at the expense of vegetative shoots. Crop load had no effect on the number of flowers per inflorescence. Reciprocity between floral vs. vegetative shoot development for on-crop vs. off-crop trees suggests that endogenous plant hormones might be playing a more important role in alternate bearing in 'Hass' avocado than resource (e.g., carbohydrate, N or other nutrient) availability, which would have resulted in a reduction in both vegetative and floral shoot development for trees carrying an on-crop. In a current study on nutrient partitioning in 'Hass' avocado (Rosecrance and Lovatt, unpublished), off-crop trees (low set in spring 2001 and remaining fruit removed in July 2001) produced significantly more reproductive structures and set more fruit for the 2002 return bloom (an average of 1.33 kg dry wt./tree per month March through June 2002) than trees that were not defruited in July 2001, which averaged only 0.08 kg dry wt./tree per month over the same period. Surprisingly, the presence of only a few fruit (2 kg, ~10 fruit) was sufficient to reduce the 2002 return bloom, indicating that the effect of fruit was not limited to the shoot on which they set.

Four questions need to be answered to solve the problem of alternate bearing of the 'Hass' avocado. (1) For on-crop trees, is reduced return bloom due to inhibition of vegetative shoot production and thus a lack of "wood" to bear next spring's inflorescences? (2) Or, alternatively is reduced return bloom for on-crop trees due to inhibition of inflorescence development on an <u>adequate number of vegetative shoots</u>? (3) Are fruit the source of hormones or other compound(s) responsible for inhibition of vegetative or floral shoot development, whichever the case proves to be? (4) Does resource availability (carbohydrate, N and other nutrient reserves) play a role in alternate bearing in the 'Hass' avocado? Preliminary results suggest that it is the inhibition of vegetative shoot growth in spring-summer when trees are carrying a heavy on-crop that results in reduced flowering the following spring (Paz-Vega, 1997). However, export of compounds (especially plant growth regulators) from the developing fruit that inhibit the transition of vegetative shoot apices to floral meristems cannot be ruled out (Paz-Vega, 1997).

The proposed research supports the industry objectives, expectations and visions of increasing grower profitability. In orchards exhibiting alternate bearing, yield is reduced below the potential of the orchard and grower income is significantly reduced. The PI has successfully reduced the impact of alternate bearing in pistachio and is working towards mitigating alternate bearing in 'Pixie' mandarin. Similarities in the physiology underlying the mechanisms of entrainment are emerging. Furthermore, our approach to identifying the physiology underlying the mechanism of entrainment has proven valid in the two systems and is easily adaptable to the 'Hass' avocado. The results of this research will significantly increase yield and grower profitability. In addition, the results will identify treatments that can be used to increase floral intensity in other situations or annually. It is clear that yield is related to inflorescence number (Salazar-Garcia et al., 1998).

The proposed research also relates to the following priority: "The role of endogenous and exogenous plant growth regulators in avocado and the evaluation of commercial growth regulators on flowering, fruit set, fruit size, yield and vegetative growth." This research will also provide data sought under the priority related to canopy management, i.e., innovative techniques to increase production. In addition, this project will save time in developing the use of exogenous foliar applications of PGRs to increase yield by identifying the specific PGR and phenological stage at which the PGR should be applied to reduce alternate bearing. It will likely also utilize the results we have obtained in our previous CAC-funded research on N fertilization which demonstrated that 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 four years of the study.

Objectives

The objectives are: (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 (or other compound) during the period critical 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 and other nutrient resources to the roots, reducing root growth and/or metabolic activity and 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

Year 1 – To determine whether reduced flowering in spring for on-crop trees is due to a reduced number of vegetative shoots, on which to bear the inflorescences the following spring or to straightforward inhibition of inflorescence development on an adequate number of vegetative branches, we will conduct the following experiments. The experiments will be conducted in a commercial orchard exhibiting strong alternate bearing starting with a heavy on-year bloom. For 10 branches on each of 10 on-crop and 10 off-crop trees in the same orchard we will quantify the amount of shoot growth on each branch monthly starting in mid-April and the amount of floral and vegetative shoot growth during next spring bloom. Using a separate set of 20 on-crop trees, each month starting in April we will remove fruit from 10 branches of 10 on-crop trees (the remaining 10 on-crop trees will not have fruit removed) and quantify vegetative shoot production in response to fruit removal vs. no fruit removed and vegetative and floral shoot production during spring bloom the following year to determine the window when fruit are inhibiting either vegetative shoot growth or floral shoot development. In preparation for Year 2, fruit will be removed from a set of 60 trees bearing light crops early in fruit set to create on-crop trees. This strategy has proven very successful in creating on-crop and off-crop trees in our nutrient uptake study in Moorpark, Calif. Trees from which fruit were removed flowered profusely compared to trees from which fruit was not removed, even if trees carried few fruit.

Year 2 – The experiment conducted in Year 1 will be repeated on one set of trees to confirm the results of Year 1 on shoot growth, return bloom and yield and repeated on another set of trees that will be destructively sampled monthly during the period(s) identified in Year 1 as the time at which the fruit are exerting their effect on vegetative shoot growth and/or floral initiation. Buds will be collected from branches without fruit from off-crop trees, branches with fruit from on-crop trees and from branches on a second set of on-crop trees that are defruited during the period from June through January to determine the time(s) when the fruit are exerting their effect on vegetative shoot growth and/or floral initiation. An aliquot of each branch itself will be analyzed to determine the concentration of C, N and other nutrients in on- versus off-crop branches. Root samples will be collected concurrently, the number of new root tips per kg soil quantified and the concentration of C, N and other nutrients in roots from on- and off-crop trees determined. Buds and root tip samples will also be analyzed for differences in PGR content. We are able to quantify changes in the auxin indoleacetic acid (IAA), the cytokinins zeatin riboside (ZR) and isopentyladenosine (IPA), gibberellin as GA_3, and abscisic acid (ABA). It is anticipated that the presence of fruit results in the accumulation of abscisic acid and/or the loss of the cytokinins zeatin riboside and isopentenyladenosine. In preliminary experiments, buds from shoots bearing fruit had higher concentrations of ABA than buds from shoots without fruit. Buds on shoots bearing fruit did not produce inflorescences, whereas buds from fruitless shoots flowered. Analysis of the PGR content of buds combined with the quantitative data on vegetative and floral shoot growth will enable us to determine exactly when and how the fruit are exerting their effect on return bloom. Developing fruit will be analyzed to determine if they export abscisic acid, IAA and other inhibitors. The results of this research also will allow us to determine if the effect of crop load on resource availability impacts root growth, thereby, reducing cytokinin synthesis and shoot growth and the resource availability in the branches necessary to support shoot growth.

Year 3 – The window during which fruit are exerting their negative effect will be confirmed by removing fruit from 20 on-crop trees just prior to this window and leaving fruit on 20 trees. Vegetative shoot growth, if appropriate, return bloom and yield will be quantified. Buds will be collected from both sets of trees and analyzed microscopically to assess floral shoot development and for PGRs to confirm the effects of the treatments. In addition, 20 trees with fruit will be treated with the appropriate PGRs (most likely cytokinins) with and without nitrogen just prior to and during the window identified in year 2. Buds will be collected and analyzed microscopically and for PGRs to confirm the effects of the PGR treatments. Vegetative shoot growth, if appropriate, return bloom and yield will be quantified. Specific treatments will be based on the results obtained in Years 1 and 2.

Year 4 – The treatments used to eliminate alternate bearing in Year 3 will be used on the on-crop trees in Year 4 to confirm their effectiveness.

All data will be statistically analyzed by analysis of variance using SAS at $P \leq 0.05$.

Summary

In 2002-2003, trees were selected for the experiment based on the number of fruit on each tree and assigned to a treatment. Within the two groups (high yield on-crop trees or low yield off-crop trees), treatments were assigned in a randomized complete block design. Mature fruit were harvested in May 2003 and the crop loads were compared to the assigned treatments. As anticipated trees with little-to-no 2003 crop had the highest yield of mature fruit (61-68 kg/tree) in 2004 ($P \leq 0.0001$). Trees with a good 2003 set fell into two groups: trees that yielded ~20 to 27 kg mature fruit/tree and those that yielded ~11 to 18 kg mature fruit/tree in 2004. The 2003 spring crop was removed from a set of 10 trees in June. At that time the crop weighed an average of 1.5 kg/tree.

Results collected during spring bloom 2004 clearly demonstrate the repressive effect of even a modest crop (37 kg) per tree on inflorescence development (Table 1). The data were obtained for four branches 24 mm in diameter and 94 cm long on each of five trees per treatment. It can be seen that the effect of the crop is a whole tree effect with regard to branches. The presence or absence of fruit on branches on on-crop trees was without effect compared to branches without fruit on trees with off-year crops. The presence of the crop also prevented the development of apical buds (reported as inactive buds), independent of the presence or absence of fruit on the branch itself, compared to branches without fruit on off-crop trees (Table 1). In addition, the results confirmed the predominance of indeterminate inflorescences in the 'Hass' bloom in California.

Removal of all fruit (mature and setting fruit) in June from trees setting a heavy on-crop (the previous year's crop averaged only 9 kg/tree for the trees in this treatment) resulted in a significant increase in inflorescence production and decrease in the number of inactive buds compared to both on-crop and off-crop trees (Table 1). The significantly greater number of inflorescences on trees with fruit removed in June compared to off-crop trees is likely due to the fact that these trees had an off-crop (9 kg/tree) the previous year, whereas the off-crop trees had an on-crop (70 kg/tree) the previous year. This difference is consistent with a possible role for resource availability in alternate bearing of 'Hass' avocado.

Additional experiments were conducted to determine whether the effect of the on-crop was a whole tree effect at the level of small shoots (8.4 mm in diameter and 11.6 cm in length) or an effect localized only to shoots subtending fruit. Five shoots of the size given above with and without fruit were tagged on each of five on-crop trees in June. The presence of fruit reduced the production of inflorescences and increased the proportion of inactive apical buds in spring 2004 compared to shoots without fruit (Table 2). Vegetative shoots produced in spring 2003 contributed little reproductive growth to the 2004 bloom compared to shoots that developed in summer-fall 2003. The majority of inflorescences produced in spring 2004 were borne on shoots produced during the 2003 summer-fall vegetative flush. To confirm the importance of the summer-fall flush to return bloom, fall shoots or both summer and fall shoots were removed from 5 off-crop trees, respectively. These trees produced no inflorescences during spring bloom 2004.

The effect of fruit removal in June, removal of summer and fall vegetative shoots, or removal of just fall flush shoots were confirmed by the harvest of 2005. Trees with all fruit removed in June had the highest yield, followed by the yield of the off-crop trees. Trees with only their fall flush shoots removed yielded 50% less fruit than the off-crop trees. On-crop trees produce 50% less fruit than trees with only their fall flush shoots removed, and trees with both their summer and fall flush shoots removed averaged only 0.6 fruit per tree. We also quantified the number of summer and fall vegetative shoots that were produced by on- and off-crop trees and trees with all fruit removed from June through January and the contribution of the spring, summer and fall flushes to the floral intensity (number of indeterminate and determinate floral shoots), vegetative shoot growth and inactive buds produced by all trees during the return bloom of 2005. In addition, we continue to collect this data from the trees studied in previous years of this project.

This is a huge data set that we not only analyze by year but also will analyze across years to determine the cropping (alternate bearing) pattern of individual trees over the 4-year period.

The results strongly suggest that fruit exert their influence on flowering by reducing the amount of summer-fall flush produced, thereby reducing the number of inflorescences produced the following spring. The effect on yield of removing the summer and fall flush shoots or even just the fall flush shoots confirms the importance of this flush to ‘Hass’ productivity. However, at this time the possibility that fruit also inhibit the transition of the vegetative shoot apex to a floral apex cannot be ruled out. To distinguish these two possibilities the following research was conducted. Fruit were removed from each of two trees each month, starting on 15 June and continuing through 15 February. For these trees we quantified the amount of summer and fall vegetative shoot growth and return bloom and yield. We also collected apical buds that will be analyzed by Dr. Samuel Salazar-Garcia, who will determine whether the primary apical meristem underwent phase transition to a floral apex or was inhibited from doing so and remained vegetative. This data is important in order to learn whether inactive buds would develop into floral or vegetative shoots if stimulated to grow in the spring. We also quantified the effect of crop load on new root growth expressed as the number of new roots gram (g) per gram total roots. Shoot apical buds and the apical 10 mm of roots were collected and analyzed to determine their starch, arginine and proline concentrations. Next, we will analyze the concentrations of hormones in these tissues.

The carbohydrate status and arginine and proline concentrations of apical buds and root apices were analyzed 2 and 4 months after each fruit removal date. Only the starch data are presented here. The carbohydrate analyses are provided 1 year ahead of schedule. In August, trees with fruit removed in June had root starch concentrations equal to those of both on- and off-crop trees, but by September, trees with fruit removed in July had significantly greater root starch concentrations than either on- or off-crop trees, which had the equal root starch concentrations (Table 3). By October, trees with fruit removed in August had significantly greater root starch concentrations than trees with fruit removed in June or on- or off-crop trees, which all had equal concentrations of starch in their roots. By November, trees with fruit removed in September had significantly greater root starch concentrations than trees with fruit removed in July and on- or off-crop trees, which all had equal root starch concentrations. By December, trees with fruit removed in August had root starch concentrations equal to that of off-crop trees, both had root starch concentrations greater than those of on-crop trees. With regard to root starch concentrations, the advantage of fruit removal evident 2 months after fruit removal is lost by 4 months after fruit removal until the December sampling date. In January, trees with fruit removed in September had significantly greater root concentrations of starch than on-crop trees; off-crop trees had root starch concentrations that were intermediate to and not significantly different from either of these treatments.

In August, the starch concentrations of buds from on- and off-crop trees were equal and greater than those of buds from trees with fruit removed in June (Table 4). In September, bud starch concentrations for trees with fruit removed in July were greater than off-crop trees, which were greater than on-crop trees. In October, bud starch concentrations were equal for trees with fruit removed in August or June and greater than those of on-crop trees, with off-crop trees having intermediate concentrations. In September, trees with fruit removed in September had bud starch concentrations that were greater than buds of trees with fruit removed in July and buds of on-crop trees, with off-crop trees having intermediate concentrations. By December, bud starch concentrations of trees with fruit removed in August were greater than those of on-crop trees, with off-crop trees being intermediate. The starch concentrations of buds increased with time after fruit removal and were always greater than those of on-crop trees; they were only greater than the starch concentrations of buds from off-crop trees in September. By January buds of trees with fruit removed in Septmeber and off-crop trees had signifcantly greater bud starch concentrations than on-crop trees.

Starch concentrations of both root apices and shoot apical buds increased significantly from August to January for on- and off-crop trees (Tables 3 and 4). Consistent with previous reports, the increase in starch was greater for off-crop trees than on-crop trees. Our research provides evidence that the magnitude of the increase in starch is greater in shoot apical buds than root apices for both on- and off-crop trees (Tables 3 and 4), with buds of off-crop trees having 2.6-fold more starch than on-crop trees compared to only 1.8-fold more starch in roots of off-crop trees than on-crop trees.

In February, shoot apical buds and root apices were collected from all the trees in this experiment and analyzed to determine their starch, arginine and proline concentrations. Next, these samples will be analyzed to determine their hormone concentrations. The starch concentration of shoot apical buds from on-crop trees were significantly less than that of buds from trees in all other treatments (Table 5). The starch concentration of apical buds from off-crop trees were high but not signifcantly greater than the starch concentrations of apical buds from trees with fruit removed in July through Decemeber. Apical buds from trees from which fruit were removed in June had starch concentrations that were significantly less than buds of off-crop trees and trees with fruit removed in November, but equal to the starch concentrations in buds of trees which had their fruit removed in July, August, September, October, December and January. Apical buds from trees from which fruit were removed in January had starch concentrations that were significantly less than buds of off-crop trees and trees with fruit removed in July, October and November, but equal to the starch concentrations in buds of trees which had their fruit removed in June, August, September, and December. In contrast, by February there were no differences in the starch concentrations of root apices from on- versus off-crop trees (Table 5). Moreover, removal of all fruit from trees monthly from June through January had no significant effect on root starch concentrations by February. Since the fruit removal treatments resulted in differences in the carboydrate status of the trees, it will be possible to determine whether carbohydrate availability plays a critical role in altrnate bearing or not.

The arginine and proline concentrations of shoot apical buds were not influenced by crop load (Table 5). In contrast, root arginine concentrations were significantly affected by crop load (*P*=0.0093). (Table 6). Fruit removal from trees in November, December and January resulted in significantly more arginine in the roots compared to those of on-crop trees and trees with fruit removed in June through September. Off-crop trees and trees with their fruit removed in October had arginine concentrations that were intermediate to and not significantly different from those in all other treatments. Thus, late fruit removal increased the amount of nitrogen stored as arginine in the roots in February. Crop load had no effect on the proline concentration of the roots by February.

Year 3 – To overcome the inhibitory effects of fruit on the development of the summer and fall vegetative shoot flush we injected on-crop trees with CPPU, a powerful diphenylurea-type cytokinin, and with benzyladenine, a commonly used commercial cytokinin with the purine ring structure of naturally occurring cytokinins. These treatments are designed to stimulate bud break and increase summer-fall vegetative shoot development to increase the number of sites on which to bear inflorescences during spring bloom. Cytokinins can also overcome the effect of IAA that might be accumulating in the buds and preventing their growth, the situation we found in citrus. Cytokinins can also cancel the effect of ABA that might be accumulating in the buds, the situation we found in pistachio. We (Lovatt and Ferguson, 2001, 2005) used foliar-applied cytokinins combined with foliar-applied low-biuret urea in the on-crop year to successfully increase pistachio yield in the off-crop year. We injected GA_3 to stimulate summer-fall vegetative shoot growth in a separate set of trees. We injected 2,3,5-triiodobenzoic acid (TIBA), an auxin-transport inhibitor, in another set of trees. This treatment is designed to release buds from apical dominance to increase summer-fall vegetative shoot development. In early spring, additional sets of trees will be injected with these PGRs to increase spring bud break and floral shoot number. A set of untreated control trees was included in the experiment. The experimental design is a randomized complete block. For all trees in this experiment, we will quantify the number of summer and fall vegetative shoots that develop, the number of spring vegetative and floral shoots that develop, the number of inactive buds and the contribution of each vegetative flush to spring bloom.

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Table 1. Effect of crop load on spring 2004 growth.

Treatment	Branch	Yield 2004	% Inflorescence Indeterminate	Determinate	% Vegetative shoot	% Inactiv e buds
		Kg/tree				
On-crop trees	+ fruit	36.82 a	15.71 b[z]	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

[z] 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 of on-crop trees on total spring 2004 growth borne on spring and summer-fall 2003 shoots.

Treatment	Branch	Yield 2004	% Inflorescence Indeterminate	Determinate	% Vegetative shoot	% Inactiv e buds
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

[z] Means followed by different letters within a vertical column are significantly different by Tukey HSD test, *P*=0.05.

Table 3. Effect of crop load on the starch concentration (mg/g dry weight) root apices.

	Aug. 2004	Sept. 2004	Oct. 2004	Nov. 2004	Dec. 2004	Jan. 2005
On-crop trees	21.02	22.03 b[z]	21.79 b	30.71 b	26.93 b	83.30 b
Off-crop trees	26.17	29.60 b	25.35 b	40.91 b	52.20 a	149.20 ab
Fruit removed						
June	24.60	–	30.75 b	–	–	–
July	–	44.53 a	–	44.52 b	–	–
August	–	–	45.50 a	–	65.47 a	–
September	–	–	–	80.52 a	–	288.84 a
P-value	0.2520	0.0013	0.0109	0.0003	0.0083	0.0545

[z] 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 crop load on the starch concentration (mg/g dry weight) of shoot apical buds.

	Aug. 2004	Sept. 2004	Oct. 2004	Nov. 2004	Dec. 2004	Jan. 2005
On-crop trees	22.95 a[z]	19.31 c	20.50 b	50.25 b	79.53 b	154.27 b
Off-crop trees	25.61 a	25.29 b	23.56 ab	94.05 ab	206.20 ab	403.72 a
Fruit removed						
June	19.21 b	–	25.07 a	–	–	–
July	–	32.97 a	–	80.82 b	–	–
August	–	–	25.90 a	–	292.01 a	–
September	–	–	–	147.96 a	–	374.09 a
P-value	0.0144	<.0001	0.0679	0.0187	0.0326	0.0060

[z] 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 crop load on the starch, arginne and proline concentrations (mmols/g dry weight) of shoot apical buds in February.

	Starch	Arginine	Proline
On-crop trees	45.46 e[z]	21.69	13.54
Off-crop trees	115.19 ab	24.99	15.88
Fruit removed			
June	86.26 cd	20.47	12.84
July	106.18 abc	22.45	14.73
August	97.92 abcd	21.63	14.88
September	94.41 bcd	22.33	16.67
October	104.82 abc	21.37	15.21
November	122.62 a	19.33	12.99
December	101.86 abcd	21.86	14.37
January	76.59 d	21.66	14.40
P-value	<0.0001	0.1546	0.3532

[z] 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 crop load on the starch, arginne and proline concentrations (mmols/g dry weight) of root apices in February.

	Starch	Arginine	Proline
On-crop trees	27.47[z]	24.32 b	17.13
Off-crop trees	30.38	29.20 ab	17.948
Fruit removed			
June	37.42	24.93 b	15.82
July	55.57	23.60 b	16.30
August	31.80	24.52 b	15.91
September	27.62	24.79 b	14.10
October	48.89	29.26 ab	19.23
November	23.06	31.90 a	15.98
December	28.04	31.22 a	15.68
January	43.74	34.88 a	17.75
P-value	0.22130	0.0093	0.9489

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