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Citrus Fruit Reduce Summer and Fall Vegetative Shoot Growth and Return Bloom

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Abstract. **Alternate bearing citrus trees produce a heavy (on) crop followed by a lighter (off) crop. Whereas it is well documented that crop load affects return bloom, both the mechanism and underlying physiological basis by which fruit influence flowering the next spring remain unknown. In preparation for studies elucidating the role of plant growth regulators in relation to carbohydrate and nutrient reserves in the physiology of alternate bearing, the mechanism by which fruit cause the cyclic differences in floral intensity was determined. Using 'Pixie' mandarin (*Citrus reticulata* Blanco) as the model system, two hypotheses were tested. (1) The on-crop reduces summer and fall vegetative shoot growth and, thereby, decreases the number of sites that can bear flowers the next spring. (2) The on-crop reduces the transition of vegetative buds to reproductive buds. In hypotheses 1 and 2, fruit exert their effect during the summer or winter, respectively. Vegetative shoot growth and return bloom were quantified for shoots with and without fruit for both on- and off-trees. Removal of fruit from individual shoots on-trees bearing on-crops provided evidence that fruit removal in June or July increased summer and fall vegetative shoot growth, resulting in a greater number of leafless floral shoots and flowers the following spring compared with shoots or trees with no fruit removed. Fruit removal from shoots in December did not affect flowering. The effect of fruit was not exclusively localized; individual shoots were influenced by the on- or off-condition of the tree.**

Introduction

Alternate bearing (also called biennial or uneven bearing) is the tendency of a fruit tree to produce a heavy crop in one year (on-year) followed by a light crop or no crop (off-year). The phenomenon is widespread, occurring in both deciduous and evergreen trees (Monselise and Goldschmidt, 1982). Alternate bearing may occur over an entire region, for a block of trees, for an individual tree, or even for part of the tree or one branch (Monselise and Goldschmidt, 1982). Alternate bearing is initiated by a favorable or unfavorable environmental trigger that results in a heavy on-crop or light off-crop, respectively (Hield and Hilgeman, 1969). Alternate bearing is a major problem in citrus production all over the world, especially in mandarin varieties (Wheaton, 1992). Many marketing problems result from alternate bearing. On-crop trees produce a large number of small size fruit (Hield and Hilgeman, 1969) and off-crop trees produce a small number of large, unattractive fruit with coarse rinds (Moss et al., 1974). In addition, this alternation in crop load, especially for trees within a block, makes orchard management practices difficult.

The alternate bearing habit in citrus is known to be due to a lack of flowering in the spring following a heavy on-crop year (Goldschmidt and Golomb, 1982; Hield and Hilgeman, 1969), rather than to poor fruit set (Goldschmidt and Golomb, 1982). Floral intensity (number of flowers) and yield and, therefore, the severity of alternate bearing, are inversely proportional to the size of the preceding year's crop load (number of fruit) (Becerra and Guardiola, 1984; Moss, 1971; 1973). Heavy crops are normally still on the tree during floral induction (Plummer et al., 1989) and sometimes during anthesis and initial fruit set (Monselise and Goldschmidt, 1982). Delaying harvest in an on-crop year further reduces flowering in the following year (Hilgeman et al., 1967a; 1967b)

For alternate bearing in citrus, the effect of fruit on floral intensity is due to the effect of crop load on floral shoot production each spring. Effects of fruit on a branch include decreased sprouting percentage and a decreased number of floral shoots in the return bloom (Plummer et al., 1989; Koshita et al., 1999). Fruit-bearing shoots normally have a lower number of leafless and leafy inflorescences, but a higher percentage of vegetative shoots (Koshita et al., 1999). The inhibitory effect of fruit extends to adjacent branches, but not to adjacent limbs (Mullins et al., 1989; Plummer et al., 1989). Most studies suggest that fruit exert their inhibitory effect on flowering during the period of floral induction (Plummer et al., 1989; Garcia-Luis et al., 1995a; 1995b) and that removal of fruit causes a decrease in vegetative shoots and an increase in reproductive shoots in the spring (Garcia-Luis et al., 1995a; 1995b). Effects of fruit removal on a branch include increased number of sprouting buds per shoot (Monselise et al., 1981), increased number of flowers, increased number of generative and mixed shoots, and a decreased number of vegetative shoots (Becerra and Guardiola, 1984; Garcia-Luis et al., 1995a). Monselise and Goldschmidt (1982) suggested that biennial bearing was induced through a lack of flowering positions after a heavy-bearing year. Some studies state the importance of spring vegetative shoot growth on the return bloom (Ehara et al., 1981; Plummer et al., 1989). Few studies, however, show the importance of summer and fall vegetative shoot growth to the return bloom. Monselise and Goldschmidt (1982) and Monselise et al. (1981) found that summer vegetative shoot growth was inhibited on trees with heavy crops.

Thus, the mechanism by which fruit exert their inhibitory effect on return bloom is unresolved, and the physiological basis of the inhibitory effect is unknown. In preparation for studies elucidating the physiology underlying the mechanism by which fruit cause the cyclic differences in floral intensity, the following two hypotheses were tested to identify the mechanism leading to alternate bearing in ‘Pixie’ mandarin *(Citrus reticulata* Blanco). (1) The on-crop reduces summer and fall vegetative shoot growth and, thereby, decreases the number of sites that can bear flowers the next spring. If this hypothesis is valid, removal of fruit just prior to or during sprouting of the summer vegetative flush will increase the number and length of vegetative shoots (if environmental conditions permit growth) and increase floral intensity in the spring on these shoots. (2) The heavy on-crop reduces the transition of vegetative buds to reproductive buds, resulting in more vegetative shoots and less reproductive shoots, a decrease in flower number and an off-crop. In ’Navel’ orange (*C. sinensis* L.), and presumably other *Citrus* spp., phase transition occurs approximately mid-December to mid-January in California (Lord and Eckard, 1987). If this hypothesis is valid, removal of fruit from approximately November to early January will increase the number of reproductive shoots and reduce the number of vegetative shoots formed during spring bloom. ‘Pixie’ mandarin, a strong alternate bearer grown in the Ojai Valley, Calif., USA, was used as the model system. In the case of ‘Pixie’ mandarin, the previous season’s crop is normally still on the tree during floral induction (December-January) and through anthesis (March-April). The crop reaches maturity in April-May. The effect of crop load and fruit removal from June through January on return bloom in spring was quantified in two separate studies.

Materials and Methods

Determining the effect of fruit removal. To determine the effect of fruit removal on return bloom, heavily bearing 10-year-old ‘Pixie’ mandarin trees on ‘Carrizo’ citrange (*C. sinensis* x *Poncirus trifoliata* [L.] Raf.) rootstock, in a commercial orchard in the Ojai Valley, Calif., USA, (34°27′ N, 119°15′ W) were used. Only visually healthy trees, with uniform canopy size, setting an on-crop (based on 4 years’ of yield data and visual confirmation) were selected for the experiment. The following treatments were replicated on 16 single-tree replicates: (*i*) one shoot with no fruit, (*ii*) one shoot with fruit, and (*iii*) eight shoots from which fruit were removed from one shoot per month from June through January, a total of 8 months. Selected (tagged) parent shoots were ≥1 year old. The number of nodes on each parent shoot was recorded, as well as the number of fruit per shoot. The number of summer and fall shoots produced, as well as the number of nodes per shoot, was determined until spring bloom. At full bloom, the number of leafless and leafy floral shoots, flowers, and vegetative shoots produced by each parent shoot was quantified. Harvest of mature fruit was after spring bloom.

Determining the effect of crop load. In a separate study, 12 on-crop and 12 off-crop 10-year-old ‘Pixie’ mandarin trees on ‘Troyer’ citrange rootstock in a commercial orchard in the Ojai Valley, were used. For on-crop trees, three fruit-bearing shoots and one non-bearing shoot (vegetative shoot) in each of the four quadrants of the tree (N, S, E and W) were selected and tagged for analysis. For the off-crop trees, one fruit-bearing and three non-bearing shoots in each of the four quadrants of the tree were selected and tagged. Shoots selected and tagged (parent shoots) were ≥1 year old. Only visually healthy tees, with uniform canopy size and on- and off-crops, respectively (based on 4 years’ of yield data and visual confirmation), were selected for the experiment. The number of nodes and fruit per parent shoot were recorded. The number of summer and fall shoots produced, as well as the number of nodes per shoot, was determined until spring bloom. At full bloom, the number of leafless and leafy floral shoots, flowers, and vegetative shoots produced by each parent shoot was quantified. Harvest of mature fruit was after spring bloom.

Statistical analysis. Analysis of variance was used to test for treatment effects on summer/fall vegetative shoot growth, floral intensity and production of leafless, leafy and vegetative shoots and yield at bloom using the General Linear Models procedure of the SAS statistical program (SAS Inst. Inc., Cary, N.C.). Means were separated using Duncan’s multiple range test at $P = 0.05$.

Results

Effect of fruit removal. All data are expressed as number per 100 total nodes, which includes the number of nodes on the selected parent shoot (≥1 year old) and the number of nodes on new shoots that developed until the next spring bloom. Removal of fruit from parent shoots of on-crop trees in June or July significantly increased the number of summer and fall vegetative shoots that developed and the number of nodes on these shoots compared to both non-bearing and fruit-bearing parent shoots (Table 1). These summer/fall shoots produced significantly more flowers during spring bloom than the summer/fall shoots borne on fruit-bearing parent shoots. Only the summer/fall shoots on parent shoots with fruit removed in June produced significantly more flowers than summer/fall shoots borne on non-bearing parent shoots. Flowers were predominantly borne on leafless floral shoots compared to leafy floral shoots (data not shown). Fruit removal in June or July significantly increased the number of leafless floral shoots produced on summer/fall shoots compared to the summer/fall shoots of both fruit-bearing and non-bearing shoots. Fruit removal in August produced an intermediate response. These shoots produced a greater number of summer/fall shoots than fruit-bearing shoots but not greater than non-bearing shoots. However, fruit removal in August resulted in more nodes on summer/fall shoots compared to summer/fall shoots on fruit-bearing and non-bearing shoots. Despite the increased number of nodes, there was no difference in the number of flowers or leafless floral shoots produced by summer/fall shoots for the August fruit removal treatment, fruit-bearing shoots or non-bearing shoots. Removal of fruit from parent shoots each month from September through January had no effect on the number of summer/fall vegetative shoots that developed or the number of nodes on these shoots and no effect on flowering or production of leafless floral shoots compared to non-bearing and fruit-bearing shoots.

The total number of shoots produced during spring bloom was the same for non-bearing parent shoots and those parent shoots with fruit removed in June or July (Table 2). For each of these treatments, total spring shoot production was significantly greater than for parent shoots with fruit removed in January and fruit-bearing shoots. Fruit removal from parent shoots from August through December only increased spring shoot production over that of fruit-bearing parent shoots. Non-bearing parent shoots and those with fruit removed in June, July or August produced significantly more flowers on the new spring growth than fruit-bearing parent shoots or parent shoots with fruit removed in January. In addition, parent shoots with fruit removed in June produced more flowers on spring shoots than parent shoots with fruit removed in September through December. All flowers were borne predominantly on leafless floral shoots compared to leafy floral shoots (data not shown). Non-bearing parent shoots and those with fruit removed in June or July produced significantly more leafless floral shoots than fruit-bearing shoots and parent shoots with fruit removed in January. Parent shoots with fruit removed in August only produced more leafless floral shoots than fruit-bearing parent shoots. It was of interest that fruit removal from parent shoots in June, July or August also significantly increased the number of flowers borne on the parent shoots themselves, i.e., on wood ≥1 year old, compared to fruit-bearing parent shoots (data not shown).

Table 1. Effect of fruit removal from shoots of on-crop trees from June through January on summer and fall vegetative shoot growth (S/F) and return bloom in spring.

Factor	S/F shoots	Nodes on S/F shoots	Flowers on S/F shoots	Leafless floral shoots on S/F shoots
	number per 100 nodes			
Non-bearing shoot	1.5 bc[z]	6.4 b	8.7 bc	5.4 b
Fruit removed				
June	5.3 a	21.0 a	21.0 a	17.5 a
July	5.3 a	21.2 a	18.3 ab	16.0 a
August	3.2 b	16.4 a	8.4 bc	4.3 b
September	1.4 bc	6.4 b	2.3 c	1.3 b
October	1.1 c	5.1 b	1.4 c	1.4 b
November	0.0 c	0.0 b	0.0 c	0.0 b
December	0.7 c	2.0 b	1.5 c	1.0 b
January	0.6 c	3.0 b	1.6 c	0.6 b
Fruit-bearing shoot	0.7 c	2.3 b	2.1 c	1.2 b
P-value	0.0001	0.0001	0.0001	0.0001

[z]Means in a vertical column followed by different letters are significantly different at the 5% level.

Table 2. Effect of fruit removal from shoots of on-crop trees from June through January on the return bloom in spring.

Factor	Total spring shoots	Total flowers	Total leafless floral shoots
	number per 100 nodes		
Non-bearing shoot	40.3 a[z]	40.7 ab	28.4 ab
Fruit removed			
June	41.4 a	43.2 a	31.7 a
July	42.9 a	39.2 ab	31.9 a
August	37.4 ab	38.3 ab	23.8 abc
September	30.3 ab	27.4 bc	17.5 bcd
October	32.4 ab	25.7 bc	15.4 bcd
November	33.1 ab	26.5 bc	13.3 cd
December	31.4 ab	26.0 bc	17.8 bcd
January	25.5 b	17.5 c	11.1 cd
Fruit-bearing shoot	12.5 c	11.7 c	7.4 d
P-value	0.0001	0.0001	0.0003

[z]Means in a vertical column followed by different letters are significantly different at the 5% level.

Effect of crop load. All data are expressed as number per 100 total nodes, which includes the number of nodes on the selected parent shoot (≥1 year old) and the number of nodes on new shoots that developed up until the next spring bloom. The on- or off-crop status of trees influenced flowering on summer/fall vegetative shoots and during return bloom in spring, independent of whether fruit were present on the parent shoot. Parent shoots of either type (fruit-bearing or non-bearing) on on-crop trees produced significantly fewer flowers on summer/fall vegetative shoots than off-crop trees, despite the lack of effect of crop load on the production of summer/fall vegetative shoots and the number of nodes on these shoots (Table 3). In addition, during return bloom both fruit-bearing and non-bearing shoots on on-crop trees produced significantly fewer total shoots, leafless floral shoots and flowers than these shoots on off-crop trees (Table 4).

Table 3. Effect of crop load on summer and fall vegetative shoot growth (S/F) and return bloom in spring.

Factor	S/F shoots	Nodes on S/F shoots	Flowers on S/F shoots
	number per 100 nodes		
Tree status			
On	0.2	1.2	0.3 b
Off	0.5	4.8	5.9 a
Shoot type			
Fruit-bearing	0.0 b[z]	0.1 b	0.1 b
Non-bearing	0.7 a	5.8 a	6.1 a
On tree			
Fruit-bearing shoot	0.0	0.0	0.0
Non-bearing shoot	0.7	4.6	1.2
Off tree			
Fruit-bearing shoot	0.1	0.5	0.4
Non-bearing shoot	0.7	6.2	7.7
Significance of F tests			
Tree status (T)	0.8551	0.2555	0.0645
Shoot type (S)	0.0001	0.0001	0.0216
T x S	0.6139	0.6698	0.0998

[z]Means in a vertical column followed by different letters are significantly different at the 5% level.

Table 4. Effect of crop load on the return bloom in spring.

Factor	Total spring shoots	Total flowers	Total leafless floral shoots
	number per 100 nodes		
Tree status			
On	10.6 b[z]	6.4 b	2.8 b
Off	46.4 a	59.9 a	18.8 a
Shoot type			
Fruit-bearing	6.8 b	4.1 b	1.6 b
Non-bearing	49.9 a	61.9 a	19.9 a
On tree			
Fruit-bearing shoot	3.1	0.2	0.1
Non-bearing shoot	32.9	25.2	10.6
Off tree			
Fruit-bearing shoot	18.3	16.3	6.1
Non-bearing shoot	55.6	74.2	23.0
Significance of F tests			
Tree status (T)	0.0001	0.0002	0.0050
Shoot type (S)	0.0001	0.0001	0.0001
T x S	0.0916	0.0002	0.0972

[z]Means in a vertical column followed by different letters are significantly different at the 5% level.

Fruit-bearing parent shoots on either on- or off-crop trees produced significantly fewer summer/fall vegetative shoots, significantly fewer nodes on summer/fall shoots and less flowers on these shoots compared to non-bearing parent shoots (Table 3). Moreover, fruit-bearing parent shoots produced significantly fewer spring shoots, leafless floral shoots and flowers than non-bearing shoots independent of the on- or off-crop status of the whole tree (Table 4).

The number of flowers produced by summer/fall vegetative shoots was weakly affected by the interaction between the on- or off-crop status of the tree and the fruit-bearing or non-bearing status of the parent shoot ($P = 0.0998$) (Table 3). However, the interaction between on- or off-crop status of the tree and parent shoot type (fruit-bearing or non-bearing) significantly affected the total number of flowers produced in the return spring bloom ($P = 0.0002$) (Table 4). The interaction had weak effects on the total number of shoots produced in the spring ($P = 0.0916$) and on the number of leafless floral shoots ($P = 0.0972$). The effect of the on-crop (whole tree effect) is evident on the non-bearing shoots of on-crop trees (Tables 3 and 4), whereas the localized effect of fruit on individual shoots is observed for fruit-bearing shoots on off-crop trees (Tables 3 and 4).

Discussion

The results of these studies provide evidence in support of hypothesis 1, that fruit are exerting an inhibitory effect in the summer (June to July) that reduces summer and fall vegetative shoot growth and, thereby, reduces the number of sites on which to bear flowers the following spring. Fruit removal from shoots in June and July increased the number of summer and fall vegetative shoots that developed and the number of flowers on the summer/fall shoots. Summer/fall vegetative shoots on parent shoots with fruit removed in June or July, respectively, contributed 49% and 47% of the total flowers in the return spring bloom. Parent shoots with fruit removed in June, July and August resulted in a higher number of leafless floral shoots in the return bloom compared to fruit-bearing shoots. Similar results were obtained for *C. sinensis* and *C. unshiu* when fruit were removed September through December, with increased flower number due to the increased number of leafless floral shoots (Becerra and Guardiola, 1984; Garcia-Luis et al., 1986). Fruit removal from parent shoots in June, July or August also significantly increased the number of flowers borne on the parent shoots themselves, i.e., on wood ≥1 year old, compared to fruit-bearing parent shoots. Fruit removal in September through January did not increase the number of summer/fall shoots that developed, nor the number of flowers on these shoots compared to fruit-bearing shoots. At spring bloom, these treatments also did not increase floral intensity compared to fruit-bearing shoots. An additional effect of fruit on spring shoot development and flowering cannot be ruled out since mature fruit remained on the trees past spring bloom.

In the present study, no evidence was obtained to support hypothesis 2. Fruit removal in December and January significantly increased total shoot production in spring but had no effect on floral intensity or the number of leafless (or leafy) floral shoots. Similar results were obtained for *C. unshiu* when fruit were removed in January or later (Garcia-Luis et al., 1986). During the return bloom in spring, the number of flowers on summer and fall vegetative shoots and the total number of flowers produced were each influenced by the interaction between the on- or off-crop status of the tree and the presence or absence of fruit of the parent shoot. Additional studies are being conducted to further establish that a heavy on-crop exerts a significantly greater effect during the summer, by reducing summer and fall vegetative shoot growth and the number of flowers borne on the old wood of the parent shoots, compared to the effect of the crop in winter in reducing return bloom in the spring. In these studies, the underlying physiological basis for the inhibitory effect of fruit on summer and fall vegetative shoot growth is being contrasted with the apparent lack of effect of fruit on phase transition in winter. Subsequently, management strategies to mitigate the negative effects of the on-crop on return bloom will be developed.

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