

# The Effect of Crop Load on Budbreak Influences Return Bloom in Alternate Bearing ‘Pixie’ Mandarin

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**ABSTRACT.** Alternate bearing trees produce a heavy (on) crop followed by a light (off) crop. Whereas it is well documented for citrus that fruit number in the current crop inversely affects flower number in the return bloom, when in the phenology of the tree and how fruit exert an effect on floral intensity the following spring remained unresolved. ‘Pixie’ mandarin (*Citrus reticulata*) was used as the model system to investigate when and how fruit perpetuate cyclic differences in floral intensity. Parent shoots (current spring flush shoots) were tagged on on-crop trees and fruit were removed from individual shoots or whole trees. The number of summer and fall (summer/fall) vegetative shoots that developed on parent shoots with and without fruit and the contribution of spring shoots (floral and vegetative) made by parent shoots alone (now 1 year old) and by their summer/fall shoots to return spring bloom was quantified. Removal of fruit from individual shoots on on-crop trees in June or July had no effect on the number of flowers contributed by parent (current spring) shoots to return bloom, but increased total flower number 4-fold because summer/fall shoot number increased more than 8-fold. Removal of fruit from individual shoots of on-crop trees after July had no effect on flower number. In the whole tree experiment, parent + summer/fall shoots of off-crop trees produced more flowers the following spring than on-crop trees due to greater flower production by both parent shoots and their greater number of summer/fall shoots. Removal of all fruit in July from on-crop trees resulted in 2-fold more flowers in spring compared with off-crop trees due to the increased number of flowers contributed by both parent shoots (75% of the total) and the increased number of summer/fall shoots. The importance of summer/fall shoots to return bloom was confirmed by removing all summer/fall shoots from off-crop trees. This reduced floral intensity to that of on-crop trees. Removing all fruit from on-crop trees in December increased the percentage of budbreak in spring and flower number on parent shoots to that of off-crop trees, whereas the number of summer/fall shoots and the number of flowers the parent shoots contributed to bloom were both less than that of off-crop trees. For the branch and whole tree experiments, flower number was significantly correlated with the percentage of spring budbreak on parent + summer/fall shoots ( $r^2 = 0.88$ ,  $P \leq 0.0001$  and  $r^2 = 0.71$ ,  $P \leq 0.0001$ ; respectively). Taken together, the results of this research provide evidence that fruit of the ‘Pixie’ mandarin reduce floral intensity of the return bloom by inhibiting budbreak, which reduces summer/fall shoot growth and thus the number of nodes that can bear inflorescences and development of spring shoots, which are predominantly floral.

Alternate bearing (also called biennial or uneven bearing) is the tendency of a fruit tree to produce a heavy crop (on-crop year) followed by a light crop or no crop (off-crop year). The phenomenon is widespread, occurring in deciduous and evergreen trees (Monselise and Goldschmidt, 1982). Alternate bearing may occur over an entire region or block of trees, for an individual tree, part of a tree, or even for one branch (Monselise and Goldschmidt, 1982). Alternate bearing is initiated by an environmental trigger that is favorable or unfavorable to crop production, resulting in excessive fruit set or extreme thinning of reproductive structures, respectively (Hield

and Hilgeman, 1969). Alternate bearing is a major problem in citrus (*Citrus* spp.) production worldwide, especially with mandarin cultivars (Wheaton, 1992). Many marketing problems result from alternate bearing (Hield and Hilgeman, 1969; Moss et al., 1974). On-crop trees produce a large number of small size fruit of little commercial value (Hield and Hilgeman, 1969) and off-crop trees produce a small number of large size fruit, a high proportion of which have unattractive, thick coarse rinds and are culled in the packinghouse (Moss et al., 1974). In addition, this alternation in crop load, especially among trees within a block, makes orchard management 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), and not due to a negative effect of the heavy on-crop on fruit set (Goldschmidt and Golomb, 1982). Floral intensity (number of flowers) and yield are inversely proportional to the number of fruit produced the preceding year (Becerra and Guardiola, 1984; Moss, 1971, 1973). The inhibitory effect of fruit on flowering was reported to extend to adjacent branches, but not to adjacent limbs (Mullins et al., 1989; Plummer et al., 1989).

The severity of alternate bearing is reported as the alternate bearing index (I), which is equal to

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$$I = \frac{\sum_{i=1}^n \frac{|a_{i+1} - a_i|}{a_{i+1} + a_i}}{n - 1}$$

n = number of years for which the alternate bearing index is calculated  
a<sub>i+1</sub> + a<sub>i</sub> a<sub>i</sub> = yield in the i<sup>th</sup> year, with a<sub>1</sub> being the year 1 harvest

When I is 1, alternate bearing is 100%, and when I is 0, there is no alternate bearing (Pearce and Dobersek-Urbanc, 1967). For many citrus cultivars, the crop is typically 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 is known to further reduce return bloom (El-Otmani et al., 2004a; Hilgeman et al., 1967a, 1967b). Thus, it was suggested that fruit reduce flowering by inhibiting floral induction (Garcia-Luis et al., 1995, Koshita et al., 1999; Plummer et al., 1989). Consistent with this proposal, fruit removal during this period increased floral shoot number in spring with a concomitant decrease in vegetative shoot number (Garcia-Luis et al., 1995). Similarly, earlier fruit removal in summer or 1 month before harvest in October increased the number of buds that sprouted per shoot (Monselise et al., 1981), the number of leafless (one apical flower with or without additional lateral flowers and no leaves on a single shoot) and leafy (one apical flower with or without additional lateral flowers with one or more leaves on a single shoot) floral shoots, and the number of flowers, but reduced the number of vegetative shoots (Garcia-Luis et al., 1995).

Monselise and Goldschmidt (1982) suggested that biennial bearing was induced through a loss of flowering positions after a heavy on-crop year. The authors cited the inhibitory effect of the heavy on-crop on summer vegetative shoot growth (Monselise and Goldschmidt 1982; Monselise et al., 1981). Others also noted the inhibitory effect of fruit on shoot emergence and return bloom (Ehara et al., 1981; Plummer et al., 1989). However, no studies have quantified the contribution of summer and fall vegetative shoot growth to return bloom.

The objective of the research presented herein was to determine when in the phenology of the tree the setting on-crop negatively impacts floral intensity of the return bloom, hence reducing return yield to perpetuate alternate bearing in 'Pixie' mandarin. The following three hypotheses were tested: 1) the on-crop reduces summer and fall vegetative shoot growth and thereby decreases the number of nodes that can bear flowers the next spring; 2) the heavy on-crop reduces the transition of vegetative buds to floral buds, resulting in more vegetative shoots and less floral shoots; and 3) the on-crop inhibits budbreak in the spring. 'Pixie' mandarin is a strong alternate bearer, which might be due in part to the fact that the mature crop is normally still on the tree during floral induction through anthesis and early fruit set. For navel orange (*Citrus sinensis*), and presumably other *Citrus* species in California, the transition from vegetative to reproductive development occurs about in mid-December to mid-January (Lord and Eckard, 1987). Thus, if fruit reduce floral intensity at return bloom by inhibiting phase transition, removal of fruit from about November to early January of an on-crop year should increase the number of floral shoots and reduce the number of vegetative shoots formed during spring bloom. Alternatively, if fruit reduce floral

intensity by inhibiting summer and fall shoot growth, summer through fall fruit removal should increase the number of vegetative shoots in these flushes and, hence, the number of nodes that bear flowers in spring. Thus, removing the summer and fall shoots from off-crop trees should greatly reduce the floral intensity of these trees. To determine when crop load exerts an effect on return bloom, fruit were removed from shoots of on-crop trees from June through January or from entire on-crop trees in July and in December before irreversible commitment to flowering. The number of floral shoots, flowers, and vegetative shoots contributed by parent shoots (current spring flush shoots) alone or including their summer/fall shoots to bloom the following spring was quantified in the two separate experiments, respectively.

## Material and Methods

### Plant material

Ten-year-old 'Pixie' mandarin trees on 'Troyer' citrange (*C. sinensis* × *Poncirus trifoliata*) or 'Carrizo' citrange (*C. sinensis* × *P. trifoliata*) rootstocks were used in two separate experiments, respectively. The trees were located in commercial orchards in the Ojai Valley, CA (lat. 34°27'N, long. 119°15'W).

### Treatments and measurements

**FRUIT REMOVAL FROM SHOOTS OF ON-CROP TREES.** Visually healthy trees of uniform canopy size and setting an on-crop were selected for the experiment. The following treatments were replicated 16 times in a randomized complete block design in which a single tree equals a block: 1) one shoot setting no fruit, 2) one shoot setting fruit, and 3) eight shoots setting fruit, from which fruit were removed from one shoot per month from June through January. These shoots were current spring flush shoots and were referred to as parent shoots. With the exception of parent shoots in treatment 1, shoots set an average of 3.5 fruit per shoot, with no significant differences in fruit number per parent shoot among treatments. The number of nodes on each parent shoot, the number of summer/fall shoots produced by each parent shoot, and the number of nodes on the summer/fall shoots were determined through the following spring bloom. At full bloom, the number of leafless and leafy floral shoots, flowers, and vegetative shoots produced by each parent shoot (now 1 year old) and summer/fall shoot was quantified. The total productivity of a parent shoot, including the contribution of the summer/fall shoots, is referred to as parent + summer/fall.

**WHOLE TREE FRUIT AND SHOOT REMOVAL.** Visually healthy trees of uniform canopy size and setting an on-crop or off-crop were selected for the experiment. The following treatments were replicated eight times in a randomized complete block design in which an individual tree equals a replicate: 1) on-crop control trees; 2) removal of all fruit on 23 July from on-crop trees; 3) removal of all fruit on 11 Dec. from on-crop trees; 4) off-crop control trees; and 5) removal of all summer (1 Aug.) and fall (29 Oct.) vegetative shoots from off-crop trees. Parent shoots (current spring flush shoots) were selected and tagged. For on-crop trees, three fruit-bearing and one nonbearing (vegetative) parent shoot in each of the four quadrants of the tree (north, south, east, and west) were tagged for analysis. For the off-crop trees, one fruit-bearing and three nonbearing parent shoots in each of the four quadrants of the tree were tagged. The ratio of bearing to nonbearing parent shoots that were tagged

reflected that of on- and off-crop trees, respectively. Fruit-bearing parent shoots had an average of 2.9 fruit per shoot and there were no significant differences in fruit number on parent shoots for trees in different treatments. The number of nodes per parent shoot, the number of summer/fall shoots produced by each parent shoot, and the number of nodes on the summer/fall shoots were determined through spring bloom. At full bloom, the number of flowers, leafless and leafy floral shoots, and vegetative shoots produced by each parent (now 1 year old) and summer/fall shoot was quantified. The percentage budbreak was calculated by dividing the total number of floral and vegetative shoots produced by parent or summer/fall shoots in spring by the total number of nodes on the parent or summer/fall shoots, respectively. Total productivity of parent shoots including the contribution of the summer/fall shoots is referred to as parent + summer/fall. Yield data were collected at commercial harvest.

### Statistical analysis

All data are reported as mean number per shoot unless stated otherwise. 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 at bloom and yield using the General Linear Models procedure of SAS (version 6.12; SAS Institute, Cary, NC). Means were separated using Duncan's multiple range test at  $P \leq 0.05$ . In addition, regression analysis was used to determine the relationship between the number of flowers per node of the parent + summer/fall shoots and budbreak per node of the parent + summer/fall shoots.

## Results

### Effect of fruit removal from shoots of on-crop trees

**PARENT SHOOTS INDEPENDENT OF SUMMER/FALL SHOOTS.** Yield for the on-crop trees in this orchard was  $\approx 120$  kg per tree at commercial harvest. Removal of fruit each month from June through January from shoots of on-crop trees significantly increased the percentage of budbreak on parent shoots (now 1

year old) during return bloom in spring compared with the fruit-bearing parent shoots (control) that did not have fruit removed (Table 1). Removing fruit from June through January had no significant effect on the number of nodes per parent shoot. Despite the increasing lateness of the month in which the fruit were removed, including January, the percentage of budbreak in each case was equal to that of the nonbearing parent shoots. This demonstrates the inhibitory effect of fruit on budbreak of the parent shoots during return bloom. The greater budbreak in spring on nonbearing parent shoots and on bearing shoots with fruit removed only resulted in a numerical, not a statistically significant, increase in flower number per parent shoot compared with that of fruit-bearing shoots (Table 1). There were strong, significant, and positive relationships between budbreak and the number of flowers and the number of leafless floral shoots per parent shoot ( $r^2 = 0.83$ ,  $P \leq 0.0001$  and  $r^2 = 0.75$ ,  $P \leq 0.0001$ ; respectively), but only a weak significant positive relationship between budbreak and the number of leafy floral shoots produced per parent shoot ( $r^2 = 0.36$ ,  $P \leq 0.0001$ ). There was no relationship between spring budbreak and the number of vegetative shoots produced per parent shoot ( $r^2 = 0.00$ ,  $P \leq 0.7352$ ).

Removal of fruit from parent shoots of on-crop trees in June significantly increased the number of summer/fall vegetative shoots, the number of nodes on summer/fall shoots, and the percentage of budbreak on summer/fall shoots compared with nonbearing and fruit-bearing parent shoots (Table 2). The increase in summer/fall vegetative shoot growth in response to June fruit removal resulted in a significantly greater number of flowers borne on a significantly greater number of leafless floral shoots compared with summer/fall shoots of nonbearing or fruit-bearing shoots.

July fruit removal from parent shoots of on-crop trees significantly increased the number of summer/fall vegetative shoots and the number of nodes on these shoots compared with nonbearing and fruit-bearing parent shoots. The effect of fruit removal in July on these two parameters was not significantly

Table 1. Effect of fruit removal from parent shoots of on-crop 'Pixie' mandarin trees from June through January on the contribution of the parent shoot independent of the contribution of the summer/fall vegetative shoots to return bloom in spring. The number of flowers, leafless and leafy floral shoots, and vegetative shoots are expressed as the mean number per parent shoot.

	Budbreak <sup>y</sup> (%)	Nodes	Flowers	Leafless floral shoots <sup>x</sup>	Leafy floral shoots <sup>w</sup>	Vegetative shoots
		(mean no. per parent shoot)				
Nonbearing shoot	34.6 a <sup>z</sup>	51.1 a	17.6 a	12.9 a	3.0 a	1.9 a
Fruit removed						
June	31.9 a	60.7 a	19.4 a	12.4 a	3.6 a	3.1 a
July	35.6 a	51.4 a	16.1 a	12.3 a	2.3 a	3.1 a
August	37.9 a	52.3 a	20.9 a	12.3 a	3.6 a	2.6 a
September	29.8 a	53.0 a	15.6 a	10.3 a	4.4 a	2.5 a
October	32.0 a	51.1 a	14.5 a	9.4 a	4.1 a	3.8 a
November	33.1 a	50.8 a	15.0 a	8.6 a	5.4 a	3.2 a
December	30.5 a	51.8 a	11.4 a	7.6 a	3.8 a	3.1 a
January	25.3 a	55.1 a	8.6 a	5.4 a	3.6 a	4.3 a
Fruit-bearing shoot	10.6 b	61.0 a	6.7 a	4.5 a	1.8 a	1.0 a
P value	0.0020	0.7918	0.1597	0.2002	0.3345	0.2282

<sup>z</sup>Means in a vertical column followed by different letters are significantly different at the 5% level by Duncan's multiple range test.

<sup>y</sup>Budbreak is the total number of floral and vegetative shoots produced in spring expressed as a percentage of the total number of nodes on the parent shoot only.

<sup>x</sup>Leafless floral shoots have one apical flower with or without additional lateral flowers and no leaves on a single shoot.

<sup>w</sup>Leafy floral shoots have one apical flower with or without additional lateral flowers with one or more leaves on a single shoot.

Table 2. Effect of fruit removal from parent shoots of on-crop 'Pixie' mandarin trees from June through January on the contribution of the summer/fall vegetative shoots to return bloom in spring. The number of summer/fall shoots and the number of nodes on the summer/fall shoots, number of flowers, leafless and leafy floral shoots, and vegetative shoots are expressed as the mean number per parent shoot.

	Summer/fall shoots	Summer/fall nodes	Budbreak <sup>y</sup> (%)	Flowers	Leafless floral shoots <sup>x</sup>	Leafy floral shoots <sup>w</sup>	Vegetative shoots
	(mean no. per parent shoot)			(mean no. per parent shoot)			
Nonbearing shoot	1.3 cd <sup>z</sup>	5.5 bc	38.5 b	8.1 bc	5.6 bc	1.5 a	0.2 a
Fruit removed							
June	4.9 a	21.0 a	96.1 a	22.4 a	19.1 a	1.4 a	0.3 a
July	4.1 ab	17.5 a	41.3 b	16.0 ab	14.4 ab	0.6 a	0.6 a
August	2.5 bc	12.8 ab	21.4 b	7.0 bc	3.4 c	1.5 a	0.3 a
September	0.6 cd	2.8 bc	13.3 b	1.2 c	0.6 c	0.4 a	0.1 a
October	0.7 cd	3.3 bc	9.7 b	0.9 c	0.9 c	0.0 a	0.6 a
November	0.0 d	0.0 c	0.0 b	0.0 c	0.0 c	0.0 a	0.0 a
December	0.4 cd	1.1 c	13.3 b	0.7 c	0.4 c	0.3 a	0.0 a
January	0.3 cd	1.7 c	7.9 b	0.9 c	0.4 c	0.1 a	0.1 a
Fruit-bearing shoot	0.5 cd	1.7 c	22.7 b	1.6 c	0.8 c	0.6 a	0.2 a
<i>P</i> value	0.0001	0.0001	0.0293	0.0003	0.0004	0.0724	0.4884

<sup>z</sup>Means in a vertical column followed by different letters are significantly different at the 5% level by Duncan's multiple range test.

<sup>y</sup>Budbreak is the total number of floral and vegetative shoots produced in spring expressed as a percentage of the total number of nodes on the summer/fall shoots.

<sup>x</sup>Leafless floral shoots have one apical flower with or without additional lateral flowers and no leaves on a single shoot.

<sup>w</sup>Leafy floral shoots have one apical flower with or without additional lateral flowers with one or more leaves on a single shoot.

different from the effect of fruit removal in June or August. Fruit removal in July had no significant effect on budbreak on summer/fall vegetative shoots during return bloom relative to other treatments. However, removal of fruit in July from parent shoots of on-crop trees resulted in summer/fall shoots having an equal number of flowers and leafless floral shoots during return bloom as summer/fall shoots on nonbearing shoots or those with fruit removed in June. July fruit removal resulted in a significantly greater number of flowers borne on a significantly greater number of leafless floral shoots than was produced by summer/fall vegetative shoots of fruit-bearing parent shoots and those shoots with fruit removed in September through January (Table 2).

Removal of fruit from parent shoots of on-crop trees in August did not increase the number of summer/fall shoots, the percentage of budbreak on summer/fall shoots, or the number of flowers or leafless floral shoots that developed on summer/fall shoots compared with nonbearing and fruit-bearing parent shoots or shoots with fruit removed in September through January, despite a greater number of nodes than summer/fall shoots on fruit-bearing shoots or shoots with fruit removed from November through January (Table 2). Removal of fruit from parent shoots of on-crop trees each month from September through January had no significant effect on the number of summer/fall vegetative shoots, the number of nodes on summer/fall shoots, budbreak on summer/fall shoots, or on the number of flowers or leafless floral shoots borne on the summer/fall shoots during return bloom compared with both nonbearing or fruit-bearing parent shoots (Table 2). No treatment had an effect on the number of leafy floral shoots or vegetative shoots produced by summer/fall vegetative shoots during return bloom (Table 2).

The number of flowers and the number of leafless floral shoots produced in the spring was significantly related to the mean percentage of budbreak of summer/fall shoots per parent shoot ( $r^2 = 0.96$ ,  $P \leq 0.0001$  and  $r^2 = 0.94$ ,  $P \leq 0.0001$ ; respectively) to a greater degree than to the number of summer/fall shoots per parent shoot ( $r^2 = 0.84$ ,  $P \leq 0.0001$  and  $r^2 = 0.77$ ,

$P \leq 0.0001$ ; respectively) or to the total number of nodes present on summer/fall shoots ( $r^2 = 0.77$ ,  $P \leq 0.0001$  and  $r^2 = 0.68$ ,  $P \leq 0.0001$ ; respectively).

**PARENT + SUMMER/FALL SHOOTS.** Fruit removal from parent shoots of on-crop trees in June or July increased the number of flowers and total spring flush shoots that developed on parent + summer/fall shoots to a value that was significantly greater than that of fruit-bearing parent + summer/fall shoots, but equal to that of nonbearing parent + summer/fall shoots (Table 3). The greater number of flowers and total shoots that developed on parent + summer/fall shoots in response to June or July fruit removal compared with fruit-bearing parent + summer/fall shoots was due to a significant increase in the number of flowers and total shoots produced by summer/fall shoots, not parent shoots, during return bloom (Table 3). Only fruit removal in June and July increased the number flowers and total shoots contributed by summer/fall shoots to a number equaling the contribution of parent shoots in each treatment (Table 3). For shoots with fruit removed in June, summer/fall shoots produced, respectively, 57% of the flowers and 56% of the total shoots in spring, whereas for nonbearing shoots, summer/fall shoots produced only 32% of the flowers and 29% of the total spring shoots. Delaying fruit removal to August or later dramatically reduced the contribution of the summer/fall shoots to total flower and shoot number (budbreak) relative to the parent shoots. Fruit removal from September through January did not significantly increase flower number in the return bloom above that of fruit-bearing parent + summer/fall shoots. Total number of flowers produced by parent + summer/fall shoots was significantly correlated with spring budbreak ( $r^2 = 0.88$ ,  $P \leq 0.0001$ ).

#### Whole tree fruit and shoot removal

On-crop trees used in this experiment yielded 177 kg of fruit per tree, whereas off-crop trees yielded only 51 kg of fruit per tree. Yield was significantly different between on- and off-crop trees ( $P \leq 0.05$ ). In two subsequent years, 'Pixie' mandarin trees bearing on- and off-crops were selected (different trees

Table 3. Effect of fruit removal from parent shoots of on-crop 'Pixie' mandarin trees from June through January on the contribution of the parent shoot plus the contribution of the summer/fall vegetative shoots to return bloom in spring. The number of total flowers and total shoots produced during the return bloom in spring on parent + summer/fall shoots, parent shoots minus the contribution of the summer/fall shoots, and on summer/fall shoots are expressed as the mean number per parent shoot.

	Total flowers on parent + summer/fall shoots	Total spring shoots on parent + summer/fall shoots (mean no. per parent shoot)	Total flowers on parent shoots	Total flowers on summer/fall shoots	<i>P</i> value	Total spring shoots on parent shoots (mean no. per parent shoot)	Total spring shoots on summer/fall shoots	<i>P</i> value
Nonbearing shoot	25.7 abcd <sup>z</sup>	25.1 ab	17.6 a <sup>Ay</sup>	8.1 bc <sup>A</sup>	0.2446	17.8 a <sup>A</sup>	7.3 bc <sup>A</sup>	0.1579
Fruit removed								
June	39.2 a	37.5 a	19.4 a <sup>A</sup>	22.4 a <sup>A</sup>	0.6641	19.1 a <sup>A</sup>	20.9 a <sup>A</sup>	0.8047
July	32.1 ab	33.3 a	16.1 a <sup>A</sup>	16.0 ab <sup>A</sup>	0.9847	17.6 a <sup>A</sup>	15.7 ab <sup>A</sup>	0.7730
August	27.9 abc	23.6 abc	20.9 a <sup>A</sup>	7.0 bc <sup>A</sup>	0.0722	18.4 a <sup>A</sup>	5.1 bc <sup>B</sup>	0.0178
September	16.8 bcd	18.3 bc	15.6 a <sup>A</sup>	1.2 c <sup>B</sup>	0.0066	17.2 a <sup>A</sup>	1.1 c <sup>B</sup>	0.0016
October	15.4 bcd	18.8 bc	14.5 a <sup>A</sup>	0.9 c <sup>B</sup>	0.0043	17.3 a <sup>A</sup>	1.5 c <sup>B</sup>	0.0008
November	15.0 bcd	17.2 bc	15.0 a <sup>A</sup>	0.0 c <sup>B</sup>	0.0106	17.2 a <sup>A</sup>	0.0 c <sup>B</sup>	0.0023
December	12.1 cd	15.2 bc	11.4 a <sup>A</sup>	0.7 c <sup>B</sup>	0.0023	14.5 a <sup>A</sup>	0.7 c <sup>B</sup>	0.0002
January	9.5 cd	13.9 bc	8.6 a <sup>A</sup>	0.9 c <sup>B</sup>	0.0047	13.3 a <sup>A</sup>	0.6 c <sup>B</sup>	0.0001
Fruit-bearing shoot	8.3 d	8.9 c	6.7 a <sup>A</sup>	1.6 c <sup>B</sup>	0.0108	7.3 a <sup>A</sup>	1.6 c <sup>B</sup>	0.0108
<i>P</i> value	0.0013	0.0006	0.1597	0.0003		0.1421	0.0004	

<sup>z</sup>Means in a vertical column followed by different lower case letters are significantly different at the 5% level by Duncan's multiple range test.

<sup>y</sup>Means in adjoining cells in a horizontal row followed by different upper case letters are significantly different at the 5% level by paired Student's *t* test.

each year) to quantify the effect of crop load on return bloom and return yield. In both years, the heavy on-crop significantly reduced the number of floral shoots, but not the number of vegetative shoots, in the return bloom compared with the effect of the light off-crop (Table 4). In both cases, the reduction in floral intensity resulted in the production of an off-crop the year following the on-crop (Table 4). Thus, there was an inverse relationship between the current crop yield and the total number of floral shoots produced in the return bloom the following spring ( $r = -0.63, P \leq 0.0007$ ) and the resulting return yield ( $r = -0.57, P \leq 0.0081$ ). The severity of alternate bearing in the orchard is reflected in the alternate bearing index of 0.57 calculated using 4 years (consecutive) of yield data from 24 trees per year.

**PARENT SHOOTS INDEPENDENT OF SUMMER/FALL SHOOTS.** The greater number of fruit present on on-crop trees significantly reduced the percentage of budbreak, the number of flowers, and the number of leafless and leafy floral shoots produced by parent shoots (now 1 year old) during return bloom compared with off-crop trees (Table 5). Removal of all fruit in July from

on-crop trees significantly increased the percentage of budbreak, the number of flowers, and the number of leafless and leafy floral shoots produced by parent shoots in the return bloom compared with parent shoots of on-crop and even off-crop trees and off-crop trees with summer and fall flush vegetative shoots removed on 1 Aug. and 29 Oct., respectively. Removing all fruit 5 months later in December also significantly increased the percentage of budbreak and the number of flowers and the number of leafless and leafy floral shoots produced by parent shoots to values greater than parent shoots on on-crop trees and equal to those of parent shoots on off-crop trees, with the exception that leafy floral shoot number was significantly greater than that of off-crop trees (Table 5). Parent shoots of off-crop trees and off-crop trees with all summer/fall shoots removed were similar with regard to percentage of budbreak, number of flowers, and number of leafless and leafy floral shoots (Table 5). No treatment had a significant effect on the number of nodes per parent shoot. Thus, the effects of crop load and fruit removal on percentage of budbreak were independent of node number. No treatment had a significant

Table 4. Effect of crop load on the number of inflorescences and vegetative shoots produced during return bloom the following spring and on the resulting return crop for two separate sets of 12 off-crop and 12 on-crop 'Pixie' mandarin trees selected in years 1 and 2, respectively.

	Current crop from spring bloom year 1 (kg/tree)	Floral shoots from spring bloom year 2 (mean no. per parent shoot)	Vegetative shoots from spring bloom year 2	Return crop from spring bloom year 2 (kg/tree)
Off-crop trees	24.8 b <sup>z</sup>	2.59 a	0.33 a	103.5 a
On-crop trees	84.7 a	0.52 b	0.44 a	40.0 b
	Current crop from spring bloom year 2 (kg/tree)	Floral shoots from spring bloom year 3 (mean no. per parent shoot)	Vegetative shoots from spring bloom year 3	Return crop from spring bloom year 3 (kg/tree)
Off-crop tree	6.2 b	3.33 a	0.10 a	199.8 a
On-crop trees	124.9 a	0.30 b	0.30 a	27.0 b

<sup>z</sup>Means for separate sets (selected annually) of off- and on-crop trees in a vertical column followed by different letters are significantly different at the 5% level by Duncan's multiple range test.

Table 5. Effect of removing all fruit (July or December) or removing summer (August) and fall (October) vegetative shoots from on- and off-crop 'Pixie' mandarin trees, respectively, on the contribution of parent shoots independent of the contribution of the summer/fall vegetative shoots to return bloom in spring. The number of flowers, leafless and leafy floral shoots, and vegetative shoots are expressed as the mean number per parent shoot.

Treatment	Budbreak <sup>y</sup> (%)	Nodes	Flowers	Leafless floral	Leafy floral	Vegetative shoots
				shoots <sup>x</sup>	shoots <sup>w</sup>	
(mean no. per parent shoot)						
On tree	5.4 c <sup>z</sup>	35.5 a	0.8 d	0.2 c	0.5 c	0.8 a
Fruit removed (July)	43.2 a	33.2 a	19.8 a	8.6 a	4.9 a	0.7 a
Fruit removed (December)	34.8 ab	34.3 a	13.5 b	3.4 b	6.1 a	1.7 a
Off tree	26.3 b	29.8 a	8.8 bc	3.9 b	2.5 b	0.7 a
Summer/fall shoots removed	28.7 b	28.1 a	7.3 c	3.0 bc	2.8 b	1.4 a
<i>P</i> value	0.0001	0.9455	0.0001	0.0074	0.0004	0.0943

<sup>z</sup>Means in a vertical column followed by different letters are significantly different at the 5% level by Duncan's multiple range test.

<sup>y</sup>Budbreak is the total number of floral and vegetative shoots produced in spring expressed as a percentage of the total number of nodes on the parent shoot only.

<sup>x</sup>Leafless floral shoots have one apical flower with or without additional lateral flowers and no leaves on a single shoot.

<sup>w</sup>Leafy floral shoots have one apical flower with or without additional lateral flowers with one or more leaves on a single shoot.

effect on the number of vegetative shoots produced by parent shoots in the spring. The failure of the fruit removal or on- and off-crop status to influence vegetative shoot growth was also observed in the first experiment.

**SUMMER/FALL SHOOTS.** Parent shoots on off-crop trees produced a significantly greater number of summer/fall shoots than parent shoots on on-crop trees and trees in all other treatments (Table 6). In addition, summer/fall shoots on off-crop trees had more nodes and a greater percentage of budbreak resulting in more flowers borne on more leafless floral shoots during the return bloom than summer/fall shoots produced by parent shoots of on-crop trees. Removal of all fruit from on-crop trees in July resulted in the production of significantly more summer/fall shoots than on-crop trees, but significantly less summer/fall shoots than off-crop trees. However, fruit removal in July resulted in summer/fall shoots with a mean number of nodes, percentage of budbreak, flower number, and number of leafless floral shoots equal to summer/fall shoots of off-crop trees and greater than summer/fall shoots of on-crop trees (Table 6). Parent shoots of trees with all fruit removed in December produced significantly more summer/fall shoots than parent shoots of on-crop trees, but significantly less than off-crop trees

or trees with all fruit removed in July. Although the number of summer/fall shoots per parent shoot of trees with all fruit removed in December was significantly greater than that of on-crop trees, during return bloom, they had the same percentage of budbreak and floral intensity as summer/fall shoots on on-crop trees (Table 6). Off-crop trees with all summer/fall shoots removed also mimicked on-crop trees during return bloom. In this experiment, no treatment affected the number of leafy floral shoots produced by summer/fall shoots. In addition, crop load had no effect on the number of vegetative shoots produced by summer/fall shoots per parent shoot during the return bloom, as was the case in the previous experiment.

For off-crop trees, the number of summer shoots that developed was greater than the number of fall shoots. Compare a mean number of 1.9 summer flush vegetative shoots per parent shoot to 0.1 fall flush vegetative shoots per parent shoot. Summer shoots had fewer nodes (4.2) per shoot than fall shoots (6.0). Due to their greater number, summer shoots contributed more flowers (4.5) and leafless floral shoots (3.3) than fall flush shoots (1.2 and 0.2, respectively) per parent shoot during spring bloom. For off-crop trees, summer vegetative shoots and fall vegetative shoots contributed 31% and 8% of the total

Table 6. Effect of removing all fruit (July or December) or removing summer (August) and fall (October) vegetative shoots from on- and off-crop 'Pixie' mandarin trees, respectively, on the contribution of the summer/fall vegetative shoots to return bloom in spring. The number of summer/fall shoots and the number of nodes on the summer/fall shoots, number of flowers, leafless and leafy floral shoots, and vegetative shoots are expressed as the mean number per parent shoot.

Treatment	Summer/fall	Nodes	Budbreak <sup>y</sup> (%)	Flowers	Leafless floral	Leafy floral	Vegetative shoots
	shoots			shoots <sup>x</sup>	shoots <sup>w</sup>		
(mean no. per parent shoot)							
On tree	0.2 d <sup>z</sup>	1.5 b	2.0 b	0.2 b	0.1 b	0.1 a	0.0 a
Fruit removed (July)	1.4 b	7.1 a	29.9 a	6.6 a	2.5 a	1.7 a	0.0 a
Fruit removed (December)	0.7 c	3.2 b	8.7 b	2.2 b	0.8 b	0.6 a	0.1 a
Off tree	2.0 a	8.5 a	26.8 a	5.8 a	3.5 a	0.7 a	0.2 a
Summer/fall shoots removed	0.1 d	0.7 b	0.7 b	0.1 b	0.0 b	0.0 a	0.0 a
<i>P</i> value	0.0001	0.0009	0.0002	0.0182	0.0004	0.0725	0.0706

<sup>z</sup>Means in a vertical column followed by different letters are significantly different at the 5% level by Duncan's multiple range test.

<sup>y</sup>Budbreak is the total number of floral and vegetative shoots produced in spring expressed as a percentage of the total number of nodes on the summer/fall shoots.

<sup>x</sup>Leafless floral shoots have one apical flower with or without additional lateral flowers and no leaves on a single shoot.

<sup>w</sup>Leafy floral shoots have one apical flower with or without additional lateral flowers with one or more leaves on a single shoot.

number of flowers produced during return bloom, respectively. For summer flush shoots, 79% of the flowers produced were borne on leafless floral shoots, which comprised 88% of the total floral shoots. In contrast for fall vegetative shoots, leafless floral shoots were only 50% of the total. The number of leafy floral shoots and vegetative shoots that developed in spring was low and not significantly different for summer and fall flush shoots.

**PARENT + SUMMER/FALL SHOOTS.** Fruit removal from on-crop trees in July resulted in a significantly greater number of flowers and total shoots produced by parent + summer/fall shoots in spring compared with all other treatments (Table 7). These high values were due to an increase in the number of total shoots produced by parent shoots and summer/fall shoots compared with on-crop trees. However, parent shoots on trees with fruit removed in July contributed more flowers and total spring shoots to return bloom (75% and 77%, respectively) than summer/fall shoots. No other treatment increased floral intensity over that of the off-crop trees. As anticipated, the total number of flowers produced by parent + summer/fall shoots of off-crop trees with their summer/fall shoots removed was equal to that of parent + summer/fall shoots of on-crop trees and significantly lower than that of off-crop (control) trees without the summer/fall shoots removed. For this experiment, 71% of the variation in flower number during return bloom was due to budbreak on parent + summer/fall shoots ( $r^2 = 0.71$ ,  $P \leq 0.0001$ ), but budbreak on parent shoots alone explained 69% of the variation in flower number at spring bloom ( $r^2 = 0.69$ ,  $P \leq 0.0001$ ).

### Discussion

Results obtained in this research using 'Pixie' mandarin as the model system are consistent with earlier reports that the alternate bearing habit in citrus is due to a lack of flowers in spring following a heavy on-crop year (Goldschmidt and Golomb, 1982; Hield and Hilgeman, 1969). Quantifying the return bloom and yield of two separate sets of on- and off-crop 'Pixie' mandarin trees for 2 years (consecutive) provided strong evidence that floral shoot number and yield were greatly reduced the year following the on-crop compared with the year following the off-crop (Table 4). Results obtained with 'Pixie' mandarin did not support the suggestion that yield following a heavy on-crop could be equal to or greater than the yield

produced by the intense bloom following a light off-crop due to the greater fruit set potential of leafy floral shoots comprising the bloom following the heavy on-crop. Hence, the results obtained with the 'Pixie' mandarin were consistent with earlier reports (Becerra and Guardiola, 1984; Moss, 1971, 1973) that floral intensity and yield are inversely proportional to the number of fruit produced the previous year. For the 'Pixie' mandarin these relationships were also negative and significant ( $r = -0.63$ ,  $P \leq 0.0007$  and  $r = -0.57$ ,  $P \leq 0.0081$ ; respectively).

Results of the present research provide evidence in support of hypothesis 1, that young developing fruit exert a significant inhibitory effect, as early as June, that reduces the number of summer/fall shoots that develop and, thereby, reduces the number of nodes that can bear flowers the following spring. For example, parent shoots on on-crop trees with fruit removed in June or July produced significantly more summer/fall shoots than fruit-bearing shoots with no fruit removed and significantly more than even nonbearing shoots. The summer/fall shoots in these two treatments produced a net increase in total flowers per parent shoot of 115% and 99%, respectively, during spring bloom (Table 3). Parent shoots of on-crop trees with fruit removed from the entire tree in July also produced more summer/fall shoots than parent shoots on on-crop trees, with the summer/fall shoots increasing the number of flowers in the return bloom by 33% (Table 6). Consistent with the negative effect of fruit on the contribution of summer/fall shoots to return bloom, parent shoots of off-crop trees produced significantly more summer/fall vegetative shoots than parent shoots on on-crop trees. These summer/fall shoots increased the number of flowers per parent shoot in the return bloom by 66% (Table 6). For both experiments, at budbreak in spring, summer/fall shoots produced predominantly floral shoots. Whereas inhibition of summer/fall vegetative shoot growth by a heavy on-crop had been noted (Monselise and Goldschmidt, 1982; Monselise et al., 1981) and recent experiments using plant growth regulators to mitigate alternate bearing have provided evidence suggesting that summer/fall vegetative shoot growth might be important to return bloom (Benhamou et al., 2004; El-Otmani et al., 2004b), the direct contribution of summer/fall shoots to return bloom had not been previously quantified. For off-crop 'Pixie' mandarin trees, summer flush vegetative shoots contributed  $\approx 4$ -fold more flowers to return bloom than fall flush shoots. Moreover, in the present research,

Table 7. Effect of removing all fruit (July or December) or removing summer (August) and fall (October) vegetative shoots from on- and off-crop 'Pixie' mandarin trees, respectively, on the contribution of parent shoots plus the contribution of the summer/fall vegetative shoots to return bloom in spring. The number of total flowers and total shoots on parent + summer/fall shoots, total shoots on parent shoots minus the contribution of the summer/fall shoots, and total shoots on summer/fall shoots produced in the return bloom in spring are expressed as the mean number per parent shoot.

Treatment	Total flowers on parent + summer/fall shoots	Total spring shoots on parent + summer/fall shoots	Total spring shoots on parent – summer/fall shoots	Total spring shoots on summer/fall shoots
	(mean no. per parent shoot)			
On tree	1.0 c <sup>z</sup>	1.7 d	1.5 c	0.3 b
Fruit removed (July)	26.4 a	18.4 a	14.1 a	4.3 a
Fruit removed (December)	15.7 b	12.7 b	11.2 a	1.5 b
Off tree	14.6 b	11.4 b	7.1 b	4.4 a
Summer/fall shoots removed	7.3 c	7.3 c	7.3 b	0.1 b
P value	0.0001	0.0001	0.0011	0.0034

<sup>z</sup>Means in a vertical column followed by different letters are significantly different at the 5% level by Duncan's multiple range test.

the importance of the summer/fall vegetative shoots to return bloom was confirmed by removing these shoots from off-crop trees. This treatment resulted in parent + summer/fall shoots of off-crop trees producing a low number of flowers that was equal to that of on-crop trees and significantly less than off-crop trees from which the summer/fall vegetative shoots were not removed (Table 7).

Summer fruit removal also resulted in a significant increase in the number of flowers produced by parent shoots on on-crop trees that was independent of summer/fall shoot number. Parent shoots on on-crop trees from which all fruit were removed in July produced significantly more flowers on significantly more leafless and leafy floral shoots than parent shoots of on- or off-crop trees (Table 5). Thus, this treatment not only increased the number of flowers borne on an increased number of summer/fall vegetative shoots produced by the parent shoot, but also increased the number of flowers produced by the parent shoot itself. When fruit were removed in July, the parent shoots on average produced 75% of the flowers in the return bloom. Parent shoots on off-crop trees produced 60% of the total flowers in the return bloom. In contrast, removing fruit from parent shoots on on-crop trees (not the entire tree) in June or July had no effect on the number of flowers or leafless floral shoots that developed on parent shoots during the return bloom compared with fruit-bearing shoots from which fruit were not removed, demonstrating the significant over-riding effect of the on-crop status of the tree (Table 1).

In the present study, removing fruit from entire on-crop trees in December increased the number of flowers produced by parent + summer/fall shoots to a value equaling that of parent + summer/fall shoots on off-crop trees and greater than those of on-crop trees with no fruit removed (Table 7). The increase in flower number was due to the significant increase in the number of flowers produced on leafy inflorescences by the parent shoots alone, a number significantly greater than that of parent shoots on on- or off-crop trees. The number of flowers produced by parent + summer/fall shoots of on-crop trees with all fruit removed in December was significantly less than the number of flowers produced by parent + summer/fall shoots on on-crop trees with all fruit removed in July, due to a significantly lower number of flowers produced on significantly fewer summer/fall vegetative shoots. For parent shoots, July fruit removal increased the number of flowers borne on leafless and leafy inflorescences to values significantly greater than on- and off-crop trees. Fruit removal from entire Satsuma mandarin (*Citrus unshui*) trees from September through December resulted in more flowers on a greater number of leafless floral shoots (Becerra and Guardiola, 1984; Garcia-Luis et al., 1986), but the contribution of spring, summer, and fall shoots was not reported. The results of the research presented here are the first to quantify the effect of crop load on the contribution of each flush to return bloom.

Several researchers have proposed that fruit reduce flowering at return bloom by inhibiting floral induction in winter (Garcia-Luis et al., 1995; Plummer et al., 1989). Evidence for this effect is that removing fruit at this time increases floral shoot development at the expense of vegetative shoot development in the spring (Garcia-Luis et al., 1995; Monselise et al., 1981; Okuda, 2000). Consistent with the proposed inhibitory effect of fruit on the transition of vegetative shoot apices to floral apices, Monselise et al. (1981) and Okuda et al. (2002a, 2002b) reported that during spring bloom of Satsuma mandarin

trees, fruit-bearing shoots and fruit-bearing trees had a lower number of leafless and leafy floral shoots but a greater number of vegetative shoots compared with nonbearing shoots or nonbearing trees. The results of the research reported herein do not support these findings. The increase in the number of flowers and floral shoots observed during return bloom on parent + summer/fall shoots of on-crop trees when fruit were removed from the entire tree in July or December was not at the expense of vegetative shoot development in spring (Tables 5–7). Conversely, reduced flowering during spring bloom following a heavy on-crop was not associated with greater number of vegetative shoots that developed relative to that of off-crop trees. In part, the contrasting results reported here might be due to how the data are presented. If the number of vegetative shoots produced during spring bloom is expressed as a percentage of the total shoots produced rather than the mean number per parent shoot of on- and off-crop trees, vegetative shoot production does appear to increase at the expense of floral shoots in the return bloom following an on-crop even though the mean number of vegetative shoots per parent shoot is not significantly different. For example, in the present study, when expressed as a percentage, vegetative shoots were only 11% of the total shoots produced by off-crop trees, which produced many floral shoots and flowered intensely during return bloom. In contrast, an equal number of vegetative shoots is 54% of the total shoots produced by on-crop trees, which produced fewer floral shoots and flowered poorly during return bloom. As reported herein for ‘Pixie’ mandarin, fruit-bearing shoots of the ‘Valencia’ orange (*C. sinensis*) had a reduced number of floral shoots accompanied by a reduced number of vegetative shoots during the spring bloom relative to nonbearing shoots (Moss, 1971). In both experiments reported here, the number of vegetative shoots that developed during return bloom was low and only rarely affected by the presence or absence of fruit on a shoot or the on- or off-crop status of the tree. Thus, the results of this research provide no evidence to suggest that fruit inhibit transition from vegetative to reproductive development.

As previously reported by Becerra and Guardiola (1984), the results of the current research provided evidence that the number of flowers produced by parent + summer/fall shoots is directly related to the total number of shoots that develop during the return bloom. For both experiments, greater than 71% of the variation in flower number in the return bloom was due to the amount of budbreak on the parent + summer/fall shoots, consistent with hypothesis 3.

Thus, for the ‘Pixie’ mandarin in California, the alternating cycles of on- and off-crops appear to be perpetuated by a crop load-dependent inhibitory effect of fruit on budbreak. Early in their development, fruit repress the growth of the vegetative shoots that would comprise the summer flush and, subsequently, the fall flush. Later in their development, fruit inhibit spring budbreak on the parent shoots and the summer/fall vegetative shoots borne on the parent shoot. Summer (June and July) fruit removal had a more positive effect on return flower number than later fruit removal not only because earlier fruit removal resulted in a greater number of summer/fall vegetative shoots, but also because these shoots were highly floral. Moreover, summer fruit removal had a significant positive effect on budbreak on the parent shoot itself during spring bloom. Removal of all fruit in December from on-crop trees was sufficient to restore flowering on the parent shoots and on

the reduced number of summer/fall shoots present to that of the off-crop trees. Persistence of mature fruit on the tree through commercial 'Pixie' mandarin harvest in May significantly inhibited spring budbreak and reduced the contribution to flowering made by the parent shoots and the summer/fall vegetative shoots. These findings are consistent with the effect of early (October) harvest of on-crop 'Nour' Clementine mandarin trees, which increased the number of inflorescences per 100 nodes on spring (parent) and summer vegetative shoots the following spring compared with trees harvested in January. It is important to note that early harvest had a positive effect on return bloom of 'Nour' Clementine mandarin only if crop load was below a threshold value by October (El-Otmani et al., 2004a).

In light of the above, 'Pixie' mandarin growers should investigate the effects of degrees of fruit thinning or pruning to reduce fruit number in early summer of the on-crop year. In addition, for mandarin cultivars that mature sufficiently early, they should harvest all, or at least a significant portion, of the on-crop before or during December. The degree to which spring budbreak is affected by the on-crop for 'Nules' Clementine or navel oranges harvested as early as November or December in parts of California remains to be determined. However, for 'Pixie' mandarin, Valencia and other cultivars that mature during or after spring bloom, to mitigate alternate bearing it is important that on-crop trees be harvested as soon as possible after the fruit reach legal maturity to avoid having two crops on the trees into early summer. The results of the research presented here support those of El-Otmani et al. (2004a), Hilgeman et al. (1967b), Jones and Cree (1954), and Jones et al. (1964) that the cultural practice of holding fruit on the tree to extend the commercial harvest period during an on-crop year exacerbates alternate bearing.

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