Alternate bearing in olive

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Abstract

Alternate bearing (AB), a low-yield "off" crop (OFF tree, OFF year) followed by a high-yield "on" crop (ON tree, ON year), is initiated in perennial tree crops by adverse climate events that occur during bloom or fruit set and affect not only the crop trees, but also the pollinizer trees, causing poor flowering, reduced pollination and fruit set, or excessive flower and fruit drop. The result is an OFF crop that is typically followed by an ON crop. Conversely, optimal climate conditions during bloom and fruit set such that normal crop thinning fails to take place result in an ON crop, which is followed by an OFF crop. Globally, AB is a serious economic problem for oil and table olive growers. In OFF years, trees produce large fruit but too few to provide a good income. In ON years, trees produce a large number of small fruit of reduced commercial value that take longer to mature, attain size and accumulate oil. The delayed harvest exacerbates AB. For 'Manzanillo' olive (*Olea europaea* L.) in California, our results documented that the setting ON crop reduced spring and summer vegetative shoot growth, thereby reducing the number of nodes that could bear inflorescences the following spring. The ON crop further reduced floral intensity by inhibiting spring bud break. The negative effects of the ON crop of fruit on summer vegetative shoot growth and spring bud break were partially mitigated with cytokinin plant growth regulators.

Keywords: ON-crop tree/year, OFF-crop tree/year, vegetative shoot growth, spring bud break, plant growth regulators, auxin-transport inhibitor, cytokinin

INTRODUCTION

Alternate bearing (AB), repeating cycles of a low-yield "off" crop (OFF tree, OFF year) followed by a high-yield "on" crop (ON tree, ON year), occurs in perennial fruit and nut crops and in forest species (where it is called masting). AB is initiated by adverse climate events (low or high temperatures, drought, soil waterlogging, etc.) during bloom or fruit set that negatively impact not only the crop trees, but also pollinizer trees, causing poor flowering, reduced pollination and fruit set, or excessive flower and fruit drop. The result is an OFF crop that is typically followed the next year by an ON crop, depending on how long it takes the trees to recover. Conversely, optimal conditions during bloom and fruit set such that normal crop thinning fails to take place result in an ON crop, which is followed by an OFF crop. Worldwide, AB is a serious problem of economic consequence to oil and table olive growers (Sibbett, 2000). In OFF years, trees produce commercially valuable large fruit, but too few to provide a good income to the growers. In ON years, trees produce a large number of small fruit with reduced commercial value. Delaying the ON year harvest so the fruit can attain a greater size and accumulate oil to improve fruit quality exacerbates AB.

Once initiated, AB becomes entrained until reset by a second climate event or implementation of cultural management practices typically designed to reduce crop load (number of fruit per tree) in the ON year. Perpetuation of the alternating cycles of ON and OFF crops is due to the effect of crop load on endogenous tree factors that ultimately impact floral intensity, such that the ON crop reduces return bloom the following spring, whereas the OFF crop results in an intense return bloom. According to Sibbett (2000), "olives, for all practical purposes, are borne on one-year-old shoots (i.e. grown the previous season). In the

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year of the heavy crop, shoot growth that will bear the inflorescences for the subsequent crop is physically depressed – without fruitful shoots, no crop will occur the following year." This is strikingly similar to AB in mandarin (*Citrus reticulata* Blanco 'Pixie') (Verreynne and Lovatt, 2009). During the OFF year, the spring flush of vegetative shoots produces summer and fall vegetative shoot growth. These shoots bear inflorescences the following spring, resulting in an intense ON bloom. In contrast, the ON crop reduces the extension growth of spring, summer and fall vegetative shoots, resulting in a light OFF bloom and OFF crop. In *C. reticulata*, the ON crop also inhibits bud break the following spring, which also reduces floral intensity.

The research objectives were to determine for 'Manzanillo' olive: (i) when the ON crop reduces vegetative shoot growth; (ii) which vegetative shoot flushes contribute the majority of inflorescences to the following spring bloom, and (iii) whether the ON crop, which is harvested in September to October, inhibits spring bud break. The final objective was to use the results to develop and test plant growth regulator (PGR) strategies to mitigate the negative effects of the ON crop on return bloom.

MATERIALS AND METHODS

Plant material and plant growth regulator treatments

The research was conducted in a commercially bearing 'Manzanillo' olive orchard located in Exeter, CA, USA (36.3°N 119.15°W; 106 m a.s.l.). The 17-year-old trees were planted on their own roots at a spacing of 7.3×3.7 m. 'Barouni' olive pollinizer trees were planted at a ratio of one to ten. In year 1, seven OFF and seven ON (control) trees were selected at bloom. Five shoots without inflorescences (non-bearing; NBS) were tagged at a height of 1.5 m around the trees; five heavily flowering (bearing; BS) shoots were tagged on ON trees only. An additional 77 ON trees were selected at bloom and five NBS and five BS were tagged on each. The following spring (January through April of year 2), scaffold branches were injected with the following PGRs to identify the best treatment and application time for increasing bud break and return bloom: (i) tri-iodobenzoic acid (TIBA), an auxin-transport inhibitor, plus 6-benzyladenine (BA), a cytokinin, in January; (ii) TIBA + BA in February; (iii) a proprietary natural auxin-transport inhibitor (NATI) + BA in February; (iv) TIBA + a proprietary natural cytokinin (PCK) in February; (v) NATI + PCK in February; (vi) BA alone in February; (vii) PCK alone in February; (viii) TIBA alone in February; (ix) NATI alone in February; (x) TIBA + BA in March; and (xi) TIBA + BA in April. Each treatment was injected at the rate of 1 g active ingredient (a.i.) in 50 mL appropriate solvent divided between two syringes per compound per one main scaffold branch per tree. A randomized complete block (RCB) design with seven individual tree replications per 13 treatments was used. The following year, a second set of five OFF and five ON (control) trees and 40 additional ON trees were selected at bloom and 10 shoots per tree were tagged as described above. In July of year 1, scaffold branches were injected with the following PGRs to identify the best treatment for increasing summer vegetative shoot extension growth: (i) TIBA + BA; (ii) TIBA + PCK; (iii) NATI + BA; (iv) NATI + PCK; (v) TIBA alone; (vi) NATI alone; (vii) BA alone; and (viii) PCK alone. The RCB design had five individual tree replications per eight treatments.

Statistical analysis

Analysis of variance (ANOVA) was used to test for treatment effects on the number of nodes produced each month, inflorescence number per node pair, and flower number per inflorescence averaged across five NBS and five BS, per individual tree replication. When ANOVA output indicated significant differences, post-hoc comparisons were run using Fisher's least significant difference (LSD) test with a family error rate of $\alpha \leq 0.05$.

RESULTS

Effect of crop load on floral intensity the following spring

The most dramatic effect of crop load on return bloom was on BS of ON trees the next spring (year 2) (Table 1). The combined effects of crop load and the local effect of fruit borne on the shoot reduced inflorescence number per BS of ON trees 16.6-fold compared with NBS of ON trees and nearly 20-fold compared with NBS of OFF trees (P=0.0018). For BS of ON trees, the majority of inflorescences were produced at the apical first five node pairs (last year's vegetative shoot growth) (P=0.0438), whereas NBS of OFF and ON trees produced inflorescences through node pair 15 (Table 1). Despite a significant decrease in inflorescence number with increasing distance (shoot age) from the shoot apex (P<0.0001), NBS of OFF and ON trees produced significantly more inflorescences than BS of ON trees for node pairs 6 through 10 (P=0.0069) and 11 through 15 (P=0.0357). In addition, NBS on OFF and ON trees produced 3-fold more flowers (11.2) per inflorescence than BS of ON trees (3.7 flowers/inflorescence) (P<0.0001). Clearly, the localized effect of fruit borne on a shoot had a more negative impact on flowering than crop load, leaving NBS of ON trees as the major contributor of inflorescences the following spring. The proportion of NBS to BS was determined after fruit set for 50 shoots in each of four quadrants (N, E, W, S) of ON and OFF trees. ON trees had 39.9% NBS and 60.1% BS; OFF trees had 99.5% NBS but only 0.5% BS, explaining the ON bloom the following spring.

Table 1. Effect of nonbearing and bearing shoots of OFF and ON 'Manzanillo' olive trees in year 1 on inflorescence number at spring bloom in year 2.

Year 1 tree/shoot crop status	Number of inflorescences per node pair per shoot (spring year 2)					*P* value
	Total	1-5	6-10	11-15	16-20	
OFF/nonbearing	15.4 a[1]	7.1 a^{A}	5.3 a^{B}	2.2 a^{C}	0.4 a^{D}	<0.0001
ON/nonbearing	13.3 a	6.5 a^{A}	4.5 a^{B}	2.3 a^{C}	0.2 a^{D}	<0.0001
ON/bearing	0.8 b	0.7 b^{A}	0.0 b^{B}	0.1 b^{B}	0.0 a^{B}	0.0438
P value	0.0018	0.0002	0.0069	0.0357	0.2853	

[1]Values in a column followed by different lowercase letters and rows followed by different uppercase letters are significantly different at specified *P* values by Fisher's LSD test.

Effect of crop load on spring and summer vegetative shoot growth

For NBS and BS of ON trees, summer vegetative shoot growth was reduced 5-fold from July through October by the developing ON crop compared with NBS of OFF trees (P=0.0059) (Table 2). Crop load had no effect on shoot growth during November to December or January to February. However, in March through May of year 2, when NBS of OFF trees were now producing an ON bloom, shoot extension growth was reduced 40% compared with BS of ON trees, which were now producing very few inflorescences (P=0.0078) (Table 2). Similarly, NBS of ON trees, now the major source of inflorescences at spring bloom, also exhibited reduced spring vegetative shoot growth (25%) compared with BS of ON trees producing only a few inflorescences (P=0.0078). These results document that, when 'Manzanillo' olive trees produce an ON-bloom, spring vegetative shoot growth is reduced and, with the setting of the ON crop, summer vegetative shoot growth is also reduced.

Effects of PGRs on spring bud break and floral intensity

Both cytokinins, BA and PCK, applied in February following the ON year, significantly increased the number of buds that underwent bud break and the number of inflorescences produced by NBS of ON trees by more than 40% compared with NBS of OFF control trees and more than 66% compared with NBS of ON control trees (P<0.0001) (Table 3), consistent with the ON crop inhibiting spring bud break. Significant increases in inflorescence number were achieved by one or both cytokinins at node pairs 6-10, 11-15 and 16-20 on NBS of ON trees. These node pairs corresponded approximately to vegetative shoot growth that developed in the spring of year 1 and the previous summer and spring, respectively. No treatment significantly increased floral intensity of BS of ON trees.

Table 2. Effect of nonbearing and bearing shoots of OFF and ON 'Manzanillo' olive trees on vegetative shoot growth (net increase in number of node pairs) during the summer of year 1 (harvest was in October) and winter and spring of year 2.

Year 1 tree/shoot crop status	Net number of node pairs				*P* value
	Jul-Oct	Nov-Dec	Jan-Feb	Mar-May	
OFF/nonbearing	3.3 a^{A}[1]	0.1 a^{B}	0.2 a^{B}	1.5 b^{B}	0.0019
ON/nonbearing	0.7 b^{B}	0.0 a^{C}	0.2 a^{BC}	1.9 b^{A}	<0.0001
ON/bearing	0.6 b^{B}	0.1 a^{B}	0.1 a^{B}	2.5 a^{A}	0.0003
P value	0.0059	0.8732	0.4096	0.0078	

[1]Values in a column followed by different lowercase letters and rows followed by different uppercase letters are significantly different at specified *P* values by Fisher's LSD test.

Table 3. Effect of plant growth regulators (PGRs) injected into scaffold branches of ON-crop 'Manzanillo' olive trees the following January, February, March or April on the number of inflorescences produced by nonbearing and bearing shoots at spring bloom in year 2.

Year 1 tree/shoot crop status, PGRs[1]	Number of inflorescences per node pair per shoot (year 2)					*P* value
	Total	1-5	6-10	11-15	16-20	
OFF/nonbearing	15.4 b[2]	7.1 ab^{A}	5.3 bcd^{B}	2.2 cdef^{C}	0.4 cd^{D}	<0.0001
ON/nonbearing	13.3 bc	6.5 abcd^{A}	4.5 cde^{B}	2.3 cdef^{C}	0.2 cd^{D}	<0.0001
Jan TIBA+BA	10.5 bcd	4.4 cdefghi^{A}	4.1 cde^{A}	2.0 defg^{B}	1.1 abcd^{B}	0.0060
Feb TIBA+BA	16.3 ab	6.1 abcde^{A}	6.0 abc^{A}	3.7 bcde^{B}	1.4 abc^{C}	0.0002
Feb NATI+BA	16.9 ab	5.6 abcdefg^{A}	6.3 abc^{A}	4.9 ab^{A}	1.3 abcd^{B}	<0.0001
Feb TIBA+PCK	15.8 ab	6.1 abcde^{A}	5.5 bcd^{A}	3.4 bcde^{B}	2.4 a^{B}	0.0004
Feb NATI+PCK	8.7 cde	3.3 fghij^{A}	3.5 de^{A}	2.0 defg^{AB}	0.7 bcd^{B}	0.0245
Feb TIBA	14.8 bc	5.4 abcdefgh^{A}	5.5 bcd^{A}	3.9 bcd^{A}	0.7 bcd^{B}	0.0002
Feb NATI	8.7 cde	2.8 ijk^{A}	3.1 ef^{A}	1.9 efgh^{AB}	1.2 abcd^{B}	0.0293
Feb BA	22.0 a	7.8 a^{A}	7.8 a^{A}	5.0 ab^{B}	2.0 ab^{C}	<0.0001
Feb PCK	22.2 a	6.9 abc^{A}	7.5 ab^{A}	5.9 a^{A}	1.9 ab^{B}	<0.0001
Mar TIBA+BA	15.3 b	5.1 bcdefghi^{A}	6.3 abc^{A}	3.5 bcde^{B}	1.2 abcd^{C}	<0.0001
Apr TIBA+BA	16.0 ab	5.8 abcdef^{A}	6.1 abc^{A}	4.1 abc^{B}	1.2 abcd^{C}	<0.0001
ON/bearing	0.8 f	0.7 k^{A}	0.0 g^{B}	0.1 h^{B}	0.0 d^{B}	0.0438
Jan TIBA+BA	3.3 ef	3.0 hijk^{A}	0.3 g^{B}	0.0 h^{B}	0.0 d^{B}	0.0006
Feb TIBA+BA	3.6 ef	3.1 ghijk^{A}	0.4 g^{B}	0.0 h^{B}	0.0 d^{B}	0.0002
Feb NATI+BA	3.9 ef	3.4 fghij^{A}	0.4 g^{B}	0.0 h^{B}	0.0 d^{B}	<0.0001
Feb TIBA+PCK	4.9 def	3.9 efghij^{A}	0.8 g^{B}	0.3 gh^{B}	0.0 d^{B}	<0.0001
Feb NATI+PCK	2.1 f	1.7 jk^{A}	0.3 g^{B}	0.0 h^{B}	0.0 d^{B}	0.0063
Feb TIBA	4.7 def	4.3 defghi^{A}	0.4 g^{B}	0.0 h^{B}	0.0 d^{B}	0.0001
Feb NATI	3.9 ef	3.5 efghij^{A}	0.3 g^{B}	0.1 h^{B}	0.0 d^{B}	0.0002
Feb BA	4.1 def	3.3 fghij^{A}	0.6 g^{B}	0.3 gh^{B}	0.0 d^{B}	<0.0001
Feb PCK	5.1 def	3.5 efghij^{A}	1.1 fg^{B}	0.5 fgh^{B}	0.2 cd^{B}	<0.0001
Mar TIBA+BA	4.8 def	4.0 defghij^{A}	0.5 g^{B}	0.2 gh^{B}	0.1 cd^{B}	<0.0001
Apr TIBA+BA	4.2 def	3.7 efghij^{A}	0.6 g^{B}	0.0 h^{B}	0.0 d^{B}	<0.0001
P value	<0.0001	<0.0001	<0.0001	<0.0001	0.0006	

[1]TIBA, tri-iodobenzoic acid; NATI, natural auxin-transport inhibitor; BA, 6-benzyladenine; PCK, proprietary natural cytokinin.

[2]Values in a column followed by different lowercase letters and rows followed by different uppercase letters are significantly different at specified *P* values by Fisher's LSD test.

Effects of PGRs on summer vegetative shoot growth

All July PGR treatments significantly increased growth (number of node pairs) of NBS of ON trees during July to October (up to 5.6-fold) compared with NBS of ON control trees (P<0.0001) and to a value in all cases equal to that of NBS on OFF control trees (Table 4). All July PGR treatments also significantly increased shoot growth of BS of ON trees in July to October by more than 4.0-fold compared with BS of ON control trees (P<0.0001). Only PCK, NATI, TIBA+PCK and NATI+BA increased extension growth of BS of ON trees equal to that of NBS of OFF control trees during July through October.

Table 4. Effect of plant growth regulators (PGRs) injected into scaffold branches of ON-crop 'Manzanillo' olive trees in July of year 1 on the net increase in the number of node pairs from July to October of year 1.

Year 1 tree/shoot crop status, PGRs[1]	Net number of node pairs, July-Oct
OFF/nonbearing	3.3 abcde[2]
ON/nonbearing	0.7 ij
TIBA+BA	3.0 abcdefg
TIBA+PCK	3.6 ab
NATI+BA	3.9 a
NATI+PCK	3.5 abcd
TIBA	3.6 abc
NATI	3.2 abcdef
BA	2.6 bcdefgh
PCK	3.5 abcd
ON/bearing	0.6 j
TIBA+BA	1.9 ghi
TIBA+PCK	2.4 defgh
NATI+BA	2.4 cdefgh
NATI+PCK	2.1 fgh
TIBA	2.0 gh
NATI	2.2 efgh
BA	1.9 hi
PCK	2.6 bcdefgh
P value	<0.0001

[1]TIBA, tri-iodobenzoic acid; NATI, natural auxin-transport inhibitor; BA, 6-benzyladenine; PCK, proprietary natural cytokinin.

[2]Means followed by different letters are significantly different at P<0.0001 by Fisher's LSD test.

DISCUSSION

To evaluate the contribution of different vegetative shoot flushes to return bloom, extension growth was quantified as net increase in node pairs. In 'Manzanillo' olive, two opposing leaves identify a node pair, having two potential floral buds in the axil of each leaf (four potential inflorescences per node pair). Typically, two inflorescences developed at node pairs 1-5, but this number decreased to one inflorescence per node pair with increasing distance (shoot age) from the apex. The NBS of OFF and ON trees produced significantly more inflorescences the following spring (year 2) than BS of ON trees, predominantly at node pairs 1-5 and 6-10, which represent, moving back in time, the previous year's summer and spring vegetative shoot growth. Importantly, the spring following the OFF and ON crops, NBS produced inflorescences at node pairs 16-25, i.e., sections of the shoot definitely older than 1 year. The NBS of OFF trees, depending on crop load, produced approximately three to six node pairs during the OFF bloom in spring and another three to ten node pairs during OFF crop fruit development through harvest in October, such that summer shoots contributed the majority of inflorescences at spring bloom. The BS of ON trees produced only a few inflorescences the following spring, located at nodes 1-5, i.e., on the limited spring and summer vegetative shoot extension growth of a tree producing an ON bloom and setting an ON crop, respectively, and did not produce inflorescences on older sections of the shoot. The data also showed that the ON crop reduced summer vegetative shoot growth (number of node pairs) 5-fold in July through October for both NBS and BS compared with NBS of OFF trees, with greater reductions in shoot growth occurring in July to August than September to October. In addition, the data provided evidence that the ON bloom reduced spring vegetative shoot growth by 40% compared with OFF-bloom trees. Auxin-transport inhibitors and cytokinins, either alone or in combination, increased summer vegetative shoot growth for both NBS and BS of ON-crop 'Manzanillo' olive trees to equal to that of NBS of OFF, consistent with the potential role of the ON crop in correlative inhibition of the apical bud of vegetative shoots in summer, which was first proposed by Verreynne (2005) for 'Pixie' mandarin. Correlative inhibition is due to accumulation of auxin relative to cytokinin in the shoot apical bud. Consistent with inhibition of spring bud break by the ON crop, both cytokinins, when applied to ON trees in February, increased bud break and inflorescence number on NBS to a value significantly greater than that of NBS of OFF control trees, with a nonsignificant increase in inflorescence number on BS of ON trees. This is the first evidence that the ON crop of olive fruit inhibits spring bud break.

The results presented here show that the reduced number of inflorescences following the ON crop in 'Manzanillo' olive was due to: (i) reduced summer vegetative shoot growth (fewer node pairs, fewer inflorescences); (ii) few to no inflorescences produced on older shoot sections (after node pair 5); (iii) reduced spring vegetative shoot growth (fewer node pairs); (iv) inhibition of spring bud break; and (v) fewer flowers per inflorescence. These effects of the ON crop were more negative for BS, which were impacted by both crop load and fruit borne on the shoot, compared with NBS. The PGRs used in these experiments to mitigate the negative effects of the ON crop on summer vegetative shoot growth and spring bud break showed promise. Future research will test the successful PGRs as whole-canopy sprays to ON trees in summer plus spring to increase summer vegetative shoot growth and bud break, respectively, and, thus, increase return bloom and yield following the ON year.

ACKNOWLEDGMENTS

The authors thank the University of California (UC)-Riverside, NIFA, UC Cooperative Extension-Tulare County, and California Olive Committee for funding, C. Hill for use of his orchard, E. Jorgensen and M. Jorgensen for PGR injections, and T. Khuong for data analysis.

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