The floral biology of the olive II. The effect of inflorescence load and distribution per shoot on fruit set and load

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Abstract

The effect of inflorescence number and distribution along the shoot on the level of fruit-set was studied using 'ON' year olive trees with a high level of floral differentiation. Reduced levels and different inflorescence distribution patterns were created artificially by hand inflorescence thinning. In most cases, removal of up to 50% of the inflorescences had either no effect on the total amount of fruit load per shoot or increased it significantly. Thus, the percentage of fruit set increased with the reduction in inflorescence number due to both, a higher percentage of fruitful inflorescences and higher numbers of fruits per inflorescence. Inflorescences on the distal half of cv. Barnea shoots were less fruitful than on the proximal half. With cv. Manzanillo no such difference was found. Single inflorescence distribution significantly raised the level of both, the fruit load and fruit set compared with distribution of the inflorescences along the shoot in pairs, although the amount of this increase varied with the different thinning levels. The actual percent of fruit set on a flower number basis increased in parallel with the reduction of their number in response to inflorescence thinning.

Keywords: Olive; Floral biology; Fruit set

1. Introduction

The pre-bloom removal of up to 50% of the flowers from abundantly flowering olive shoots has been shown to have no significant effect on fruit set or load

(Lavee et al., 1996). Furthermore, the removal of up to 70% of the flowers within the inflorescence at pre-bloom (Lavee et al., 1996) or 60–88% at full bloom (Rallo and Fernández-Escobar, 1985) does not affect the fruit load per shoot irrespective of flower distribution within the inflorescence. This was also the case when up to 60% of the inflorescences were removed at any time from full bloom until the onset of fruit abscission which occurs 10 days after full bloom (Suarez et al., 1984). In various plant species, partial removal of inflorescences has no effect on the final number of fruits reaching maturity (Herrera, 1991). In others, however, the amount and distribution of the inflorescences may affect pollination and fruit development (Wyatt, 1982).

Cuevas et al. (1995) reported that in 60% of all flowers produced on an olive tree (cv. Arbequina) a pollen tube reached the micropyle of one of the four ovules. Still, only 4% of those flowers set fruit which reached maturity. Competition for nutrients among fruitlets and between fruitlets and flowers has been suggested as the major factor for the intensive post-anthesis flower and fruit abscission in abundantly flowering olive shoots. This assumption is based on: (a) the reported thinning experiments (Lavee et al., 1996; Rallo and Fernández-Escobar, 1985; Suarez et al., 1984), and (b) the observation that fertilization and early fruit growth precede the abscission of fertilized and unfertilized flowers (Rapoport and Rallo, 1991b; Cuevas et al., 1995). Competitive factors have also been reported as influencing olive pistil development (Uriu, 1959), indicating that competition plays a continuous role during all the stages of the development of the reproductive organs. In connection with competition among inflorescences, their distribution and position on the shoot has also to be considered. In this part of our study we examined the pre-bloom effect of inflorescence distribution, location and load on fruit set. By removing inflorescences to reduce flower number before anthesis the competition during pollination and the progamic phase was also assumed to be affected.

2. Materials and methods

In this study, we used irrigated unstressed highly-flowering olive trees (*Olea europaea* L.) cvs. Manzanillo and Barnea grown in the orchards of the Volcani Center at Bet Dagan and the Faculty of Agriculture at Rehovot in the center of the coastal plain of Israel. Uniformly long (ca. 40 cm) reproductive shoots with 90–95% axillary buds differentiated as inflorescences were tagged 10 days before flowering. Various patterns of inflorescence removal were performed 5–7 days before anthesis, using scissors to prevent damage to the nearby leaf petioles. Inflorescence removal levels were in all cases 0 (control), 25%, 50%, and 75%. In most experiments with cv. Barnea a treatment with 66% inflorescence removal was also included. The retained inflorescences were left uniformly along the

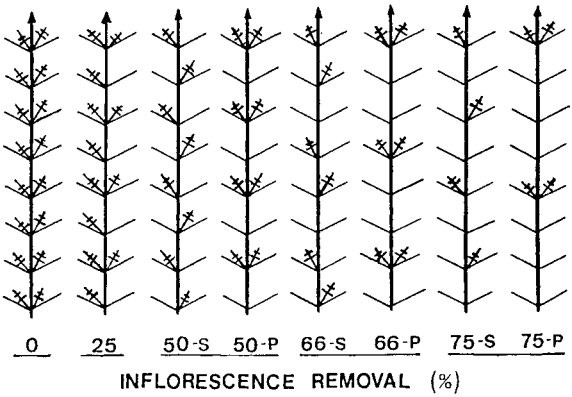

Fig. 1. A schematic representation of the main inflorescence removal treatments. Each shoot bore originally 34–40 inflorescences originating from 17–21 nodes. S, single inflorescence on the node; and P, a pair of inflorescences on the node.

shoot. In the later experiments with cv. Barnea, the retained inflorescences were left either as pairs (two per node) or singles (one per node) at all thinning levels. These different inflorescence thinning treatments are shown diagrammaticaly in Fig. 1. In addition to these treatments, inflorescence number was also reduced by removing all inflorescences either from the distal or the proximal half of the shoots.

The average inflorescence length and number of flowers was determined for each cultivar, orchard and experimental year. Fruit set was recorded eight weeks after full bloom. Results were calculated on both an inflorescence or flower basis (% set) and also on a per shoot (fruit load) basis. Any water stress was avoided throughout the experimental period.

All experiments with cv. Manzanillo were repeated four times and with cv. Barnea three or four times in different orchards or years. At least 10 shoots per treatment were tagged on each of the five trees per treatment on every occasion. Thus, each treatment was applied to 50 individual shoots per experiment. The data of each single experiment were pooled and considered as a single replication of a global randomized block design, i.e. each single experiment represents a replication of the whole experimental design. When treatments were quantitative, ANOVA and regression analysis were computed (Experiment 1, Table 1). When treatments were qualitative, ANOVA and mean separation by the Duncan test were computed (Experiment 2, Table 2). Finally, when treatments focused on the difference between the single and the paired arrangement of the inflorescences within the same level of inflorescence thinning treatment, factorial ANOVA and regression analysis were computed (Experiment 3, Tables 3–5).

In a separate experiment with cv. Barnea and another Israeli cultivar ‘Kadesh’, reproductive shoots differing in the number of inflorescence formed, were

Table 1
The effect of reduciong inflorescence number on fruit load and fruit set of cvs. Manzanillo and Barnea shoots. Results are means of four independent experiments

Thinning treatments			Fruit load fruits per shoot (No.)	Fruit set	
inflorescences		flowers per shoot (No.)		inflorescence with fruits (%)	flowers setting fruit (%)
removed (%)	retained (No.)				
cv. Manzanillo					
0	32	551	5.5	17.2	1.0
25	23	420	6.0	26.0	1.4
50	17	288	80	47.0	2.8
75	8	126	6.1	76.3	4.8
C_V (%)	—	—	2.1	4.4	9.6
Best polynomial regression (significance)			C[b] (0.03)	L[a] (0.0001)	L[a] (0.0001)
Adjusted R^2			0.60	0.91	0.87
cv. Barnea					
0	42	804	11.7	27.9	1.5
25	32	587	10.1	31.6	1.7
50	23	401	14.0	61.0	3.5
75	11	189	7.2	65.5	3.8
C_V (%)	—	—	3.7	7.5	7.97
Best polynomial regression (significance)			C[b] (0.009)	L[a] (0.001)	L[a] (0.001)
Adjusted R^2			0.67	0.73	0.78

[a] Linear.
[b] Cubic.

selected and tagged. The effect of three levels of inflorescence load per shoot on fruit set was presented, computing the means and standard errors.

3. Results

Removing inflorescences from highly flowering trees in both cultivars ‘Manzanillo’ and ‘Barnea’ promoted, respectively, a significant cubic response ($p < 0.0001$) in fruit load, with most fruits per shoot recovered at 50% inflorescence removal (Table 1). Whereas the differences in fruit load with respect to the controls were minor for 25% and 75% inflorescence removal in the case of ‘Manzanillo’, ‘Barnea’ showed a decrease in the number of fruits per

Table 2
Fruit set level on the distal or proximal halves of the fruiting shoots of cvs. Manzanillo and Barnea after rmeoval of all inflorescence on the other half of the shoots

Thinning treatments		Setting		
shoot half with inflorescence retained	inflorescence retained per shoot	per shoot		per inflorescence fruit (No.)
		fruit (No.)	inflorescence (%)	
cv. Manzanillo				
Control	31	11.5a	36.7a	1.0a
Distal half	15	7.9a	53.0b	1.0a
Proximal half	15	8.7a	46.2b	1.3b
cv. Barnea				
Control	40	10.3b	20.9a	1.2a
Distal half	19	4.6a	22.1a	1.1a
Proximal half	19	13.5b	47.6b	1.5b

Note: Results are mean values of three independent experiments. Different letters within each column and cultivar represent significance at the $P = 0.05$ level.

inflorescence at 75% of inflorescence removal. This response was due to the significant and linear increase in the percent of inflorescences and flowers producing fruits as a consequence of inflorescence removal (Table 1). The coefficient of variation (C_V) ranged from 2.1% to 9.6% for 'Manzanillo' and from 3.7% to 7.9% for 'Barnea'.

Both, in cv. Manzanillo and cv. Barnea unthinned shoots, 60–65% of the total number of fruits were set in the central half of the shoots. There was, however, no difference in the number of fruits set in the distal and proximal halves of the shoots (Data not shown). Removing the inflorescences from either the distal or the proximal half of cv. Manzanillo shoots resulted in a similar increase in the percentage of fruit set of the remaining inflorescences (Table 2). On cv. Barnea trees, however, an increase in the percentage of set occurred when the inflorescences were retained on the proximal half of the shoots, but not when they were retained on the distal half. It was noted that the inflorescences at the distal end of the cv. Barnea shoots were shorter than on the proximal half (3.6 ± 0.3 and 4.1 ± 0.4 cm, respectively) at the time of treatment. Also the flowers were somewhat smaller.

The effect of inflorescence distribution, one or two per node, on their ability to set fruit in cv. Barnea was determined at three different inflorescence levels (50%, 66% and 75% inflorescence removal; Fig. 1). Thinning of inflorescences significantly ($p < 0.0001$) increased the fruitful inflorescences per shoot at 50% inflorescence removal, but decreased it at higher levels of thinning (Table 3). This parabolic response was highly significant ($p < 0.0001$). Also single inflorescence

Table 3
The effect of inflorescence thinning and distribution patterns, on the level of inflorescence with fruit setting in cv. Barnea

Inflorescences per shoot			Fruitful inflorescences		
removed (%)	retained (No.)	distribution per node	number per shoot	as % of retained number	as % of initial number
0	30.0	pair	8.1	27	27.0
50	14.1	single	9.2	69	32.6
50	14.2	pair	8.7	63	29.4
66	9.2	single	7.5	82	25.1
66	9.4	pair	7.4	79	24.2
75	7.5	single	6.4	85	21.2
75	7.3	pair	5.9	81	19.6
C_V (%)			3.5	5.9	5.9
ANOVA effects			Significance		
Inflorescence per shoot			0.0001	0.0001	0.0001
best polynomial regression			Q[b] (0.0001)	L[a] (0.001)	Q[b] (0.001)
adjusted R^2			0.86	0.96	0.83
Inflorescence distribution			0.002	0.04	0.03
Interaction			0.05	NS[c]	NS[c]

Note: Inflorescence removed 10 days before bloom. Results recorded two months after treatment. Mean of three independent experiments.

[a] Linear.

[b] Quadratic.

[c] Nonsignificant.

distribution per node significantly increased ($p < 0.002$) the final number of fruitful inflorescences per shoot relative to paired inflorescences, but the amount of the difference with respect to two inflorescences per node was highest for 50% inflorescence thinning. This interaction was also significant ($p < 0.05$). In all the cases, the percentage of inflorescences setting fruit was considerably higher on thinned shoots than unthinned shoots. This response was linear and highly significant ($p < 0.0001$). When calculations were made based on the original inflorescence number per shoot before our thinning, inflorescence removal promoted a quadratic highly significant ($p < 0.0001$) response as the proportion of the original inflorescences that were fruitful increased with 50% of inflorescence removal, but then decreased for higher levels of inflorescence thinning. Also, fruit load and setting of inflorescences were significantly ($p < 0.002$ and $p < 0.04$,

Table 4
The effect of inflorescence number and distribution on fruit set at shoot, node and inflorescence level in cv. Barnea

Inflorescences per shoot			Shoot	Numbers of fruits per		
removed (%)	retained (No.)	distribution per node		node with inflorescence	inflorescence retained	nodes on shoot
0	30.0	pair	10.7	1.32	1.32	0.71
50	14.1	single	12.4	1.28	1.28	0.88
50	14.2	pair	10.1	2.02	1.16	0.71
66	9.2	single	13.2	1.76	1.76	0.96
66	9.4	pair	12.6	2.86	1.70	0.89
75	7.5	single	12.3	1.92	1.92	0.82
75	7.3	pair	10.1	2.66	1.71	0.69
C_V (%)			1.9	1.3	4.7	3.1
ANOVA effects			Significance			
Inflorescence per shoot			0.0001	0.0001	0.0001	0.0001
best polynomial regression			C[c] (0.02)	L[a] (0.01)	Q[b] (0.0001)	C[c] (0.02)
adjusted R^2			0.31	0.39	0.80	0.33
Inflorescence distribution			0.001	0.0001	0.006	0.0001
Interaction			0.0001	0.0001	NS[d]	0.02

Note: Inflorescences removed 10 days before bloom. Results recorded two months after treatment. Mean of three independent experiments.

[a] Linear.

[b] Quadratic.

[c] Cubic.

[d] Nonsignificant.

respectively) higher for single than for paired inflorescence distribution per node for the same level of thinning (Table 3).

The final number of fruits per shoot of cv. Barnea was slightly and significantly ($p < 0.0001$) increased up to 66% of inflorescence removal. This cubic response ($p < 0.02$) accounted for 31% of the variability (Table 4). This response was related to the increase in the percentage of fruitful inflorescences (Table 3) and to the number of fruits setting on each retained inflorescence, that increased parabolically ($p < 0.0001$) with inflorescence thinning. This behavior produced parallel fruiting patterns in the shoot and the node (Table 4). The similar performance of the inflorescence within the shoot, and of the flower within the

Table 5
Fruit set of cv. Barnea in relation to inflorescence and flower number and distribution on the shoots based on the initial and actual inflorescence number

Thinning treatments				Fruit set (%) per			
inflorescences per			flowers retained	inflorescence number		flower number	
shoot		node		ON		ON	
removed (%)	reained (No.)	distribution		initial	retained	initial	retained
0	30.0	pair	570	35.7	35.7	1.9	1.9
50	14.1	single	268	41.6	88	2.3	4.6
50	14.2	pair	270	34.1	71	1.9	3.7
66	9.2	single	175	44.2	143	2.5	7.6
66	9.4	pair	179	41.2	134	2.4	7.1
75	7.5	single	143	40.8	164	2.2	8.6
75	7.3	pair	139	33.5	139	1.8	7.3
C_V (%)				3.3	3.5	3.0	4.1
ANOVA effects				Significance			
Inflorescences per shoot				0.0001	0.001	0.001	0.001
best polynomial regression				C[b] (0.05)	Q[a] (0.001)	C[b] (0.04)	Q[a] (0.001)
adjusted R^2				0.26	0.94	0.27	0.94
Inflorescence distribution				0.0001	0.0001	0.0001	0.0001
Interaction				0.03	0.03	0.02	0.03

Note: Inflorescences removed 10 days before full bloom, results recorded after two months. Mean of three independent experiments.

[a] Quadratic.

[b] Cubic.

inflorescence, in response to inflorescence thinning accounted for the parallel fruit set results when these were expressed as a percentage of either inflorescences or flowers, and either initial or retained (Table 5).

Even though the fruit set per inflorescence retained was always significantly ($p < 0.006$) higher for single than for paired inflorescence distribution, the number of fruits per node with inflorescence was always significantly ($p < 0.0001$) lower in single than in paired inflorescence distribution (Fig. 1 and Table 4). This increase in fruit set of single vs. paired inflorescence distribution depends on the level of thinning as evidenced by the significant interaction between both these factors (Table 5). The actual percentage of fruit set on singly distributed inflorescences increased up to 4.5 times when only 25% of the inflorescences were left on the shoot. When the retained inflorescences were

Table 6
The effect of the natural level of inflorescence differentiation on the fruit set of cvs. Kadesh and Barnea shoots

Cultivar	Inflorescence load (% of buds with inflorescenes)		
	1–5	35–50	90–95
Kadesh	1.1 ± 0.3	4.5 ± 0.6	5.3 ± 0.7
Barnea	2.0 ± 0.4	5.8 ± 0.7	7.1 ± 0.9

Note: Uniform shoots 25–30 cm long with low, medium and high inflorescence load development were chosen on the same trees. Results are expressed as mean fruit per shoot ± SE.

spread along the shoots in pairs per node, fruit set per inflorescence was lower in all cases, and to a greater extent at the maximum thinning level. As flower number is basically related to the inflorescence number on the shoots, fruit set expressed on a flower number basis showed a similar pattern. It should be noted that though the natural mean percent of flowers setting fruit in these experiments was ca. 2% (Table 5), the actual fruit set increased to >8% when inflorescence, and thus flower number, was highly reduced.

All these experiments were based on reducing the number of inflorescences on highly reproductive (90–95% axillary buds differentiated into inflorescences) shoots. A preliminary experiment using shoots with different levels of natural differentiation chosen within the canopy of the same trees was also performed. The results with two cultivars Kadesh and Barnea under such conditions were generally similar. Shoots with full bud differentiation (90–95%) bore more fruit than those with medium (35–50%) differentiation (Table 6). In both cultivars, however, that difference was not statistically significant. Thus, the effect of naturally 'thinned' trees might be somewhat different from the artificial thinning of fully differentiated shoots. Shoots with a naturally determined small number of inflorescences (1–5% of full differentiation) produced, as expected, a significantly smaller amount of fruits.

4. Discussion

In the orchard, the level of flowering is inversely related to the amount of the previous year's yield. This is attributed to the inhibiting effect of developing fruits on floral induction in the summer previous to flowering (Lavee et al., 1986; Stutte and Martin, 1986; Fernández-Escobar et al., 1992). Also, pre-bloom environmental conditions, and defoliation caused by pathological factors after floral buds were induced, affected both, the inflorescence and floral development (Uriu, 1959; Hartmann and Panetssos, 1962). However, Suarez et al. (1984) and Lavee (1986) reported a higher percentage of fruit set in flowers of trees with a light flower load even when caused by a heavy yield in the previous year. In most fruit

species no clear anatomical differences between flowers in the 'ON' and 'OFF' years were observed except sometimes in flower size. Thus, the unspecific term 'flower quality' was introduced to account for the behavior differences of flowers and ovule longevity between years (Williams, 1965). In olive 'OFF' years, a lower percentage of pistil abortion than in 'ON' years was reported by Uriu (1959), who also stated that a high leaf/inflorescence ratio was required for an adequate pistil development. The higher percentage of fruit set of olive trees in the 'OFF' years was attributed to post-bloom reduced nutritional competition between fruitlets (Suarez et al., 1984: Cuevas et al., 1994).

The present study clearly indicates the existence of a control mechanism based on the fruiting potential of the individual flowering shoots within each tree. Artificial reduction of the inflorescence number on a fully reproductive-bud differentiated branch, resulted in an increased fruit set percentage for inflorescences as well as flowers within the inflorescences (Tables 1, 3–5). Thus, the number of fruits developing on the shoot was hardly changed in comparison to unthinned controls. Single inflorescence distribution on the shoots increased fruit set per inflorescence only slightly over pair-distributed inflorescences per node for the same level of thinning (Table 4). These results agree with those of previous experimental thinning of inflorescences and flowers within inflorescences (Lavee et al., 1996; Rallo and Fernández-Escobar, 1985; Suarez et al., 1984). This supports the post-bloom nutritional competition hypothesis, as in our case competition would be reduced either by fewer or by more distant inflorescences. However, some varietal differences in that behavior were noted as in cv. Barnea the fruit set potential of the inflorescences on the distal half of the shoots was significantly lower than on the proximal half (Table 2). These differences pose the question whether nutritional competition is the sole explanation for controlling the level of olive fruits on the trees. The inflorescences on the younger distal half of the shoots of cv. Barnea were smaller and less developed though the difference was not statistically significant.

It has been suggested that the low percentage of olive flowers setting fruit on the abundantly flowering trees is controlled by the first-to-set developing fruits, which prevent other fruits developing in their vicinity (Rapoport and Rallo, 1991b; Cuevas et al., 1995). This is probably governed by the developing endosperm of the fertilized ovule, as the embryo in the olive starts to form 2–3 weeks later (Rapoport, 1994). Earlier findings (Rallo and Fernández-Escobar, 1985; Rapoport and Rallo, 1991a) showed that more than half of the olive flowers have a normal developed ovary, and probably a similar basic potential to set fruit. Therefore, the amount of fruit set is not limited by inflorescence distribution or flower ability to set fruit but by a post-pollination control mechanism. Our results on fruit set would, therefore, partially support this explanation, although some pre-bloom development factor is also required to explain the differential behavior between the proximal and distal halves in cv. Barnea.

The current results were based on the 'ON' year trees with close to maximum reproductive bud differentiation. It is still questionable whether shoots with similar flowering density on 'OFF' and 'ON' trees will have the same fruit set potential. In previous studies, a relatively higher percentage of fruit set for the 'OFF' year flowers has been reported (Suarez et al., 1984; Lavee, 1986). This has to be considered since, under natural orchard conditions, the yield in 'OFF' and semi-'OFF' years is positively correlated with the number of reproductive buds which differentiate and develop (Cuevas et al., 1994). Our present data, however, indicated that inflorescence and flower number on a shoot basis could not be considered a major limiting factor of fruit load. In a preliminary experiment, shoots with different numbers of naturally developing inflorescences gave rise to different amounts of yield accordingly. Still, a partial compensation of increased fruit set did occur, but generally the yield was higher on the abundantly flowering shoots. Thus, the relation between shoot vigor, natural level of flowering and the fruit set potential was further studied. These relations in trees, differing in their natural flowering, will be described in further papers in this series.

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