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Influence of Cultivar and Flower Thinning within the Inflorescence on Competition among Olive Fruit

L. Rallo and R. Fernández-Escobar
Laboratorio de Pomologia, ETSIA, Universidad de Córdoba, Apartado 3048, Córdoba, Spain

Additional index words. fruit set, fruit abscission, pollination

Abstract. **Experiments with heavily-flowering olive trees showed only one period of abscission of flowers and fruit in the 5–6 weeks following full bloom. This abscission of flowers and fruit is responsible for the small percentage of fruit retained to maturity. Most of the fruit drop was concomitant with initial fruit growth for all cultivars. There were no differences in the number of fruit per inflorescence among cultivars, but the percentage of inflorescences with fruit at harvest was related negatively to final fruit size for each cultivar. Thinning of perfect flowers within the inflorescence did not affect fruit set at the inflorescence level; thus, the inflorescence behaved as a unit of fruitfulness. Competition among fruits played a significant role in fruit set. Initial setting induced by pollination and fertilization is counteracted early by fruit abscission originated by competition among fruit. In light of this early abscission, the use of fruit set to indicate response to pollination in previous experiments is questioned.**

Olive blooms strongly in "on" years, but only a small number of flowers are able to set fruit that remain until harvest. Griggs et al. (7) have defined a good crop as 1% of the original flowers setting fruit and remaining until harvest. Rallo et al. (16) studied the seasonal changes of fruitfulness in olive and stated that reduction in fruit number takes place within the first 5–6 weeks after full bloom, suggesting that competition among fruit, triggered by fertilization and early fruit growth, is mainly responsible for fruit abscission.

The purpose of this study was to evaluate cultivar differences and the influence of flower thinning within the inflorescence on fruit setting in order to assess the importance of competition in olive fruitfulness.

Materials and Methods

Expt. 1. Seasonal pattern of fruit set and development in 6 cultivars. Number of inflorescences, flowers, and fruit, as well as shoot growth were determined from bloom until harvest in 'Arbequina', 'Picual', 'Manzanillo', 'Lechin', 'Hojiblanca', and 'Cornicabra'. These cultivars are adapted to distinct growing areas in Spain, and differ in both fruit size and fertility. Five-year-old trees growing in a varietal plot at the Instituto Nacional de Investigaciones Agrarias farm in Alameda del Obispo, Córdoba, were chosen. The trees were trained and irrigated following locally approved practices, and continuous treatment was done from bloom to harvest to prevent *Prays oleae* Bern.

Four heavily flowering trees for each cultivar, and 10 uniformly distributed fruitful shoots per tree were selected and tagged in spring, 1980. Numbers of inflorescences and flowers per inflorescence were counted per shoot, just before full bloom (FB; the time when more than 50% of the flowers had opened in at least 75% of the inflorescences). Number of fertile inflorescences, perfect flowers, and fruit per inflorescence were determined at 5, 12, 15, 21, 26, 36, and 48 days after FB. Inflorescences were considered fertile when they bore at least one perfect flower or one persisting fruit. Perfect flowers were first determined at FB + 5, at which time petal-fall occured. Length and number of nodes, and number of leaves per fruitful shoot (corresponding to 1979 growth), were determined during the spring of 1980. Vegetative growth of 1980 was similarly determined 7, 17, and 57 days after FB, and at harvest. Average weights for 20 fruit per tree were determined at 3, 6, 9, 12, 15, 20, and 30 days after FB, and at harvest.

Expt. 2. Influence of flower thinning on fruitfulness. This experiment was planned to determine if the number and position of flowers on the inflorescence were critical for fruit set. Two identical experiments were established for 'Manzanillo' and 'Picual'.

The thinning treatments consisted of eliminating one-half, three-fourths, and seven-eights of the flowers in each inflorescence at 3 positions (basal, apical, and longitudinal) and an unthinned control. The 10 treatments were applied at random to different branches per tree. For each branch, all flowering shoots received the same treatment, and 8 of such shoots were tagged for observation. Four replications (trees) of each cultivar were used.

Observations were determined as in Expt. 1, except that perfect flower and fruit counts were done at 8, 12, 22, and 39 days after FB, and shoot measurements were made at 13 and 48 days after FB. In addition, the weight of 20 fruit per treatment was determined at harvest.

For both experiments, the influence of different fruitfulness indices on crop efficiency was evaluated by correlation analysis. The parameters used are included in Table 2. In addition, analysis of variance and the Duncan's multiple range test were used for mean separation.

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Results

Seasonal pattern of fruit set and development in 6 olive cultivars. Both the number of fruit per inflorescence and the percentage of inflorescences with fruit decreased slowly from FB + 5 to FB + 12, and then decreased sharply, except for 'Arbequina' and 'Hojiblanca', where fruit abscised in large numbers starting from FB + 5 (Fig. 1). The number of fruit per inflorescence was practically stabilized at FB + 21 for all cultivars, but abscission of fertile inflorescences lasted until FB + 36 (Fig. 1).

Fruit drop coincided with the beginning of fruit enlargement for all cultivars (Fig. 1). Fruit weight increased in 'Arbequina' and 'Hojiblanca' at FB + 3, but somewhat later (FB + 6 to FB + 9) for the other cultivars. Those differences concurred with the onset of fruit abscission, which occurred earlier in 'Arbequina' and 'Hojiblanca' than in the other cultivars. Furthermore, fruit abscission as well as fruit weight increased rapidly, starting at FB + 12. Fruit size at that time had at least doubled that at FB for all cultivars.

In spite of the initial different fruit numbers per inflorescence

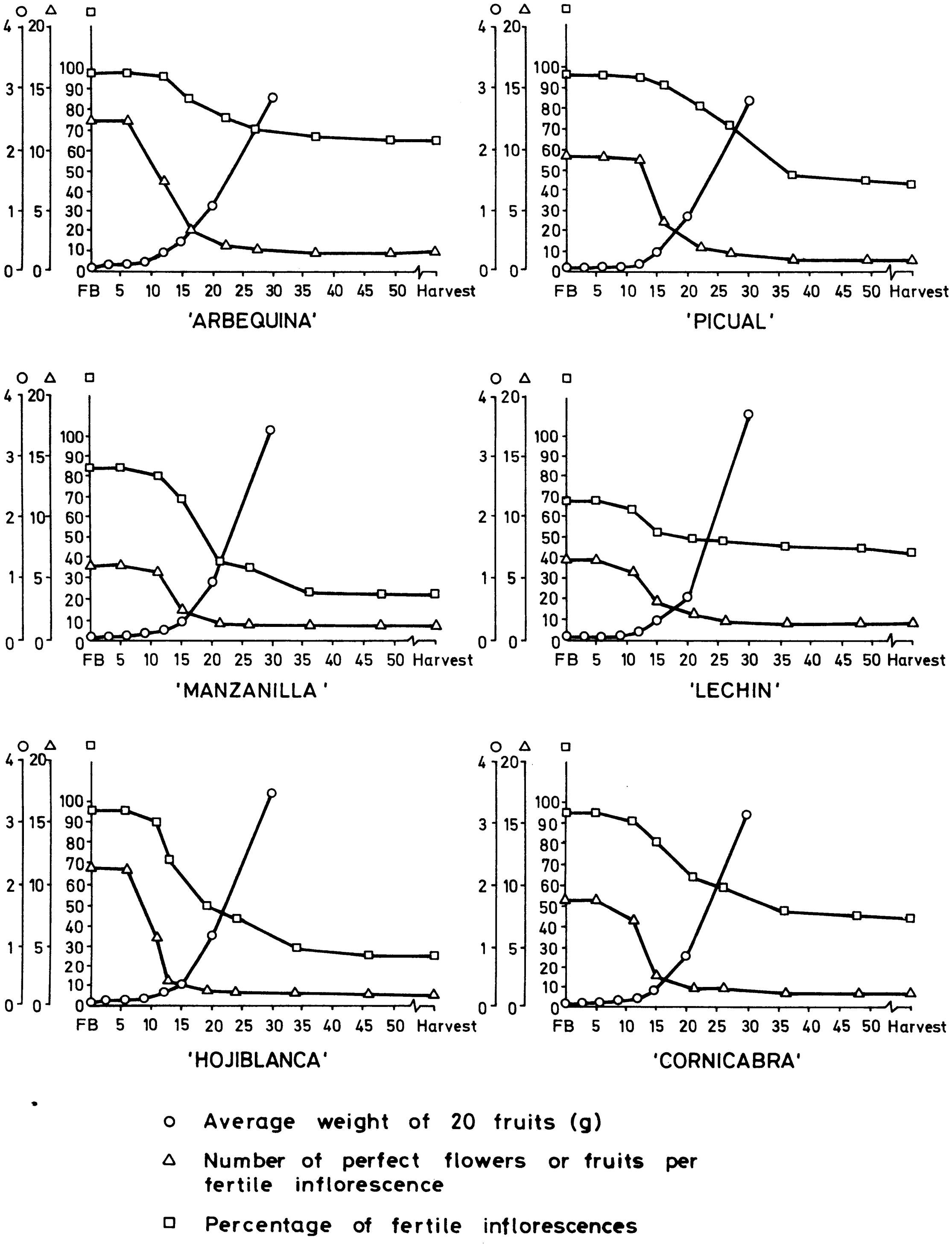

Fig. 1. Change of crop components in 6 olive cultivars

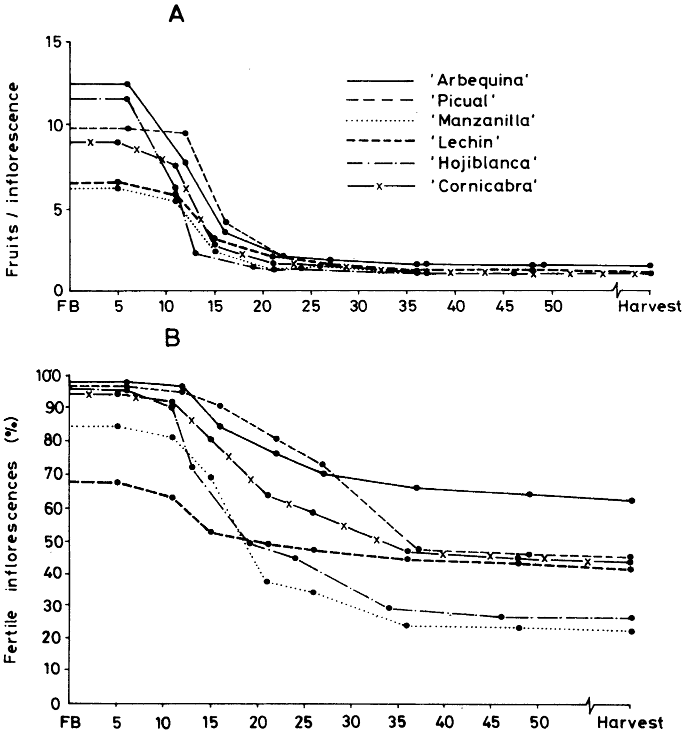

Fig. 2. Change of number of perfect flowers, or persisting fruit per fertile inflorescence (**A**), and change of percentage of fertile inflorescences (**B**) from FB to harvest in 6 olive cultivars.

there were no significant differences among cultivars in the final number of fruit per inflorescence (Fig. 2A). On the other hand, the percentage of inflorescences with fruit differed significantly ($P < 0.01$) among cultivars at harvest (Fig. 2B; Table 1). These differences were not related with the initial values but were significant and negatively related to final fruit size ($P < 0.001$). Average weight per fruit was 0.9 g for 'Arbequina', 1.8 g for 'Cornicabra', 2.0 g for 'Picual', 2.2 g for 'Lechin', 3.1 g for 'Manzanillo', and 3.4 g for 'Hojiblanca'.

Influence of flower thinning on fruitfulness. The original differences in the number of perfect flowers per inflorescence induced by flower thinning treatments disappeared by FB + 22 in 'Manzanillo' and by FB + 41 in 'Picual' (Fig. 3). The percentage of inflorescences with fruit changed similarly for all treatments in both cultivars (Fig. 3). No significant differences among treatments were observed at harvest for all parameters determined.

The increase in fruit set at the flower level compensated for the reduction in perfect flowers per inflorescence induced by thinning. This tendency started to appear at FB + 12, and was fully evident at FB + 36. Thus, the reduced fruit shedding in thinned treatments balanced the reduced number of perfect flower per inflorescence, and led to the behavior of the inflorescence as a unit of fruitfulness.

Relationship between crop efficiency and fruitfulness and vegetative indices. Crop efficiency was considered to be the number of fruit and the average fruit weight per cm of fruitful shoot. Fruit setting indices were calculated at both the flower and inflorescence levels (Table 1).

The percentage of perfect flowers and of fertile inflorescences at anthesis was not significantly correlated with crop efficiency for most cultivars (Tables 1 and 2). Initial fruit setting (recorded at FB + 12) at the flower and inflorescence levels was not related to crop efficiency for almost all cultivars (Tables 1 and 2). Fruit setting between FB + 12 and FB + 36 was significantly correlated with crop productivity for all cultivars, however, and higher correlation coefficients were obtained at the inflorescence than at the flower level (Table 2). In contrast, fruit size was negatively correlated with fruit setting at the inflorescence level for all cultivars.

When thinning treatments were applied (Expt. 2) similar results were obtained. No significant correlation between productivity and initial fruit set appeared for most treatments in both 'Manzanillo' and 'Picual'. However, crop efficiency was significantly correlated with fruit set (between FB + 12 and FB + 39) at the inflorescence level for almost all treatments and for both cultivars, and for some treatments in both cultivars at the fruit level.

The negative correlation between vegetative growth and crop efficiency was significant only for 'Lechin' (Table 2) and for 'Manzanillo' when thinning treatments were applied (Expt. 2). Vegetative growth, however, was extremely variable, with the coefficient of variation for total shoot growth from leafing to harvest reaching 54% and that of shoot growth rate (cm/day)

Table 1. Pistil abortion, fruit setting (as percentage of flowers and inflorescences), and crop efficiency in 6 olive cultivars.[z]

	Pistil abortion		Fruit setting[y]						Crop efficiency[x]	
			Initial (From FB to FB + 12)		Competition (From FB + 12 to FB + 36)		General From FB to Harvest			
Cultivar	Perfect flowers (% at FB)	Fertile inflorescences (% at FB)	Flowers (%)	Inflorescences (%)	Flowers (%)	Inflorescences (%)	Flowers (%)	Inflorescences (%)	Fruit/cm	g/cm
'Arbequina'	85.7 a	97.7 a	62.1 c	98.4 a	16.7 a	69.2 a	9.6 b	64.3 a	0.59 a	0.57 a
'Cornicabra'	62.7 b	94.9 a	81.2 b	96.4 a	8.6 b	52.0 b	6.5 bc	46.9 b	0.23 c	0.43 a
'Hojiblanca'	69.1 b	96.2 a	51.5 c	94.3 a	7.2 b	32.9 bc	3.2 c	28.0 c	0.13 d	0.45 a
'Lechin de Sevilla'	25.2 c	68.0 c	84.2 b	93.6 a	21.3 a	71.5 a	16.8 a	63.3 a	0.33 b	0.77 a
'Manzanilla'	32.2 c	84.6 b	88.9 ab	96.2 a	6.6 b	30.0 c	5.6 bc	27.3 c	0.16 cd	0.53 a
'Picual'	65.2 b	97.1 a	95.8 a	98.2 a	6.8 b	50.0 b	6.0 bc	46.0 b	0.40 b	0.87 a
Significance	**	**	*		*	*	*	*	*	
cv (%)	10.7	5.2	11.9	5.6	19.6	14.7	20.4	14.8	18.5	37.5

[z] Within columns, numbers with a different subscript are significantly different at $P<0.05$(*); $P<0.01$(**). Data transformed to arcsine for analysis.

[y] Expressed as the percentage of perfect flowers or fertile inflorescences at start of period.

[x] Expressed as number of fruit or weight (g) of fruit per cm of bearing shoot.

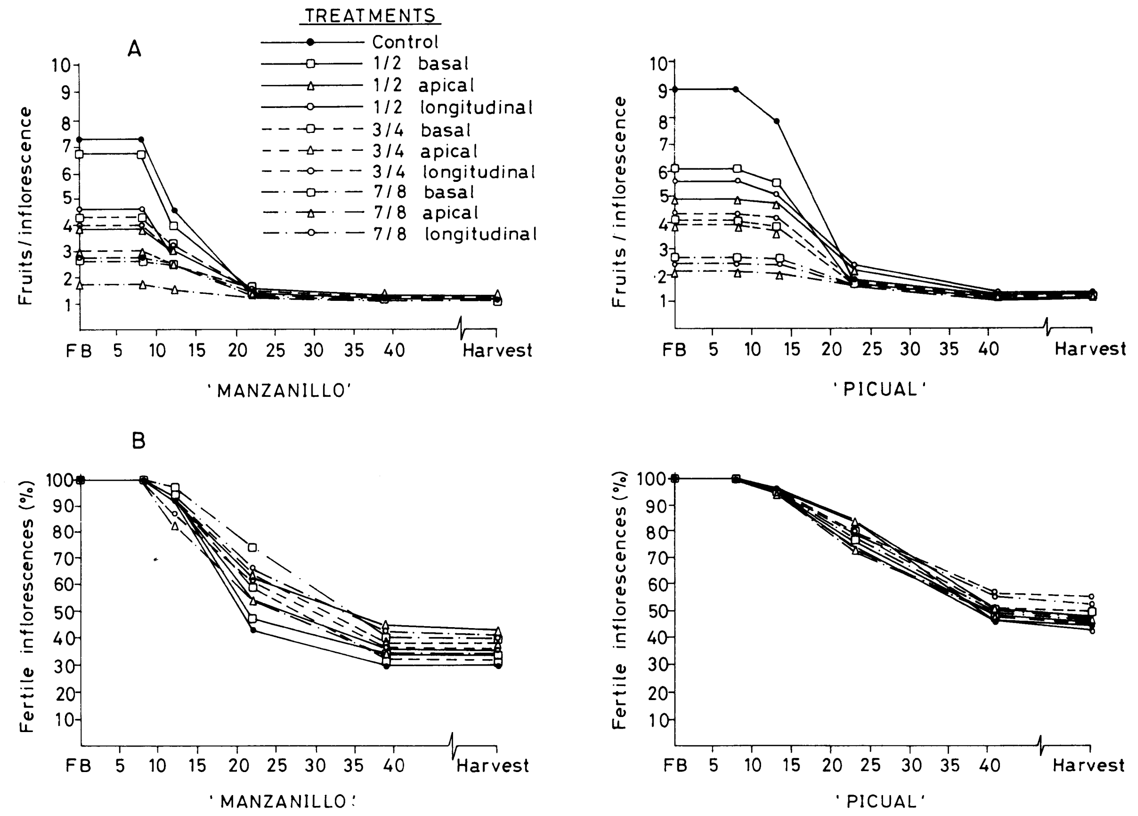

Fig. 3. Change of number of perfect flowers or persisting fruit per fertile inlorescence (**A**), and change of percentage of fertile inflorescences (**B**) in 2 olive cultivars with different thinning treatments.

Table 2. Correlation coefficients between fruitfulness and vegetative growth indices and crop efficiency in 6 olive cultivars.[z]

Fruitfulness and vegetative growth indices	Crop efficiency[y]											
	Fruits/cm						g/cm					
	'Arbequina'	'Picual'	'Manzanilla'	'Lechin'	Hojiblanca'	'Cornicabra'	'Arbequina'	'Picual'	'Manzanilla'	'Lechin'	'Hojiblanca'	'Cornicabra'
Pistil abortion												
Perfect Flowers (%)	−0.26	0.28	−0.09	0.15	0.07	−0.19	−0.34*	0.31	−0.13	0.22	0.16	−0.32*
Fertile Inflorescences (%)	0.05	0.26	0.08	0.25	0.02	0.15	0.01	0.23	0.04	0.30	0.04	0.08
Fruit setting												
From FB to FB + 12												
Flowers (%)	−0.05	−0.12	0.02	0.31*	0.27	0.03	−0.11	−0.1	0.02	0.32*	0.14	0.05
Inflorescences (%)	0.32*	−0.06	0.11	0.37*	0.15	0.27	0.32*	−0.1	0.15	0.30	0.07	0.25
From FB + 12 to FB + 36												
Flowers (%)	0.34*	0.53***	0.52***	0.45**	0.54***	0.44**	0.28	0.47**	0.57***	0.35*	0.68***	0.45**
Inflorescences (%)	0.35*	0.84***	0.78***	0.57***	0.66***	0.39*	0.34*	0.79***	0.78***	0.57***	0.75***	0.31*
General (from FB to Harvest)												
Flowers (%)	0.40**	0.51***	0.54***	0.56***	0.75***	0.62***	0.34*	0.47**	0.59***	0.46**	0.79***	0.63***
Inflorescences (%)	0.44**	0.85***	0.78***	0.71***	0.73***	0.46**	0.43**	0.79***	0.78***	0.67***	0.78***	0.37*
Vegetative growth												
From leafing to harvest (cm)	0.34	−0.01	−0.20	−0.46**	−0.19	−0.15	0.29	0.06	−0.15	−0.41**	−0.19	−0.18

[z]Significance at 5% (*), 1% (**) and 0.1% (***), 38 df.

[y]Expressed as number of fruit or weight (g) of fruit per cm of bearing shoot.

during the competition period, measured from FB + 17 to FB + 57, 67%. Thus, in spite of large mean differences in both parameters—total shoot growth in 'Lechin' was twice that in 'Arbequina' and competition period shoot growth rate in 'Lechin' was 3 times that in 'Arbequina'—the differences among cultivars were not significant. However, when growth during the competition period was expressed as the percentage of total growth, the results were significantly ($P < 0.05$) higher in 'Hojiblanca', 'Lechin', and 'Manzanillo' than in 'Arbequina' and 'Picual'. Therefore, it seems that in some cases the vegetative growth from fertilization to the end of competition period (40–45 days after FB) may be negatively related to fruit set.

Discussion

In the olive, massive abscission of flowers and fruit shortly after anthesis is responsible for the low efficiency in setting fruit which reach maturity. In different cultivars, however, the causes of flower and fruit drop and their relative contributions to final fruit production may be different. Three major causes for natural abscission of flowers and fruit may be recognized: a) shedding of staminate flowers and inflorescences without perfect flowers in the initial days after FB; b) shedding of unfertilized flowers in the days after petals fall; and c) fruit abscission by competition among fruit and between fruit and other sinks.

Staminate flowers are common in olive and are caused by pistil abortion during flower development (17). Shedding of unfertilized flowers and inflorescences due to limited pollination has been determined in this study by the abscission of perfect flowers at FB + 12, when pistil weight is at least double that of anthesis. Although fertilization was not verified, previous observation (16) and the increment in size already described would imply that most shedding occurring after FB + 12 must correspond to fertilized flowers. The abscission due to competition is presumably triggered by fertilization and early fruit growth, and proceeds until about 35–45 days after FB (16). We recorded it as abscission taking place between FB + 12 and FB + 36. Preharvest fruit drop, which usually is not an important factor in fruit production in olive, is a consequence of the ripening process and is not considered in this study.

In our experiments, heavily flowering trees were chosen. In these circumstances, whereas crop efficiency was influenced strongly by fruit abscission between FB + 12 and FB + 36, usually neither percentage of staminate flowers nor initial fruit setting (before FB + 12) affected the size of the final crop (Tables 1 and 2). In fact, most of the fruit abscission was concomitant with early fruit growth for all cultivars, although initiation of growth (and consequently fruit shedding) differed among them (Fig. 1). Thus, fertilized flowers acted as sinks that competed with each other, adjusting the fruit population in the 35–40 days after FB. The beginning of this major abscission of young fruit must overlap the shedding of unfertilized flowers, since only one continuous abscission period of perfect flowers and fruit was noticed here (Fig. 1, 2, and 3) and elsewhere (16). However, the distinction between abscission of unfertilized flowers and of young fruit must be particularly emphasized in pollination studies, as competition counteracts the increasing number of fertilized flowers due to cross-pollination. Nevertheless, fruit counts to determine fruit set in cross-pollination experiments in olive usually are done 25–30 days after FB (1, 5, 6, 12, 13, 14, 15, 18), probably adopting methods employed for other fruit species (15), where abscission of unfertilized flowers clearly precedes fruit drop due to other causes (19). The competition period in olive already has started at that time, however, and fruit counts integrate not only the response to pollination treatments but also that to competition among fruit, a process which counteracts high fertilization. This competition effect could be a major reason for the reported lack of response to cross-pollination (4, 7). Also, competition among fruit would explain why the relationship between pistil abortion and crop production was not noticed among the 6 cultivars (Tables 1 and 2) and has not been reported elsewhere (2).

Parthenocarpic fruit in olive showed attenuated competition among fruit, in contrast to normal fruit (16) where the fruit shedding period corresponds to the first rapid fruit growth period (8) and ends before pit-hardening and rapid embryo development, as described by King (9). These observations suggest that competition among fruit may be regulated by developing seeds, possibly by the formation of the cellular endosperm.

Distance between fruit seems to play an important role in competition; the shorter the distance the earlier the competition is expressed. Thus, fruit abscission proceeds first within the inflorescence and later between fruitful inflorescences within the bearing shoot (compare Fig. 1 and 3). Concomitantly, whereas number of fruit per fruitful inflorescence at harvest were neither influenced by thinning within the inflorescence nor by cultivars in spite of large differences at FB (Fig. 2A and 3A), the percentage of fruitful inflorescences differed between cultivars (Fig. 2B), and was negatively correlated with final fruit size. However, no such differences occurred between thinning treatments for the same cultivar (Fig. 3B). This sequence in the process of competition seems, therefore, responsible for the observed behavior of the inflorescence as a unit of fruitfulness, at least within the range of fruit sizes present in the cultivars considered and for the thinning treatments applied in these experiments (Table 1; Fig. 3 and 4), as previously suggested by Rallo et al. (16).

The negative correlation between fruit size and the percentage of fruitful inflorescences for the 6 cultivars studied suggests that the strength of the competition mechanism, regulating fruit number before the 1st period of fruit growth ended may be partially responsible for the differences in fruit size between cultivars. Also, in chemical thinning experiments (10, 11) where the time of thinning was just at the beginning of the competition period among fruit, the response was an increase in fruit size that compensated for the reduction in final setting.

Negative correlations between yield components have been observed frequently in many crops (3). Although often interpreted as indicating that yield is limited by the supply of assimilates, Evans (3) suggests, quoting results from Adams, that other explanations may hold. Some negative correlations between vegetative growth and crop efficiency were determined (Table 2), suggesting that when maximum vegetative growth is simultaneous with fruit growth, growing points could act as competing sinks. All these results suggest that source-sink relationships must play a relevant role in determining olive yield and merit further study.

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Root and Shoot Growth Patterns of Newly Rooted Woody Plants

Susan E. Bentz[1], Dennis P. Stimart[2], and Marla S. McIntosh
University of Maryland, College Park, MD 20742

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Abstract. **Changes in primary root number (RN), root dry weight (RDW), and shoot dry weight (SDW) on newly rooted stem cuttings of 7 woody ornamental plants were evaluated over 18 or 24 weeks after either no root removal or root removal where remaining RN equalled 25%, 50%, or 100% of the average RN at transplanting. Regardless of root removal treatment or season (February, June, or July), increases in primary RN occurred after transplanting and preceded increases in RDW and SDW. RDW and SDW increased progressively and together after primary RN ceased increasing. Cuttings started in February attained maximum RN in 12 to 18 weeks after transplanting, whereas those started in June and July required 6 weeks. Results suggest that stem cuttings of woody plants have a minimum, species dependent, primary RN which must be attained before measurable shoot growth is initiated.**

Rooted cuttings of woody plants are evaluated for future success on the quality and size of root system they produce (4, 6). Large numbers of roots on *Betula, Halesia, Malus, Prunus* and *Vitis* enhance transplant survival (2, 4) and shoot growth (16). Similarly, survival of bare root woody plants is facilitated by root development (8). Root removal studies indicate shoot growth to be related to root size: root reduction results in a decrease in shoot growth rate (7, 17, 18). Neither the aspect of root size (weight, volume, root number) nor the manner in which it mediates its influence is well understood.

Root modification of shoot growth has been attributed to control of nutrient and water uptake or to hormone synthesis (5, 15, 17). It is not clear whether reduced shoot growth following root pruning results from interference with nutrient or water uptake (3, 5, 7, 17). Resumption of shoot growth following cytokinin application to pruned roots (17, 18) indicates hormones may exert a regulatory influence. Control has been postulated to be localized in root tips since they are sites of high rates of nutrient and water uptake (2, 16, 17, 18) and of synthesis of cytokinins and gibberellins supplied to the shoot (5, 15, 17, 18).

Improved knowledge of the patterns of root change during the establishment phase of newly rooted stem cuttings of woody plants would help clarify means by which growth is integrated between root and shoot. The present study monitored changes in root number, root dry weight, and shoot dry weight during the establishment of rooted shoot tip cuttings of several woody plants.

Materials and Methods

Softwood and hardwood shoot tip cuttings were propagated at the Univ. of Maryland greenhouses, College Park, Md. (38°58′N latitude). Rooting was facilitated by dipping the lower 2.5 cm of stems into commercial rooting powder containing 1H-indole-3-butanoic acid (IBA) and Thiram (15%). Cuttings were rooted in flats containing a mixture of 1 coarse perlite (#3): 1 Canadian sphagnum peat moss v/v under intermittent mist.

Once rooted (roots 2.5 cm or longer) cuttings were lifted, treated, and planted in containers in a 40% peat : 20% perlite : 20% vermiculite : 20% topsoil mix containing fritted trace elements (#503), and limed to pH 6.5. Plants were hardened-off under polypropylene shade cloth (53% transmittance) in the greenhouse for 2 weeks, given a fungicidal drench of Banrot (0.08%), and transferred to full sun in the greenhouse or outdoors.

Controlled release fertilizer (18N–2.6P–10K) at 5 g/liter of soil was provided within 2 weeks of initial transplanting. Plants were fertilized with 20N–8.7P–16.6K at 236 ppm N every 2 weeks after transplanting except at 4 weeks when applied at 470 ppm N.

Fourteen (Expt. 1) or 25 (Expt. 2 and 3) plants per treatment of each species were selected for evaluation at transplanting and

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[1] Graduate Research Assistant, Dept. of Hort.

[2] Associate Professor of Hort.

[3] Associate Professor of Agron.