Flowering and Fruit Set of Olive Trees in Response to Nitrogen, Phosphorus, and Potassium

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ABSTRACT. The independent effects of nitrogen, phosphorus, and potassium concentrations in the irrigation solution on flowering and fruit set in olive trees (*Olea europaea* L. cv. Barnea) were studied in a container experiment. Treatments included eight levels of N ranging from 0.4 to 14.1 mM, seven levels of P ranging from 0.01 to 0.62 mM, and seven levels of K ranging from 0.25 to 5.33 mM. At low environmental concentrations of each of the minerals, additions led to large increases in their concentrations in leaves, and as the environmental concentrations became high, relative increases in leaf accumulation were reduced. Availability of N, P, and K was found to influence flowering intensity in the olive trees. Fruit set was affected by N and P, but not K levels. Total fruit load of olives was shown to be a function of flowering level multiplied by fruit set. The final number of olives per tree increased appreciably as leaf P and K increased from minimum levels, and relative increases in fruit load tapered at the highest measured leaf concentrations of the minerals. Maximum fruit load was found corresponding to $\approx 0.06 \text{ mol}\cdot\text{kg}^{-1}$ P and close to $0.35 \text{ mol}\cdot\text{kg}^{-1}$ K in leaves. Fruit load increased to a maximum as leaf N increased from 0.7 to $1.3 \text{ mol}\cdot\text{kg}^{-1}$ and then decreased as leaf N increased to $1.5 \text{ mol}\cdot\text{kg}^{-1}$. The findings indicate that each of the macronutrients plays a fundamental role in processes affecting olive tree productivity.

Olive is a traditionally important crop grown extensively in the Mediterranean basin. Recent modernization of olive cultivation has introduced and promoted densely planted orchards that are irrigated via systems that can also be used for nutrient application (Fernández-Escobar et al., 2006; Fontanazza, 1993; Tombesi, 2006). Plant growth, fruit production, and oil yield and quality are all expected to be influenced by levels of available nutrients, and manipulation of these levels in irrigation water is necessary to optimize oil production and economic returns.

Flowering and fruit set are the main processes influencing the productivity of fruit trees and are particularly important for olive, where biannual bearing is acutely experienced and where there is an apparently delicate relationship between vegetative and reproductive stages of growth (Lavee, 2006). Inflorescence in olive develops from buds borne on shoots grown in the previous year, a process that starts at the beginning of the summer (Fabbri and Benelli, 2000; Fernández-Escobar et al., 1992). Olive trees possess hermaphrodite and staminate (“male”) flowers. The relative proportion of these two flower types can vary greatly, as a function of cultivar, developmental,

and fruiting history, and specific environmental conditions (Lavee et al., 1996). In the northern hemisphere, floral differentiation is evident by March (Hartmann, 1951) and anthesis occurs by April and May. Shortly after anthesis, massive abscission of flowers and fruitlets occurs (Rallo and Fernández-Escobar, 1985; Rapoport and Rallo, 1991a, 1991b). The remaining fruit typically manage to persist on the trees until ripening, which takes place during the fall. At full bloom, some 500,000 flowers are present on a mature olive tree. Commercial yield is achieved if 1% or 2% of those flowers remain as developing fruit (Martin et al., 2005).

Substantial amounts of nutrients are lost from olive trees as a result of fruit removal, annual pruning of leaves and wood, and natural leaf drop. Removed nutrients must be replaced and, where natural levels in the soil are insufficient, appropriate fertilization is necessary to supply the minerals for new growth and for the following year’s yield. The current study concentrated on the importance of the macronutrients nitrogen, phosphorus, and potassium and their specific roles in flowering and fruit set of olive.

Olive leaves and stems represent storage organs for N and release it in response to the metabolic demands of developing reproductive and vegetative organs (Fernández-Escobar et al., 2004; Klein and Weinbaum, 1984). Under N deficiency, fruit set, yield, and shoot growth are negatively influenced (Freeman et al., 2005). In experiments in the 1950s in the United States, N

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fertilization increased fruit set in rain-fed olives grown in nutrient-poor soil (Hartmann, 1958). In Italy, N fertilization was also reported to increase fruit set in olive (Cimato et al., 1990). N was found to increase the proportion of hermaphrodite flowers, and a N concentration of less than 1% in leaves led to the formation of staminate flowers and therefore decreased the potential level of fruit set (Therios, 2006). Therios (2006) also reported that N deficiency reduces the number of flowers. Further evidence of the importance of N to olive productivity was provided by Chatzissavvidis et al. (2004), who found a correlation between a reduction in leaf N and a reduced number of flowers per inflorescence, and by Lombardo and Briccoli-Bati (1990), who showed a significant increase in flower-bud differentiation after fertilization with N of olives planted in poor soils.

Information relating P fertilization to reproductive and vegetative growth and function in olives is limited. Generally, P fertilization is not recommended or practiced in rain-fed olive orchards (Therios, 2006), and there is very little documentation of P deficiencies in this crop (Freeman et al., 2005; López Villalta, 1996). However, it is anticipated that under intensive irrigation management, P supply in many soils will eventually be diminished and that application of P will become beneficial.

Potassium fertilization is essential in olive, particularly because greater than 60% of the plant's K is located in the fruit and is removed annually with its harvest (López Villalta, 1996). Soil application of a large quantity of fertilizer containing K was shown to be responsible for major yield increases in olive orchards that had previously been seriously K deficient (Hartmann et al., 1986).

Some micronutrients have also been found to play roles in plant productivity. In olives, boron appears to be particularly important. Deficient B has been demonstrated to increase the percentage of imperfect flowers and to decrease fruit set (Perica et al., 2001).

Macronutrient mineral status influences the productive stages of olive growth, including flowering and fruit set, directly or indirectly, through its effects on other physiological processes (Fabbri and Benelli, 2000). Indeed, most studies found in the literature indicate a positive response of olive productivity to increased mineral status (Ben Rouina et al., 2002; Talaie and Taheri, 2001). However, the data supporting this have more often than not been collected under rain-fed conditions where the nutrients were applied to the soil before the rainy season or were occasionally sprayed onto the foliage. Little is known regarding the effects of nutrients supplied intensively via the irrigation water throughout the growing season, as is becoming common practice in intensively managed olive orchards. Therefore, the objective of the present work was to study the independent effects of N, P, and K concentrations in the irrigation solution on flowering and fruit set in olive trees.

Materials and Methods

Olives (cv. Barnea) were grown in containers at the Gilat Experimental Station, Israel (lat. 31°20'N, long. 34°39'E). Two-year-old seedlings, pruned to single 60-cm-high trunks, were planted in Feb. 2006 in 60-L (40.4 cm diameter and 47 cm depth) containers filled with type 4 (4–6 mm) granular perlite substrate. Perlite was chosen to be the growth medium because of the preferable physical properties (high porosity and high hydraulic conductivity) and low interaction with nutrients.

Initially, the trees were irrigated with an irrigation system including an irrigation pump to excess via a drip system twice per day with solution containing 5.9 mM nitrogen (70% NO_3^- and 30% NH_4^+), 0.51 mM P, 1.8 mM K, 1.3 mM Ca, 0.9 mM Mg, 0.6 mM S, 0.023 mM B, 10.7 μM Fe, 5.46 μM Mn, 2.31 μM Zn, 0.35 μM Cu, and 0.17 μM Mo. The irrigation solution (three replicates) was sampled and analyzed weekly, and the values above are averages of all measurements. Differential nutrient application treatments were initiated in Sept. 2006. The 20 treatments included eight levels of N, seven levels of P, and seven levels of K. To analyze effects of N concentrations on growth and reproductive variables, concentrations of P and K in the irrigation solution were maintained at 0.30 ± 0.06 (mean $\pm$ SD) and 2.6 ± 0.3 mM, respectively. To analyze effects of P concentrations, N and K in the irrigation solution were maintained at 5.4 ± 0.6 and 2.6 ± 0.3 mM, respectively, and to analyze effects of K concentrations, N and P in the irrigation solution were maintained at 5.4 ± 0.6 and 0.30 ± 0.06 Mm, respectively (Table 1). Nutrient solutions were prepared in 500-L containers containing a full regime of all additional nutrient elements. Concentrations of specific nutrients were: 1.3 mM Ca, 0.67 mM Mg, 1.1 mM S, 0.023 mM B, 9.8 μM Fe, 4.9 μM Mn, 2.1 μM Zn, 0.31 μM Cu, and 0.16 μM Mo. In all treatments, N was allocated as 90% NO_3^- and 10% NH_4^+ . Solutions were prepared by dissolving KH_2PO_4 , K_2SO_4 , KNO_3 , $\text{NH}_4\text{H}_2\text{PO}_4$, NaNO_3 , and NH_4NO_3 . Monitoring of irrigation solution minerals via measurements made every 2 to 3 weeks (collated from the 500-L containers) insured stable and correct concentrations. Average electrical conductivity (EC) values for the solutions ranged from 0.9 to 2.1 $\text{dS}\cdot\text{m}^{-1}$ (Table 1). Irrigation water pH was set to a value of 6.0 ± 0.2 using 1.15 N sulfuric acid. Irrigation quantity was set to obtain 30% drainage by volume. Volume, EC, and pH of the drainage water were routinely measured. The experiment used a randomized block design with six replications. To decrease spatial variability, rows of olive seedlings planted in additional containers were located around the perimeter of the experimental trees.

Leaves were sampled on 2 May 2007 and 50 to 100 of the youngest fully developed leaves from the previous year's growth were collected from the middle portion of nonbearing branches. Sampled leaves were rinsed for 15 s in deionized water, dried at 60 °C, and ground with in a stainless steel coffee mill to particle size less than 0.5 mm. Total N, P, and K concentrations of the leaves were determined after digestion with sulfuric acid and peroxide (Snell and Snell, 1949). The concentrations of N and P were determined with an autoanalyzer (Lachat Instruments, Milwaukee) and K concentrations were analyzed with a flame photometer (model 400; Corning, Corning, NY). Total B concentrations of the leaves were determined using the dry-ash method (Yermiyahu et al., 2001). The concentration of B was determined by the azomethine-H procedure (Page et al., 1982).

Growth parameters were measured 1 week before initiation of the treatments and then again in late Apr. 2007. Trunk circumference was measured at a marked location ≈ 10 cm above the media surface. The rate of growth (length) was measured for four labeled branches per tree.

Flowering intensity was appraised by two different methods. Each tree was visually evaluated independently by four individuals using a scale of 1 to 100, with 100% denoting full flowering potential. Additionally, the number of inflorescences per branch was counted using the same branches labeled for the

Table 1. Irrigation solution treatment levels of N, P, and K and their respective electrical conductivities (EC). Average measured increases in branch length and trunk circumference of olive trees for the experimental period (Sept. 2006–Apr. 2007).

Element	Treatment	Element concentration in irrigation solution			Irrigation solution EC (dS·m ⁻¹ ± sd)	Branch length (cm)	Trunk circumference (cm)
		N	P	K			
		-----	(mm ± sd)	-----			
N	N1	0.4 ± 0.2	0.31 ± 0.05	2.68 ± 0.2	0.87 ± 0.11	15.5 B ^z	9.1 B
	N2	1.1 ± 0.3	0.31 ± 0.04	2.54 ± 0.2	0.88 ± 0.14	18.1 B	9.0 B
	N3	1.8 ± 0.1	0.33 ± 0.04	2.65 ± 0.2	0.92 ± 0.13	28.6 A	14.4 A
	N4	3.4 ± 0.2	0.32 ± 0.04	2.70 ± 0.2	0.98 ± 0.10	25.4 AB	15.1 A
	N5	5.4 ± 0.6	0.30 ± 0.06	2.62 ± 0.3	1.08 ± 0.10	23.0 AB	12.5 AB
	N6	7.8 ± 0.8	0.33 ± 0.06	2.80 ± 0.3	1.32 ± 0.13	23.1 AB	14.8 A
	N7	10.9 ± 1.3	0.32 ± 0.06	2.84 ± 0.3	1.63 ± 0.17	25.5 AB	14.8 A
	N8	14.1 ± 1.2	0.32 ± 0.06	2.87 ± 0.3	2.12 ± 0.37	25.0 AB	14.6 A
P	P1	5.6 ± 0.5	0.01 ± 0.01	2.73 ± 0.3	1.12 ± 0.12	21.4 A	12.7 A
	P2	5.4 ± 0.4	0.02 ± 0.01	2.61 ± 0.3	1.08 ± 0.11	25.6 A	13.2 A
	P3	5.5 ± 0.6	0.04 ± 0.01	2.80 ± 0.2	1.12 ± 0.12	19.7 A	13.7 A
	P4	5.3 ± 0.4	0.06 ± 0.02	2.58 ± 0.2	1.09 ± 0.11	25.4 A	14.1 A
	P5	5.6 ± 0.4	0.14 ± 0.05	2.70 ± 0.2	1.10 ± 0.11	24.2 A	15.3 A
	P6	5.4 ± 0.6	0.30 ± 0.06	2.62 ± 0.3	1.08 ± 0.10	23.0 A	12.5 A
	P7	5.4 ± 0.4	0.62 ± 0.05	2.61 ± 0.2	1.09 ± 0.08	22.5 A	15.3 A
K	K1	5.7 ± 0.6	0.34 ± 0.05	0.25 ± 0.1	1.11 ± 0.15	28.1 A	13.3 A
	K2	5.7 ± 0.8	0.36 ± 0.04	0.49 ± 0.1	1.06 ± 0.13	28.0 A	13.4 A
	K3	5.4 ± 0.8	0.34 ± 0.08	0.73 ± 0.1	1.09 ± 0.12	24.3 A	15.9 A
	K4	5.9 ± 0.4	0.35 ± 0.03	1.33 ± 0.2	1.09 ± 0.10	22.0 A	13.1 A
	K5	5.9 ± 0.5	0.35 ± 0.06	2.05 ± 0.2	1.13 ± 0.11	24.7 A	14.5 A
	K6	5.4 ± 0.6	0.30 ± 0.06	2.62 ± 0.3	1.08 ± 0.10	23.0 A	12.5 A
	K7	5.6 ± 0.4	0.35 ± 0.03	5.33 ± 0.3	1.31 ± 0.12	20.9 A	15.5 A

^zAny two means within a column for a single element not followed by the same letter are significantly different at $P \leq 0.05$.

growth rate determination. One hundred contiguous flowers on four individual branches per tree were labeled during the flowering period. These branches, containing hermaphrodite and staminate flowers, were used to measure fruit set on 20 May 2007. Results are presented as the percentage of flowers resulting in viable fruit.

Data were analyzed using the JMP 5.0 software (SAS Institute, Cary, NC) and the curve-fitting and analysis tools of SigmaPlot 9.01 (Systat Software, San Jose, CA). Effects of the various irrigation solutions on branch lengthening and change in trunk circumference were examined by analysis of variance (ANOVA), and whenever the F statistic was significant, differences between treatments were determined using the Tukey-Kramer honestly significant difference test (at $P \leq 0.05$). The relationships between N, P, and K concentrations (in the irrigation water and leaves) and measures of flowering intensity, fruit set, and fruit number were determined using linear and nonlinear regressions. Default significance levels were set at $\alpha = 0.05$. Means are presented with ($\pm$) SDs. Calculated fruit number was compared with measured values using regression analysis with the null hypothesis that slopes and intercepts of the linear regression were not different from 1 and 0 at 95% confidence.

Results

PLANT GROWTH AND MINERAL ACCUMULATION IN LEAVES. Trunk circumference of the trees before implementation of the treatments was between 4.0 and 6.0 cm (average 5.09 ± 0.44 cm). The average increase in circumference between Sept. 2006 and Apr. 2007 was 13.7 cm (Table 1). With the exception of the two lowest N treatments, N1 and N2, for which trunk growth

was less, no significant differences were found between treatments. A similar picture arose from the branch-length data (Table 1), where only N1 and N2 treatments yielded significantly less elongation compared with all the other treatments, for which the average growth from Sept. 2006 to Apr. 2007 amounted to 25 cm. Regression analysis for trunk circumference and branch length were weak statistically and the significance of the results is easily demonstrated using ANOVA. These results implied that although vegetative growth of the trees during the experimental period was substantial, it was unaffected by P or K nutrition and was reduced only at the lowest two N concentrations. Trees receiving the N1 and N2 treatments were smaller and chlorotic and were easily visually distinguished from the trees receiving the other treatments, which were uniform in appearance.

For each of the three elements, mineral concentration in the leaves increased as a function of increasing solution concentration, with the rate of increase tapering off at high solution concentrations (Fig. 1). Nevertheless, accumulation of mineral ions in the leaves continued to increase at the highest solution concentrations, i.e., they had not reached saturation levels. For N treatments, leaf concentration of N for the lowest concentration in the irrigation solution (0.35 mM) was $0.63 \text{ mol} \cdot \text{kg}^{-1}$ and increased 2.4 times to $1.50 \text{ mol} \cdot \text{kg}^{-1}$ for the highest N concentration in the irrigation solution (14.45 mM; Fig. 1A). Similar trends were observed for the P and K treatments. The mineral concentration in the leaves for the lowest and highest concentrations in solution was 0.028 and $0.062 \text{ mol} \cdot \text{kg}^{-1}$ for P, corresponding to solution P concentrations of 0.01 and 0.626 mM, respectively (Fig. 1B), and 0.17 and $0.37 \text{ mol} \cdot \text{kg}^{-1}$ for K, corresponding to 0.21 and 5.35 mM K in solution, respectively (Fig. 1C). The substantial range of leaf mineral concentrations

Fig. 1. Leaf N concentration in olive as a function of N concentration in the irrigation solution (A). Leaf P as a function of P in the irrigation solution (B). Leaf K as a function of K in the irrigation solution (C). Symbols are averages of the measured data, error bars are standard error, and lines are best-fit regression from raw data. Data from May 2007.

enabled subsequent analysis of the elements in flowering and fruit set, not only as a function of environmental concentrations, but also as a function of biological leaf concentration as well.

FLOWERING, FRUIT SET, AND NUMBER OF FRUIT PER TREE. There was a good and significant correlation ($P < 0.001$; $r^2 = 0.81$) between the two methods of determining flowering intensity (visual evaluation of entire trees and counting on four individual labeled branches per tree). We present both sets of data in parts A and B, respectively, of Figs. 2, 3, and 4, while we use only the data from the branch counting for the generation of response curves and the calculation of regression statistics.

Full anthesis was reached on 15 Apr. 2007 for most treatments, 221 d from the beginning of the trial. There was a noticeable delay for N1, N2, and P1 treatments, which reached full anthesis, on average, 5.5, 3.3, and 4.5 d, respectively, after 15 Apr.

Results regarding flowering, fruit set, and number of fruit per tree are hereby presented individually for each nutrient variable.

NITROGEN. Flowering intensity was highly dependent on the concentration of N in the irrigation solution (Fig. 2A). Flowering at the lowest N treatment (no N addition, 0.35 mM N) was very low (0.5 inflorescences per branch). Increasing the N concentration to 3.4 mM (N4) increased flowering intensity to the maximum measured (7.0 inflorescences per branch). A further increase in irrigation N concentration to 14.1 mM decreased the flowering to 6.5 inflorescences per branch. Presentation of flowering intensity as a function of concentration in leaf matter (Fig. 2B) revealed a second-order polynomial rising and falling response curve. Maximum flower intensity was achieved when leaf N concentration was 1.29 mol·kg⁻¹.

Fruit set was affected similarly to flowering by N concentration in the irrigation solution and N concentration in the leaves (Fig. 2, C and D). Fruit set when no N was added was almost 0 and increased to 8.0% when N in solution reached 3.4 mM (Fig. 2C). The highest N concentrations caused reductions in fruit set, but relatively less so than for flowering. The maximum fruit set occurred when leaf N concentration was 1.27 mol·kg⁻¹ (Fig. 2D).

Following the trends seen for flowering and fruit set, the final number of fruit remaining on individual trees was also a function of N concentration. Fruit number per tree increased from 11 to 1122 when solution N concentration increased from 0.4 to 3.4 mM and decreased from this maximum to 531 as N concentration was further increased to 14.1 mM (Fig. 2E). Fruit number as a function of leaf N concentration was well defined ($r^2 = 0.94$) by a second-order polynomial curve with maximum fruit corresponding to 1.27 mol·kg⁻¹ N in the leaves (Fig. 2F).

PHOSPHORUS. Flowering intensity increased as a function of P solution concentration (Fig. 3A), from 3.5 to over 8.0 inflorescences per branch as P increased from 0.01 to 0.14 mM. A further increase in P did not affect the flowering levels. Flowering was seen to respond to leaf P concentration (Fig. 3B), reaching a plateau at ≈ 0.05 mol·kg⁻¹ P.

The fruit set response to P solution concentration increased with increasing solution P with a maximum level of 9.5% (Fig. 3C). The fruit set at the three lowest concentrations (P1–P3) was very similar and was less than half of that in P7. Fruit set significantly increased linearly as a function of leaf P concentration (Fig. 3D).

The total number of fruit counted was also a function of P concentration. Fruit number per tree increased from 291 to 1190 when P concentration in the irrigation water increased from 0.01 to 0.62 mM, with the rate of increase in fruit number declining at the higher P concentration treatments (Fig. 3E). Fruit number as a function of leaf P concentration increased with increasing P concentration (Fig. 3F) and was defined ($r^2 = 0.89$) by a second-order polynomial curve with maximum fruit corresponding to the maximum measured P in leaves (0.062 mol·kg⁻¹).

POTASSIUM. Flowering intensity increased as a function of solution K concentration (Fig. 4A), with flowering increasing from 3.3 to nearly 10 inflorescences per branch as K increased from 0.2 to ≈ 1.5 mM. Further increases in K did not affect the flowering levels. Flowering was seen to respond to leaf K concentration linearly (Fig. 4B), increasing from minimum values at K = 0.17 mol·kg⁻¹ to a maximum at K = 0.37 mol·kg⁻¹ in leaves.

Fig. 2. Flowering (A and B), fruit set (C and D), and total number of fruit per olive tree (E and F) as a function of irrigation solution N concentration (left) and leaf N concentration (right). Symbols are averages of the measured data, error bars are standard error, and lines are best-fit regression from raw data.

Fruit set was high ($8.4\% \pm 0.013\%$) for all K treatment levels and was not found to be a function of solution or leaf K levels (Fig. 4, C and D). The total number of fruit counted was a function of K concentration, with an increase from 793 to 1297 fruit per tree as the K in solution was raised from 0.21 to 1.34 mM (Fig. 4E). Increases from 1.34 to over 5 mM K in solution did not result in any further changes in fruit number. Fruit number as a function of leaf K concentration (Fig. 4F) increased in a generally linear fashion with increases of over 250 fruit per tree for every 0.1 mol·kg⁻¹ K increment.

CALCULATED VERSUS MEASURED FRUIT LOAD. To examine if flowering intensity and fruit set were the main factors determining fruit number, a procedure calculating fruit load was applied. Initially, normalized response equations for flowering intensity and fruit set were created by dividing results by those of the treatment common to all three data sets ($N_5 = P_6 = K_6$). Subsequently, for each nutrient, the normalized equation for flowering intensity was multiplied with the normalized equation for fruit set. Fruit set for K was taken as a constant value of 1.16. The resulting combined functions for fruit number are displayed together with data from actual fruit count at harvest in Fig. 5. The measured relative fruit numbers are very well defined by the predicted-combined response functions (Fig. 5). Regression of calculated versus measured data for N in Fig. 5A was significantly linear ($r^2 = 0.96$) with a slope of 1.003 and an intercept of 0.002 (not different from 1 and 0 at 95%

confidence). For P (Fig. 5B), the significant linear regression had $r^2 = 0.86$ and the slope and intercept of calculated versus predicted values were 0.82 and 0.18, respectively (not different from 1 and 0 at 95% confidence). For K (Fig. 5C), the significant linear regression ($r^2 = 0.50$) had slope and intercept of calculated versus predicted values of 0.49 and 0.48, respectively (different from 1 and 0 at 95% confidence).

Discussion

The lower flowering levels found at low N, P, and K concentrations were likely due to low flower-bud induction and differentiation (Lavee, 1996). The lower fruit set levels found with low concentrations of N and P were probably due to inadequate total quantities of nutrients available to the flowers as they developed into fruit. Abscission of fruitlets with insufficient nutrient supply was expected ≈ 2 weeks after full bloom (Rapoport and Rallo, 1991a, 1991b).

Regression analysis of the relationships between the nutrient concentrations in solution or leaves and the productivity parameters were statistically significant, but at times had low r^2 values (Figs. 3 and 4). When determined using means of treatments rather than the entire data set, r^2

values were substantially higher. The low r^2 values indicate high variability between replicates of treatments. This variation was found between individual trees regarding the flowering level, fruit set, and fruit number in spite of the fact that no such variability was measured for mineral concentrations in leaves (Fig. 1).

In the literature, flowering level and fruit set ratio are usually negatively correlated: reported cases of high flowering correspond with reduced fruit set and vice versa (Cuevas et al., 1994; Lavee et al., 1996, 1999). This apparent compensation essentially balances the total fruit load per branch or tree. We did not find such compensation for N, P, or K nutrition. In the present study, augmented N and P concentrations increased fruit load by boosting flowering level and fruit set. Increased K concentration, although positively affecting flowering, did not influence fruit set at all. These findings indicate that each of the macronutrients must therefore play a fundamental role in processes affecting tree productivity.

The number of fruit remaining on a single olive tree is expected to be a function of the total number of flowers multiplied by the percentage of flowers developing into fruit (fruit set). The agreement between actual fruit count at harvest per tree and predicted fruit number calculated according to multiplication of the total number of flowers by the percentage of flowers developing into fruit (Fig. 5) indicated that the fruit load was affected solely by the concentrations of N, P, and K in

Fig. 3. Flowering (A and B), fruit set (C and D), and total number of fruit per olive tree (E and F) as a function of irrigation solution P concentration (left) and leaf P concentration (right). Symbols are averages of the measured data, error bars are standard error, and lines are best-fit regression from raw data.

the irrigation water and not by other, unknown variables. The young trees exhibited substantial vegetative growth, which was observable and measurable throughout the year. Vegetative production was not influenced by nutrient treatment, with the exception of the two lowest N levels. This suggests that the amount of nutrients (especially P and K) that had accumulated in the trees before initiation of the treatments sufficiently provided for vegetative growth, even when their concentrations in leaves were reduced (Fig. 1). Therefore, we can additionally conclude that the effects on flowering and fruit set were caused directly by nutritional status and not by some other indirect effects such as the previous year's fruit load or tree size. This first season was unique; investigation of nutrients on vegetative and reproductive parameters should be continued in subsequent seasons to evaluate long-term or accumulated effects.

NITROGEN. Nutrient uptake interactions are widely described in the literature (Marschner, 1995) and are expected to be particularly salient in growth media, such as perlite, with their low buffering capacities. Leaf mineral concentration can indicate such interactions. For the case of the N treatments in the current study, the P concentration in leaves averaged 0.052 ± 0.04 mol·kg⁻¹ (data not shown), equivalent to the high P levels in the P treatments (Fig. 3), and there were no differences between treatments. In contrast to P, the K concentration in leaves increased with increasing N in solution. Potassium

concentration increased from 0.29 to 0.37 mol·kg⁻¹ for the lowest to highest N treatments (data not shown). However, that range of leaf K is all within that found for the high K treatment levels (Fig. 1C) and cannot explain the decreased olive fertility with high N treatments. Boron is known to be an important factor for olive productivity (Perica et al., 2001), but leaf B concentration was unaffected by any of the treatments and ranged between 0.0016 and 0.0024 mol·kg⁻¹ across all experiments. Therefore, B cannot explain the effect of the various N concentrations on productivity either.

Nitrogen deficiency is well established as a limiting factor for flowering and fruit set in olive fruit trees (Cimato et al., 1990; Freeman et al., 2005; Hartmann, 1958; Therios, 2006). Furthermore, correction of insufficient N has been found to reduce fruit abscission throughout all developmental stages (Cimato et al., 1990; Inglese et al., 2002). The results from the two lower N treatments in the present study support these previous findings. Without addition of N, growth of 'Barnea' olives ceased and zero reproductive productivity was observed. Nitrogen is essential for protein biosynthesis, and the fact that developing inflorescences have been shown to be strong sinks for N (Klein and Weinbaum, 1984) and water-soluble proteins (Bouranis et al., 1999) suggests that its availability is important for flowering. Furthermore, polyamine has been implicated in playing an important regulatory role in olive flower induction (Prista and Voyiatzis, 2004).

Maximum productivity was achieved for 3.4 mM N in solution, where the N concentration in leaves reached 1.2 mol·kg⁻¹. Further increases in solution N concentration, while increasing leaf N concentration, significantly decreased olive productivity. The highest N treatment had a particularly negative effect on flowering intensity, causing a 50% depletion in the number of fruit (Fig. 2). Nitrogen overfertilization has been reported to adversely affect orchard productivity due to increases in vegetative growth, which augments shading within the tree and negatively affects not only flower bud development and fruit set, but also fruit quality and shoot survival (Weinbaum et al., 1992). Nevertheless, overfertilization with N did not negatively affect tree productivity in a field study of rain-fed olives (Fernández-Escobar et al., 2002). We speculate that the availability of N in relatively dry soils, expected during much of the growing season under rain-fed conditions, is lower than that found in our experiment or that expected in orchards where fertilizers are applied via the irrigation system throughout the season, and, therefore, the negative effect of overfertilization was not as pronounced in the aforementioned study. In addition to a negative effect on

Fig. 4. Flowering (A and B), fruit set (C and D), and total number of fruit per olive tree (E and F) as a function of irrigation solution K concentration (left) and leaf K concentration (right). Symbols are averages of the measured data, error bars are standard error, and lines are best-fit regression from raw data.

tree productivity, as found in the current study, we may also expect overfertilization with N to have a negative effect on oil quality via reductions in the levels of saturated fatty acids (Simões et al., 2002) and polyphenol content (Fernández-Escobar et al., 2002, 2006).

PHOSPHORUS. Nitrogen and K concentrations in leaves increased with increasing P in solution: N increased from 1.0 to 1.4 mol·kg⁻¹ and K from 0.31 to 0.33 mol·kg⁻¹ with the increase from P1 to P7 (data not shown). These ranges of leaf mineral concentrations are equivalent to the optimum found for N and high for K and do not explain the effects of P on fertility and productivity. Leaf B did not change with the P level, averaging 0.002 mol·kg⁻¹. Therefore, P in leaves was solely a function of P concentration in solution and neither N, K, nor B were involved in the effect of P supply on olive productivity.

Little attention has been paid to the demands of olives in terms of P nutrition and there is almost no documentation of P deficiencies in this crop (Freeman et al., 2005; López-Villalta, 1996; Therios, 2006). The current study provides strong evidence for the importance of P in productivity and shows that flowering and fruit set levels can be improved by increasing P uptake and accumulation. In a review of P fertilization practices (Rickard, 2000), similar improvement in flowering and fruit set leading to increased productivity was reported for citrus.

POTASSIUM. Increasing K concentration in solution, while increasing leaf K concentration, did not influence the concen-

trations of N, P, or B in the olive leaves. The average mineral concentration in leaves across K treatments was 1.3 mol·kg⁻¹ N, 0.05 mol·kg⁻¹ P, and 0.002 mol·kg⁻¹ B. Therefore, these minerals and their possible interactions were not responsible for the responses of flowering and fruit number to K level. Correlations between high yields and high levels of leaf K have been well documented in olive (Freeman et al., 2005). Potassium, more than any other macroelement, is understood to have a positive effect on flowering (Fabbri and Benelli, 2000), as it promotes the formation of amino acids that stimulate the formation of IAA oxidase which, in turn, stimulates flower induction (Gonzalez-Garcia et al., 1972). Potassium might also promote the production of pyruvate chinase (Mazuelos et al., 1983) and thereby influence the level of a number of amino acids involved in flowering induction.

Conclusions

The results of this study clearly demonstrate that increased solution N, P, or K in the root zone increases the concentration of each of these nutrients in the leaves of olive trees. At low environmental concentrations of these minerals, additions led to large increases in leaf mineral concentration, and as the environmental concentrations became high, relative increases in leaf accumulation became less pronounced. Availability of the macronutrients N, P, and K was found to influence flowering intensity of young olive trees. Fruit set was affected by N and P but not K levels. The results also confirm that, as expected, fruit yield in olives is essentially a function of number of flowers multiplied by fruit set. Total fruit load of olives increased appreciably as P and K in the leaves increased from minimum levels, and relative increases in fruit load tapered off at the highest measured leaf concentrations of the minerals. Maximum fruit load corresponded to ≈ 0.06 mol·kg⁻¹ P and close to 0.35 mol·kg⁻¹ K in the leaves. Fruit load increased to a maximum as leaf N increased from 0.7 to 1.27 mol·kg⁻¹ and then decreased as leaf N increased to 1.5 mol·kg⁻¹.

As olive production advances into regions with less winter rainfall and as intensive cultivation practices, including season-long application of fertilizers in the irrigation water, are adopted and expanded, management of nutrient application to optimize availability for maximum production is becoming a necessity. In addition to the results of this study regarding the important roles played by N, P, and K on flowering and fruit set, information concerning long-term tree growth and, in particular, oil yield and quality as a function of nutrient status is needed for a more complete understanding of olive tree nutrition and proper horticultural management.

Fig. 5. Measured (symbols) and calculated (lines) number of olive fruit per tree as a function of leaf N (A), P (B), and K (C) concentration. Calculated curves are from multiplied normalized equations describing flowering intensity and fruit set.

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