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Mobilization of Boron in Olive Trees during Flowering and Fruit Development

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Abstract. **Change in B content of olive *(Olea europaea* L.) leaves during anthesis reveals the appearance of a potent B sink. This phenomenon was more marked in young leaves of bearing trees with a high degree of flowering than in nonbearing trees with a low degree of flowering. Applying B to the leaves at the time of anthesis increased the B concentrations in leaf blades, petioles, bark of the bearing shoot, and flowers and fruit 3 days after treatment. The results suggest that B is mobilized from young leaves during anthesis to supply the requirements of flowers and young fruit.**

Boron is an element with low phloem mobility in plants (Marschner, 1986). Several observations support this hypothesis: symptoms indicating a lack of B are found in young developing tissues (Eaton, 1944); B concentration in the phloem is usually low (Epstein, 1973); and if B is artificially increased, the phloem structure is altered (Eschrich et al., 1965). Also, Oertli and Richardson (1970) have suggested that B does not readily move out of mature leaves because of a cyclical movement of B between the phloem and the xylem within a leaf. However, in cases of plant deficiency (Campbell et al., 1975; McIlrath, 1965), B has been found to flow from mature leaves to other plant parts (Hanson, 1991).

Numerous reports indicate that B plays an important role in flowering. Boron may be necessary for flower bud formation (Kamali and Childers, 1970), production of pollen grains (Argawala et al., 1981), and pollen tube growth (Dickinson, 1978; Linskens and Kroh, 1970; Rodriguez-Rosales et al., 1989).

Woodbridge et al. (1971) observed that pear, apple, and cherry *(Pyrus communis* L., *Malus domestics* Borkh., *Prunus avium* L., respectively) buds accumulated B more rapidly by anthesis. Foliar B treatments efficiently increased B concentrations in buds (Callan et al., 1978) and increased yields in cranberry *(Vaccinium corymbosum* L.) (DeMoranville and Deubert, 1987), grape *(Vitis vinifera* L.) (Fregoni et al., 1978), and prune *(Prunus domestics* L.) (Callan et al., 1978; Chaplin et al., 1977; Hanson and Breen, 1985). Chaplin et al. (1977) suggested that transitory needs for B during floral development and fruit set can be met in certain cases by foliar treatments.

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The olive tree has a marked alternate-bearing habit. Olives flower on 1-year-old wood and display two inflorescences per node. Floral differentiation is evident by March (Hartmann, 1951), and anthesis occurs by May in the Mediterranean regions. Shortly after anthesis, massive abscission of flowers and fruit occurs (Rallo and Fernádez-Escobar, 1985). Hartmann et al. (1966) reported that olive trees require high levels of B; therefore, B is used extensively in olive production in Spain. However, little is known about B nutrition in the olive. The objective of our work was to study the changes of B concentration in bearing and nonbearing olive shoots during flowering and fruit development.

Materials and Methods

Two trials were conducted in an olive orchard located in the Experimental Farm of Alameda del Obispo at Córdoba, Spain. Drip-irrigated, 17-year-old 'Manzanillo' trees were selected for the experiments. The objective of the first experiment was to determine the changes in B concentration in leaves during the flowering period. For this purpose, four bearing trees with an average of 0.53 fruit/cm of bearing shoot and four nonbearing trees with an average of 0.08 fruit/cm were selected. Four shoots per experimental tree were collected from positions ≈90° apart on each tree on 26 Mar., 21 Apr., 28 Apr. (anthesis), 5 May, 12 May, 1 June, and 15 June (end of massive fruit abscission). Once in the laboratory, young leaves from the current-season's growth and mature leaves formed during the previous season were removed separately from each shoot, washed in deionized water, dried at 80C for 48 h, ground, and stored in an oven at 60C until B analysis.

The second experiment investigated the effect of foliar B application on B concentration in blades, petioles, bark, flowers, and fruit. Four bearing trees were selected for the experiment. Boron was applied 3 days before anthesis to one scaffold of 7- to 12-cm^2 cross-sectional area per tree. The rest of the tree was used as the control. Each leaf from the experimental scaffold was immersed for 5 sec in a solution of 0.5% (v/v) sodium borate (Solubor) (B sodium salt, Borax Holding, United Kingdom). The solution contained 1 g B/liter. Only the leaf blade was soaked. Shoots were collected as described previously from treated and nontreated scaffolds from each tree and on the same dates, starting at anthesis. Once in the laboratory, blades from young and mature leaves, petioles from mature leaves, bark from the previous-season's growth, flowers, and fruit were removed separately from each shoot, dried at 80C for 48 h, ground, and stored at 60C until B analysis. Leaves had been washed with 0.03% Triton X-100 to remove excess B adhering to the surface. Bark and fruit were rinsed in deionized water.

The stored samples were calcined at 600C, and the ash was dissolved in 0.1 N HC1. Boron was determined in the extract by calorimetry (Greweling, 1976).

Results

Changes of B concentration in olive leaves. Young leaves showed a higher B concentration than the mature leaves in bearing and nonbearing trees (Fig. 1), although B concentration in young leaves of nonbearing trees was lower than that obtained in the young leaves of the bearing trees. Boron concentration in young leaves of bearing trees strongly decreased at the time of anthesis, a change in concentration that was not observed in the mature leaves (Fig. 1A). When calculated on a per-leaf basis, B content of young leaves also decreased at the time of anthesis (Table 1). The decrease in B for leaves of the nonbearing trees occurred at anthesis over a narrow range (Fig. lB). The seasonal pattern of B concentration in mature leaves of both bearing and nonbearing trees was similar.

Effect of foliar B application on B levels in the bearing shoot. Applying B to the leaf blades increased the concentration of this element in the various parts of the bearing shoot (Fig. 2). Three days after treatment, the B concentration in the blade of the treated mature leaves was three times higher than in the control (Fig. 2A). Concentrations in treated leaves decreased thereafter and were similar to those on control leaves 50 days after treatment. The blade of the young leaves showed a similar behavior, although the differences were smaller than those found for the mature leaves (data not shown).

Boron content in the petiole at 3 days after B treatment was similar to that described for the leaf blade (Fig. 2B). In the bark, differences between treatment and control were slight, B concentration remaining stable throughout the sampling period (Fig. 2C).

The highest concentrations of B in the flower and fruit were observed 3 and 17 days after treatment, coinciding with anthesis and the beginning of the massive fruit abscission, respectively (Fig. 2D). Boron treatment nearly doubled B concentration in flowers and fruit over that of controls. Boron concentrations in fruit from control and treated branches de-

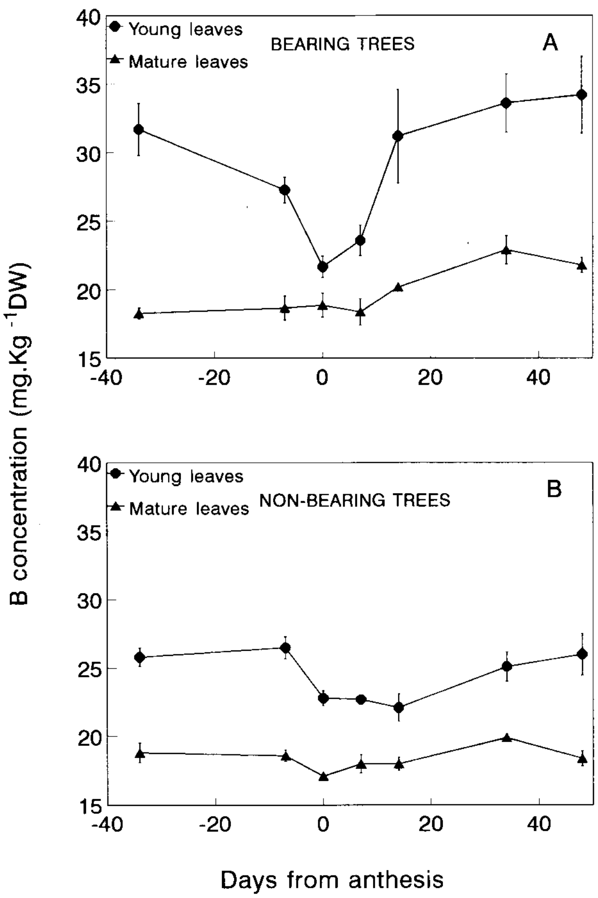

Fig. 1. Change in B concentration of young and mature leaves in bearing and nonbearing olive trees. Vertical bars indicate SE.

creased thereafter until 37 days after treatment, when fruit abscission was completed. Boron content in the fruit, expressed as accumulated B per fruit, increased throughout the sampling period; this effect was more marked in the fruit from shoots whose blades were treated with B (Fig. 3).

Discussion

The change of B concentration in young leaves, with a clear minimum coinciding with anthesis, suggests that B flows out from these leaves at this time. This change might be due to the appearance of a potent B sink during anthesis and the early phases of fruit development. The following observations support this hypothesis: a lower B content in the young leaves during anthesis, compared to that found in the days previous to and after this time; the fact that this phenomenon was more marked on bearing trees; and, finally, the rapid accumulation of B in the fruit after B treatment of the leaves.

In the olive tree, the outflow of B from the blade of the treated leaf (Fig. 2A) is slower than that obtained by Hanson (1991) for apple, pear, prune, and cherry trees. However, the flower and fruit behaved as a powerful B sink. Three days after treatment of the blade, the concentration of B in flowers at anthesis was 75% higher than that in the control. Seventeen days after treatment, B began to reach similar values to those found during anthesis. During that time period, massive fruit abscission occurred (Rallo and Fernández-Escobar, 1985). The enormous capacity for B accumulation in the fruit observed during this phase of fruit development could be a consequence of the smaller number of sinks due to fruit abscission. In other species, an increase in B accumulation in buds during anthesis has been observed by Woodbridge et al. (1971); their results agree with those described in our experiments.

Leaf age influenced the capacity to mobilize B. The young leaves had greater capacity for B mobilization than did-the mature leaves. Although B concentration was higher in young than in old leaves, both leaf types had similar B contents (Table 1). Mobilizable B in the young leaves and the immobile Bin the mature leaves may constitute, respectively, the dialyzable (soluble) and nondialyzable B fractions described by Skok and McIlrath (1958). Foliar B treatments may increase the dialyzable B fraction in the mature leaves and, therefore, promote the capacity of B mobilization in these leaves. These results suggest that, at least at a given time in the olive tree, it is possible to mobilize B from the leaves. Studies on other species support this suggestion (Campbell et al., 1975; Hanson, 1991; McIlrath, 1965).

Our results show that the flower and fruit mobilize foliar B in their early stages of development, and that the plant has the capacity to remobilize B from the leaves to meet this demand. Foliar B application, at least with our method. near anthesis can satisfv the need for B during flowering and fruit set.

Table 1. Boron content (µg/leaf) in young and mature leaves of bearing olive trees before, during, and after anthesis.

	Days from anthesis[z]		
Leaf	−7	0	+7
Young	2.35 a	1.94 b	2.26 a
Mature	2.59 a	2.62 a	2.54 a

[z]Letters indicate mean separation within each leaf type based on SE.

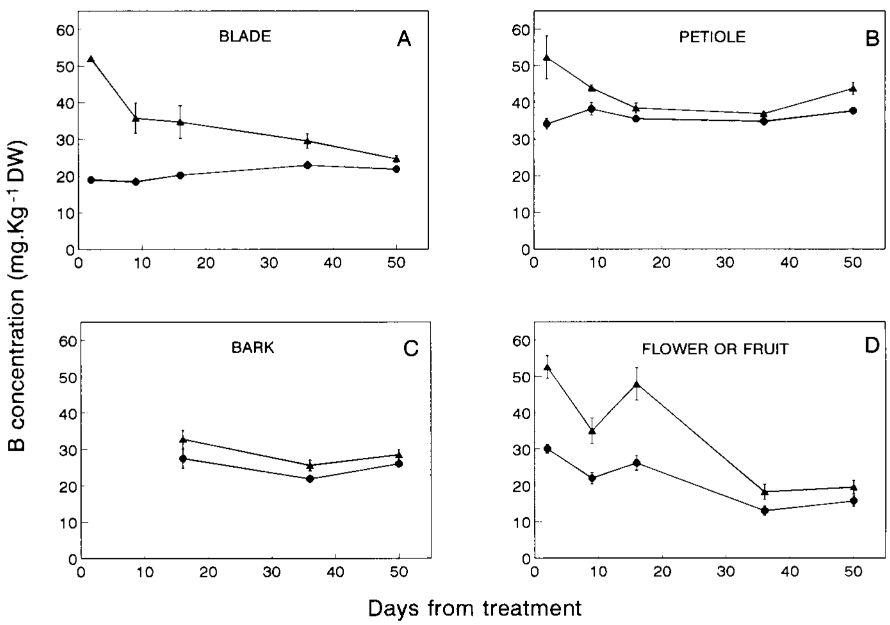

Fig. 2. Change in B concentration in various parts of the bearing shoot after B treatment with 0.5% Solubor (triangles) compared to controls (circles). Vertical bars indicate SE.

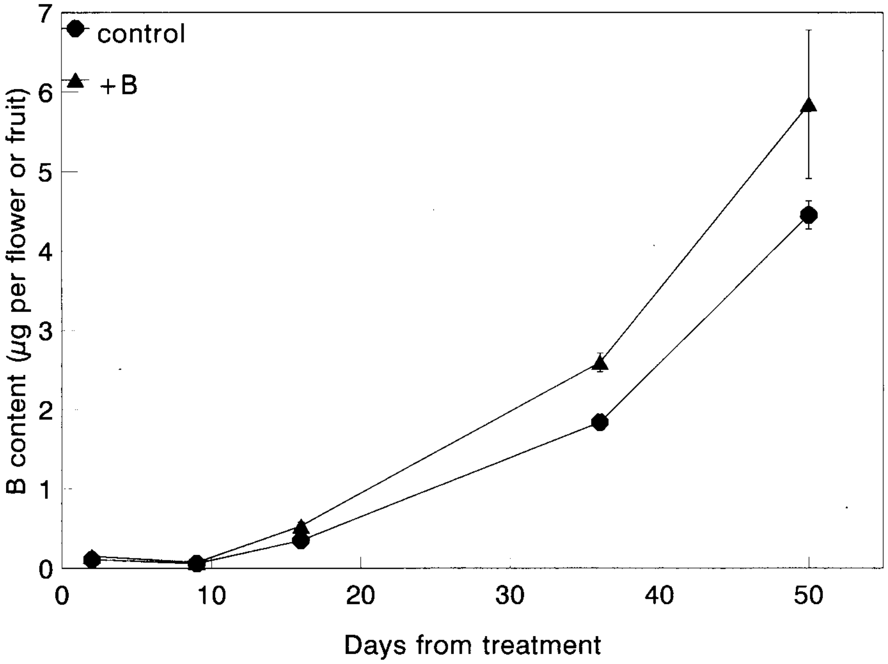

Fig. 3. Boron accumulation in flowers and fruit after foliar B treatment with 0.5% Solubor compared to controls. Vertical bars indicate SE.

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