Fall Foliar-applied Boron Increases Tissue Boron Concentration and Nut Set of Almond

Agnes M.S. Nyomora¹ and Patrick H. Brown²

Department of Pomology, University of California, Davis, CA 95616

M. Freeman³

Cooperative Extension, University of California, 1720 South Maple Avenue, Fresno, CA 93703

ADDITIONAL INDEX WORDS. *Prunus dulcis*, foliar fertilization, flowering, pollination, micronutrients

ABSTRACT. Fruit set is the major determinant of productivity in almond [*Prunus dulcis* (Mill D.A. Webb)] where seed is the commercial product. Boron influences flowering and fruit set in a number of crops, but little has been reported on this subject in almond. Here, we investigated the effect of a fall foliar application of B on fruit set and tissue B concentration in open pollinated 'Butte' and 'Mono' almond over a 2-year period. Early fall B application significantly increased the vegetative, floral, and fruit tissue B concentration in the subsequent year. The greatest increase in organ B concentration was observed in flower buds, flowers, and hulls. Recent work has demonstrated that B forms a B–sorbitol complex in *Prunus* species. This B–sorbitol complex is phloem mobile and is transported to sink organs. Here we demonstrate that fall-applied B is absorbed by the leaf and is subsequently transported (presumably as the B–sorbitol complex) to floral buds where it is available to flowers and, hence, influences fruit set and yield. It is concluded that fall foliar-applied B is a useful fertilization strategy that can be used to optimize tissue B concentration in species in which B is phloem mobile. Boron applied at 245 and/or 490 ppm significantly increased fruit set in 'Butte' and 'Mono' and increased yield of 'Butte' in 1994 on open-pollinated trees (yield was not determined in 1993). The highest initial and second fruit set was associated with either the 245 or 490 ppm B treatments in both cultivars and both years. This increased fruit set resulted in yield increases of 53% and 4%, respectively, for 'Butte' and 'Mono'. Of the two cultivars, 'Butte', which had lower tissue B concentration before B application, responded more significantly in yield to B application. Application of 735 ppm B was less effective than either 245 and 490 ppm B; however, no visual symptoms of excess B were observed.

Under normal conditions, many almond cultivars have an average fruit set of only 22% to 30% (Griggs and Iwakiri, 1975; Kester and Griggs, 1959b; Tufts and Philp, 1922). Fruit set percentage is determined by prevailing conditions at the time of pollination (weather conditions, compatibility, and flowering overlap of cultivars and pollenizers) as well as postfertilization conditions that influence resource availability and fruitlet retention. As almond is a high-value crop, even small increases in fruit set and nut retention can be economically significant.

Low B levels have been found to restrict the proportion of flowers setting fruit, reduce fruitlet retention and development, and decrease yield in a number of tree crop species (Batjer and Thompson, 1949; Chaplin and Westwood, 1980; Hanson and Breen, 1985; Shrestha et al., 1987). Batjer and Thompson (1949) and Hanson et al. (1985) observed a proportionate increase in fruit set in 'Italian' prune (*Prunus domestica* L.) and 'Anjou' pear (*Pyrus communis* L.) with increasing concentration of foliar B sprayed before anthesis. Hanson (1991a, 1991b) reported as much as a 100% increase in fruit set percentage in sour cherry (*Prunus cerasus* L.) following foliar B applications. In 'Barcelona' hazel nuts (*Corylus avellana* L.), Baron (1972, 1973) reported yield increases of between 10% and 88%, while Shrestha et al. (1987) reported a 17% to 21% yield increase of the same cultivar. Most of these experiments were conducted on trees that did not show

obvious vegetative signs of B deficiency, suggesting that there is a specific requirement for B in the reproductive processes of tree fruit and nut crops.

Despite the observed positive effects of B on fruit and nut set, the role played by B in flowering and fruiting processes is unclear. The often-reported influence of B status on ion and carbohydrate absorption and translocation processes (Parr and Loughman, 1983) may indirectly affect pollination, fertilization, and fruit development by affecting the supply of nutrients during critical developmental stages. Marschner (1986) speculated that B deficiency alters the transportation of sugars to the developing flower, thereby reducing the sugar content of the nectar. This would implicate B in the promotion of pollinator activity during flowering. Related to this function is the speculation that B increases flavonoid content of the pollen (Taylor et al., 1994). Flavonoids have been found to be important in maintaining high pollen viability and germinability (Taylor et al., 1994). There is evidence (Dickinson, 1978; Nyomora, 1995) that B deficiency results in low pollen viability, poor pollen germination, and reduced pollen tube growth, possibly through its metabolic role in controlling various biochemical reactions and also due to its general role in the structure of plant cell walls and maintenance of cell membrane integrity (Goldbach et al., 1991; Loomis and Durst, 1991). Boron is also known to play a role in the inhibition of nonpathological callose formation, a role that parallels plant defense mechanisms. Lewis (1980) speculated that B may be required in stigma and styles to physiologically inactivate callose present in pollen tube walls that would otherwise elicit phytoalexin production to inhibit pollen tube growth.

Almond presents more pollination problems than any other fruit and nut crop. First, cross pollination is almost the exclusive mode of pollination. Second, since the number of seeds contributes most to the commercial product, large numbers of flowers (up to 100%) need to be pollinated for optimal productivity (Griggs and Iwakiri, 1964; Micke and Kester, 1978). This is compared to the

Received for publication 17 May 1996. Accepted for publication 16 Dec. 1996. We acknowledge the Univ. of California, Davis, and the Almond Board of California for supporting this research. We also thank the grower, Bill Chandler, of Fresno, Calif., for accommodating this research in his orchard. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

¹Postgraduate researcher.

²Associate professor.

³Farm advisor, Fresno County.

3% to 7% pollination considered adequate to give a commercial crop in apple or pear (McGregor, 1976; Hill et al., 1985). Third, pollination and fertilization in almonds occurs over a very short period in early spring. The stigma are receptive to pollen for only 1 to 2 d following anthesis, while the ovules remain receptive for 3 to 4 d more (Pimienta and Polito, 1982a, 1982b). Finally, in almond, as in other *Prunus* sp., the presence of pollen tubes in the transmitting tissue is a prerequisite to the completion of megagametogenesis (Herrero and Arbeloa, 1989). Unlike many other fruit and nut species, the embryo sac does not begin to develop until the flowers open and the pollen tubes have reached the base of the ovary (Pimienta and Polito, 1982b). Any environmental perturbation (cold weather, wind, or rain at the critical time of pollination and fertilization), including possibly B deficiency, that may occur during anthesis may hinder rapid pollen tube growth and reduce fruit set and yield.

Almond hulls contain the highest B concentration of any almond tissue (Nyomora, 1995). The removal of the fruit from the orchard at harvest represents a significant loss of B. Large acreages of Californian, upper Sacramento valley (north of Yolo County to Chico), and eastern regions of the San Joaquin valley (from Modesto to Fresno) almond orchards are on light-textured soils that are low in B and are irrigated with low B water and, therefore, are at risk of incipient B deficiency. These factors and the long-term production of almond in these regions suggests that B deficiency may limit crop production. Low productivity due to premature flower and fruitlet drop (characteristic of B deficiency) in several orchards throughout California are symptomatic of B deficiency. The objective of this study was to investigate the effect of fall foliar application of B on tissue B concentration and fruit set in open-pollinated Butte and Mono almond cultivars.

Materials and Methods

An orchard suspected of having an incipient B deficiency (reduced productivity, flower, and fruitlet drop) was identified in Fresno County, Calif. Initial leaf samples contained B on a dry mass basis at 22 to 24 $\mu\text{g}\cdot\text{g}^{-1}$, which is below the adequate level of $>30 \mu\text{g}\cdot\text{g}^{-1}$ thought to be required in almond (Shear and Faust, 1980). Recent observations indicate a foliar B concentration of 50

$\mu\text{g}\cdot\text{g}^{-1}$ to be adequate in almond orchards (Brown et al., 1996).

In 1992, an experiment was initiated in this orchard to characterize further the role of B in almond. Boron as Solubor ($\text{Na}_2\text{B}_4\text{O}_{10}\cdot 4\text{H}_2\text{O}$), a commercial product containing 20.5% B, was foliar applied on 15 Oct. 1992 (1 month postharvest) and on 30 Sept. 1993 (2 weeks postharvest) to the same trees each year. Boron was applied at 0, 245, 490, and 735 ppm in water. Trees with uniform stem girth and appearance were sprayed using a tractor-mounted sprayer that delivered dilute sprays of about 18 L/tree. Treatments were applied to a block of three replicate trees per treatment on two compatible cultivars, Mono and Butte. Each block was then replicated five times in a randomized complete-block design (RCBD) layout for a total of 120 treated trees (60 trees each of 'Butte' and 'Mono'). Rows of 'Ruby', 'Mono', and 'Butte' alternated in the orchard. The test cultivars Butte and Mono constituted the main treatment on which B rates were superimposed.

BORON ANALYSES. For B analysis, 25 leaves were sampled in early fall before treatment, following treatment, as well as in midsummer of the following year (July) from nonfruiting shoots and spurs from around each treated tree. Leaves were washed in a 1% liquid detergent, rinsed three times in double-deionized water, and dried at 65 °C for 72 h. Dry leaves were ground (20 mesh) and samples of about 0.5 g were ashed overnight at 500 °C. The ashed samples were digested (heated in 10 mL 1 N nitric acid at 80 °C for 20 min), filtered through Whatman filter paper no. 1, diluted to 50 mL with double-deionized water, and analyzed by inductively coupled plasma-atomic emission spectroscopy (ICP-AES) (Thermo Jarrell Ash, Menlo Park, Calif.). The same tissue preparation and sampling procedure was used for the flower buds, flowers, pistils, and immature fruit. Samples were collected from treated trees in midwinter (December) for flower buds (250 g), at 50% budbreak for flowers (100 g), mid-February for pistils (10 g), and late spring (May) for immature fruit (10 fruit). Boron determination in pollen samples (collected in the spring) was performed by microwave digestion (Sah and Miller, 1992) after air drying to a constant weight at 65 °C. This overcame problems of pollen caking and incomplete ashing in the muffle furnace. A 10-nut subsample was randomly selected from the 1.8-kg subsamples taken from each treatment during the harvesting process. These nuts were separated into hulls, shells, and kernels and analyzed for B in similar manner

Table 1. Tissue B concentration ($\mu\text{g}\cdot\text{g}^{-1}$) of 'Butte' and 'Mono' almond in response to B sprays applied in September 1992.²

Cultivar	B rate (ppm)	September 1992	December 1992	February 1993		May 1993	June 1993
		Leaf before application	Flower buds	Flower	Pollen	Fruit	Midsummer leaf
Butte	0	10.8	17.9	20.1	20.6	11	17.2
	245	18.9	44.1	30.5	36	19.3	21.8
	490	13.6	58.5	37.3	29.5	24.2	27.3
	735	22.1	86.3	55.3	37.8	33.1	26.7
	LSD	11.2	5.1	8.5	19.7	6.8	5.2
Mono	0	15.5	22.1	11.3	16.3	11.0	21.9
	245	34.8	43.4	23.5	30.1	24.3	28
	490	22.8	52.5	31.7	38	24.3	31.3
	735	28.4	78.6	34.2	48	26.8	28.1
	LSD	18	9	12.2	21.7	8.2	5.8
B rate (B)		NS	**	***	***	*	**
Variety (V)		NS	**	*	***	NS	**
B × V		NS	NS	*	*	NS	NS

²Shown are means of five replications of each treatment for 'Butte' and 'Mono'.

NS, *, **, ***Nonsignificant or significant at $P = 0.05$, 0.01, or 0.001, respectively.

to the immature fruit and leaf tissue. All analyses included National Institute of Standards and Technology (NIST) calibration standards after each 10 to 15 samples.

FRUIT SET DETERMINATION. Four healthy and exposed branches each measuring 0.5 m long, were selected on each treatment tree. All flowers on each of the selected branches were counted in February 1993 and 1994 and the branches were tagged. One month after pollination, the remaining flowers and fruitlets were counted. A second count was taken in June. Fruit set was determined as the percentage of fruitlets remaining on the test branches after flower drop in March and percentage of fruitlets remaining on the test branches between the first and the second counts.

YIELD DETERMINATION. 'Mono' was harvested in mid-August 1994, while 'Butte' was harvested in early September 1994. No harvests were made in 1993. Mature nuts of both cultivars were mechanically shaken from the trees and left to dry on the ground for 1 week before windrowing. Nuts were picked from the ground on the third day of windrowing and weighed. The nut yield per plot was recorded from the nuts covering the ground area occupied by the treated trees. The nut mass per tree was then estimated from this weight. A 1.8-kg sample from each of the observations was randomly collected during the harvesting process. The nuts in this sample were counted to estimate the number of nuts per tree after considering the total nut mass of the whole tree. In addition, a 50-nut subsample was randomly selected and weighed, and nuts were separated into hulls, shells, and kernel followed by another weighing to give hulling and shelling percentages.

STATISTICAL ANALYSES. SUPERANOVA and STATVIEW programs (Abacus Concepts Inc., Berkeley, Calif.) were used for statistical analysis. Protected least significant differences (LSDs) were used for the mean separation.

Results

INFLUENCE OF FALL FOLIAR B APPLICATION ON TISSUE B CONTENT. Before B application in 1992, leaf B concentrations, on a dry mass basis, in this orchard averaged 18 to 25 $\mu\text{g}\cdot\text{g}^{-1}$ in 'Butte' and 'Mono', respectively (Table 1). In 1993, pretreatment leaf B values for the two cultivars were 21 and 25 $\mu\text{g}\cdot\text{g}^{-1}$ respectively. Pretreatment leaf

B values did not differ between 1992 and 1993. In 1993, fall foliar B sprays significantly increased B concentrations in leaves sampled 48 h after application (Table 2), an increase that was directly proportional to the concentration of the applied B. Fall B applications also significantly increased B concentration in dormant flower buds, flowers, pollen, and young fruit (May sample) in both years (Tables 1 and 2). Boron application also increased stylar B in 'Mono' (Table 2), although the low B concentrations in styles coupled with the difficulty in collecting adequate tissue for sampling resulted in high variability in these results. In both years, the highest concentration of B was found in the entire flower buds, while the lowest B concentration was found in styles and midsummer leaves (Tables 1 and 2).

After foliar B was first applied in October 1992, there was minor residual B at the end of the following season, as evidenced by a slight increase in leaf B concentrations in June 1993 (Table 1). In contrast, when the same trees were sprayed in September 1993, leaf B measured in June 1994 clearly reflected the previous B application. Boron concentrations in the entire flower, immature fruit, and midsummer leaves in both years and in pollen and styles in 1994 all reflected the B applications made the previous year (Tables 1 and 2).

Boron application significantly increased B concentration in all fruit tissues during 1993–94. Hulls had the highest B concentration, while lower concentrations were found in kernels and shells.

FRUIT SET. Foliar B treatment significantly increased initial fruit set in both cultivars in 1993 and 1994 (Fig. 1). In 'Butte' in 1993, the initial fruit set was highest with application of 245 ppm B. In 1994, 245 and 490 ppm B resulted in higher initial set. In 'Mono' in 1993 and 1994, fruit set was greatest with either 245 or 490 ppm B. In 1992–93, application of 490 ppm B to 'Mono' and 245 ppm B to 'Butte' resulted in the highest initial fruit set (28% and 36%, respectively), which is a 130% and 50% increase in set over nontreated trees. Boron application at higher and lower rates resulted in lower fruit set percentages in both cultivars (Fig. 1). Fruit set (second set) measured in June 1993 was also increased by B application and was generally higher in trees receiving moderate B (245 and 490 ppm) than in untreated trees; this was most evident in 'Mono', where fruit set at 490 ppm B was >200% higher than in

Table 2. Tissue B concentration ($\mu\text{g}\cdot\text{g}^{-1}$) of 'Butte' and 'Mono' almond in response to B sprays applied in September 1993.^z

Cultivar	September 1993			December 1993		February 1994			May 1994	June 1994	September 1994		
	B rate	Leaf before	After	Flower									
	(ppm)	application	48 h	buds	Flower	Pollen	Style	Fruit	Leaf	Hull	Shell	Kernel	
Butte	0	22.2	25.9	28.6	18.4	12.1	---	16.9	20.2	40.8	33.4	17	
	245	23.8	69.2	60.9	34.2	34.4	---	27.3	31.4	54.1	34.2	17.1	
	490	21.8	106.7	87.1	44.8	42.1	---	33.5	32.1	61.5	40.7	20.8	
	735	20.1	148.6	91.7	60.5	40.6	---	56.1	39	70.5	72.2	27.8	
LSD ^x		17.7	53.4	18.9	7.5	---	11.1	8	6.1	24	4.4	7.7	
Mono	0	21.9	35.2	27.6	18.5	---	19	18.2	32.6	13.6	9	13	
	245	34.9	93.5	46	38.4	---	24.8	35.2	36.1	49.6	16.4	20.9	
	490	22.8	148.6	76.1	45.5	---	33.6	38.9	38.4	65.5	20.8	26.2	
	735	31.7	191.1	97.1	62.4	---	50.5	52.6	44.6	89.4	32.1	31	
LSD		17.7	53.4	18.9	7.5	---	11.1	8	6.1	23.9	4.4	7.7	
B rate (B)		NS	***	***	***	**	**	***	***	***	***	***	
Variety (V)		*	NS	**	NS	NS	---	---	NS	NS	NS	***	
B × V		NS	NS	**	NS	NS	---	---	NS	NS	NS	***	

^zShown are means of five replicates of each treatment for 'Butte' and 'Mono'.

^yNo data available.

*Mean separation by protected LSD ($P = 0.05$).

NS, **, *** Nonsignificant or significant at $P = 0.05$, 0.01, or 0.001, respectively.

nontreated trees. The increase in the second fruit set for 'Butte' averaged 25% greater than the control across all B application rates. Except for the initial set in 1994, B application resulted in an increase in set when applied at 245 and 490 ppm B and a decline in set at higher rates (735 ppm) when compared to nonsprayed trees.

During 1993–94, B applications (September 1993) resulted in a significant increase in the initial fruit set (Fig. 1). The highest increase in the initial fruit set of 70% and 40% over the control was observed with B application of 490 and 245 ppm treatments, respectively, for 'Mono' and 'Butte'. The increase in the second fruit set in 1994 was highest (50%) at the 245 ppm rate for 'Mono', while for 'Butte' the highest (240%) was at 735 ppm. As in 1993, no visual symptoms of B toxicity were observed at any B application rate. The lower initial fruit set percentages observed during 1993 compared to 1994 were in part due to a delay in assessment (May instead of April).

The reduction in fruit set over the season (i.e., difference between the initial and second fruit set) varied with season and treatment and showed no clear pattern within treatments or cultivars.

YIELD. Yield was not collected in 1993. In 1994, the yield of 'Butte' was increased by B applications, while in 'Mono' it was not. This occurred despite significant effects of B application on fruit set. Yield, in fruit numbers and mass per tree, was significantly enhanced by B fertilization in Butte (Fig. 1). On average, across all treatments, 'Butte' yielded 32 kg/tree while 'Mono' yielded 21 kg/tree. The nut yield of 'Butte' trees treated with 490 ppm B was 39 kg/tree, equivalent to a 53% increase in yield over the control, while 'Mono' yielded only 4% over the untreated trees.

The highest number of nuts in 'Butte' (12,287 nuts/tree) was found in plots that had been fertilized with 245 ppm B, while in 'Mono' the highest numbers (6543 nuts/tree) was obtained in trees treated with 490 ppm equivalent, respectively, to a 75% and 7% increase in nut numbers compared to the untreated trees. Within a cultivar, yields from the two intermediate B rates (245 and 490 ppm) did not differ significantly.

Boron application and cultivars significantly influenced the hull percentage of the fruit (Table 3). Moderate B application to 'Butte' (245 and 490 ppm) reduced the hull proportion of the nuts by 8% compared to untreated trees and trees treated with the highest B rate of 735 ppm. Hull proportions of 'Mono' were not affected by B application. The decrease in hull proportion resulted in a similar increase in percentage nutmeat in 'Butte'. Boron application did not affect the shelling percentage, which averaged 25% in 'Butte' and 28% 'Mono'. Regardless of the B rate, 'Mono' had heavier nuts (3.5 g/nut) than 'Butte' (3.0 g/nut)

Discussion

Before B application in October 1992, the average leaf B concentrations of 18 and 25 ppm dry matter ('Butte' and 'Mono', respectively) in this orchard was below the generally accepted adequate levels of 30 ppm B dry matter (Shear and Faust, 1980). Foliar applications of B in fall consistently increased the B concentrations in all sampled tissues the following season but had no effect on visible tree appearance or growth. A highly significant increase in B concentration was observed in dormant buds, flowers,

immature fruit, and hulls. Although fall B applications always increased tissue B levels in the following season, there was no evidence of carryover of the 1992 sprays in the 1994 tissue samples. These results, in part, agree with the findings of Baron (1973), Hanson and Breen (1985), Hanson et al. (1985), and Hanson (1991b) in other fruit and nut crops, where it was observed that foliar B applications in the previous fall or dormant period could influence tissue B concentration in the subsequent spring. We observed that B application consistently influenced fruit and leaf B concentration in spring and summer. These results contrast with those of Hanson (1991b), who observed no increase in summer leaf B concentration of prune following fall foliar application of B. Similarly, Callan et al. (1978) and Hanson (1991a) reported no residual effect of fall-applied B on leaves in the season following fall foliar B application. Callan et al (1978) and Hanson (1991a) proposed that most of the foliar-applied B was used by reproductive tissues, leaving little additional B for leaves. Differences in initial B concentrations, fruit load, or other environmental conditions may account for this discrepancy.

Fig. 1. Effect of B application on almond nut set and yield (1994 season). Error bars if not visible are smaller than the symbol.

Table 3. Effect of fall foliar-applied B on proportions of hull, shell, and seed.²

Treatment (ppm)	Butte			Mono		
	Hull	Shell	Seed	Hull	Shell	Seed
0	51	24	24	47	28	24
245	47	25	26	45	28	23
490	47	26	26	46	30	24
735	50	25	23	49	27	23
LSD ³	2.0	2.3	2.0	2.3	3.0	1.1

²Shown are means of five replicates of each treatment in 'Butte' and 'Mono' during 1993–94.³Mean separation by protected LSD ($P = 0.05$).

A significant increase in B concentrations in leaf tissue was observed 24 h after B application. In an experiment by our group (Brown and Hu, 1996; Picchioni et al., 1995) and others (Hanson, 1991a; Hanson et al., 1985), a similar rapid increase in leaf B has been observed. This increase is only transient, and, within 5 d, most foliar applied B had disappeared from the leaf. This has been interpreted as evidence of rapid phloem mobility of B in *Prunus* sp. (Brown and Hu, 1996). In both years following B application, there was a significant increase in leaf B concentration. These results clearly demonstrate a significant phloem mobility of foliar applied B within these trees. Recently, using ¹⁰B isotope tracing, it has been demonstrated that foliar-applied B is readily retranslocated out of the mature leaves of *Prunus*, *Pyrus*, and *Malus* and is retranslocated to currently active sink tissue (Brown and Hu, 1996; Hanson, 1991a). This movement is the result of the phloem mobility of B-sorbitol complexes (Brown and Hu, 1996; Hu et al., 1997).

In the experiment reported here, fall-applied B to trees with incipient B deficiency increased the initial fruit set in almond. Similar effects have been observed in pear (Batjer and Thompson, 1949), hazel nut (Baron, 1972, 1973; Shrestha et al., 1987), Italian prunes (Chaplin et al., 1977; Hanson et al., 1985), and sour cherry (Hanson, 1991b). Boron application at 245 or 490 ppm gave the highest increase in the initial and second fruit set in both years. Boron application rates in excess of 490 ppm decreased yield suggesting an optimal B concentration at which fruit set and consequently yield is maximized. Initial fruit set is a measure of the number of fertilized flowers, while the second set measures the proportion of the fertilized flowers that are retained at a certain fruit developmental stage. While it may be possible that the positive effect of B on first and second fruit set could be directly correlated, we speculate that there may be a dual role of B in fruit set. Boron is known to be required for pollination and fertilization success (initial set) and apparently also influences subsequent fruitlet retention (second set). The causes of fruit drop have been variously attributed to factors such as an inability of the endosperm to maintain the embryo development (Murneek, 1954), hormone imbalance in favor of abscission (Luckwill, 1953), and resource limitations, particularly of C and N (Chandler, 1957; Deng et al., 1991; Stephenson, 1981). All these causes can generally be related to B in so far as B is known to affect carbohydrate and hormone metabolism and translocation (Shelp, 1993).

The highest B application rate of 735 ppm was less effective at increasing fruit set than the middle and lower rates. This high rate may have been toxic to the reproductive structures, although the mechanism involved is unknown. Loomis and Durst (1991) speculated that, under B toxicity situations, cell expansion is inhibited by an abnormal excess of cell wall cross-links. This may cause abnormal pollen tube growth and/or ovule development resulting in reduced fertilization rates. There may also be disruption of membrane bound enzymes as well as disruptions to the transport of ions, metabolites, and hormones, thus resulting in fertilization

failure or further developmental limitations (Luckwill, 1953; Parr and Loughman, 1983).

The cultivars used here differed in their responsiveness to B supply. 'Butte', which is known to be more affected by B deficiency (unpublished observations), was also more responsive to B application, even at lower application rates than 'Mono'. This may not indicate that 'Butte' has a higher B requirement than 'Mono', but rather is more sensitive to changes in B levels. It is also possible that bloom time may affect responsiveness to B during the critical time of pollination and fertilization. Earlier blooming usually coincides with lower temperatures compared to later blooming (Griggs and Iwakiri, 1964) and, therefore, increases the risks of fertilization failure and consequently low fruit set. Low temperatures may also affect the use of B within the plant. Thompson and Liu (1973) showed that at postbloom mean temperatures of 7.7 to 10.7 °C, Italian prune pollen tubes grew so slowly that none had effective fertilization after 13 d. In contrast, at mean temperatures of 14.0 to 17.3 °C, only 3% of the tubes had not penetrated the micropyle in 11 d. Under prolonged cool weather, many of the embryo sacs began to degenerate before pollen tubes reached them, thus eliminating any chance for fruit set. Sufficient B may therefore moderate the adverse effects of low temperature, since B accelerates pollen tube growth (Griggs and Iwakiri, 1975; Nyomora, 1995).

Yield nut numbers and total mass of 'Butte' increased in response to B application, while the hull percent decreased with increasing B application. This is consistent with findings of most of the earlier investigators in other tree species. In macadamia (*Macadamia intergrifolia* Maiden and Bette), Stephenson and Gallagher (1987) found a higher percentage kernel recovery, first-grade kernels and mean kernel mass from B treated trees than from untreated non-B-deficient trees. The initial B concentration of 'Mono' was higher than that of 'Butte' and B application caused differential responses in fruit set in these two cultivars. Since the same trees were treated in 1993 and 1994, the applied B plus the residual B from the previous season could have elevated B concentration in 'Mono' and may have been adequate to ensure optimal fruit set in all treatments.

Fruit set is affected by factors other than B nutrition, such as weather, the size of pollinator population, and cross-fertilization events; all of these factors interactively contribute to set and final yield (DeGrande-Hoffman et al., 1989). It is possible that factors other than pollination limitations and B status affected the results presented here. Nevertheless, foliar B application was remarkably effective at influencing fruit set in both cultivars and yield in 'Butte'.

The increase in B concentration in various tissues following B application to the leaves suggest that applied B is absorbed by leaves and is redistributed to developing sinks. In woody Rosaceae species of Prunoideae and Pomoideae, B supplied to leaves is translocated and remobilized to the strongest sinks (Brown and

Hu, 1996) as a B-sorbitol complex (Hu et al., 1997). In this experiment, we supplied B to leaves following fruit harvest; at this growth stage, the buds and storage tissue represented the strongest sinks. Boron stored in these tissues is then available for remobilization into developing tissue in the spring. The high B concentration in the hulls and the sensitivity of these tissue to B application is further evidence of phloem B mobility. The accumulation of B in hull tissue further suggests that hull tissue may be a good indicator of general B content of almond. Recent discoveries on the mechanism of phloem mobility provide a physiological rationale for the results observed here. Further, an understanding of the mechanism of B mobility allow a reexamination of previous reports of plant responses to foliar B application in *Prunus* species. We conclude that fall foliar applications are a valid method of enhancing tissue B levels in the subsequent spring. Optimal B nutrition is required for maximal fruit set. This conclusion is likely true for any species for which B is freely phloem mobile including all *Malus*, *Pyrus*, *Prunus*, and *Oleaceae* (Brown and Hu, 1996; Hu et al., 1997).

Literature Cited

- Baron, L.C. 1968. Waking the sleeping giants. Nut Growers Soc. Oregon and Washington. Proc. 54th Annu. Mtg., Salem, Ore., 13 Dec. 1968. Nut Growers Soc. Oregon and Washington 54:22-28.
- Baron, L.C. 1973. The value of boron sprays on filberts. Nut Growers Assn. of Oregon and Washington. Proc. 58th Annu. Mtg., Portland, Ore., 30-31 Jan. 1973. Nut Growers Assn. Oregon and Washington 58:43-44.
- Batjer, L.P. and A.H. Thompson. 1949. Effects of boric acid sprays applied during bloom upon the set of pear fruits. Proc. Amer. Soc. Hort. Sci. 53:141-142.
- Brown, P.H. and H. Hu 1996. Phloem mobility of boron is species dependent. Evidence for phloem mobility in sorbitol rich species. Ann. Bot. 77:497-505.
- Brown, P.H., H. Hu, A. Nyomora, and M. Freeman. 1996. Foliar application enhances almond yields. Better Crops with Plant Food, No. 1. Potash and Phosphate Inst. Ref. No. 323054/95223.
- Callan, N.W., M.M. Thompson, and M.N. Westwood. 1978. Effects on fruit set of Italian prune following fall foliar and spring B sprays. J. Amer. Soc. Hort. Sci. 103:253-257.
- Chandler, W.H. 1957. Deciduous orchards. 3rd ed. Lee and Febiger, Philadelphia.
- Chaplin, M.H., R.L. Stebbins, and M.H. Westwood. 1977. Effect of fall applied boron sprays on fruit set and yield of Italian prune. HortScience 12:500-501.
- Chaplin, M.H. and M.N. Westwood. 1980. Relationship of nutritional factors to fruit set. J. Plant Nutr. 2:477-505.
- DeGrande-Hoffman, G., S.A. Roth, and G.M. Lopper. 1989. ALMOPOL: A cross-pollination and nut set simulation model for almond. J. Amer. Soc. Hort. Sci. 114:170-176.
- Deng, X., S.A. Weinbaum, T.M. DeJong, and T.T. Muraoka. 1991. Pistillate flower abortion in 'Serr' walnut associated with reduced carbohydrate and nitrogen concentrations in wood and xylem sap. J. Amer. Soc. Hort. Sci. 116:291-296.
- Dickinson, D.B. 1978. Influence of borate and pentaerythritol concentrations on germination and tube growth of *Lilium longiflorum* pollen. J. Amer. Soc. Hort. Sci. 103:413-416.
- Goldbach, H.E., J.B. Grill, N. Lendeman, M. Porzelt, C. Horrmann, B. Lupp, and B. Gessmer. 1991. Influence of boron on net proton release and its relation to other metabolic processes. Current Topics Plant Biochem. Physiol. 10:195-220.
- Griggs, W.H. and B.T. Iwakiri. 1964. Timing is critical for effective cross pollination of almond flowers. Calif. Agr. 18(1):6-7.
- Griggs, W.H. and B.T. Iwakiri. 1975. Pollen tube growth in almond flowers. Calif. Agr. 29(7) 4-7.
- Hanson, E.J. 1991a. Movement of boron out of tree leaves. HortScience 26:271-273.
- Hanson, E.J. 1991b. Boron requirements and mobility in tree fruit species. Current Topics Plant Biochem. Physiol. 10:240-246.
- Hanson, E.J. and P.J. Breen. 1985. Xylem differentiation and boron accumulation in Italian prune flower buds. J. Amer. Soc. Hort. Sci. 110:566-570.
- Hanson, E.J., M.H. Chaplin, and P.J. Breen. 1985. Movement of foliar applied boron out of leaves and accumulation in flower buds and flower parts of 'Italian' prune. HortScience 20:747-748.
- Herrero, M. and A. Arbeloa. 1989. Influence of the pistil on pollen tube kinetics in peach (*Prunus persica*). Amer. J. Bot. 76:1441-1447.
- Hu, H., S.G. Penn, C.B. Lebrilla, and P.H. Brown 1997. Isolation and characterization of soluble B-complexes in higher plants. Plant Physiol. (In press.)
- Hill, S.J., D.W. Stephenson, and B.K. Taylor. 1985. Almond pollination studies: Pollen production and viability, lower emergence and cross pollination tests. Austral. J. Expt. Agr. 25:697-704.
- Kester, D.E. and W.H. Griggs. 1959b. Fruit setting in Almond: The effect of cross pollinating various percentages of flowers. J. Amer. Soc. Hort. Sci. 74:206-213.
- Lewis, D.H. 1980. Are there interrelations between metabolic role of boron, synthesis of phenolic phytoalexin and the germination of pollen? New Phytol. 84:261-270.
- Loomis, W.D. and R.W. Durst. 1991. Boron and cell walls. Current Topics Plant Biochem. Physiol. 10:149-178.
- Luckwill, L.C. 1953. Studies of fruit development in relation to plant hormones. I. Hormone production by the developing apple seed in relation to fruit drop. J. Hort. Sci. 28:14-24.
- Marschner, H. 1986. Mineral nutrition of higher plants. Academic Press, London.
- McGregor, S.E. 1976. Insect pollination of cultivated crop plants. Agr. Hdbk. 496. USDA-ARS, Washington, D.C.
- Micke, W. and D.E. Kester. 1978. Almond bud development, pollination and fertilization, p. 52-56. In: Micke, W. and D.E. Kester (eds.). Almond orchard management. Univ. California Div. Agr. Sci. Publ. 4092.
- Murneek, A.F. 1954. The embryo and endosperm in relation to fruit development, with special reference to apple, *Malus sylvestris*. Proc. Amer. Soc. Hort. Sci. 64:573-582.
- Nyomora, A.M.S. 1995. The effect of boron deficiency on the reproductive processes of almond (*Prunus dulcis* [Mill] D.A. Webb). PhD diss. Univ. California, Davis, Diss. Abstr.
- Parr, A.J. and B.C. Loughman. 1983. Boron and membrane function in plants, p. 86-103. In: Robb, D.A. and W.S. Pierpoint (eds.). Metals and micronutrients: Uptake and utilization by plants. Academic Press, London.
- Picchioni, G.A., S.A. Weinbaum, and P.H. Brown. 1995. Retention and the kinetics of uptake and export of foliage-applied, labelled boron by apple, pear, prune, and sweet cherry leaves. J. Amer. Soc. Hort. Sci. 120:28-35.
- Pimienta, E. and V.S. Polito. 1982a. Ovule abortion in 'Nonpareil' almond (*Prunus dulcis* [Mill] D.A. Webb). Amer. J. Bot. 69:913-920.
- Pimienta, E. and V.S. Polito. 1982b. Embryo sac development in almond (*Prunus dulcis* [Mill] D.A. Webb). Ann. Bot. 51:469-479.
- Sah, R.N. and R.O. Miller. 1992. Spontaneous reaction for acid dissolution of biological tissue in closed vessels. Anal. Chem. 64:230-303.
- Shear, C.B. and M. Faust. 1980. Nutritional ranges in deciduous tree fruits and nuts. Hort. Rev. 2:142-163.
- Shelp, B.J. 1993. Physiology and biochemistry of boron in plants, p. 53-85. In: U.C. Gupta (ed.). Boron and its role in crop production. CRC Press, Boca Raton, Fla.
- Shrestha, G.K., M.M. Thompson, and T.L. Righetti. 1987. Foliar applied B increases fruit set in Barcelona hazelnut. J. Amer. Soc. Hort. Sci. 112:421-416.
- Stephenson, A.G. 1981. Flower and fruit abortion: Proximate causes and ultimate functions. Annu. Rev. Ecol. Systematics 12:253-279.
- Stephenson, R.A. and E.C. Gallagher. 1987. Effects of foliar boron sprays on yield and quality of macadamia. Scientia Hort. 32:97-103.
- Taylor, L.P., T. Vogt, and M.P. Turcich. 1994. Flavonols and functional pollen, p. 62-77. In: A.G. Stephenson and Teh-hui Kao (eds.). Current topics in plant physiology. Amer. Soc. Plant Physiol. Ser., vol. 12.
- Thompson, M.M. and L.J. Liu. 1973. Temperature, fruit set and embryo sac development in 'Italian' prune. J. Amer. Soc. Hort. Sci. 98:193-197.
- Tufts, W.P. and G.L. Philp. 1922. Almond pollination. Univ. of California Agr. Expt. Sta. Publ. 4092.