CALIFORNIA

Boron Mobility and Consequent Management in Different Crops

By Patrick H. Brown and Hening Hu

Boron deficiency and toxicity occur throughout agricultural regions worldwide. To identify and correct an imbalance of B requires knowledge of the processes governing uptake, remobilization and distribution in the plant.

Mobile or Not Mobile in Plant Tissue?

Boron is now known to be mobile in the phloem of all species that utilize polyols (complex sugars) as a primary photosynthetic metabolite. In these species a polyol-B-polyol complex is formed in the photosynthetic tissues and is transported in the phloem to currently active sink regions such as vegetative or reproductive meristems. In species that do not produce significant quantities of polyols, B once delivered to the leaf in the transpiration stream cannot reenter the phloem, resulting in essentially complete phloem immobility.

In species for which B is immobile, B moves with the transpiration stream and once it enters a leaf it tends to remain. Thus, B will accumulate at the sites of termination of leaf veins. A steep gradient in B concentration has often been found such that B concentration in petioles and midribs < middle of lamina < margins and tips. This principle is illustrated in **Figure 1** in which the distribution of B within a mature leaf of walnut and apple is contrasted. In walnut, in which B is immobile, the highest B accumulation occurred at the tip and margin of the leaf.

Boron Distribution in Plant Tissue

Figure 1 also illustrates B distribution in apple. In this species leaf B concentrations were significantly lower than in walnut, and there was very little difference in B accumulation across the leaf.

> It has been accepted that the uptake of boron (B) is a passive (non-metabolic) process and that it is a phloem immobile element, so once incorporated into tissue, it cannot be remobilized to supply the needs of other plant tissues. Recent work by Brown and co-workers, however, has now demonstrated that the physiology (mobility) of B varies dramatically between plant species and that our current knowledge of the symptoms and management of B nutrition must be re-examined on a species by species basis.

TABLE 1. Boron concentration (ppm dry wt.) in leaf and fruit organs of four tree species.

	B mobile		B immobile	
Organ	Almond	Apple	Pistachio	Walnut
Leaf	42	41	130	295
Hull	170	51 (peel)	33	40
Shell	34	34 (pulp)	2	9
Kernel	43	54 (core)	1	4

This uniform low distribution of B in apple does not correlate with leaf venation pattern and is not consistent with the hypothesis that B distribution is determined solely by transpiration. This same leaf distribution was observed in almond, peach and plum, suggesting that B distribution in these species is not governed by transpiration and is suggestive of phloem B mobility. Evidence of phloem B mobility or immobility can also be discerned from the distribution of B within different organs of a given species. For example, under field conditions pistachio and walnut both contain the highest B concentration in mature leaves and the lowest B concentration in fruit and seed tissue (**Table 1**). In contrast, almond or apple grown at the same site had highest B concentration in hull (fruit tissue), with much lower B in the leaves (**Table 1**).

The concentration of B in leaves of different ages within a species can also provide evidence of B mobility. The occurrence of higher B concentrations in old or mature leaves in comparison to younger leaves is evidence of B immobility, while higher B concentrations in younger leaves is an indication of B mobility since these leaves have transpired less water than older leaves. The results in **Table 2** suggest that B is phloem immobile in pecan, tomato, strawberry and walnut, while B is phloem mobile in apple, apricot, pear, grape, loquat, peach, celery, olive, and pomegranate. These differences in the site of accumulation of B in tissues will, in turn, determine where within a plant the symptoms of B toxicity will occur.

Boron Toxicity Symptoms

The difference in B mobility also results in difference in the expression of B toxicity symptoms. Because plants in which B is immobile always accumulate B in the tip and edge of old leaves like walnut in **Figure 1**, B toxicity symptoms in those species are always exhibited as leaf tip and edge burn (**Figure 2a**, pistachio). On the other hand, for those plants in which B is mobile, instead of the marginal leaf burn, these species exhibit B toxicity as die back in young shoots (**Figure 2b**, almond), profuse gumming in the leaf axil and the appearance of brown, corky lesions along stems and petioles (**Figure 2c**, almond). Die back induced by B toxicity has been reported in almond, apple, apricot, cherry, peach, pear, plum, and prune etc. The occurrence of these 'unusual' symptoms of B toxicity are not,

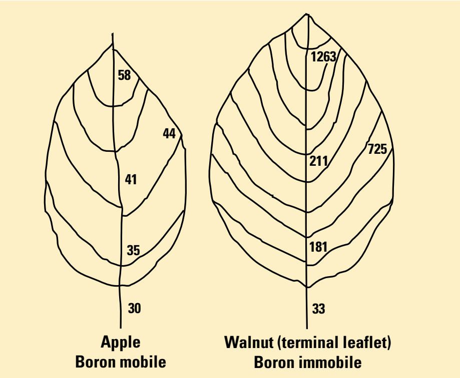

Figure 1. Leaf B concentration (ppm) in field grown apple and walnut. Leaves were collected at the end of the growing season. The two species were grown in close proximity and received the same irrigation.

Figure 2a. Boron is immobile in pistachio, so toxicity symptoms appear as leaf tip and edge burn.

however, restricted solely to the members of the Prunus, Malus and Pyrus genera as discussed earlier. For example, celery responds to B toxicity by producing deformed young leaves, "bitter" and misshapen stems, while the tip burn symptom is absent. Boron is known to be phloem mobile in celery, since celery like the members of the Prunus genera, utilizes a polyol as a primary transported photosynthate. The two kinds of B toxicity symptoms described above are a consequence of the difference in B mobility. In short, for those species in which B is immobile, B toxicity is exhibited as tip/edge burn of old leaves, while for those in which B is mobile, meristematic dieback is the primary symptom of B toxicity.

Diagnosis and Fertilization

In general, for the majority of plant species, B is phloem immobile, however B is phloem mobile in many important crop species such as those presented in **Table 2**. Preliminary evidence also suggests that many other crop species may exhibit phloem B mobility (i.e. coffee) though this is yet to be verified.

The difference in B mobility indicated above also profoundly influences the diagnosis of plant B status and the correction of deficiencies and toxicities. Currently practiced sampling techniques and symptom descriptions have been based on the premise that B is not mobile in the plant. Selection of tissue samples and determination of critical nutrient concentrations are all fundamentally dependent on the phloem mobility of B. **Table 2** illustrates that B does not accumulate in the older leaves of species in which B is mobile. Thus, old leaves are not suitable for determination of B toxicity. Rather young apical leaves or fruit tissue may be a superior indicator in these species (**Table 1, 2**). This observation has led to the widespread use of hull B as a determinant of B status in almond in California. In species with limited B mobility however, the B concentration in the old leaves (**Table 2**) remains a good indicator of B toxicity.

TABLE 2. Leaf B concentration (ppm dry wt.) along a shoot in various plant species.

Species	Basal	Middle	Apical	Remarks
Pecan	303	119	30	B-immobile
Tomato	721	318	94	B-immobile
Strawberry	512	176	68	B-immobile
Walnut	304	127	48	B-immobile
Apple	50	56	70	B-mobile
Apricot	45	60	81	B-mobile
Pear	42	57	62	B-mobile
Celery	32	49	104	B-mobile
Grape	74	55	88	B-mobile
Loquat	72	101	162	B-mobile
Olive	42	51	56	B-mobile
Peach	53	57	208	B-mobile
Pomegranate	21	20	111	B-mobile

For the diagnosis of B deficiency, the use of a recently matured, or fully expanded leaf is inappropriate if B is phloem immobile since the B concentration of a developed leaf may not reflect the B status of growing tissues for which a constant B supply is most critical. This can only be achieved by sampling growing tissues. This is an inherently difficult and inconsistent process. However, it is the only valid approach. By contrast, in species that exhibit mobility, mature leaves are appropriate for assessing B deficiency since their content reflects the B status of the entire plant, including young growing tissues. In these species B depletion in the soil will not impact meristematic growth until the soluble B pool of mature tissues has also been depleted.

The management of B fertilization in plants is directly influenced by patterns of B mobility. Experimental evidence clearly demonstrates that foliar applied B can be retranslocated to the growing organs in species with significant phloem B mobility. This suggests that foliar B application can be used effectively at any time functional leaves are present to correct B deficiency, and to supply B to future flower and fruit tissue. The significant benefits of foliar B application on fruit set that has been observed in many tree species such as almond, plum, prune and others is a consequence of this mobility. In species in which B is immobile, however, foliar applied B cannot be retranslocated from the site of application and cannot supply the B requirements of tissue not yet formed. Hence, in these species B applications must be made directly to the tissue of interest. In fruit crops, where B is essential for the flowering process, this means that B applications can only be effectively used if applied directly to the flower buds or flowers themselves.

Figure 2b. (At left) Boron is mobile in almond, and toxicity may cause dieback in young shoots.

Figure 2c. (At right) Profuse gumming in the leaf axil and appearance of brown, corky lesions along stems and petioles are symptoms of B toxicity in almond.

Summary

Knowledge of the relative mobility of B within a particular species determines the approach that should be used to sample and diagnose B status. This knowledge also determines the optimum fertilization strategy that should be used and helps in our understanding of the causes and consequences of B deficiency. Further work is underway to fully characterize the patterns of B mobility in diverse plant species. However, the following predictions can now be made about several important field crops.

- In corn, wheat, alfalfa and vegetable crops except those mentioned earlier, B is immobile and must, therefore, be supplied at all stages of plant growth.
- Foliar application can be used to correct deficiency in current tissues but will have minimal effect on new plant growth.
- In some species, there may be cultivars in which a small amount of mobility may occur.

This may explain the differences in sensitivity to B deficiency that are occasionally observed between cultivars. Further work on this topic is required.

Dr. Brown is Associate Professor and Dr. Hening Hu is a Postdoctoral Research Scientist, Department of Pomology, University of California, Davis.