

A survey of tropical species for boron retranslocation

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Abstract

The mobility in phloem of boron (B) has been reported to vary among plant species. Boron is phloem immobile in many species and completely mobile in others. Recent reports regarding phloem B mobility or immobility only considered temperate plants, and there is no information on tropical species. Information of phloem B mobility is useful for improving the diagnosis of B deficiency and management of B status in crop production. This study aimed to survey tropical species for their B mobility. Leaf samples of 17 species, including coffee (*Coffea arabica* L.), custard apple (*Annona squamosa* L.), guava (*Psidium guajava* L.), jackfruit (*Artocarpus heterophyllus* Lamk.), lime (*Citrus aurantifolia* Swingle.), cashew (*Anacardium occidentale* L.), mango (*Mangifera indica* L.), papaya (*Carica papaya* L.), passion fruit (*Passiflora edulis* Sims.), teak (*Tectona grandis* L.), cassava (*Manihot esculenta* Crantz.), Cork wood tree (*Sesbania grandiflora* (L.) Pers.), Indian walnut (*Samanea saman* (Jacq.) Merrill.), Tamarind (*Tamarindus indica* L.), Lychee (*Lychi chinensis* Sonn.), Longan (*Euphoria longana* Lam.) and Star fruit (*Averrhoa carambola* L.), were collected in the position of the youngest fully expanded leaf (YFEL), the middle leaf age of branch (ML) and the oldest leaf (OL). Based on a premise that nutrient concentration gradient between young and old leaf will be steeper in those species in which B is immobile, B concentrations in the different leaf positions was examined in comparison with calcium (Ca is phloem immobile) and potassium (K is phloem mobile). Concentrations of K in all leaf types were not significantly different or decreased with leaf age, while Ca concentrations were always higher in the older leaves. Seven species; coffee, guava, jackfruit, papaya, teak, tamarind and longan, showed concentration gradients of B that were similar to K. The results suggested that B may be retranslocated from older to younger leaves of these species, hence indicating that B may be phloem mobile in these species. However, this hypothesis needs conformation through studies examining retranslocation of B using B¹⁰ isotope or identification of B-complexing molecules in the phloem, e.g. sugar alcohols.

Media summary

Some tropical species may retranslocate boron via the phloem.

Key Words

Boron, retranslocation, phloem mobility, tropical species

Introduction

When nutrients are absorbed by roots and translocated in xylem sap by water movement to shoots, they may be transferred to phloem sap or exported and stored in roots, stems and leaf cells. However, nutrients that are stored in tissues and organs may be retranslocated and transported to other plant parts which transpire less, e.g. new shoot, reproductive tissues, via the phloem (Smith and Loneragan, 1997).

While all nutrients move readily in the xylem, they vary widely in the extent of their mobility in the phloem. Nutrient retranslocation or phloem mobility can be determined by a number of criteria, including direct analysis of nutrient concentration in phloem sap, movement of isotopes, development of deficiency symptoms, measurement the rates of influx of an element during fruit development, comparison of measured contents in different plant parts, and determination of concentration gradients in plants from older to younger leaves (Van Goor and Van Lune, 1980; Marschner, 1995).

Boron (B) is unique amongst the essential elements in that its mobility varies among species (Brown and Shelp, 1997). In most species B mobility is insignificant. Evidence for this type of behavior is widespread. Hu and Brown (1994) found that symptoms of B deficiency in young squash (*Cucurbita sp.*) occurred rapidly after withdrawal of B supply. In tomato (*Lycopersicon esculentum*) plants, which were grown with an excessive supply of B, the first symptoms of B toxicity appeared in the form of chlorosis at the margins and tips of leaves having high B concentrations, in contrast to the other plant parts. When B supply was interrupted, B deficiency symptoms developed immediately in younger and immature leaves (Oertli, 1993).

However, many observations have indicated mobility of B in plants. Hanson (1991) reported that B concentrations in leaves of apple (*Malus domestica* Borkh.), pear (*Pyrus communis* L.), plum (*Prunus domestica* L.) and cherry (*Prunus ceasus* L.) which were treated by foliar B spray (500 mg/L) decreased to levels similar to non-treated leaves and the highest B concentrations were found in buds. Applying B to leaves of olive at anthesis also increased B concentrations in leaf blades, petioles, bark of bearing shoots, flowers and fruits (Delgado *et al.*, 1994). The mechanisms of B remobilization in these studies were not clear. One possible mechanism is transport of B in the phloem through a complex with sugar alcohol, such as sorbitol, which has been found in apple, pear, plum, cherry (Brown and Hu, 1996), celery and peach (Hu *et al.*, 1997). Those species produce sorbitol as primary translocated photosynthates.

These studies all examined B translocation in temperate plants and there are few data for tropical species. Accordingly, this study aimed to survey B mobility in tropical species, by examining the nutrient concentration gradient between young to old leaves. The assumption was that this gradient will increase with leaf age in those species in which B is immobile. Information on mobility of B in phloem is useful for improving the diagnosis of B deficiency and management of B in crop production.

Methods

Leaf samples were collected from tropical trees (Table 1), growing in low B soil (0.10–0.15 mg/kg). The leaves of seven trees were collected from the position of the youngest fully expanded leaf (YFEL), the middle leaf age of branch (ML) and the oldest leaf (OL). Leaves from branches around the tree were pooled to one sample for each leaf position.

Table 1. Tropical species which were verified for boron retranslocation.

Common name	Scientific name	Family	Time of collecting
Coffee	<i>Coffea Arabica</i> L.	Rubiaceae	December 2002
Custard apple	<i>Annona squamosa</i> L.	Annonaceae	June 2002
Guava	<i>Psidium guajava</i> L.	Myrtaceae	June 2002
Jackfruit	<i>Artocarpus heterophyllus</i> Lamk.	Moraceae	June 2002
Lime	<i>Citrus aurantifolia</i> Swingle.	Rutaceae	November 2002
Cashew	<i>Anacardium occidentale</i> L.	Anacardiaceae	June 2002

Mango	<i>Mangifera indica</i> L.	Anacardiaceae	December 2002
Papaya	<i>Carica papaya</i> L.	Caricaceae	November 2002
Passion fruit	<i>Passiflora edulis</i> Sims.	Passifloraceae	Nov. – Dec. 2002
Teak	<i>Tectona grandis</i> L.	Verbenaceae	June 2002
Cassava	<i>Manihot esculenta</i> Crantz.	Euphorbiaceae	June 2002
Cork wood tree	<i>Sesbania grandiflora</i> (L.) Pers.	Leguminosae	June 2003
Indian walnut	<i>Samanea saman</i> (Jacq.) Merril.	Leguminosae	June 2002
Tamarind	<i>Tamarindus indica</i> L.	Leguminosae	June 2002
Lychee	<i>Lychi chinensis</i> Sonn.	Sapindaceae	June 2003
Longan	<i>Euphoria longana</i> Lam.	Sapindaceae	June 2003
Star fruit	<i>Averrhoa carambola</i> L.	Oxalidaceae	June 2003

Leaf samples were oven dried at 80 °C for 48 hours and ground to pass 1-mm mesh. Samples were extracted by dry-ashing, the azomethine-H method was used for determination of B (Lohse, 1982) and calcium (Ca) and potassium (K) concentrations were determined by atomic absorption spectrophotometry. Boron concentrations in leaves from the different positions were compared with Ca, (phloem immobile) and K (phloem mobile).fc.

Data of nutrient concentration in leaves was calculated by analysis of variance (ANOVA) and concentration means in different position of each species were separated by least significance difference (LSD) at 95 % probabilities.

Results

Distributions of nutrients in each species are shown in Table 2, 3 and 4. There were no significant differences in K concentrations of coffee, lime, cork wood tree and tamarind leaves at different positions. In the remaining species, concentration of K in YFEL was the highest and decreased with leaf age (Table 2). This is the characteristic of highly mobile elements where the concentrations in the oldest leaves is recycled to new growth (Greenway and Pitman, 1965; Smith and Loneragan, 1997). In the other hand, increasing elemental concentration with leaf age is in accordance with immobility in the phloem, e.g. Ca, which showed concentration gradients across leaf ages very different to K. Concentrations of Ca were lower in the younger leaves and higher in the older leaves (Table 3). In contrast to K and Ca, B concentrations of most species were similar to Ca, except coffee, guava, jackfruit, papaya, teak, tamarind and longan, which showed distribution of B similar to K (Table 4). These data suggest that B may be retranslocated from older to younger leaves in some species.

Table 2. K concentration (% dry wt.) of leaf different position in tropical species.

Species	Leaf Position ^a			LSD _{0.05}
	YFEL	ML	OL	
Coffee	1.23	1.13	1.19	ns
Custard apple	1.42 c	1.16 b	0.90 a	0.22
Guava	1.39 b	0.75 a	0.67 a	0.21
Jackfruit	2.09 b	1.94 b	1.45 a	0.31
Lime	1.56	1.42	1.46	ns
Cashew	0.98 b	0.76 a	0.77 a	0.15
Mango	0.80 b	0.68 ab	0.56 a	0.13
Papaya	2.81 b	2.08 a	1.88 a	0.65
Passion fruit	3.89 b	3.77 ab	3.37 a	0.46
Teak	2.47 b	1.04 a	0.90 a	0.46
Cassava	2.10 b	1.29 a	1.33 a	0.13
Cork wood tree	2.77	2.33	2.16	ns
Indian walnut	1.25 b	1.06 a	1.19 ab	0.18
Tamarind	0.88	0.89	0.84	ns
Lychee	1.59 c	0.79 b	0.64 a	0.13
Longan	1.46 b	1.29 a	1.32 a	0.13
Star fruit	3.47 b	3.25 b	3.19 a	0.15

^a Leaf Position: YFEL - the youngest fully expanded leaf, ML - the middle age leaf of branch, OL - the oldest leaf

ns = not significant ($p < 0.05$).

Means within a row within the same letter do not differ significantly at 5 % with LSD.

Table 3. Ca concentration (% dry wt.) of leaf different position in tropical species.

Species	Leaf Position ^a			LSD _{0.05}
	YFEL	ML	OL	
Coffee	1.55 a	2.23 b	2.38 b	0.19
Custard apple	1.24 a	1.73 b	2.39 c	0.21
Guava	0.82 a	1.31 b	1.77 c	0.19
Jackfruit	1.03 a	1.47 b	2.00 c	0.21
Lime	2.20 a	2.25 a	2.83 b	0.21
Cashew	0.16 a	0.37 b	0.44 c	0.03
Mango	1.77 a	2.05 b	2.56 c	0.22
Papaya	1.40 a	2.52 b	2.88 c	0.23
Passion fruit	1.91 a	1.84 a	2.47 b	0.27
Teak	1.04 a	1.87 b	2.46 c	0.31
Cassava	0.53 a	0.99 b	1.81 c	0.11
Cork wood tree	1.14 a	2.17 b	2.66 c	0.16
Indian walnut	0.71 a	1.00 b	1.03 b	0.09
Tamarind	0.80 a	1.22 b	1.63 c	0.09
Lychee	0.60 a	2.44 b	2.85 c	0.13
Longan	0.34 a	0.65 b	0.71 c	0.05

Star fruit	0.65 a	1.16 b	1.10 b	0.15
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^a Leaf Position: YFEL - the youngest fully expanded leaf, ML - the middle age leaf of branch, OL - the oldest leaf

ns = not significant ($p < 0.05$).

Means within a row within the same letter do not differ significantly at 5 % with LSD.

Table 4. B concentration (mg B/kg dry wt.) of leaf different position in tropical species.

Species	Leaf Position ^a			LSD _{0.05}
	YFEL	ML	OL	
Coffee	34.50	38.79	40.47	ns
Custard apple	23.47 a	34.61 b	53.17 c	2.31
Guava	21.88 b	21.70 b	17.91 a	1.80
Jackfruit	20.99 ab	22.38 b	20.00 a	1.47
Lime	35.83 a	42.68 b	61.00 c	1.42
Cashew	7.45 a	8.53 b	9.75 c	0.82
Mango	20.83 a	22.00 ab	23.19 b	1.33
Papaya	35.42	33.76	34.68	ns
Passion fruit	24.76 a	25.23 a	29.19 b	1.21
Teak	29.00 c	26.36 b	20.84 a	1.78
Cassava	20.10 a	24.96 b	32.51 c	0.65
Cork wood tree	36.17 a	52.41 b	74.95 c	6.10
Indian walnut	8.14 a	8.06 a	9.50 b	0.47
Tamarind	22.89 b	22.10 ab	19.96 a	2.57

Lychee	22.00 a	28.52 b	24.47 b	3.81
Longan	16.03	17.12	15.53	ns
Star fruit	49.52 a	67.49 b	73.16 c	5.49

^a Leaf Position: YFEL - the youngest fully expanded leaf, ML - the middle age leaf of branch, OL - the oldest leaf

ns = not significant ($p < 0.05$).

Means within a row within the same letter do not differ significantly at 5 % with LSD.

Conclusion

These results suggested that B was phloem immobile in custard apple, lime, cashew, mango, passion fruit and cassava whereas it may be phloem mobile in coffee, guava, jackfruit, papaya, teak, tamarind and longan. However, B retranslocation in these species needs to be confirmed and the mechanisms investigated with more precise methodologies, such as B¹⁰ isotope or identification of B-complexing molecules, e.g. sugar alcohols, which are essential for B translocation in the phloem.

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References

- Brown PH and Hu H (1996). Phloem mobility of boron is species dependent. Evidence for phloem mobility in sorbitol rich species. *Annals of Botany* 77, 497-505.
- Delgado A, Benlloch M and Fern?ndez-Escobar R (1994). Mobilization of Boron in Olive Trees During Flowering and Fruit Development. *HortScience* 29(6), 616-618.
- Greenway H and Pitman MG (1965). Potassium retranslocation in seedlings of *Hordeum vulgare*. *Australian Journal of Biological Science* 18, 235-247.
- Hanson EJ (1991). Movement of Boron out of Tree Fruit Leaves. *HortScience* 26(3), 271-273.
- Hu H. and Brown PH (1994). Localisation of boron in cell walls of squash and tobacco and its association with pectin. *Plant Physiology* 105, 681-689.
- Hu H, Penn SG, Lebrilla CB and Brown PH (1997). Isolation and Characterization of Soluble Boron Complexes in Higher plants. *Plant Physiology* 113, 649-655.
- Loshse G (1982). Microanalytical azomethine-H method for boron determination in plant tissues. *Communication in Soil Science & Plant Analysis*.13, 127-134.
- Marschner H (1995). Long- Distance Transport in the Xylem and Phloem and Its Regulation. In 'Mineral Nutrition of Higher Plants'. 2nd edition, pp. 79-115. (Academic Press, New York).
- Oertli JJ (1993). The mobility of boron in plants. *Plant and Soil* 155/156, 301-304.

Smith FW and Loneragan JF (1997). Interpretation of Plant Analysis: Concepts and Principles. In 'Plant Analysis and Interpretation Manual' (Ed. D.J. Reuter and J.B. Robinson) 2nd edition, pp. 3-33. (Collingwood Vic.: CSIRO).

Tenner W and Beevers H (2001). Transpiration, a prerequisite for long-distance transport of minerals in plants? *Plant Biology* 98(16), 9443-9447.

Van Goor B and Van Lune P (1980). Redistribution of Potassium, boron, iron, magnesium and calcium in apple trees determined by an indirect method. *Physiologia Plantarum* 48, 21-26.