Plant Prod. Sci. 8(3) : 338 — 341 (2005)

A Survey of Woody Tropical Species for Boron Retranslocation

Sawika Konsaeng[1], Bernard Dell[2] and Benjavan Rerkasem[1]

([1]Agronomy Department, Faculty of Agriculture, Chiang Mai University, Chiang Mai, Thailand, 50200;
[2]School of Biological Sciences and Biotechnology, Murdoch University, Perth, Australia 6150
Corresponding author: Email g4468103@cm.edu)

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 cashew (*Anacardium occidentale* L.), mango (*Mangifera indica* L.), custard apple (*Annona squamosa* L.), papaya (*Carica papaya* L.), cassava (*Manihot esculenta* Crantz.), Indian walnut (*Samanea samen* (Jacq.) Marrill.), cork wood tree (*Sesbania grandiflora* (L.) Pers.), tamarind (*Tamarindus indica* L.), jackfruit (*Artocarpus heterophyllus* Lamk.), guava (*Psidium guajava* L.), star fruit (*Averrhoa carambola* L.), passion fruit (*Passiflora edulis* Sims.), coffee (*Coffea arabica* L.), lime (*Citrus aurantifolia* Swingle.), longan (*Euphoria longana* Lam.), lychee (*Lychi chinensis* Sonn.) and teak (*Tectona grandis* L.) were collected in the position of the youngest fully expanded leaf (YFEL), the middle leaf age of a branch (ML) and the oldest leaf (OL). Based on a premise that the nutrient concentration gradient between young and old leaves will be steeper in those species in which B is immobile, B concentration 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. Three species; tamarind, guava and teak, 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 confirmation through studies examining retranslocation of B using ^{10}B isotope or identification of B-complexing molecules in the phloem, e.g. sugar alcohols.

Key words : Boron, Phloem mobility, Retranslocation, Tropical species.

When nutrients are absorbed by roots and translocated in xylem sap by water movement to shoots, they may be transferred to phloem sap and retranslocated to sinks in roots, stems and leaf cells. However, nutrients that are stored in tissues and organs may be retranslocated via the phloem to other plant parts which transpire less, e.g. new shoot and reproductive tissues (Smith and Loneragan, 1997). While all mineral 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 of the rate 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 B supply, 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). By contrast, other observations indicate that B is phloem mobile in some plants. Hanson (1991) reported that the B content in leaves of apple (*Malus domestica* Borkh.), pear (*Pyrus communis* L.), plum (*Prunus domestica* L.) and cherry (*Prunus ceasus* L.) which were treated with foliar B (500 mg L^{-1}) decreased to levels similar to non-treated leaves and the highest B concentration was found in untreated 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). One possible mechanism of B transport in

Received 1 September 2004. Accepted 1 February 2005.

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

Family	Common name	Scientific name	Time of collecting	Season
Anacardiaceae	Cashew	*Anacardium occidentale* L.	June 2002	Wet
Anacardiaceae	Mango	*Mangifera indica* L.	Dec. 2002	Dry
Annonaceae	Custard apple	*Annona squamosa* L.	June 2002	Wet
Caricaceae	Papaya	*Carica papaya* L.	Nov. 2002	Dry
Euphorbiaceae	Cassava	*Manihot esculenta* Crantz.	June 2002	Wet
Leguminosae	Indian walnut	*Samanea samen* (Jacq.) Marrill.	June 2002	Wet
Leguminosae	Cork wood tree	*Sesbania grandiflora* (L.) Pers.	June 2003	Wet
Leguminosae	Tamarind	*Tamarindus indica* L.	June 2002	Wet
Moraceae	Jackfruit	*Artocarpus heterophyllus* Lamk.	June 2002	Wet
Myrtaceae	Guava	*Psidium guajava* L.	June 2002	Wet
Oxalidaceae	Star fruit	*Averrhoa carambola* L.	June 2003	Wet
Passifloraceae	Passion fruit	*Passiflora edulis* Sims.	Nov. – Dec. 2002	Dry
Rubiaceae	Coffee	*Coffea arabica* L.	Dec. 2002	Dry
Rutaceae	Lime	*Citrus aurantifolia* Swingle.	Nov. 2002	Dry
Sapindaceae	Longan	*Euphoria longana* Lam.	June 2003	Wet
Sapindaceae	Lychee	*Lychi chinensis* Sonn.	June 2003	Wet
Verbenaceae	Teak	*Tectona grandis* L.	June 2002	Wet

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

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

[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 with the same letter do not differ significantly at $p<0.05$ with LSD.

the phloem is through a complex with sugar alcohols, such as sorbitol which is a primary photosynthate translocated in apple, pear, plum, cherry (Brown and Hu, 1996), celery and peach (Hu *et al.*, 1997).

These studies all examined B translocation in temperate plants and there are few data for tropical species. Accordingly, this study investigated possible B mobility in tropical species, by surveying the nutrient concentration gradients between young and old leaves. The assumption was that the gradients will increase with leaf age in those species in which B is immobile.

Materials and Methods

Leaf samples were collected from seventeen woody tropical species (Table 1), growing in low B soil (0.10 – 0.15 mg kg^{-1} hot water soluble extract). The leaves of seven replicate trees were collected from the position of the youngest fully expanded leaf (YFEL), the middle leaf age of a branch (ML) and the oldest leaf (OL). Leaves from branches around the tree were pooled to one sample for each leaf position.

Leaf samples were oven dried at 80°C for 48 hours

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

Species	Leaf Position[a]			
	YFEL	ML	OL	$LSD_{0.05}$
Cashew	0.16 a	0.37 b	0.44 c	0.03
Mango	1.77 a	2.05 b	2.56 c	0.22
Custard apple	1.24 a	1.73 b	2.39 c	0.21
Papaya	1.40 a	2.52 b	2.88 c	0.23
Cassava	0.53 a	0.99 b	1.81 c	0.11
Indian walnut	0.71 a	1.00 b	1.03 b	0.09
Cork wood tree	1.14 a	2.17 b	2.66 c	0.16
Tamarind	0.80 a	1.22 b	1.63 c	0.09
Jackfruit	1.03 a	1.47 b	2.00 c	0.21
Guava	0.82 a	1.31 b	1.77 c	0.19
Star fruit	0.65 a	1.16 b	1.10 b	0.15
Passion fruit	1.91 a	1.84 a	2.47 b	0.27
Coffee	1.55 a	2.23 b	2.38 b	0.19
Lime	2.20 a	2.25 a	2.83 b	0.21
Longan	0.34 a	0.65 b	0.71 c	0.05
Lychee	0.60 a	2.44 b	2.85 c	0.13
Teak	1.04 a	1.87 b	2.46 c	0.31

Abbeviations as in Table 2

Table 4. B concentration (mg B/kg dry wt^{-1}.) of different leaf position in tropical species.

Species	Leaf Position[a]			
	YFEL	ML	OL	$LSD_{0.05}$
Cashew	7.45 a	8.53 b	9.75 c	0.82
Mango	20.83 a	22.00 ab	23.19 b	1.33
Custard apple	23.47 a	34.61 b	53.17 c	2.31
Papaya	35.42	33.76	34.68	ns
Cassava	20.10 a	24.96 b	32.51 c	0.65
Indian walnut	8.14 a	8.06 a	9.50 b	0.47
Cork wood tree	36.17 a	52.41 b	74.95 c	6.10
Tamarind	22.89 b	22.10 ab	19.96 a	2.57
Jackfruit	20.99 ab	22.38 b	20.00 a	1.47
Guava	21.88 b	21.70 b	17.91 a	1.80
Star fruit	49.52 a	67.49 b	73.16 c	5.49
Passion fruit	24.76 a	25.23 a	29.19 b	1.21
Coffee	34.50	38.79	40.47	ns
Lime	35.83 a	42.68 b	61.00 c	1.42
Longan	16.03	17.12	15.53	ns
Lychee	22.00 a	28.52 b	24.47 b	3.81
Teak	29.00 c	26.36 b	20.84 a	1.78

Abbreviations as in Table 2

and ground to pass a 1-mm mesh. Samples were dry-ashed at 500°C and the azomethine-H method was used for determination of B (Lohse, 1982). Boron concentration in leaves from the three positions was compared with potassium (K: phloem mobile) and calcium (Ca: phloem immobile) which were determined by atomic absorption spectrophotometry. Nutrient concentrations in leaves were compared by analysis of variance (ANOVA) and concentration means in different position of each species were separated by least significant difference (LSD) at P = 0.05%.

Results and Discussion

Distributions of nutrients in each species are shown in Tables 2, 3 and 4. There were no significant differences in K concentrations of cork wood tree, tamarind, coffee and lime 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 nutrient in the oldest leaves is recycled to new growth (Greenway and Pitman, 1965; Smith and Loneragan, 1997). On the other hand, increasing 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). The results of B concentration, when compared to K and Ca, could be arranged into 3 group of species. In the first group, B concentration gradients were the same as Ca, including, cashew, mango, custard apple, cassava, Indian walnut, cork wood tree, star fruit, lime, passion fruit and lychee. The second group contained species which showed B concentration gradients similar to K, including, tamarind, guava and teak. The third group was inconclusive for B mobility, including, papaya, jackfruit, coffee and longan. B concentrations of papaya, coffee and longan were not significantly different with leaf age. B concentrations of jackfruit increased in middle age and decreased in old leaves. That may be caused by seasonal effects (Fernández-Escobar et al., 1999).

Conclusions

The foliar nutrient gradients suggest that B is phloem immobile in cashew, mango, custard apple, cassava, Indian walnut, cork wood tree, star fruit, passion fruit, lime and lychee whereas it may be phloem mobile in tamarind, guava and teak. The mobility of B in the phloem of papaya, jackfruit, coffee and longan was inconclusive in this experiment. B retranslocation in these species needs to be confirmed and the mechanisms investigated with more precise methodologies, including use of B^{10} feeding experiments and identification of any B-complexing molecules in the phloem such as sugar alcohols, which are essential for B translocation.

Acknowledgements

We wish to acknowledge financial support from the Thailand Research Fund for RGJ Ph.D. Scholarship to the first author and Mr. Sittichai Lordkaew for help with analysis at the Multiple Cropping Center Laboratory.

References

Brown, P.H. 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.

Brown, P.H. and Shelp, B.J. 1997. Boron mobility in plants. Plant and Soil 193 : 85-101.

Delgado, A., Benlloch, M. and Fernández-Escobar, R. 1994. Mobilization of boron in olive trees during flowering and fruit development. HortScience 29(6) : 616-618.

Fernández-Escobar, R., Moreno, R. and García-Creus, M. 1999. Seasonal changes of mineral nutrients in olive leaves during the alternate-bearing cycle. Scientia Horticulturae 82 : 25-45.

Greenway, H. and Pitman, M.G. 1965. Potassium retranslocation in seedlings of *Hordeum vulgarae*. Australian Journal of Biological Science 18 : 235-247.

Hanson, E.J. 1991. Movement of boron out of tree fruit leaves. HortScience 26(3) : 271-273.

Hu, H. and Brown, P.H. 1994. Localisation of boron in cell walls of squash and tobacco and its association with pectin. Plant Physiology 105 : 681-689.

Hu, H., Penn, S.G., Lebrilla, C.B. and Brown, P.H. 1997. Isolation and characterization of soluble boron complexes in higher plants. Plant Physiology 113 : 649-655.

Lohse, 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. Academic Press, New York. 79-115.

Oertli, J.J. 1993. The mobility of boron in plants. Plant and Soil 155/156 : 301-304.

Smith, F.W. and Loneragan, J.F. 1997. Interpretation of Plant Analysis: Concepts and Principles. In D.J. Reuter and J.B. Robinson eds., Plant Analysis and Interpretation Manual. 2nd edition, CSIRO, Collingwood, Australia. 3-33.

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.