PELTOPHORUM DASYRACHIS SEEDLING GROWTH RESPONSE TO DIFFERENT LEVELS OF BORON

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ROSE, R., ROYO, A. & HAASE, D. L. 1999. *Peltophorum dasyrachis* seedling growth response to different levels of boron. Five boron treatments (0, 10, 20, 40, and 60 ppm) were applied to *Peltophorum dasyrachis* (Kurz) seedlings. Height and diameter were measured after one month. In addition, leaves were partitioned as damaged or undamaged and measured for dry weight and nutrient concentrations and contents. The results demonstrate that boron had both a growth enhancement and a toxic impact on the seedlings. The 10-ppm boron treatment enhanced growth (albeit non-significantly) relative to the control, while the 20-, 40-, and 60-ppm treatments were detrimental to growth. With higher boron treatment levels, the number and dry weight of damaged leaves were significantly higher. Foliar concentrations of potassium, magnesium, and especially boron also increased significantly with higher treatment levels.

Keywords: Toxicity - Thailand - micronutrients - nutrition

ROSE, R., ROYO, A. & HAASE, D. L. 1999. Tindak balas pertumbuhan anak benih *Peltophorum dasyrachis* terhadap boron yang berbeza tahapnya. Lima rawatan boron (0, 10, 20, 40, dan 60 ppm) dilakukan terhadap anak benih *Peltophorum dasyrachis* (Kurz). Ketinggian dan garis pusat diukur selepas satu bulan. Di samping itu, daun dibahagikan kepada rosak atau tidak rosak. Berat kering, kepekatan dan kandungan nutrien daun-daun tersebut disukat. Keputusan menunjukkan bahawa boron meningkatkan pertumbuhan dan memberikan kesan toksik terhadap anak benih. Rawatan 10-ppm boron meningkatkan pertumbuhan (walaupun tidak bererti) secara relatif dengan kawalan, manakala rawatan 20, 40, dan 60 ppm menyebabkan pertumbuhan merosot. Tahap rawatan boron yang lebih tinggi menyebabkan bilangan dan berat kering daun-daun yang rosak lebih tinggi. Kepekatan potasium, magnesium dan terutamanya boron dalam daun juga meningkat dengan bererti dengan tahap rawatan yang lebih tinggi.

Introduction

Boron is an essential micronutrient in plants and one whose role is not fully understood. Boron deficiency is the most widespread micronutrient deficiency in forestry, particularly in the tropics. Boron is thought to be passively taken up by plant roots as undissociated boric acid and translocated to the foliage (Hu & Brown 1997). Until recently, boron has been considered to be phloem-immobile. Although this is true for most species, boron can be readily transported in the phloem of species rich in polyols (Brown & Shlep 1997). Boron plays an important role in cell wall structure, cell membrane integrity, enzyme interactions, sugar transport and other plant functions (Marschner 1995, Matoh 1997, Power & Woods 1997).

Although boron deficiency and toxicity can be common, this micronutrient has received relatively little attention in the literature for tree species, especially for native tropical tree species. One study (Robinson & Edgington 1942) showed that the leaves of hardwoods such as hickory (*Carya* spp.), walnut (*Juglans* spp.), black locust (*Robinia pseudocacia*) and creosote bush (*Larrea mexicana*) can have boron levels of ~40 to 77 ppm. A few researchers report beneficial effects of boron for trees. Mitchell *et al.* (1987) found that 25 ppm borate applied as a mist to the foliage or as a soil drench significantly promoted the colonisation of ectomycorrhizae on shortleaf pine (*Pinus echinata*). Stone *et al.* (1982) suggest that southern pines suffering from boron deficiency do poorly after outplanting. Atalay *et al.* (1988) found significant increases in sugars in both ectomycorrhizal and non-mycorrhizal roots of shortleaf pine in response to boron fertilisation. Other researchers have reported the effects of boron toxicity (Glaubig & Bingham 1985, Vimmerstedt & Glover 1984, Timmer 1991, Nable *et al.* 1997).

This paper reports on the effect of boron on the important timber species *Peltophorum dasyrachis* (Kurz) (Family: Caesalpiniaceae). This species is native to southeast Asia and grows in many areas throughout Thailand and neighbouring countries, where it is used for everything from wood carvings to furniture. It was chosen for study because Thailand is known to be an area of the world where some soils are deficient in boron (Shorrocks 1997). While not as commercially valuable as teak (*Tectonia grandis*), *P. dasyrachis* is an important species for ecological restoration and conservation and is commonly grown in Thai nurseries.

In a nursery setting, *P. dasyrachis* seedlings are commonly grown in polybags in a medium consisting of local clay soil, rice husks, and chicken manure in various unknown ratios. The formula varies greatly from one area and nursery to another. In some cases, burnt rice husks are added as fertiliser. It can take more than two years for seedlings to reach plantable size (50 cm tall). Sporadic watering, the absence of commercial fertilisers with micronutrients such as boron, and the low fertility of the media greatly contribute to the slow growth.

In 1995 a successful demonstration project carried out by Oregon Woods, Inc. (Eugene, OR) in cooperation with the United States Agency for International Development (USAID) and the Royal Forest Department of Thailand showed that quality *P. dasyrachis* seedlings could be grown in styro-8 (8 cubic inch) containers with modern soluble fertilisers (Peters®) and a peat-vermiculite media mix. With constant fertilisation and irrigation, seedling growth was very rapid. The root systems filled the styro-8 cavities in less than four months.

The objective of this study was to test the null hypothesis that variations in soil boron do not affect growth of *P. dasyrachis* seedlings. Our approach was to vary the level of boron in the media while holding all other growth factors (such as light, temperature, fertilisation, and irrigation) as constant as possible. To the best of our knowledge, this is the first experiment of its kind to look at the influence of boron nutrition on early *P. dasyrachis* seedling growth.

Materials and methods

Seedlings

Peltophorum dasyrachis seed was obtained from Nursery No. 4 of the Royal Forest Department in Korat, Thailand; the seed source is unknown. Seeds were pretreated by pouring boiling water over them and allowing them to soak for 12 h until cool. They were then surface sown in flats containing a peat medium and covered with grit. Seeds were allowed to germinate and grow for several weeks before being transplanted to pots. On 21 June 1996, seedlings (approximately 5 cm tall) were pricked out of a flat bed container and transplanted to individual 15-cm (diameter) x 17-cm (height) pots (approximately 3 l). The medium was Black Gold® (a peat and vermiculite mixture) and a silt loam soil in a 1:1 (v:v) ratio.

The transplanted seedlings were grown on raised benches under ambient light conditions in a Forest Research Laboratory greenhouse, College of Forestry, Oregon State University. The fiberglass roof reduced the amount of full sunlight by as much as 50%. Temperatures in the greenhouse fluctuated from 20 to 35 °C during the day and from 10 to 20 °C at night. These conditions were much cooler than those in northeast Thailand. Another factor that was difficult to control was the cool (7 °C) temperature of the irrigation water. However, the seedlings grew very well under the circumstances.

Treatments

Five boron treatments were used: 0, 10, 20, 40, and 60 ppm of boron. These treatment levels were selected based on their expected ability to bracket responses ranging from deficient to toxic. The source of the boron was Solubor™ (U.S. Borax, Inc., Valencia, CA), which is 20.5% boron. Treatments were applied by pouring 1 l of boron solution (diluted to achieve the desired treatment) into the media of each pot. For each treatment, 20 seedlings were treated on 15 July

1996, and again on 5 August 1996. In addition, each pot was fertilised with other nutrients by adding 400 ml of Peters® 20–20–20 fertiliser diluted to 100 ppm nitrogen 1 day after the initial boron treatment and approximately twice per week until the end of the experiment. Pots were watered daily or as needed. The level of boron in the Peters® fertiliser (undiluted) was low (0.0068%). Other micronutrient levels were iron 0.05%, magnesium 0.05%, manganese 0.025%, copper 0.0036%, zinc 0.0025%, and molybdenum 0.0008%. The boron contributed by the tap water used in the experiment was considered negligible.

Measurements

Height was measured to the nearest centimeter (cm) from groundline to the highest tip of the plant. Diameter was measured to the nearest millimeter (mm) at groundline. Height and diameter were measured initially on 16 July 1996. Final height and diameter were measured, the number of leaves per plant was counted, and plant parts were harvested on 18 and 19 August 1996. Damage from boron toxicity was assessed visually as chlorosis on the leaflet edges of the pinnately compound leaves (Figure 1). A damaged leaf was defined as having at least 25% chlorosis of the leaflet surface area. Damaged and undamaged leaves were snipped off, counted, pooled together by damage category, and dried in an oven at 65 °C for 48 h. Dry weights of damaged and undamaged leaves were measured separately. There were no damaged leaves in the control treatment.

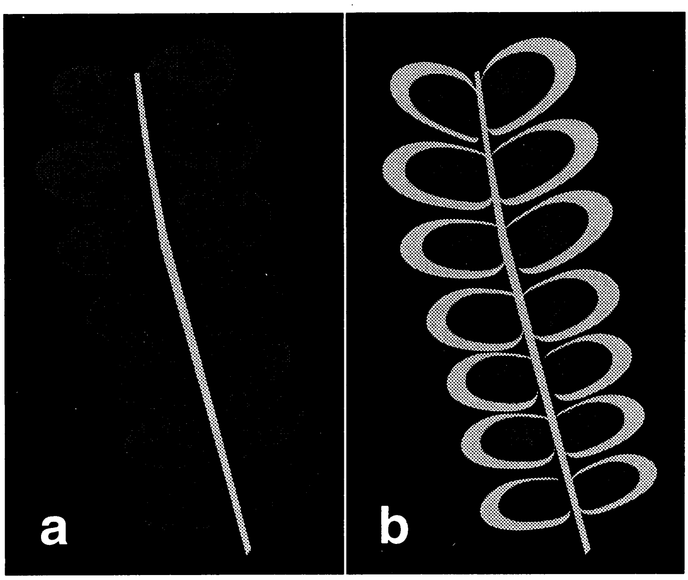

Figure 1. Effect of boron toxicity on leaflets of *Peltophorum dasyrachis:* a) undamaged and b) damaged (chlorosis on leaflet edges)

Nutrient analyses were done at the Soil and Plant Analysis Laboratory at Oregon State University using standard laboratory techniques. The leaves of each plant were separated into two categories: undamaged and damaged. There were four composited samples (consisting of 4 to 5 seedlings each) of damaged and undamaged leaves for each boron treatment. A total of 36 samples were analysed [(5 treatments × 4 undamaged leaf samples) + (4 treatments × 4 damaged leaf samples)].

Nutrient concentration is the percentage of an element in the dried leaf material. Nutrient content is the dry weight of the element in the dried leaf material (nutrient concentration x leaf dry weight). Estimates for nutrient concentrations and contents in the total foliage (i.e. damaged leaves + undamaged leaves) were calculated by adding the data and weighting by leaf dry weight as follows:

$$\text{Total foliar nutrient concentration} = \frac{\text{undamaged DW}}{\text{total DW}}(\text{undamaged concentration}) + \frac{\text{damaged DW}}{\text{total DW}}(\text{damaged concentration})$$

$$\text{Total foliar nutrient content} = \frac{\text{undamaged DW}}{\text{total DW}}(\text{undamaged content}) + \frac{\text{damaged DW}}{\text{total DW}}(\text{damaged content})$$

where DW = leaf dry weight (mg); (un)damaged concentration = nutrient concentration (%) in (un)damaged leaves; and (un)damaged content = nutrient content (mg) in (un)damaged leaves.

To aid in nutrient data interpretation, vector diagrams were plotted according to Haase and Rose (1995). Vector analysis is a technique that allows simultaneous comparison of plant biomass, nutrient concentration, and nutrient content in an integrated graphic format. Nutrient ratios were calculated for each nutrient as a percentage of nitrogen.

Design and experimental analysis

The study was a completely randomised design with 5 treatments and 20 seedlings per treatment. All data were analysed with a one-way ANOVA. Tests for normality, linearity, and constant variance of the residuals were performed, and transformations were made where necessary to assure the validity of these assumptions. Fisher's Protected Least Significant Difference procedure was used to determine significant differences among treatments at the $\alpha < 0.05$ level. Statistical Analysis System software (SAS Institute Inc. 1989) was used for analysis of all data.

Results

Boron treatments significantly influenced the growth of *Peltophorum dasyrachis* seedlings. In general, the 10-ppm boron treatment enhanced growth relative to the control (although the difference was not statistically significant), while 20-, 40-, and 60-ppm treatments were significantly detrimental to growth.

Morphology

Seedling morphology was significantly influenced by the boron treatments (Table 1). As expected, initial height and stem diameter were not significantly different among treatments. However, by the end of the experiment, seedlings receiving the 10-ppm boron treatment had the largest total height, stem diameter, height growth, and diameter growth (although not significantly different from the control).

Table 1. Seedling morphology by treatment

Measurement	Boron treatment (ppm)				
	0	10	20	40	60
Seedling height (cm)					
Initial–16 July (p = 0.1679)	9.55a	10.55a	9.76a	9.08a	10.55a
Final–19 August (p = 0.0199)	15.42abc	16.94c	15.68bc	13.5a	14.73ab
Growth (p = 0.0002)	5.87b	6.47b	5.92b	4.43a	4.18a
Stem diameter (mm)					
Initial–16 July (p = 0.2606)	1.97a	2.03a	1.86a	1.76a	2.04a
Final– 19 August (p = 0.0006)	3.38cd	3.57d	3.08bc	2.67a	2.82ab
Growth (p = 0.0001)	1.41bc	1.55c	1.22b	0.91a	0.78a
Final harvest—19 August					
Damaged leaves per plant (%) (p = 0.0001)	0.0a	27.83b	50.62c	68.00d	72.01d
No. leaves per plant					
Undamaged[1] (p = 0.0001)	10.14d	7.51c	4.74b	2.81a	2.31a
Damaged[1] (p = 0.0001)	0.00a	2.11b	4.86c	6.07c	6.11c
Total[1] (p = 0.0009)	10.13c	10.65c	9.65bc	9.60ab	8.48a
Dry Weight (g)					
Undamaged leaf[1] (p = 0.0001)	1.24c	1.37c	0.86b	0.41a	0.35a
Damaged leaf[1] (p = 0.0001))	-	0.14a	0.28b	0.34b	0.50c
Total leaf[1] (p = 0.0001)	1.23bc	1.55c	1.13b	0.77a	0.84a
Stem[1] (p = 0.0010)	0.30c	0.37c	0.27bc	0.19a	0.20b

Note: Within each row, means followed by the same letter are not significantly different at the $\alpha \leq 0.05$ level using Fisher's Protected Least Significant Difference procedure;
[1]Values were back-transformed from log values used for analysis and are estimates of the median.

Leaf damage reflected the level of the boron treatments (Table 1). The proportion of damaged leaves per plant was higher with higher levels of boron. The influence of the boron treatments was also readily apparent in the dry weights. Seedlings from the 10-ppm boron treatment had the highest undamaged leaf dry weight, total leaf dry weight and stem dry weight, while those treated with 40 and 60 ppm boron tended to be significantly smaller than the other treatments.

Foliar nutrients

The boron treatments significantly affected the concentrations of most nutrients (Table 2). With higher boron treatment levels, the concentrations of potassium, magnesium, and especially boron in the undamaged leaves, damaged leaves, and total foliage increased significantly. None of the other nutrients had significant differences among concentrations in total foliage. However, these nutrients are included in the tables to give the reader an overall understanding of *P. dasyrachis* nutrient levels since this important species has not previously been represented in the literature. Nitrogen and phosphorous concentrations in the damaged leaves were significantly higher in the 40- and 60-ppm treatments than in the 10- and 20-ppm treatments; phosphorous concentrations in undamaged leaves also increased significantly with higher treatment levels. Calcium was the only nutrient that had significantly lower concentrations in the undamaged and damaged leaves with higher treatment levels. Concentrations of manganese, copper, and zinc in undamaged leaves, damaged leaves, or total foliage were not significantly different among the treatments (Table 2).

Foliar nutrient contents (Table 3) showed more significant differences than the foliar nutrient concentration data. This is not surprising given that nutrient content is a function of dry weight, which differed significantly by treatment. With the exception of boron content, higher treatment levels of boron resulted in significantly lower nutrient contents in undamaged leaves and in total foliage, and significantly higher nutrient contents in damaged leaves.

Figure 2 shows vector diagrams for total estimated foliar boron, nitrogen, and potassium. Relative to the control, nutrient content (nitrogen and potassium only) and foliar dry weight were higher for the 10-ppm boron treatment and lower for the 20-, 40-, and 60-ppm treatments.

The nutrient ratios relative to nitrogen provide another look at the effects of the boron treatments on the various elements (Table 4). Ratios of phosphorus, potassium, and magnesium to nitrogen tended to be higher with higher levels of boron. However, the ratios of calcium to nitrogen in damaged and undamaged leaves were significantly lower with higher treatment levels of boron. As expected, the boron/nitrogen ratio showed highly significant changes.

Table 2. Nutrient concentrations (ppm or %) for undamaged leaves, damaged leaves and total foliage (estimated). p values are given in parentheses for each group of means. Note: there were no damaged leaves in the control treatment (0 ppm).

Measurement	Boron treatment (ppm)				
	0	10	20	40	60
Nitrogen (%)					
Undamaged leaves (p = 0.0764)	3.17a	3.33a	3.80a	3.61a	3.58a
Damaged leaves (p = 0.0011)	–	2.00a	2.35a	2.77b	2.96b
Total foliar estimate (p = 0.5301)	3.17a	3.17a	3.45a	3.18a	3.20a
Phosphorus (%)					
Undamaged leaves (p = 0.0001)	0.31a	0.34b	0.37c	0.40d	0.40a
Damaged leaves (p = 0.0001)	–	0.19a	0.19a	0.28b	0.28b
Total foliar estimates (p = 0.1063)	0.31a	0.32a	0.32a	0.34a	0.33a
Potassium (%)					
Undamaged leaves[1] (p = 0.0001)	1.65a	1.95b	1.93b	2.26c	2.29c
Damaged leaves (p = 0.0001)	–	1.14a	1.48b	1.91c	1.98c
Total foliar estimate (p = 0.0001)	1.65a	1.85b	1.82b	2.10c	2.10c
Calcium (%)					
Undamaged leaves (p = 0.0001)	1.47bc	1.50c	1.38bc	1.33b	1.06a
Damaged leaves (p = 0.0311)	–	2.24b	2.26b	2.05ab	1.87a
Total foliar estimate (p = 0.0781)	1.47a	1.58a	1.59a	1.66a	1.55a
Magnesium (%)					
Undamaged leaves (p = 0.0001)	0.30a	0.29a	0.33b	0.39c	0.36c
Damaged leaves (p = 0.0093)	–	0.29a	0.29a	0.35b	0.33b
Total foliar estimate (p = 0.0001)	0.30ab	0.29a	0.32b	0.37d	0.35c
Manganese (ppm)					
Undamaged leaves (p = 0.0829)	59.75a	57.00a	52.50a	48.25a	39.75a
Damaged leaves (p = 0.1970)	–	87.25a	79.75a	81.00a	68.50a
Total foliar estimate (p = 0.8928)	59.75a	60.27a	59.14a	63.69a	56.97a
Copper (ppm)					
Undamaged leaves (p = 0.1814)	2.50a	2.50a	2.00a	3.25a	2.00a
Damaged leaves (p = 0.1522)	–	3.25a	3.75a	3.25a	3.00a
Total foliar estimate (p = 0.2449)	2.50a	2.57a	2.43a	3.25a	2.60a
Boron (ppm)					
Undamaged leaves[1] (p = 0.0001)	51.03a	144.42b	217.13c	271.31d	265.87d
Damaged leaves (p = 0.0001)	–	336.75a	623.25b	878.25c	970.25c
Total foliar estimates[1] (p = 0.0001)	51.03a	165.50b	315.37c	552.14d	686.67e
Zinc (ppm)					
Undamaged leaves (p = 0.0551)	22.75a	23.00a	23.50a	26.00a	26.00a
Damaged leaves (p = 0.6348)	–	20.25a	19.50a	21.00a	20.50a
Total foliar estimate (p = 0.7161)	22.75a	22.63a	22.52a	23.92a	22.81a

Note: Within each row, means followed by the same letter are not significantly different at the $\alpha \leq 0.05$ level using Fisher's Protected Least Significant Difference procedure;

[1]Values were back-transformed from log values used for analysis and are estimates of the median.

Table 3. Nutrient contents (mg) for undamaged leaves, damaged leaves and total foliage (estimated). p values are given in parentheses for each group of means. Note: there were no damaged leaves in the control treatment (0 ppm).

Measurement	Boron treatment (ppm) 0	10	20	40	60
Nitrogen					
Undamaged leaves (p = 0.0001)	43.0bc	50.7c	35.4b	15.4a	13.6a
Damaged leaves[1] (p = 0.0001)	–	3.9a	6.9b	10.6c	16.7d
Total foliar estimate (p = 0.0001)	43.0a	54.6b	42.3a	25.6c	30.6c
Phosphorus					
Undamaged leaves (p = 0.0001)	4.2c	5.1d	3.8b	1.8a	1.5a
Damaged leaves[1] (p = 0.0001)	–	0.4b	0.6c	0.1a	1.6d
Total foliar estimate (p = 0.0001)	4.2bc	5.5c	4.0b	2.9a	3.1a
Potassium					
Undamaged leaves (p = 0.0001)	22.4c	29.7d	18.0b	10.2a	8.7a
Damaged leaves[1] (p = 0.0001)	–	2.2a	4.4b	7.3c	11.2d
Total foliar estimate (p = 0.0001)	22.4b	31.9c	22.3b	17.6a	20.0ab
Calcium					
Undamaged leaves (p = 0.0001)	19.8c	22.8d	12.8b	6.1a	4.0a
Damaged leaves[1] (p = 0.0001)	–	4.3a	6.7b	7.8b	10.5c
Total foliar estimate (p = 0.0001)	19.8b	27.2c	19.5b	13.9a	14.8a
Magnesium					
Undamaged leaves (p = 0.0001)	4.0c	4.4c	3.1b	1.7a	1.4a
Damaged leaves[1] (p = 0.0001)	–	0.6a	0.9b	1.3c	1.9d
Total foliar estimates (p = 0.0007)	4.0b	5.0c	3.9b	3.1a	3.3ab
Manganese					
Undamaged leaves (p = 0.0001)	0.0818c	0.0862c	0.0492b	0.0219a	0.0150a
Damaged leaves (p = 0.0001)	–	0.0169a	0.0237b	0.0312c	0.0385d
Total foliar estimate (p = 0.0006)	0.0818b	0.1032c	0.0730ab	0.0530a	0.0535a
Copper					
Undamaged leaves (p = 0.0001)	0.0033c	0.0039c	0.0019b	0.0015ab	0.0008a
Damaged leaves[1] (p = 0.0001)	–	0.0006a	0.0011b	0.0012b	0.0017c
Total foliar estimate[1] (p = 0.0196)	0.0033ab	0.0044b	0.0030a	0.0026a	0.0025a
Boron					
Undamaged leaves[1] (p = 0.0001)	0.0688a	0.2191c	0.2008c	0.1205b	0.1002b
Damaged leaves[1] (p = 0.0001)	–	0.0644a	0.1839b	0.3372c	0.5453d
Total foliar estimate[1] (p = 0.0001)	0.0688a	0.2840b	0.3851c	0.4597c	0.6471d
Zinc					
Undamaged leaves (p = 0.0001)	0.0310c	0.0350c	0.0218b	0.0113a	0.0093a
Damaged leaves[1] (p = 0.0001)	–	0.0039a	0.0058b	0.0083c	0.0116d
Total foliar estimate (p = 0.0001)	0.0310b	0.0389c	0.0276b	0.0201a	0.0201a

Note: Within each row, means followed by the same letter are not significantly different at the $\alpha \leq 0.05$ level using Fisher's Protected Least Significant Difference procedure;
[1]Values were back-transformed from log values used for analysis and are estimates of the median.

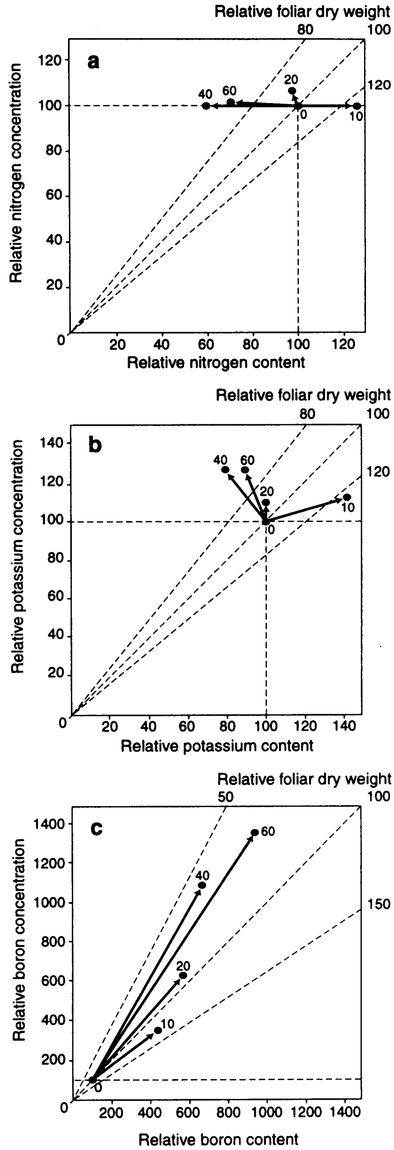

Figure 2. Relative effect of boron treatments on nutrient concentration, nutrient content, and foliar dry weight for a) nitrogen, b) potassium, and c) boron. The control (0–ppm treatment) was normalised to 100.

Table 4. Nutrient concentration ratios relative to nitrogen (nitrogen = 1) for undamaged leaves, damaged leaves and total foliage (estimated). p values are given in parentheses for each group of means. Note: there were no damaged leaves in the control treatment (0 ppm).

Measurement	Boron treatment (ppm)				
	0	10	20	40	60
Phosphorus/Nitrogen					
Undamaged leaves (p = 0.0154)	0.098a	0.101a	0.097a	0.113b	0.111b
Damaged leaves[1] (p = 0.3572)	–	0.092a	0.083a	0.101a	0.096a
Total foliar estimate (p = 0.0887)	0.098a	0.101a	0.095a	0.111a	0.103a
Potassium/Nitrogen					
Undamaged leaves (p = 0.0016)	0.520a	0.586b	0.518a	0.630b	0.641b
Damaged leaves (p = 0.3448)	–	0.574a	0.642a	0.698a	0.670a
Total foliar estimate (p = 0.0009)	0.520a	0.585a	0.537a	0.667b	0.656b
Calcium/Nitrogen					
Undamaged leaves (p = 0.0001)	0.463c	0.450c	0.367b	0.370b	0.297a
Damaged leaves[1] (p = 0.0005)	–	1.121b	0.967b	0.742a	0.641a
Total foliar estimate (p = 0.2861)	0.463a	0.499a	0.468a	0.521a	0.483a
Magnesium/Nitrogen					
Undamaged leaves (p = 0.0087)	0.094ab	0.087a	0.088a	0.109c	0.101bc
Damaged leaves (p = 0.0470)	–	0.146b	0.124ab	0.127ab	0.113a
Total foliar estimate (p = 0.0024)	0.094a	0.091a	0.094a	0.118b	0.108b
Manganese/Nitrogen					
Undamaged leaves (p = 0.0516)	0.00189a	0.00172a	0.00144a	0.00142a	0.00111a
Damaged leaves[1] (p = 0.1970)	–	0.00433a	0.00340a	0.00292a	0.00230a
Total foliar estimate (p = 0.0090)	0.00189a	0.00191a	0.00177a	0.00209a	0.00178a
Copper/Nitrogen					
Undamaged leaves (p = 0.0425)	0.000079ab	0.000076ab	0.000054a	0.000100b	0.000056a
Damaged leaves (p = 0.0113)	–	0.000162b	0.000163b	0.000120a	0.000102a
Total foliar estimate (p = 0.1239)	0.000078a	0.000083a	0.000070a	0.000113a	0.000083a
Boron/Nitrogen					
Undamaged leaves (p = 0.0001)	0.0016a	0.0044b	0.0058c	0.0078d	0.0075d
Damaged leaves (p = 0.0002)	–	0.0171a	0.0268b	0.0321bc	0.0328c
Total foliar estimate (p = 0.0001)	0.0016a	0.0053b	0.0093c	0.0178d	0.0215e
Zinc/Nitrogen					
Undamaged leaves (p = 0.5647)	0.00071a	0.00069a	0.00063a	0.00071a	0.00071a
Damaged leaves[1] (p = 0.0766)	–	0.00100a	0.00083a	0.00078a	0.00069a
Total foliar estimate (p = 0.7894)	0.00072a	0.00071a	0.00067a	0.00075a	0.00070a

Note: Within each row, means followed by the same letter are not significantly different at the $\alpha \leq 0.05$ level using Fisher's Protected Least Significant Difference procedure;
[1]Values were back-transformed from log values used for analysis and are estimates of the median.

Discussion

The treatments in this study bracketed a level of boron that appears to have stimulated growth as well as levels that are clearly toxic. However, despite the growth response, some toxicity symptoms were still evident in seedlings treated with 10 ppm of boron. It is unfortunate that this study did not include boron treatment levels below 10 ppm, which might have resulted in a significant growth response without toxicity symptoms. No plants died in this experiment even though the concentration of boron in leaves of some plants exceeded 1000 ppm. The leaves may have maintained adequate turgor pressure, which perhaps helped mitigate cell damage and stave off leaf abscission.

The use of *P. dasyrachis* in this study had several advantages. This species has a pinnately compound leaf, which allows for easy tracking of boron toxicity symptoms. The plants grew rapidly, and thus toxicity symptoms could be observed easily across the gradient from older foliage at the base of the plant to the newer foliage at the top. Furthermore, this species appears to be tolerant of abnormally high levels of boron.

Partitioning the leaves according to leaf damage allowed us to examine the concepts of nutrient dilution, toxicity, and mobility in a tropical seedling species as a result of boron application.

> "There seems considerable merit...to compare B [boron] concentrations in healthy regions of leaves with those in necrotic/chlorotic regions. If there is a large gradient between these regions, then it is very likely that B toxicity is the causal agent, not other factors such as climate or pathogens. Such an approach could be very informative in species that accumulate B in their leaves." (Nable *et al.* 1997).

The pattern of boron toxicity shows that boron is an immobile element in the phloem for *P. dasyrachis* (i.e. the undamaged leaves were primarily at the top of the plant, where foliage is newer, while the damaged leaves were primarily toward the base, where foliage is older). The pattern was similar for immobile elements calcium and manganese: the damaged leaves had higher nutrient concentrations than the undamaged leaves. The opposite was true for mobile elements nitrogen, phosphorus, and potassium. Oertli and Kohl (1961) partitioned leaves of several boron-treated herbaceous plant species into three categories (necrotic, chlorotic, and green) and measured the boron concentration in each. They found concentrations of 800–12000 ppm in necrotic tissue, 400–3000 ppm in chlorotic tissue, and 40–1000 ppm in green tissue. The toxicity symptoms observed in this study are similar to those described by Bradford (1966) and Scott (1960), in which the leaflets displayed marginal chlorosis or necrosis.

Although there is literature on boron deficiency and toxicity in numerous plant species, especially agricultural crops, we were unable to find any sources on deficiency or toxicity levels in *P. dasyrachis.* This study provided some insights into how this tropical timber species grows in the presence of various levels of boron. The tendency toward increased growth in seedlings receiving the 10-ppm boron treatment is similar to results from deficiency studies with other species, in which the addition of boron had a positive effect on growth (Stone & Will 1965, Bradford 1966, Stone 1990, Will 1990). In the current study, total foliar boron concentration for the 10-ppm treatment showed a growth enhancement at a level of 165.50 ppm.

By known standards for boron in plants (Marschner 1995), the concentrations found in leaves from the 10- to 60-ppm boron treatments were high. In many species, the range between toxicity and deficiency of boron can be quite narrow

(Eaton 1940, Gupta *et al.* 1985). In the current study, the highest average boron concentration found in undamaged foliage was 265.87 ppm (60-ppm treatment), while the lowest boron level in damaged leaves averaged 336.75 ppm (10-ppm treatment).

Although the data in Tables 2 and 3 are useful for the quantitative measure of each nutrient, vector diagrams (Haase & Rose 1995) provide a means of visualising shifts in nutrient concentration, nutrient content, and foliage dry weight relative to one another. All three of the vector diagrams in Figure 2 reveal the higher foliar dry weight found in seedlings from the 10-ppm treatment relative to the control. This is especially dramatic in the nitrogen vector diagram, in which there was very little difference in nitrogen concentration but significant differences in dry weight and, hence, nutrient content (Figure 2a). The potassium diagram also shows a similar effect, as well as significantly higher concentrations for the higher boron treatments (40 and 60 ppm) (Figure 2b). The boron diagram shows the huge difference in relative boron concentration as a result of the treatments (Figure 2c).

Conclusion

The on-going reforestation programme in Thailand can greatly benefit from research to determine the optimum levels of boron and other nutrients in the leaves of forest tree seedlings grown in nurseries. Based on our experience, it is obvious how well *P. dasyrachis* and other Thai species respond to full-spectrum soluble fertilisers. In fact, the slow growth of seedlings in polybags could be shortened to as little as four months. Given that boron is not currently used as a supplement in Thailand and that seedlings in this experiment showed some evidence of a positive response to low levels of boron, it is advisable to follow up this experiment with other trials using treatment levels of 10 ppm boron or less.

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