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ORIGINAL PAPER

Optimum Boron Supplementation Enhances Growth and Nutrient Uptake of Broad-Leaved Tree Seedlings

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Abstract

Boron (B) is a well-known essential element for plant growth, but B supplementation is not widely considered for broad-leaved seedlings because of the lack of B deficiency symptoms. The effects of B on various broad-leaved seedlings in tree nurseries need to be discovered and studied. We selected five native hardwood species commonly used in plantation forestry in Taiwan. Moreover, five concentrations of B supplementation were designed to determine the growth response and nutrient uptake of these seedlings. Supplementation with 10 mg L^{-1} B nutrient solution, corresponding to 2 kg ha^{-1} B, in the growing season significantly increased the growth of most species. Excluding *Zelkova serrata*, which was confirmed as a B-sensitive species in our study, the seedling height, dry weight, and total leaf area of the other species were increased by 21.2–30.3%, 23.2–41.3%, and 14.2–37.9%, respectively, by B supplementation versus the control, suggesting the existence of a hidden hunger effect. Additionally, moderate B supplementation increased the levels of other nutrients, such as nitrogen, phosphorus, magnesium, sodium, and potassium, whereas decreases of calcium levels were observed under the highest B supplementation. Moreover, visible toxic symptoms such as chlorosis and necrosis of leaves and growth inhibition were observed and enhanced by increasing the concentration of B. Our results demonstrated that the B management in the tree nurseries of broad-leaved species is a key factor for obtaining high-quality seedlings, as optimum B supplementation helps improve their growth and nutrient uptake.

Keywords Tree nursery · Different plant organs · Fertilization · Native hardwood species · Hidden hunger

1 Introduction

Boron (B) is an essential element for plants, and its beneficial effects on plant growth and development have been described for more than a century (Mousavi and Raiesi 2022). Studies revealed that B deficiency decreases plant yields (Rerkasem et al. 2020), root dry weight (Räisänen et al. 2007), and antioxidant enzyme levels (Wimmer and Eichert 2013). B deficiency also inhibits root elongation (Zhou et al. 2014), causes the loss of apical dominance (Lehto et al. 2010), alters membrane potential and permeability (Mühling et al. 1998), and impairs the structure and functioning of the cell wall (Hu and Brown 1994). However, the required quantities of B are small, and soils with excessive B levels cause obvious damage in plants. Many studies exposed seedlings to different B concentrations, and higher concentrations had toxic effects, leading to symptoms such as inhibition of metabolic processes; decreased root growth, plant height, and biomass; and leaf chlorosis and/or necrosis (Ou et al. 2019; Reid et al. 2004; Riaz et al. 2021; Yıldırım and Uylaş 2016). A number of review articles demonstrated the important effects of B on plant growth (Brdar-Jokanović 2020; Camacho-Cristóbal et al. 2008; García-Sánchez et al. 2020; Shireen et al. 2018). Although B has been proven to improve plant growth, its metabolic role and essentiality remain under debate (González-Fontes 2019; Lewis 2019; Wimmer et al. 2019).

The interactions of B with other nutrients have been widely discussed (Nejad and Etesami 2020). Most published reports focused on the antagonistic effect of many nutrients in countering the toxicity of B. For example, ion competition is considered to exist between phosphate and borate because they share similarities in their physiological

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and biochemical functions, as they both act as active esters and generate polyhydroxy complexes in conjunction with certain organic compounds (Behera et al. 2023). This phenomenon has been observed through studies showing that phosphorus (P) supplementation decreased the B content in plant tissue (Adak et al. 2018; Kaya et al. 2009). Similar effect was found in silicon (Si) because both Si and B share the same transporters (Celikkol Akcay and Erkan 2016). Furthermore, ion competition is reported between B and other nutrients or elements such as nitrate (Ouzounidou et al. 2013), zinc (Zn) (Hosseini et al. 2007), copper (Cu) (Hippler et al. 2016), and calcium (Ca) (Esringü et al. 2011). However, Goldberg et al. (1996) noted that the competitive effect on B adsorption with other anions was small, and the B-adsorbing sites act independently of competitive anions. Moreover, due to the dilution effect of biomass increment induced by other nutrients, it is difficult to confirm whether B uptake was inhibited by ion competition (Hua et al. 2021). Nevertheless, confirming changes in nutrient levels in different parts of seedlings when using B to improve seedling quality can help determine if the quality changes are related to uptake of other nutrients.

An adequate supply of high-quality seedlings is one component of successful afforestation/reforestation initiatives (Dey et al. 2010; He et al. 2012). For example, a retrospective study spanning 25 years has proven that the greater morphological attributes enhance seedling growth after planting on forest restoration sites (Grossnickle and MacDonald 2018). In addition, the silvicultural techniques in particular optimum nutrition used in tree nurseries will determine seedling quality and lead to a better field performance (Chirino et al. 2009). The improvement of fertilization in nurseries can significantly reduce the high field mortality of seedlings while also offsetting the need for early field fertilization (Villar-Salvador et al. 2004; Schott et al. 2016). Previous studies examined the effects of B on the morphological, physiological, and biochemical responses of plants; however, many of these studies investigated food crops (Landi et al. 2019). Meanwhile, Lehto et al. (2010) reviewed the role of B in forest trees and forest ecosystems and identified some gaps in understanding B uptake by different tree species, as well as the management of B fertilization for many tree plantations. South (2021) summarized the research on B treatments that caused toxic symptoms in tree seedlings, but most of these studies were conducted in *Pinus* species. Additionally, B deficiency in broad-leaved seedlings in nurseries is rare (May et al. 2009), leading to limited studies compared to the number conducted using conifer species. Nevertheless, the general B condition in regular nurseries might limit plant growth without causing deficiency symptoms, a phenomenon termed "hidden hunger" (South 2021). Therefore, verifying the effect of B fertilization on seedlings of different broad-leaved species might increase the efficiency of silviculture.

In this study, we hypothesized that (1) the supplementation of B increases the B concentration in plants, but the response varies among different plant organs and species; (2) the content of various nutrients in different plant organs and species is influenced by the supplemental B concentration; and (3) moderate concentrations of B supplementation improve the growth performance of broad-leaved seedlings. To test these hypotheses, we investigated the benefits of optimal B fertilization management on improving the quality of broad-leaved tree seedlings through the application of different B concentrations.

2 Materials and Methods

2.1 Plant Materials and Growth Conditions

Five native broad-leaved tree species of Taiwan, namely, *Fraxinus griffithii* C. B. Clarke, *Cinnamomum camphora* (L.) Presl, *Bischofia javanica* Bl., *Michelia compressa* (Maxim.) Sargent, and *Zelkova serrata* (Thunb.) Makino, were selected as the experimental materials. Seeds of the species were collected from tall, straight, thick, and rounded mother trees in natural evergreen broad-leaved forests in Wulai, New Taipei City, Taiwan (24° 50′ 27″ N, 121° 32′ 01″ E; 300–400 m above sea level). Seeds with dormancy need to be treated before planting. For *C. camphora*, this involves breaking dormancy through cold-wet stratification (at 4 °C for 3 months) followed by immersion in a 15% hydrogen peroxide solution for 30 min. For *M. compressa*, cold-wet stratification alone is sufficient. Seeds of the other species were reduced the moisture content to 5% and then stored at 4 °C until planted. The pre-treated seeds of the five species were kept for emergence on sand beds in February. Afterward, the seedlings were transplanted into tubes (diameter: 9 cm, depth: 15 cm, volume: 630 cm^3) containing vermiculite and peat moss (1:9, v/v) in April. Seedlings were grown in an insect-free greenhouse constructed with 0.1-mm polyethylene film, which was covered with a shading screen and has a transparency of approximately 60%. In addition, seedlings were fertilized biweekly with Peter's 20–20-20 fertilizer (JR Peters, Allentown, PA, USA) until the end of the experiment. The fertilizer was diluted to achieve concentrations of 100 mg L^{-1} nitrogen (N), 44 mg L^{-1} P, 83 mg L^{-1} potassium (K), 0.25 mg L^{-1} magnesium (Mg), 0.034 mg L^{-1} B, 0.020 mg L^{-1} Cu, 0.250 mg L^{-1} iron, 0.130 mg L^{-1} manganese, 0.005 mg L^{-1} molybdenum, and 0.0125 mg L^{-1} Zn, and 150 mL of the diluted fertilizer was applied per tube. The fertilizer diluted at 100 mg L^{-1} N was used in other woody species in previous reports (Pomper et al. 2003; Struve 2002).

Seedlings were watered with tap water (no B detected). Thus, the background B supplementation for each time was estimated to be 0.00108 kg ha^{-1}. For each species, we selected 240 healthy and homogeneous seedlings for the B supplementation experiment, which used 5 $B(OH)_3$ concentrations (0 [control], 5, 10, 20, and 40 mg L^{-1}), 4 replicates, and 12 seedlings per replicate using a completely randomized design (average value from 12 seedlings was used for each replicate). B was supplied at 2 and 4 months after transplantation by immersing the tubes in $B(OH)_3$ solution for approximately 30 s (filled the medium pores with B solution, which was allowed to seep naturally). For example, 5 mg L^{-1} B supplementation corresponded to 0.99 kg ha^{-1}; thus, the highest B concentration (40 mg L^{-1}) was estimated to be approximately 8 kg ha^{-1}. The seedlings were harvested, and the experiment was terminated 6 months after transplantation (in October). The average temperature in different months during transplantation ranged from 19 to 24 °C. The pH of the growing medium was tested, and a narrow pH range was identified among different B treatments and species (5.4–6.5).

2.2 Determination of Growth Parameters

At the end of the experiment, the seedling height and root collar diameter of each species were measured immediately. The total leaf area was determined using a portable leaf area meter (Model LI-3000, LI-COR, Lincoln, NE, USA). Afterward, the seedlings were separated into roots, shoots, lower leaves, and upper leaves (distinguished through the middle of the crown length) and dried at 75 °C for 3 days, and their dry weights were determined. Furthermore, we calculated growth associated parameters, including the specific leaf area (SLA) and leaf area ratio (LAR) as allometric indices, and slenderness index (SI), shoot/root (SR) ratio, and Dickson quality index (DQI) as quality indices (Dickson et al. 1960; Thompson 1985), using the following equations:

$$\mathrm{SLA} = \frac{\text{Leaf area (cm2)}}{\text{Leaf dry weight (g)}}$$

$$\mathrm{LAR} = \frac{\text{Leaf area (cm2)}}{\text{Seedling dry weight (g)}}$$

$$\mathrm{SI} = \frac{\text{Seedling height (cm)}}{\text{Root collar diameter (mm)}}$$

$$\text{SR ratio} = \frac{\text{Shoot dry weight (g)}}{\text{Root dry weight (g)}}$$

$$\mathrm{DQI} = \frac{\text{Seedling dry weight (g)}}{\mathrm{SI} + \text{SR ratio}}$$

2.3 Determination of the Nutrient Content in the Growing Medium and Different Plant Organs

After the end of the experiment, the growing medium of each species was collected, air-dried, and ground to pass through a 2-mm sieve. N content in the medium was analyzed using the adjusted Kjeldahl method (Bremner 1960). Specifically, 1 g of medium, 3.5 g of the catalyst (K_2SO_4:$CuSO_4$:Se at 10:10:0.1), 3 mL of ultrapure water, and 15 mL of 36 N H_2SO_4 were placed in a digestion flask, then placed on a hot plate that was pre-heated to 100 °C, and then heated to 375 °C until the digest cleared. The final volume of the solution was increased to 75 mL using ultrapure water, and 10 mL of the digested solution was then analyzed by the Kjeldahl method using an automatic analyzer (Kjeltec Auto Sampler System 1035 Analyzer, Tecator AB, Höganäs, Sweden). Moreover, the levels of minerals in the medium, including Ca, Mg, K, sodium (Na), P, and B, were analyzed using the Mehlich-3 extraction procedure (Mehlich 1984). These nutrients were extracted by shaking 5 g of each medium with 50 mL of Mehlich-3 solution (0.2 N CH_3COOH, 0.25 N NH_4NO_3, 0.015 N NH_4F, 0.013 N HNO_3, 0.001 M EDTA [pH 2.5]) for 5 min at 25 °C. The supernatant was filtered using 0.45-µm nylon syringe filters (Pall, Port Washington, NY, USA) and analyzed by inductively coupled plasma atomic emission spectroscopy (ICP-AES; ULTIMA 2000, Horiba Jobin Yvon, Longjumeau, France).

Different plant organs of the seedlings were dried at 75 °C for 3 days and ground to pass through a 0.38-mm sieve. For N determination, 0.2 g of the plant material was placed in a digestion flask with 1 g of the catalyst (K_2SO_4:$CuSO_4$:Se at 50:10:1), 2 mL of ultrapure water, and 10 mL of 36 N H_2SO_4 and analyzed as previously described. For the determination of other nutrients, the dry-ashing procedure was used (Munter et al. 1984). Dried plant tissues (1 g) were weighed in silica crucibles and ashed in an electric muffle furnace (CWF 1100, Carbolite, Sheffield, UK) at 200 °C for 2 h, followed by 400 °C for 1 h, and 550 °C for 3 h. The residue was dissolved in 5 mL of 2 N HCl and then passed through 0.45-µm PTFE syringe filters (Pall). The solution was made to a final volume of 20 mL with ultrapure water and analyzed by ICP-AES as previously mentioned.

2.4 Statistical Analysis

To test whether the growth parameters varied among different tree species and B treatments, two-way analysis of variance (ANOVA) with replication (5 species × 5 boron treatments) was performed, followed by application of

the Holm–Šídák method ($\alpha = 0.05$). The B content in each growth medium was analyzed using the same method. Moreover, one-way ANOVA followed by the same post-hoc analysis was performed to determine the difference in the content of multiple nutrient elements between different B treatments in the organs of each tree species. All analyzed data had passed the normality (Shapiro–Wilk) and equal variance (Brown-Forsythe) tests before conducting the two-way ANOVA. For the one-way ANOVA, if either of the aforementioned tests failed, the Kruskal–Wallis one-way ANOVA by ranks was used instead, followed by application of the Tukey method ($\alpha = 0.05$). Statistical analyses and graph drawing were performed using SigmaPlot 14.0 (Systat Software Inc., Chicago, IL, USA).

3 Results

3.1 B Content in Different Plant Organs and the Growing Medium

A significant two-way interaction between species and B treatment was found in all plant organs. Regarding plant organs, B was abundant in lower leaves, whereas its levels were relatively lower in shoots and roots (Fig. 1). Generally, the B content in different plant organs increased with increasing concentrations of B supplementation; however, different trends were observed in different tree species. For example, *F. griffithii* exhibited changes of lower significance in B levels in upper and lower leaves, whereas more significant and dramatic increases were detected in other species, in particular *C. camphora* and *B. javanica* (Fig. 1a, b). Under 40 mg L^{-1} B supplementation, the B levels in the lower leaves of *C. camphora* and *B. javanica* were 334.5 ± 22.5 and 400.8 ± 32.3 mg kg^{-1}, respectively, which were 7–eightfold higher than those in *F. griffithii*. Conversely, significant and large increases of B content in shoots and roots were detected in *F. griffithii* under 40 mg L^{-1} B supplementation (Fig. 1c, d). It is worth noting that under the moderate B supplementation (10 mg L^{-1}), no significant differences were found in the upper and lower leaves of *Z. serrata* (Fig. 1a, b). Moreover, excluding *F. griffithii*, other species exhibited similar B contents in shoots under different B concentrations (8.0–14.9 mg kg^{-1}) (Fig. 1c). In contrast, significant increases with the increasing B levels can be found in the root of all the species (Fig. 1d). The B content in the growing medium increased significantly with increasing concentrations of B supplementation (Fig. 1e). Under B supplementation at 0 and 40 mg L^{-1}, the B levels in the growing medium were 0.29 ± 0.14 and 2.65 ± 0.51 mg kg^{-1}, respectively.

3.2 Content of Nutrients in Different Plant Organs

Generally, the Ca content in different organs decreased with increasing B concentrations in most plant species, especially for *F. griffithii* (Fig. 2). Significant decreases were observed mostly under 40 mg L^{-1} B supplementation compared to the control. By contrast, moderate B supplementation (10 mg L^{-1}) did not cause significant decreases of Ca content in most of the plant organs among the plant species. Moreover, Mg and K levels were significantly higher than the control levels under moderate B supplementation among the plant species excluding *M. compressa* and *Z. serrata* (Fig. 2). By contrast, no significant decreases occurred under the 40 mg L^{-1} B supplementation versus the control in most plant organs among the plant species. In addition, a significant increase of Na content occurred in the roots of most species under 5 mg L^{-1} B supplementation, whereas other organs exhibited higher content under 10 or 20 mg L^{-1} B supplementation compared to the control. Furthermore, P and N levels mostly increased among different species under 10 mg L^{-1} B supplementation (Fig. 2). For example, in the roots of *F. griffithii* and *B. javanica*, significant increases of approximately 20% in P content were found compared to the control. Moreover, the N content in the lower leaves of *C. camphora* and the shoots of *B. javanica* showed a significant twofold increase versus the control under 10 mg L^{-1} B treatment. Similarly, the N content in the roots of *M. compressa* and *Z. serrata* also increased significantly under 10 mg L^{-1} B supplementation. Conversely, under 40 mg L^{-1} B treatment, the P and N levels in the shoots of *F. griffithii*, *C. camphora*, and *B. javanica* generally decreased. The P content in the roots of *M. compressa* also decreased with increasing B concentrations. Additionally, no significant differences in the nutrient contents of the growing medium were found among each species under different B treatments (Table S1), suggesting that the mineral levels were sufficient for plant growth.

3.3 Growth Responses of Different Species

The seedling height of most species increased significantly following supplementation with 10 or 20 mg L^{-1} B, while *Z. serrata* showed significant decreases, particularly at 20 and 40 mg L^{-1} B, compared to the control (Fig. 3a). Similar results were found for the seedling dry weight and total leaf area (Fig. 3c, g). Under 10 mg L^{-1} B treatment, the seedling height, dry weight, and total leaf area of all species excluding *Z. serrata* increased by 21.2–30.3%, 23.2–41.3%, and 14.2–37.9%, respectively, compared to the control. Contrarily, under 40 mg L^{-1} B treatment, *Z. serrata* exhibited significant decreases of the seedling height, dry weight, and total leaf area (26.6%, 37.1%, and 29.3%, respectively), whereas no significant differences were found at this concentration

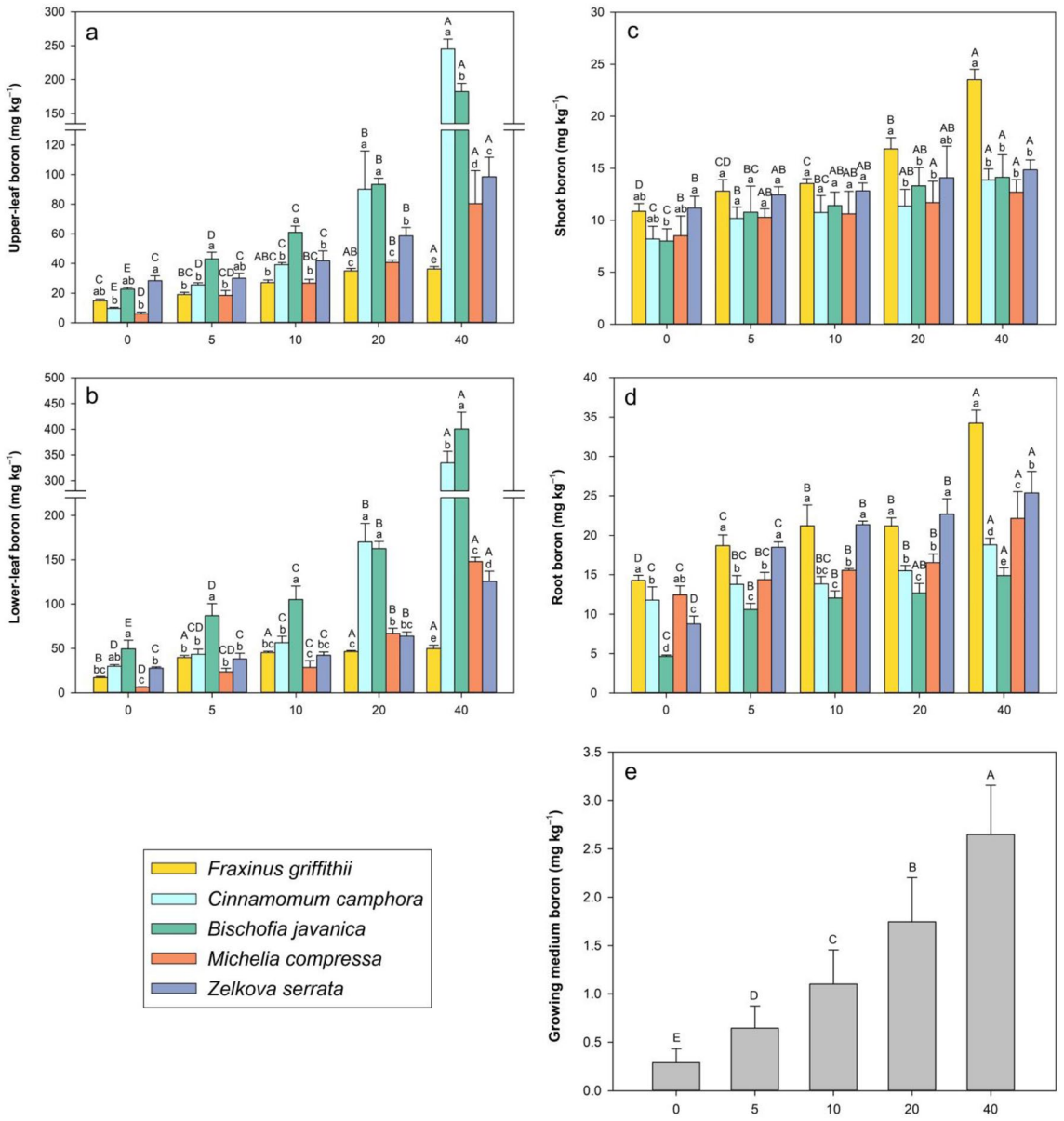

Fig. 1 Boron content in the **a** upper leaf, **b** lower leaf, **c** shoot, **d** root, and **e** growing medium under different boron treatments (boron concentration ranges between 0 and 40 mg $L.^{-1}$; data represent the mean and standard deviation of the dry weight; the capital letters indicate significant differences between boron concentrations; and the lower-case letters indicate significant differences between species [two-way analysis of variance, Holm–Šídák method, $\alpha = 0.05$, $n = 4$]; only the significant main effect of boron treatment was observed in the growing medium)

in other species compared to the control, except for the seedling dry weight of *C. camphora*. In addition, similar patterns were found for the dry leaf, stem, root, and total seedling weights in each species, indicating that the dry weight changes occurred simultaneously in different plant parts (Fig. 3c, d, e, f). Furthermore, most species exhibited a significant increase in root collar diameter by 4.7 to 23.9% under 10 or 20 mg L^{-1} B treatment, while *Z. serrata* showed a decreasing trend with increasing B levels, and a significant decrease of 19.8% under 40 mg L^{-1} B supplementation was observed (Fig. 3b). Moreover, visible toxic symptoms such as chlorosis/necrosis (tips of mature leaves), twisted leaf edges, and/or defoliation were observed only in *C. camphora* and *Z. serrata* under 20 and 40 mg L^{-1} B treatment, and the obvious toxic symptoms first occurred after 30 (Fig. 4a) and 14 days (Fig. 4b) of 40 mg L^{-1} B supplementation, respectively.

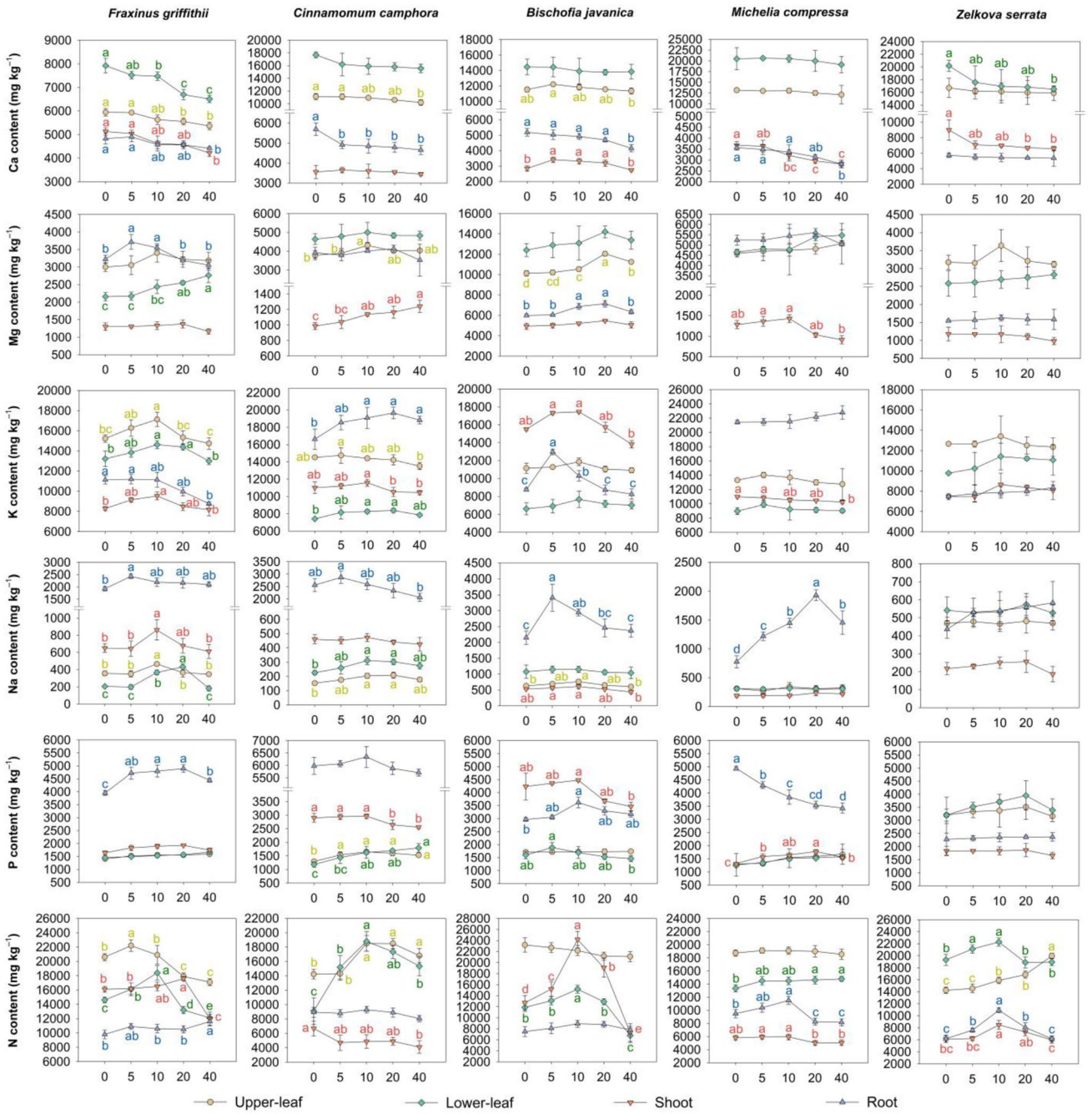

Fig. 2 Nutrient content in various plant organs under different boron treatments (boron concentration ranges between 0 and 40 mg $L.^{-1}$; data represent the mean and standard deviation; the lowercase letters indicate significant differences between boron concentrations [one-way analysis of variance, Holm–Šídák method, $\alpha = 0.05$, $n = 4$]

3.4 Growth Associated Parameters of Different Species

The results for SLA and LAR were similar in each species, and significant changes were mostly recorded in *C. camphora* and *M. compressa* (Table 1). We observed that 5 mg L^{-1} B treatment significantly decreased SLA and LAR in *M. compressa*, whereas it significantly increased these variables in *C. camphora*. In addition, the SI was smallest in *B. javanica* (total mean, 6.81) and highest in *F. griffithii* (total mean, 13.1); however, no significant differences were found among different B treatments in these two species. Conversely, 10 mg L^{-1} B treatment significantly increased SI in the other species compared to the control (15.3–21.6%). Moreover, no significant two-way interaction was found for the SR ratio, and the main effect was significant only for

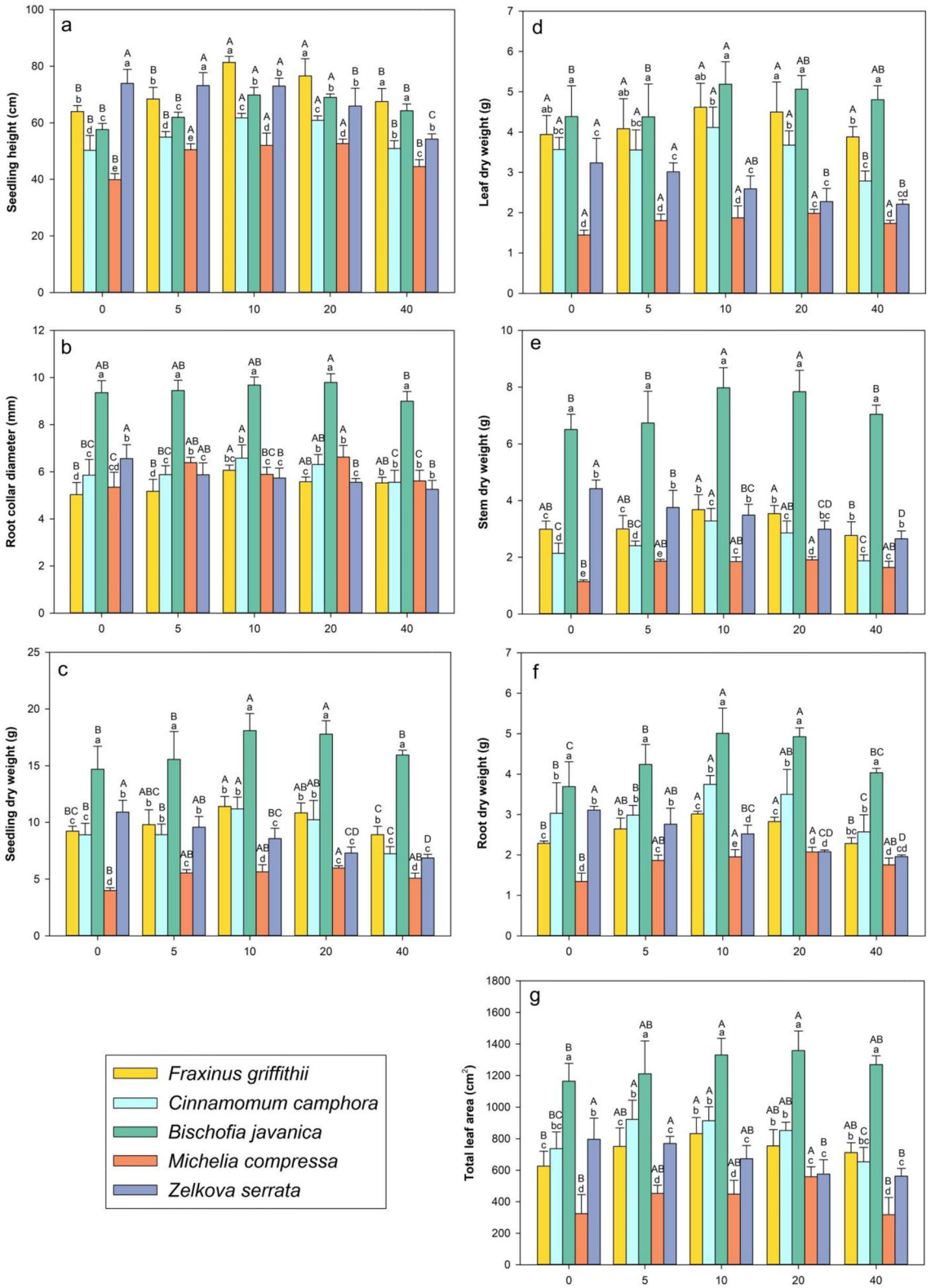

Fig. 3 Growth responses of the experimental tree species under different boron treatments including **a** seedling height, **b** root collar diameter, **c** seedling dry weight, **d** leaf dry weight, **e** stem dry weight, **f** root dry weight, and **g** total leaf area (boron concentration ranges between 0 and 40 mg $L.^{-1}$; data represent the mean and standard deviation; the capital letters indicate significant differences between boron concentrations, and the lowercase letters indicate significant differences between species [two-way analysis of variance, Holm–Šídák method, $\alpha = 0.05$, $n = 4$]

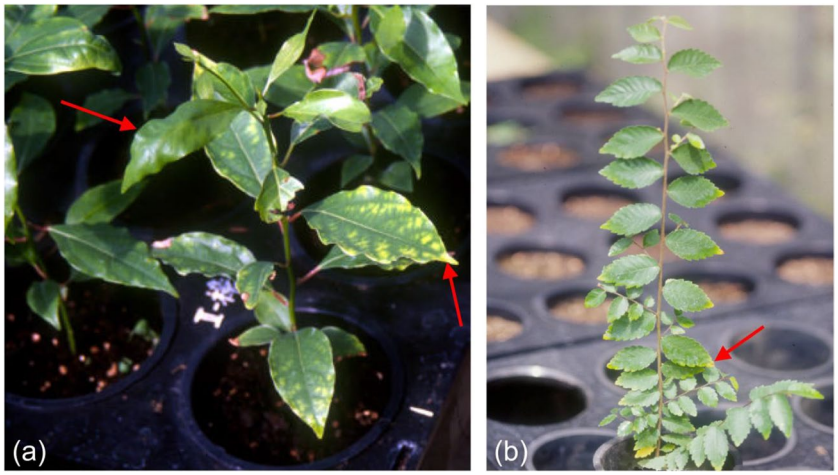

Fig. 4 Toxic symptoms in seedlings appeared **a** after 30 days of 40 mg L^{-1} boron supplementation in *Cinnamomum camphora* and **b** after 14 days of 40 mg $L.^{-1}$ B supplementation in *Zelkova serrata* (arrows denote the toxic symptoms including chlorosis, necrosis, and twisted leaf edges)

Table 1 Growth associated parameters of the experimental tree species under different boron treatments

Traits	Boron treatment (mg L^{-1})	*Fraxinus griffithii*		*Cinnamomum camphora*		*Bischofia javanica*		*Michelia compressa*		*Zelkova serrata*	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
SLA ($cm^2\ g^{-1}$)	0	171.186^{Ac}	9.001	208.652^{Bb}	21.652	260.383^{Aa}	25.485	242.545^{Aa}	26.285	250.950^{Aa}	11.063
	5	184.733^{Ad}	8.337	250.590^{Ab}	23.399	273.867^{Aa}	16.597	212.827^{Bc}	9.992	253.927^{Aab}	8.196
	10	178.615^{Ac}	9.411	233.083^{ABb}	21.078	257.817^{Aa}	6.049	236.098^{ABab}	25.437	258.712^{Aa}	6.025
	20	177.803^{Ad}	14.592	234.508^{Abc}	6.348	275.578^{Aa}	15.756	220.882^{ABc}	10.003	250.532^{Ab}	12.397
	40	172.462^{Ac}	4.290	228.517^{ABb}	19.649	282.257^{Aa}	14.033	241.140^{ABb}	19.813	242.140^{Ab}	15.659
LAR ($cm^2\ g^{-1}$)	0	76.407^{Aab}	6.291	87.152^{Ba}	17.373	79.295^{ABab}	6.966	85.937^{Aa}	9.049	69.175^{Ab}	5.720
	5	81.388^{Ab}	8.831	104.283^{Aa}	12.255	83.365^{ABb}	9.295	70.857^{Bb}	8.283	80.403^{Ab}	7.238
	10	69.748^{Ac}	10.528	92.247^{ABa}	7.017	75.648^{Bbc}	7.349	86.195^{Aab}	13.950	77.233^{Abc}	3.330
	20	72.145^{Ab}	3.137	90.865^{ABa}	6.645	80.633^{ABab}	6.311	75.742^{ABb}	8.307	73.862^{Ab}	7.634
	40	71.642^{Ab}	1.840	89.895^{Ba}	5.211	90.580^{Aa}	8.351	81.715^{ABab}	14.016	79.742^{Aab}	6.446
SI ($cm\ mm^{-1}$)	0	12.631^{Aa}	0.728	8.290^{Bc}	1.089	6.184^{Ad}	0.428	7.363^{Bc}	0.839	11.273^{BCb}	1.441
	5	13.560^{Aa}	0.777	9.367^{ABc}	0.781	6.595^{Ae}	0.568	8.068^{ABd}	0.670	12.503^{ABb}	0.669
	10	13.433^{Aa}	0.452	9.697^{Ab}	1.250	7.175^{Ac}	0.359	8.953^{Ab}	0.891	13.002^{Aa}	1.097
	20	13.626^{Aa}	1.021	9.638^{ABc}	0.825	6.951^{Ad}	0.310	7.799^{ABd}	0.598	12.350^{ABb}	1.374
	40	12.443^{Aa}	0.946	8.995^{ABc}	0.740	7.152^{Ad}	0.375	7.951^{ABcd}	0.374	10.242^{Cb}	1.144
SR ratio*	0	3.017	0.130	1.898	0.279	2.972	0.280	2.036	0.253	2.453	0.229
	5	2.801	0.292	1.913	0.175	2.663	0.304	1.974	0.169	2.450	0.334
	10	2.750	0.266	1.927	0.162	2.613	0.323	1.907	0.074	2.490	0.210
	20	2.880	0.229	1.934	0.037	2.605	0.171	1.881	0.037	2.503	0.200
	40	2.937	0.209	1.928	0.347	2.946	0.080	1.921	0.023	2.530	0.092
DQI	0	0.652^{Ac}	0.054	0.951^{ABb}	0.163	1.865^{ABa}	0.368	0.494^{Ac}	0.097	0.856^{Ab}	0.089
	5	0.666^{Ac}	0.127	0.887^{ABb}	0.178	1.862^{ABa}	0.219	0.611^{Ac}	0.073	0.693^{ABbc}	0.100
	10	0.786^{Ac}	0.085	1.071^{Ab}	0.167	2.041^{ABa}	0.209	0.577^{Ad}	0.108	0.623^{ABcd}	0.138
	20	0.716^{Ac}	0.097	0.980^{ABb}	0.206	2.091^{Aa}	0.161	0.679^{Ac}	0.043	0.537^{Bc}	0.044
	40	0.661^{Ab}	0.087	0.746^{Bb}	0.120	1.806^{Ba}	0.132	0.564^{Ab}	0.046	0.597^{Bb}	0.061

The capital superscript letters indicate significant differences between boron concentrations, and the lowercase superscript letters indicate significant differences between species (two-way analysis of variance), Holm–Šídák method, $\alpha = 0.05$, $n = 4$. *No significant two-factor interaction. Abbreviations: *SLA*, specific leaf area; *LAR*, leaf area ratio; *SI*, slenderness index; *SR*, shoot/root; *DQI*, Dickson quality index; *SD*, standard deviation

species differences (Table 1). DQI was highest under 10 or 20 mg L^{-1} B treatment in all species excluding *Z. serrata*, but the differences versus the control were not significant. Additionally, 40 mg L^{-1} B treatment significantly decreased DQI in *C. camphora*, *B. javanica*, and *Z. serrata*.

4 Discussion

B accumulation in different plant organs among different species decreased in the order of mature leaves > young leaves > roots ≈ stems, in line with previous findings (García-Sánchez et al. 2020; Gimeno et al. 2012; Rees et al. 2011). Generally, plants can regulate B levels in cells through protein tunnels (major intrinsic protein family) and BOR-type borate transporters (Onuh and Miwa 2021). In the presence of sufficient concentrations, B in plants is primarily transported passively along the transpiration streams, leading to accumulation at the end of the streams (Yoshinari and Takano 2017), thereby leading to higher B content in leaves. This is also why toxic symptoms such as chlorosis/necrosis mostly occurred at leaf margins. Moreover, mature leaves had higher B content than young leaves, proving the limitation of B mobility (Brown and Hu 1998). Furthermore, B accumulation in plants varies by species. For example, *Puccinellia distans* was proven to tolerate > 6000 mg kg^{-1} B in its shoots (Stiles et al. 2010). By contrast, B content is relatively lower in monocotyledonous plants such as wheat, barley, and maize, and toxic symptoms were observed in these plants at tissue levels < 100 mg kg^{-1} (Coskun et al. 2014; Gotz et al. 2021). Concerning tree species, in Norway spruce, B levels of approximately 400 mg kg^{-1} in needles did not exert harmful effects on the growth or morphology of the seedlings (Riikonen et al. 2013). Moreover, large chlorotic and necrotic leaf areas developed when the B content exceeded 900 mg kg^{-1} in a *Populus* species (Rees et al. 2011). In our study, *C. camphora* and *B. javanica* accumulated B mostly in the lower leaves. However, only *C. camphora* exhibited chlorosis at the leaf tips, suggesting that *B. javanica* better resists B-induced toxicity. Previous studies revealed that *B. javanica* grew rapidly, in line with our results regarding growth response, and it was also considered a stress-tolerant species with high light acclimation potential (Abe et al. 2020; Kamaluddin and Grace 1993; Yazaki et al. 2015). Conversely, *Z. serrata* was identified as a B-sensitive species in this study. The species displayed moderate B accumulation in different organs, exhibited toxic symptoms under B concentrations of ≥ 20 mg L^{-1}, and the B content in the lower and upper leaves was approximately 60 mg kg^{-1}. *F. griffithii* is considered a pioneer species that is similar to *Z. serrata* (Chen et al. 2021; Yulistyarini et al. 2020). However, *F. griffithii* accumulated relatively lower B levels in leaves, and no visible toxic symptoms were found. Generally, broad-leaved trees are considered more sensitive to high B levels (Lehto et al. 2010). For example, nine broad-leaved tree species, such as American sycamore, water tupelo, and various oak species, exhibited leaf damage (necrotic spotting) under treatment with 2 mg L^{-1} B, and the B content in leaves ranged from 61 to 210 mg kg^{-1} (McLeod and Ciravolo 1998). The present study demonstrated a significant increase in B content in the organs of various tree species with increasing concentrations of B application. However, certain species, specifically *C. camphora* and *Z. serrata*, exhibited adverse effects. Moreover, high concentrations of B application in other species, which appeared visually normal, led to an inhibition of growth-promoting effects. Overall, our results revealed differences in B accumulation and tolerance among various broad-leaved species, suggesting that B supplementation strategies in tree nurseries should better be optimized for individual species. However, the results of this study on different tree species indicate that the use of 10 mg L^{-1} B treatment in nursery management may be a widely applicable method for broad-leaved seedlings, effectively increasing the B content in various organs of different species, promoting the growth of most plants, and avoiding adverse effects on appearance.

The cell wall is the main binding site of B, and the role and function of B in cell wall assembly and growth involving the cross-linking of pectin (rhamnogalacturonan II) are well-documented (Blevins and Lukaszewski 1998; Kobayashi et al. 1996; O'Neill et al. 2004). Similarly, Ca and B are both considered apoplastic elements, and the maintenance of cell wall integrity and rigidity via interactions with pectic polymers relies on their collaboration (Matoh and Kobayashi 1998). Combined treatment with Ca and B leads to the highest marketable yield of tomatoes (Huang and Snapp 2004). However, B localization in the cell wall can decrease the cell wall permeability of Ca, highlighting a negative relationship between these elements (Turan et al. 2018). Similarly, excess B was associated with reduced Ca content in different plant organs and species in our study. Moreover, significant decreases of Ca content under the highest B supplementation (40 mg L^{-1}) occurred in *Z. serrata*, which was the B-sensitive species displaying visible adverse symptoms in our experiment. Notably, except for Ca, no significant reductions in other nutrient contents were observed in *Z. serrata* under 40 mg L^{-1} B supplementation compared to the control, indicating a strong correlation between Ca and the appearance of harmful symptoms in *Z. serrata*. This phenomenon suggests that the tolerance of B-sensitive species is associated with the maintenance of Ca levels. Previous studies reported that Ca supplementation can alleviate the toxic effects of excess B (Metwally et al. 2018). Thus, the Ca/B ratio could be an important factor for optimal plant growth (Kanwal et al. 2008). Furthermore, ion competition occurred between P (PO_4^{3-}) and B (BO_3^{3-}) because of their similar

physiological transport mechanisms (Günes and Alpaslan 2000). This effect was also found between N (NO_3^-) and B (BO_3^{3-}) (Zhen et al. 2019). The aforementioned phenomena were obvious in our results for the highest B concentration. However, moderate B treatment (10 mg L^{-1}) drastically increased N levels in various plant organs among different species, which agreed with the results of Koohkan and Maftoun (2016), who identified the important relationship between N and B and discovered that the application of B to soil significantly increased the N content by 1.74-fold in the shoots of *Brassica napus*. Similar increasing results were also found in previous studies (Hosseini et al. 2007; Inal and Tarakcioglu 2001). The increased N content could be attributed to the enhanced nitrate reductase activity (Shen et al. 1993) and rhizobia-mediated N fixation (Redondo-Nieto et al. 2003) resulting from B application. Furthermore, our results indicated that moderate B supplementation increases Mg and K content in different plant organs, demonstrating the effects of B application on macronutrient accumulation. An optimum level of B has been proven to increase membrane permeability of K^+ (Schon et al. 1990). Additionally, research on the interactions between B and Mg in plants is limited (Long and Peng 2023). In a previous study of tobacco, it was found that increased B application led to a decrease in Mg uptake and translocation. This effect was attributed to the increased K and Na levels, which can compete with Mg for uptake sites (López-Lefebre et al. 2002). However, we did not observe this phenomenon in different species under the moderate B treatment, suggesting an enhanced effect of comprehensive nutrient uptake by optimum B supplementation. It is worth noting that the increasing content of these nutrients in plants might contribute to the concentration effect attributable to the decrease in biomass (Simón et al. 2013), whereas both the dry mass and content of many nutrients particularly increased under 10 mg L^{-1} B treatment in our experiments, suggesting that nutrient uptake was enhanced. Overall, B plays an important role in the accumulation of other nutrients, and ion competition might represent a solution to mitigate the toxic effect of excess B in the environment (Hua et al. 2021). By contrast, proper B concentrations can improve both the nutritional and morphological quality of broad-leaved seedlings.

Generally, B deficiency was proven to cause leader dieback, reduce root growth, and inhibit the growth of pollen tubes (García-Sánchez et al. 2020), whereas the use of common growing media (such as peat moss) in tree nurseries did not result in these symptoms. Our growth results for *Z. serrata* proved that the B concentration in the growing medium for the control was sufficient for seedling growth; however, other species displayed greater growth responses under 10 or 20 mg L^{-1} B treatment, suggesting the existence of a hidden hunger effect. This effect was widely recognized in cauliflower with the recommended B content in soil, which was not lower than 0.48 mg kg^{-1} (Batabyal et al. 2015; Raja 2007). In this study, excluding *Z. serrata*, the critical B point for the experimental species was 10 or 20 mg L^{-1} B, corresponding to final B contents of 1.1–1.7 mg kg^{-1} in the growing medium. By contrast, Ou et al. (2019) found that the adverse effects of B application, such as chlorosis, necrosis, and growth inhibition, on *Populus russkii* worsened with increasing B levels in soil (10–50 mg kg^{-1}) versus the control (0.64 mg kg^{-1}). Similar results were observed in black poplar under soil B concentrations of 5.7–22.8 mg kg^{-1} (Yıldırım and Uylaş 2016). Moreover, in studies of *Citrus* species grown in nutrient solution, a B concentration of 0.5 mg L^{-1} was considered most suitable for growth (Boaretto et al. 2008; Mesquita et al. 2016). These results suggest that B application should be considered carefully, and the difference between effective and toxic concentrations is small. South (2021) summarized a list of B treatments that produced toxic symptoms in seedlings, but the limitation of B supplementation varied drastically across different studies because of differences in experimental species, application methods, soil types, extraction methods, and compound solubilities from different B products. Some studies reported the solution concentration of B but not the total rate of application, leading to difficulty in discussing the operational use of B. In addition to the level of B supplementation, Sutinen et al. (2007) noted that B supplementation should be applied at the beginning of the growing season in pine and spruce to prevent the appearance of negative structural symptoms. Overall, 10 mg L^{-1} B supplementation, corresponding to the application of 2 kg ha^{-1} B (twice) in the growing season, could be the optimal strategy for most broad-leaved species that avoids visible toxic symptoms and severe growth inhibition for certain species (i.e., *Z. serrata*). The aforementioned treatment also improved the growth of leaves without causing noticeable changes of leaf traits. Furthermore, DQI, an integrated measure of morphological traits combining aspects of the SR ratio, SI, and seedling dry mass, is considered a good indicator of seedling quality (Binotto et al. 2010; Dickson et al. 1960; Nyoka et al. 2018; Tsakaldimi et al. 2013). Although not statistically significant, the increase of DQI under moderate B supplementation in most species supported the effectiveness of this strategy for obtaining seedlings of better quality.

Nutrient management is a key factor in obtaining high-quality seedlings in tree nurseries. Major elements such as N, P, and K have received most of the attention; however, B, as a trace element, is not additionally supplied in regular tree nurseries in Taiwan. Moreover, slow-release fertilizers wrapped in plastic polymers contain diverse micronutrients could be another option for fertilization. However, these fertilizers are typically expensive and it is unclear whether the B content is sufficient. The experimental results of this study provide a simple and low-cost B fertilization method

with a specific B application rate that effectively enhances the growth of seedlings. Satisfying the hidden hunger of seedlings is an important issue because successful afforestation or reforestation relies on a sufficient supply of high-quality seedlings. For example, *M. compressa* is considered one of the top five hardwood species in Taiwan because of its valuable dark and dense heartwood with a fine texture, decay resistance, and anticancer potential (Chan et al. 2014; Chen 2012; Wu et al. 2012). However, it is a slow-growing species compared to other broad-leaved species, and 10 mg L^{-1} B supplementation significantly improved its seedling height and total dry mass by approximately 30% and 41%, respectively. This effect shortened the nursery time, avoided the waste of manpower and resources, and accelerated the process of transplanting seedlings to the field, which could be considered both economical and sustainable.

5 Conclusions

This study demonstrated that the B management in the tree nurseries of broad-leaved species is a key factor for obtaining high-quality seedlings, and the discrepancies between different species should be considered and discussed. We investigated the effects of B supplementation on five common broad-leaved tree species in Taiwan, which exhibited varying effects of B accumulation, growth responses, and nutrient uptake characteristics in response to B application. Moderate B supplementation effectively improved the growth and nutrient uptake of slow-growing species such as *Michelia compressa*. However, for B-sensitive species such as *Zelkova serrata*, moderate B supplementation did not significantly affect its growth, and Ca supplementation may be a key factor in further improving its quality. This study proved the great potential of optimum B supplementation for improving seedling growth. Supplementation with 10 mg L^{-1} B nutrient solution, corresponding to 2 kg ha^{-1} B, in the growing season significantly increased the growth responses of most broad-leaved species, which may be a widely applicable method for seedling nurseries. Nevertheless, more experiments are required to verify the effect of B supplementation on different tree species and fill the knowledge gaps for various broad-leaved species.

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Data Availability All data are available on request from the authors.

Declarations

Competing Interests The authors declare no competing interests.

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