REGULAR ARTICLE

Effects of nitrogen deposition on growth and phosphate efficiency of *Schima superba* of different provenances grown in phosphorus-barren soil

Rui Zhang · ZhiChun Zhou · WenJian Luo · Yi Wang · ZhongPing Feng

Abstract

Aims We determined whether nitrogen (N) deposition on phosphorus (P)-limited soil could increase *Schima superba* growth or alter root formation or P efficiency. The effects of N deposition on *S. superba* were also used to investigate the N/P requirements of plants of different provenances.

Methods One-year-old *S. superba* seedlings from eight geographic areas were grown in P-limited soil and treated with N (0, 50, 100, and 200 -kg N ha^{-1} year^{-1}; *i.e.*, control, N50, N100, or N200, respectively). Seedling growth, root development, phosphorus acquisition efficiency (PAE), and phosphorus utilization efficiency (PUE) were measured.

Results *S. superba* responded positively to N supplementation. Seedling growth and dry biomass were highest with N100 treatment and lowest with N200.

Root biomass and acquisition of soil P were greatest with N100. Significant differences were observed among plants of different geographical provenances. PAE and PUE had a strong relationship with root growth in plants subjected to N100 treatment.

Conclusion A threshold for N and P requirements related to different genetic conditions and soil nutrients may exist for *S. superba*. Root growth and PAE can be divided into three categories based on soil nitrate levels. Nutrients were found to control root morphology and to enhance aboveground differences.

Keywords Nitrogen deposition · Phosphorus limitation · Provenance · Root growth · Phosphorus acquisition efficiency (PAE) · Phosphorus utilization efficiency (PUE)

Abbreviations
PAE   Phosphorus Acquisition Efficiency
PUE   Phosphorus Utilization Efficiency
RAR   Root:Aboveground Ratio
SBD   Stem Base Diameter

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Introduction

The macronutrient phosphorus (P) is essential to plant growth and development, but it is usually present at only low levels in subtropical soils, particularly forest soils (Holford 1997; He et al. 2003). Overall soil P levels are roughly <0.3 mg g^{-1} across most areas of

southern China, which is well below the global average (National Soil Office of China 1998; Han et al. 2005). P deficiency is a major factor limiting the primary productivity of forests (Darrell and Fownes 1995; Feller et al. 1999; Davidson et al. 2004; Wassen et al. 2005; Elser et al. 2007). The P concentration in plants is maintained by the balance between by P uptake and the plant's growth rate. Phosphorus acquisition efficiency (PAE) and phosphorus utilization efficiency (PUE) are two important indices of plant growth. PAE here refers to the ability of the plant to acquire P from the soil, and PUE is the amount of biomass produced per unit of acquired P (Huang et al. 2011). PAE and PUE may be affected by several environmental and genetic factors (Pearse et al. 2006).

The rate of deposition of nitrogen (N) is high in subtropical forests in southern China, and it is expected to increase further in the coming decades (Xu et al. 2001; Zheng et al. 2007; Mo et al. 2008; Hu et al. 2010; Ti and Yan 2010). N deposition leads to soil acidity, causes depletion of base cations, and mobilizes Al. The concentration of Al^{3+} has been found to increase the levels of Al-P compounds and so reduce the content of soluble phosphate (Pi) available in the soil. High N input into forests has been linked to nutritional disorders in plants and to reduced growth and productivity (Vitousek et al. 1997; Emmett 2007; Moore and Houle 2009). However, moderate amounts of added N have been found to increase the net photosynthetic rate and biomass production of seedlings (Nakaji et al. 2001, 2002; Mo et al. 2008). Nitrogen deposition affects the concentration of P in the soil, which in turn influences PAE and PUE. The differential responses of root growth and morphology to N (which are related to different genotypes), suggest that N plays an important role in nutrient uptake (Sas et al. 2002; Wang et al. 2006; Zhang et al. 2007; Ge et al. 2008; Magaña et al. 2009; Richardson et al. 2009).

Schima superba is a representative, widely distributed species of broadleaf tree found in the subtropical forests of southern China. This species is valued commercially for its timber. It can also prevent the spread of fire and thus help protect forests (Luo 2009; http://www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=200014158). In general, *S. superba* grows in relatively nutrient-poor soils; and its root system, PAE, and PUE vary greatly across regions (Lin et al. 2009; Lin and Zhou 2009). However, the changes in the PAE and PUE of *S. superba* under different N-

deposition and P-limitation conditions have not been documented.

This study focuses on the effects of N deposition and P limitation on *S. superba* plants of different provenances and addresses the following questions: (a) What is the combined effect of increased N deposition and P limitation on seedling growth, root system growth, PAE, and PUE of *S. superba*? (b) Is there any difference in the response to N and P availability among *S. superba* from different places?

Materials and methods

Experimental conditions

This study was executed from March to November 2011 in a glass house. The glass house was not climate controlled. The temperature in the glass house ranged from 5 to 15 °C from December to the following February and from 26 to 34 °C from July to September. *S. superba* seeds from eight provenances were germinated in normal forest soil (see below) in March 2011. The seeds were collected from Hangzhou (HZ) and Longquan (LQ) in Zhejiang province and at altitudes of 100 m, 300 m, and 600 m in Jian'ou (JO100, JO300 and JO600, respectively); Gutian (GT) in Fujian Province; Guiyang (GY) in Hunan Province; and Xinfeng (XF) in Jiangxi Province (Fig. 1). When the seedlings produced two cotyledons between 2 and 3 cm in height, they were planted in plastic containers 15 cm in diameter and 18 cm in height in April 2011, two seedlings per container. The seedlings were watered every other day. If both seedlings in a given container survived, one was removed to maintain the one seedling/container planting density. A double layer of root-cloth was laid inside the container to prevent the roots from growing out of the drainage hole. The soil used was regular forest soil (P limited) from Zhejiang province. The soil pH was 5.06 (potentiometric method, LY/T 1239–1999), total nitrogen was 0.41 gkg^{-1} (semi-micro Kjeldahl method, LY/T 1228–1999), hydrolyzable nitrogen was 46.43 $mgkg^{-1}$ (alkaline hydrolysis diffusion method, LY/T 1229–1999), available phosphorous was 13 mg kg^{-1} (hydrochloric acid-sulfuric acid extraction method, LY/T 1233–1999), available potassium was 130.08 mg kg^{-1} (1 $molL^{-1}$ ammonium acetate extraction-flame photometry method, LY/T 1236–1999), and organic
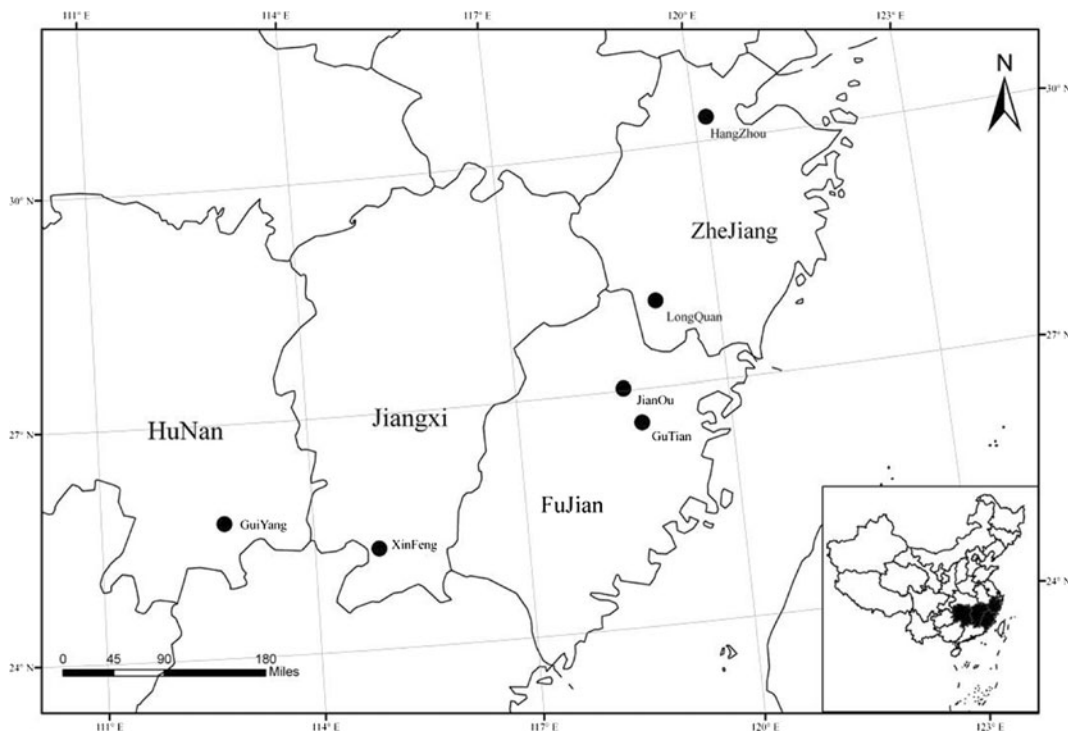
Fig. 1 Geographical distribution of southern China provenances containing *S.superba* for use in the present study

matter was 6.68 g kg^{-1} (potassium dichromate oxidation-external heating method, LY/T 1237–1999).

The factorial design of the experiment included *S. superba* seedlings of eight provenances and four levels of N addition using NH_4NO_3 (0, 50, 100, and 200 kg Nha^{-1}year^{-1}; N deposition mainly contained NH_4^+ and NO_3^- forms under natural conditions). There were 18 replicates per treatment with a total of 576 individuals. The four levels of N addition included very low levels of N deposition (0 kgNha^{-1}year^{-1}, N0), which served as a control treatment, low-to-medium deposition (50 kgNha^{-1}year^{-1}, N50), high deposition (100 kgNha^{-1}year^{-1}, N100), and very high deposition (200 kgNha^{-1}year^{-1}, N200). These levels were determined based on current and historical deposition levels in southern China (He 1993; Zheng et al. 2007; Ti and Yan 2010; Hu et al. 2010). The added N was applied once every 2 weeks for a month, and then once a month for the next 6 months, beginning when the leaves started to bud (from the April 20, 2011 to the October 20, 2011). Whole plants were sprayed using dissolved NH_4NO_3, and the concentrations were 0.0016, 0.0031, and 0.0062 molL^{-1}, for the N50, N100, and N200 treatments, respectively. Seedlings were watered with distilled water until harvest during the first week of November 2011. Pests and weeds were controlled manually.

Measurements

Seedling height and stem increments were measured each month. At the final harvest, roots were carefully separated from the soil and rinsed with water for later measurement. Root images were acquired using a scanner. Morphological and architectural parameters of the roots, such as root length and root volume, were quantified using computer image analysis software (WinRhizo Pro STD1600$^+$, Regent Inc. Canada). The biomass of roots, stems, and leaves was determined. The plant materials were dried at 105 °C for 1 h, followed by 80 °C for 48 h. They were then cooled in a desiccator filled with silicon dioxide gel until they reached a constant mass. To determine the mineral composition, plant materials were dried, ground up, and passed through a 1 mm sieve. They were then digested with H_2SO_4 and H_2O_2 was added as a catalyst. Then they were cooled and diluted with deionized water to 50 ml. Total nitrogen content was determined using the standard Kjeldahl method (Bremner and Mulvaney 1982). Total phosphorous was determined

using Mo-Sb antispetrophotography method (Anderson and Ingram 1993).

Statistical analysis

Eighteen plants were used to determine average seedling height and stem base diameter (SBD). Nine seedlings were used to measure the average dry mass of roots, stems, and leaves, calculate the root:aboveground ratio (RAR, root mass divided by aboveground mass), determine root length, diameter, and volume. Six were used to evaluate average PAE and PUE. The data were analyzed using the SAS statistical program (version V8, SAS Institute, Cary, NC, U.S.). Two-way ANOVA was performed at a significance level of 0.05, with provenance and nitrogen levels as the independent factors. All variables were normally distributed and did not need to be transformed. A Duncan's multiple-range test was used to determine whether significant ($P<0.05$) differences existed between and among treatments.

Results

Overall response of aboveground and root growth to addition of N

The growth of *S. superba* from all eight provenances was generally faster in the presence of added N. Early on, plant height and SBD were the highest among specimens subjected to N50 treatment. At the end of the growing season, however, these parameters were highest among plants subjected to N100 treatment (14.4 cm and 3.1 mm, respectively). These values were 40 % and 23 % higher, respectively, than those of plants exposed to no added N (10.3 cm and 2.5 mm, respectively). The stimulatory effect was lower among plants subjected to N200 than among plants subjected to N50 or N100. The height and SBD of plants subjected to the N200 treatment were higher than those of controls. The differences were 14 % and 9 %, respectively (Fig. 2).

Nitrogen addition significantly increased the growth in root diameter. The growth rate was significantly higher among plants subjected to N100 and N200 treatments than among controls (Fig. 3). RAR was significantly lower among plants subjected to N100 and N200 than among controls.

Overall response of biomass allocation, PAE, and PUE to the addition of N addition

Increased accumulation of dry biomass was found to be associated with the addition of N. Leaf, root, and total dry biomass among plants subjected to N50 treatment were higher than among plants exposed to no added N (Fig. 4). Dry biomass was 1.9 g for leaves, 1.6 g for roots, and 4.1 g for whole plants subjected to N100 treatment (the highest among all treatments; Figs. 3d and 4). These values were smaller with the N200 treatment (1.7 g, 1.5 g, and 3.7 g for leaves, roots, and total dry biomass, respectively).

N addition had a positive effect on PAE and PUE (Tables 1 and 2). PAE was greater among plants subjected to N100 treatment than among controls. This indicated that the addition of N promoted P acquisition. The PUE of the stems and leaves of plants subjected to N100 treatment increased by 92 % and 51 %, respectively, relative to controls. However, the PUE of the roots increased steadily as the amount of N added increased, peaking at 1.86 gmg^{-1} with N200 treatment.

Seedling and root growth in plants of various provenances

Provenance was found to significantly affect the characteristics of seedling growth in this experiment (Table 3). For example, the increase in seedling height and SBD of HZ, GT, XF, and GY provenances were the greatest among plants subjected to N50 treatment (Fig. 5a, b). JO100 and LQ had the highest seedling heights and SBD values of any provenance when subjected to N100 treatment, but the highest values for JO300 and JO600 were observed with the N200 treatment. The standard deviations for seedling height and SBD from the different provenances in the N treatment groups were greater than those for the controls (Fig. 5a, b).

Nitrogen addition clearly stimulated the growth of root length and volume in plants from the JO100 (N100), JO300 (N50), GT (N200), and GY (N50) provenances more than in plants from other provenances (Fig. 5e, f). The length and the volume of root systems of the JO600 group subjected to N200 treatment and of the LQ group subjected to N50 treatment, conversely, were smaller than those of controls. In the N treatment groups, the standard deviations of root

Fig. 2 Effects of nitrogen addition on seedling height and stem base diameter of *S. superba*. *Vertical bars* represent standard deviations from the mean (*n*=18)
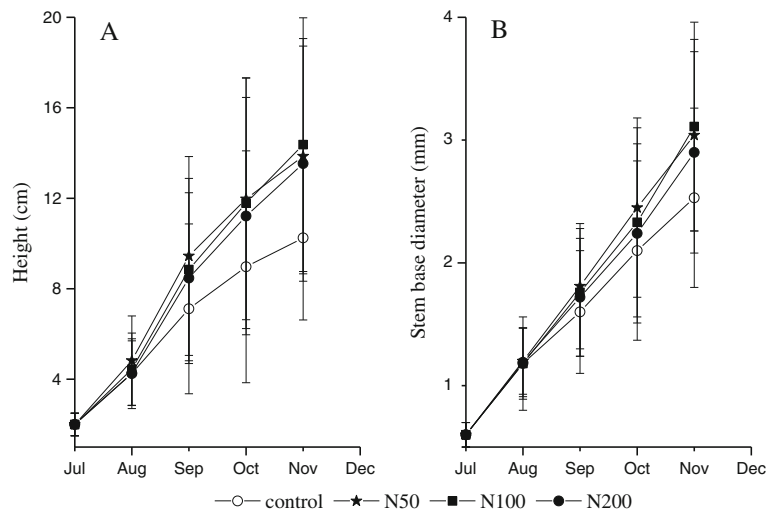
length and volume were lower than among the controls, but they increased as the level of N increased. The root:aboveground ratios for the JO100, HZ, and GT groups were greater with the N50 treatment than in the controls, but the opposite was true of plants from the other provenances (Fig. 5d).

Biomass allocation, PAE, and PUE in different provenances

N addition significantly affected biomass growth rate, and the JO100, JO300, and GT groups benefited the most from treatment. The JO100 group showed the
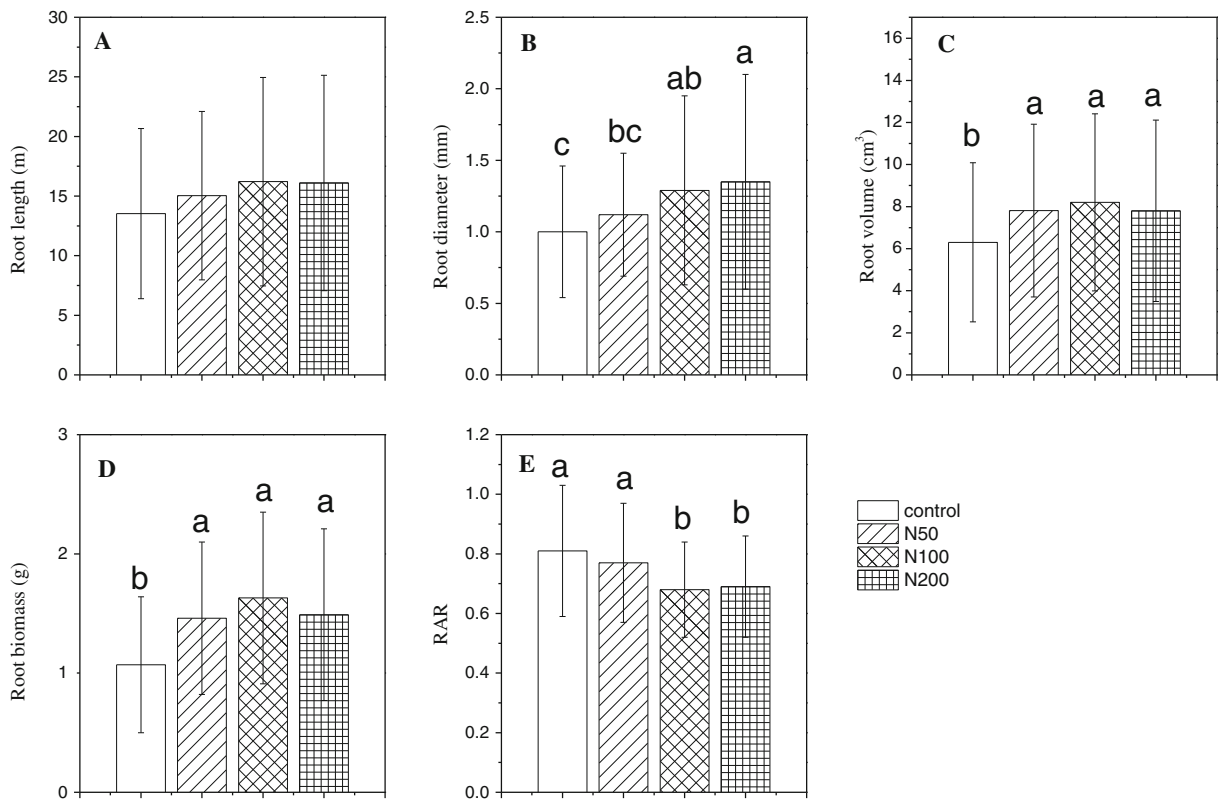

Fig. 3 Effect of nitrogen addition on the root system of *S. superba*. *Vertical bars* represent standard deviations from the mean (*n*=9)
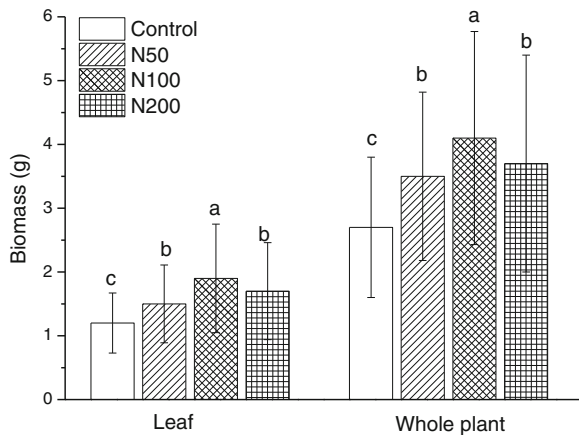
Fig. 4 Effect of nitrogen addition on dry biomass of *S.superba*. *Vertical bars* represent standard deviations from the mean (*n*=9)

highest biomass growth rate of any provenance or treatment group when subjected to the N100 treatment, 2.6 times that of the controls. The next highest rate was observed in the GT group subjected to N200 treatment and the JO300 group subjected to N100 treatment, both 2.1 times that of the controls. Although *S. superba* from the LQ provenance showed the highest biomass value, its growth rate when exposed to added N was the lowest among all the provenances (Fig. 5c). Nitrogen addition changed the biomass allocation among roots, stems, and leaves. The stem and leaf biomass of the LQ, GT, and GY groups exposed to N100 treatment increased by more than 10 % relative to the controls. GT and GY groups showed the highest

increase in stem biomass of any provenance or treatment group when subjected to N100 treatment (Fig. 6).

The plant PAE of *S. superba* from the JO600, XF, and GY groups was greater than that of controls among plants subjected to N50 treatment. The PAE of the JO300 and HZ groups was greater than that of controls among plants subjected to the N100. The PAE of the JO100, LQ, and GT groups was greater than that of controls among plants subjected to the N200 treatment. The plant PAE of *S. superba* from the HZ, LQ, and GT provenances showed the lowest values with the N50 treatment. (Table 1). The PUE of the LQ and GY groups, especially the stem PUE at the N100 level (PUE$_{stem\ LQ}$=3.24 and PUE$_{stem\ GY}$=2.73), was higher than that of plants from the other provenances. Five provenances, HZ, LQ, GT, XF, and GY, showed the highest values of leaf PUE of any provenance or treatment when subjected to N100 treatment. Plants from the JO300, JO600, HZ, GT, and XF groups showed the highest values for root PUE of any provenance or treatment when subjected to N200 treatment (Table 2).

Discussion

Our results indicated that N addition had a positive effect on the height, SBD, root system development, and biomass production of *S. superba*; but a decreasing trend was observed when N treatment was increased to N200 levels (200 kg N ha^{-1} year^{-1}) (Figs. 2

Table 1 PAE of plants after 6 months of N addition (Means with S.E. in parentheses, *n*=6 for all samples)

	Provenance	N0	N50	N100	N200	F value		
						Provenance	N	Provenance × N
PAE$_{plant}$ (mg)	JO100	2.35(0.84)	3.31(0.94)	4.25(1.22)	4.43(1.35)			
	JO300	2.52(0.59)	3.32(0.72)	3.49(1.25)	2.58(0.94)			
	JO600	2.93(0.64)	3.08(0.88)	2.35(0.67)	2.13(0.44)			
	HZ	2.33(0.68)	1.74(0.36)	3.04(1.19)	2.68(0.91)			
	LQ	2.78(0.77)b	1.83(0.48)b	2.90(0.92)b	4.58(1.10)a			
	GT	2.36(0.66)	2.05(0.52)	3.21(0.82)	3.29(1.07)			
	XF	2.13(0.62)	2.69(0.80)	2.42(0.79)	1.58(0.33)			
	GY	1.91(0.57)	2.35(0.74)	2.08(0.61)	1.88(0.55)			
	mean	2.41(0.72)	2.55(0.77)	2.97(1.12)	2.89(0.93)	4.09**	2.45+	1.86*

Different letters within a row signify statistical significance

n.s. not significant

** *P*<0.01; * 0.01<*P*<0.05; + 0.05<*P*<0.1

Table 2 PUE in seedling roots, stems and leaves after 6 months of N addition (Means with S.E. in parentheses, $n=6$ for all samples)

	Provenance	N0	N50	N100	N200	F value		
						Provenance	N	Provenance × N
PUE_{root} (g mg^{-1})	JO100	1.25(0.46)a	1.40(0.19)a	1.37(0.18)a	1.29(0.21)a			
	JO300	1.02(0.38)b	1.11(0.32)b	1.27(0.40)b	1.95(0.16)a			
	JO600	1.27(0.35)b	1.92(0.44)a	1.73(0.42)a	2.23(0.16)a			
	HZ	1.16(0.26)b	1.70(0.22)a	1.25(0.10)b	1.86(0.41)a			
	LQ	1.23(0.55)b	2.26(0.92)a	2.19(0.28)a	2.18(0.57)a			
	GT	1.07(0.38)b	1.75(0.50)a	1.78(0.31)a	1.98(0.62)a			
	XF	1.11(0.28)b	1.31(0.31)ab	1.81(0.44)a	1.82(0.34)a			
	GY	1.04(0.33)b	2.10(0.54)a	2.39(0.68)a	2.07(0.63)a			
	mean	1.14(0.37)b	1.69(0.58)a	1.79(0.54)a	1.86(0.49)a	2.30*	34.31**	3.74**
PUE_{stem} (g mg^{-1})	JO100	1.64(0.72)a	2.07(0.56)a	2.62(0.63)a	1.81(0.60)a			
	JO300	1.07(0.46)b	1.35(0.52)b	1.58(0.59)b	2.73(0.51)a			
	JO600	1.63(0.55)b	2.41(0.64)a	1.92(0.52)a	2.64(0.61)a			
	HZ	1.33(0.29)b	2.36(0.32)a	1.57(0.45)ab	2.33(0.67)a			
	LQ	1.18(0.41)b	1.49(0.36)b	3.24(0.30)a	2.79(0.86)a			
	GT	0.96(0.18)b	1.91(0.77)a	2.04(0.49)a	2.11(0.54)a			
	XF	1.09(0.43)b	1.51(0.51)b	2.32(0.67)a	2.35(0.34)a			
	GY	1.01(0.21)b	2.62(0.74)a	2.73(0.68)a	1.73(0.81)b			
	mean	1.22(0.52)c	1.96(0.69)b	2.34(0.72)a	2.22(0.69)a	7.87**	27.85**	2.30**
PUE_{leaf} (g mg^{-1})	JO100	1.24(0.28)b	1.88(0.18)a	1.86(0.37)a	1.66(0.47)ab			
	JO300	1.28(0.47)b	1.57(0.21)a	1.69(0.34)a	1.99(0.36)a			
	JO600	1.45(0.38)b	1.96(0.31)a	1.67(0.36)ab	1.97(0.12)a			
	HZ	1.10(0.26)a	1.38(0.11)a	1.44(0.28)a	1.34(0.19)a			
	LQ	1.55(0.41)b	2.22(0.29)a	2.34(0.17)a	1.63(0.42)ab			
	GT	1.15(0.35)b	1.56(0.32)ab	2.10(0.53)a	1.95(0.23)a			
	XF	1.28(0.36)b	1.36(0.31)b	1.96(0.46)a	1.92(0.25)a			
	GY	1.27(0.34)b	1.88(0.26)ab	2.22(0.61)a	1.63(0.56)ab			
	mean	1.29(0.36)c	1.73(0.37)b	1.95(0.42)a	1.76(0.40)b	6.61**	27.20**	1.49 n.s.

The PUE was calculated as the reciprocal of the P concentration

Different letters within a row signify statistical significance

n.s. not significant

** $P<0.01$; * $0.01<P<0.05$

and 3c, d). These results suggested that N was probably a limiting factor for the growth of *S. superba* seedlings in P-deficient soils (Hermans et al. 2006). Our findings are consistent with the results of a seedling experiment performed on evergreen conifer species (*Cryptomeria japonica*) and evergreen broadleaved species (*Cryptocarya concinna*), which showed that the height and SBD of seedlings increased with N5 (5 gN m^{-2}year^{-1}) treatment and decreased with increasing levels of N from N5 to N30 (30 gN m^{-2}year^{-1}) (Nakaji et al. 2001; Mo et al. 2008).

In our study, aboveground growth was found to be more sensitive to added N than root growth was. When levels of added N were low (N50), the growth and PUE of the aboveground tissues increased, peaking under moderate N addition (N100) (Table 2 and Fig. 6). Roots showed a delayed response to N addition, and their growth and PUE increased at higher levels of added N (N200) (Table 2 and Fig. 3a, b).

Nitrogen addition was found to increase the number, diameter, and length of roots (Hermans et al. 2006; Wang et al. 2006; Magaña et al. 2009). It also

Table 3 Results of two-way ANOVA of plant characteristics by provenance, N addition, and their interactions

Dependent variable	Source of variation		
	Provenance	N	Provenance × N
Seedling height (cm)	3.18**	4.34**	1.71*
SBE (mm)	4.84**	5.94**	1.49 n.s.
Dry biomass (g)	7.86**	18.74**	2.46**
RAR	12.35**	9.48**	0.63 n.s.
Total root length (m)	13.03**	2.29+	1.95 **
Root average diameter (mm)	9.71**	7.19**	3.20**
Root volume (cm^3)	6.22**	3.57 *	1.62 *
PAE (mg)	4.09**	2.45+	1.86*
PUE (g mg^{-1})	6.65**	37.43**	2.36**

Numbers represent F-values

n.s. not significant

** $P<0.01$; * $0.01<P<0.05$; + $0.05<P<0.1$

enhanced root uptake of nutrients (Wang et al. 2006; Magaña et al. 2009). Our study showed the relationships between root growth and PAE of *S. superba* of different geographic provenances after N addition to be complicated. For example, root development promoted the PAE at the N100 level in plants from the JO100, JO300, and GT provenances. However, they were less well correlated among plants subjected to N200 treatment (Table 1 and Fig. 5e, f). These results suggested that the provenances could be divided into three categories based on the relationships among plants exposed to high levels of added N (Fig. 7). The first category was characterized by efficient absorption; it included JO100 and LQ provenances. These plants maintained a high rate of phosphorus acquisition when exposed to high levels of added N but did not show pronounced root development. The second category manifested higher rates of root growth and lower P absorption; it included plants of JO300, HZ, and GT provenances. The root growth from these provenances was not found to increase
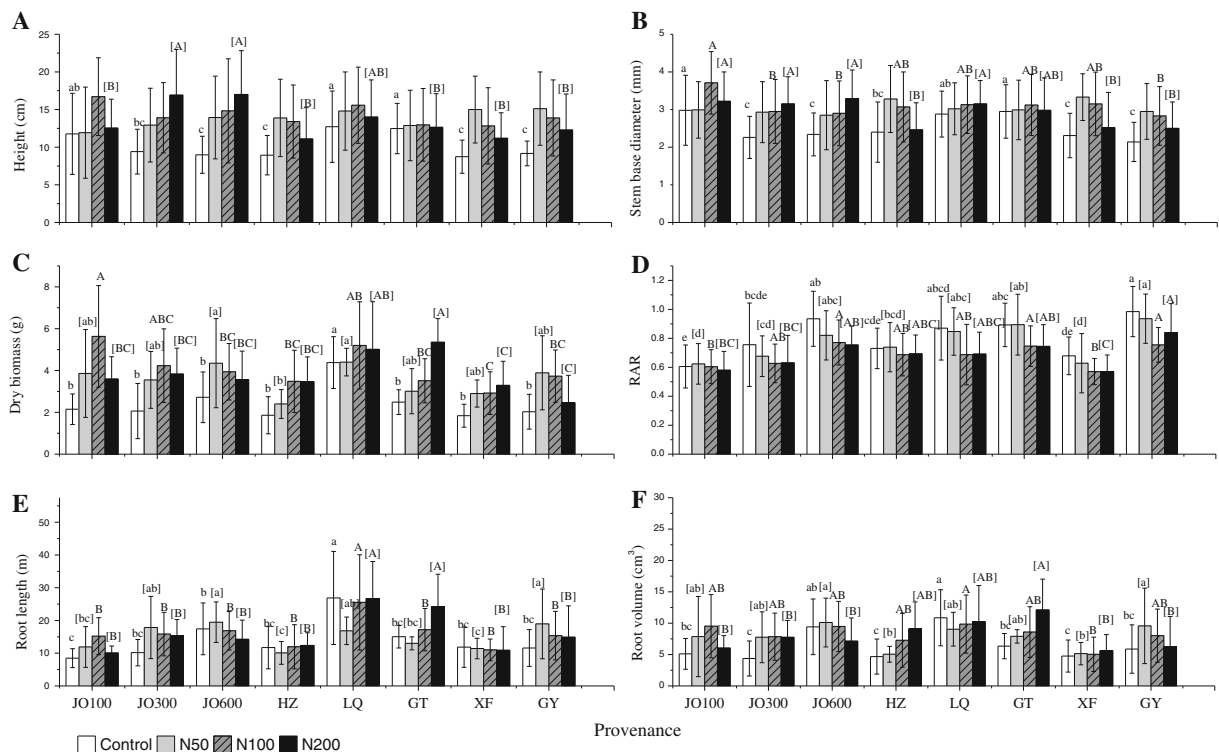

Fig. 5 Differences in seedling growth traits of *S.superba* from provenances under N addition and P-limitation treatments. Each *column* represents the mean value in a given treatment within the same provenance. *Vertical bars* represent standard deviations from the mean (n=18 for A and B, n=9 for C, D, E and F).

Different *letters* above the columns indicate significant differences among provenances ($p<0.05$). *Lowercase letters* denote controls; *lowercase letters within brackets* denote N50 treatment; *uppercase letters* denote N100 treatment; and *uppercase letters within brackets* denote N200 treatment
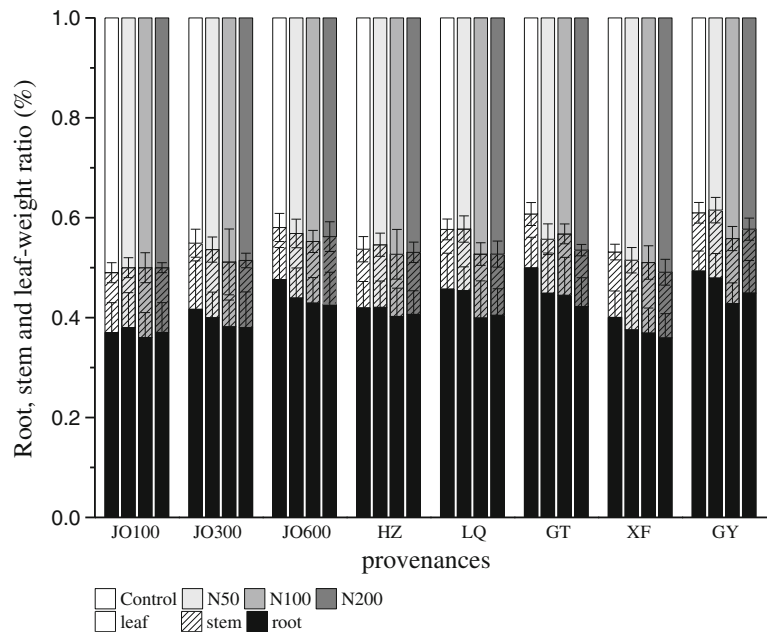
plant PAE. This may be because soil nitrate was in-sufficient for growing conditions in these prove-nances. Although an extra supply of N may promote root development, it can also fix soil-available phos-phorus (Liu et al. 2006). In addition, the N:P ratios in the plants were reported to be strongly correlated with the N:P supply ratio (Koerselman and Meuleman 1996; Güsewell 2004). This shows that the plant reg-ulates its metabolic progress to maintain a high N:P ratio by increasing N acquisition, reducing P acquisi-tion, or both (Hermans et al. 2006; Marschner 2012). The third category is characterized by negative root growth and lower PAE; it includes plants from JO600, XF, and GY. This may be because soil nitrate was saturated with respect to growing conditions in these provenances, and even a small amount of N addition can harm the roots. In this way, N and P requirements may be affected by different genetic combinations and levels of available soil nutrients (Güsewell 2004; Hammond et al. 2004; Zhang et al. 2004; Schulze et

al. 2006; Liu et al. 2006; Ristvey et al. 2007; Miller and Smith 2008).

Significant differences in seedling growth, root sys-tem growth, and phosphorus efficiency were found among plants of different provenances exposed to added N in P-limited soil. When no N was added, the LQ provenance exhibited greater seedling and root growth, PAE, and PUE in P-limited soil; but the HZ and XF groups had lower values for these same pa-rameters. When N was added, plants of all provenances except LQ and GT, gave a positive response and showed high growth rates (Fig. 5). This suggested that the LQ and GT groups possessed a more pronounced ability to resist external disturbances. Similar results were ob-served in water- and phosphorus-limited experiments with *S. superba* (Lin and Zhou 2009). The addition of nitrogen produced a positive effect on aboveground growth and biomass, which induced growth in plants from all provenances except LQ; this approached a level similar to that of the controls in the LQ provenance and

Fig. 7 Categories within
the eight provenances based
upon their relationships to
root growth and PAE under
high N addition
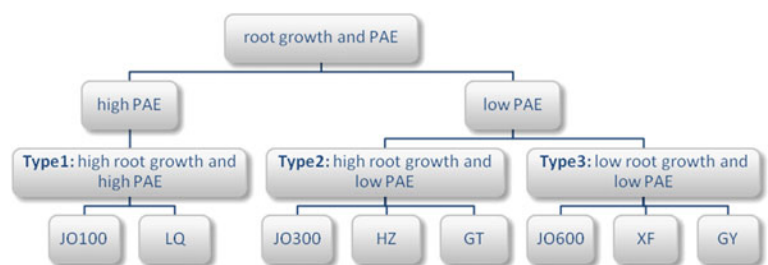
significantly reduced the difference among provenances (Fig. 5).

One of the findings of the present work was that the standard deviation in seedling and root growth showed a regular pattern with all levels of N exposure. Nitrogen deposition augmented the standard deviation of aboveground seedling growth while minimizing standard deviations of the root system (Fig. 5a, b, e, and f). This signified that root growth was more homogeneous and the aboveground growth more heterogeneous among individuals exposed to added N. This also implies that sufficient nutrient supply in the soil may control root morphology and architecture and that excess nutrients (such as N) are probably converted to storage compounds in the aboveground tissues, especially in stems (Limpens and Berendse 2003). PUE also confirmed that the stems and leaves utilized more P than the roots for equivalent biomass production. The difference between individuals with respect to aboveground growth was augmented by the addition of N, which facilitated the selection of seedlings with higher growth rates and biomass yield under N deposition conditions.

Summary

The effect of N deposition on *Schima superba* from eight different geographic areas was compared to determine whether N deposition on P-limited soil could increase *S. superba* growth or alter root formation or P efficiency. We found that *S. superba* responded positively to the addition of N. Seedling growth and dry biomass were the highest in plants subjected to N100 and lowest in plants subjected to N200. Root biomass was greatest, and plants acquired and utilized the most soil P with the N100 treatment. There was a significant difference among geographical provenances with respect to root growth, PAE, and PUE. PAE and PUE from plants of different provenances had a stronger relationship with root growth under N100 treatment. A threshold for nitrogen and phosphorus requirements (N:P ratios) related to different genetic combinations and to the availability of soil nutrients may exist for *S. superba*. Root growth and PAE can be divided into three categories based on soil nitrate levels.

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