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ORIGINAL PAPER

Long-term nitrogen addition regulates root nutrient capture and leaf nutrient resorption in *Larix gmelinii* in a boreal forest

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Abstract

Human activities accelerate global nitrogen (N) deposition, and elevated N availability may alter the stoichiometric balance of nutrients and then affect nutrient absorption by plants. The boreal forest is considered one of the world's most N-limited ecosystems, and its response to N deposition is already a hot issue. In order to explore how long-term nitrogen addition influences nutrient uptake and distribution in *Larix gmelinii* in a boreal forest, four N treatment levels (0, 25, 50 and 75 kg N ha^{-1} yr^{-1}) have been applied in a boreal forest since May 2011. Nitrogen addition significantly reduced the soil pH, significantly changed the soil N availability, increased the total N and N/P in needles and fine roots, and decreased the total P in needles and the C/N in soil. Nitrogen addition significantly reduced nitrogen resorption efficiency, and its impacts on *P* resorption efficiency were not significant. Nitrogen addition significantly increased the root length, surface area and diameter of 4th- and 5th-order transport fine roots. The N and N/P of needles showed seasonal variation. The needle N concentration and N/P were positively correlated with N addition, while the needle P was negatively correlated with nitrogen addition. With increase in nitrogen addition, *Larix gmelinii* increased its investment in its belowground parts, which may explain why *Larix gmelinii* tended to put more C in long-lived roots to improve its C utilization efficiency. Given the P deficiency caused by N addition, *Larix gmelinii* may be more likely to absorb P from the soil and adjust its C distribution to meet its P demand rather than relying on internal nutrient resorption.

Keywords Nitrogen deposition · Stoichiometry · Fine root · Root nutrient capture · Leaf nutrient resorption · Boreal forest

Introduction

In the past several decades, human activities have doubled the global reactive nitrogen (N) supply as fertilizer use and fossil fuel combustion have increased (Galloway et al. 2008; Bobbink et al. 2010). Increased N deposition may lead to unbalanced inputs of N and phosphorus (P) in ecosystems (Clark and Tilman 2008), altering the environment for plants and affecting nutrient uptake and resorption by plants (Stevens et al. 2010; Zhan et al. 2017). Changes in soil and plant nutrient status can have an impact on plant nutrient conservation strategies (Vergutz et al. 2012; See et al. 2015). It is generally considered that soil nutrient availability has a negative impact on nutrient uptake (Tully et al. 2013; See et al. 2015; Yuan and Chen 2015). However, studies have shown that plants growing in low-fertility soils do not have higher nutrient uptake rates than plants in fertile soils (Aerts 1996), and fertilization studies have not shown a consistent

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response of nutrient uptake to an increase in soil nutrient availability (Midgley et al. 2016; Han et al. 2019).

Nitrogen and phosphorus are generally considered to be the two most limiting elements for net primary productivity (NPP) in terrestrial ecosystems (Koerselman and Meuleman 1996; Güsewell 2004; Kang et al. 2011; Zhu et al. 2016). The nitrogen to phosphorus ratio in plants can be used as an indicator of nutrient supply, and it can also be characterized as the plant nutrient assimilation status of nitrogen and phosphorus (Zhang et al. 2018). Touratier et al. (2001) found that leaf N/P ratio was affected by sampling time (growing month). Agren (2008) showed that N/P ratio of leaves decreased with plant growth in terrestrial ecosystems. However, some studies had shown a seasonal variation pattern of increasing in summer then decreasing in autumn (Orgeas et al. 2003), which indicated that the changes of N and P patterns in plant leaves were regulated by many factors. Plants absorb nitrogen and phosphorus in a certain proportion for their own growth. When one element is scarce and another element is relatively abundant, the scarce element becomes the main limiting factor for plant growth. Carbon (C), N and P in plants and soils are interrelated due to their atmospheric and terrestrial cycling (Elser et al. 2010). The continuous increase in anthropogenic N deposition leads to an imbalance in N and P inputs in ecosystems, changes plant resource acquisition strategies and affects the nutrient cycle of the ecosystem (Mahowald et al. 2008; Peñuelas et al. 2012).

In theory, plants exhibit a certain degree of morphological plasticity and nutritional balance in individual organisms (Sterner and Elser 2002; Augusto et al. 2008). Through long-term natural selection, the whole plants have developed a set of absorption strategies to adapt to environmental changes (Reich et al. 2003). Plants may maintain their stoichiometric homeostasis via regulating root nutrient capture (acquisition) and/or leaf nutrient resorption (Kobe et al. 2005; Vergutz et al. 2012; Zhang et al. 2017). Plant nutrient conservation efficiency in nutrient-poor environments is higher, which may be due to the increased nutrient absorption by leaves (Vergutz et al. 2012). The distribution of the nutrients captured through roots and leaf resorption depends on the availability of environmental nutrients and the costs involved in these processes (Wright and Westoby 2003; Wang et al. 2014). In nutrient-deficient environments, energy costs are usually proportional to the nutrient uptake, and exploring for nutrients requires a substantial investment to construct longer roots (Hodge 2004). Therefore, nutrient resorption may play a key role in balancing the stoichiometry of plants under these conditions. As the efficiency of nutrient use increases, the cost for plants to obtain nutrients from the soil decreases. Nutrients acquired from root uptake are less costly than those acquired from leaf nutrient resorption, and plants are more inclined to choose root capture strategies (Huang et al. 2015; Kou et al. 2017).

Fine roots, as the most active part of roots, account for more than 30% of the NPP in terrestrial ecosystems (Jackson et al. 1997). Their morphological and chemical characteristics are very sensitive to environmental changes, which can effectively indicate changes in the nutrient cycle (Bardgett et al. 2014; Wurzburger and Wright 2015). Fine root diameter, specific root length (SRL), specific root area, root surface area, branching rate and root tissue density are the key characteristics of root resource capture (Eissenstat et al. 2015; Wang et al. 2017). Plant roots play an important role in the belowground processes of ecosystems. Many studies have shown that different levels of fine roots have different physiological functions (Pregitzer et al. 2002; McCormack et al. 2015). In addition, the morphological characteristics of fine roots are also affected by atmospheric nitrogen deposition (Kou et al. 2015). Changes in soil nutrient cycles can be effectively reflected in root morphology and chemical changes (Zhu et al. 2013; Xia et al. 2017; Yan et al. 2017).

The boreal forest area accounts for about 14.5% of the total land area and 30% of the forest area, which is the second largest forest biome on land, and it is recognized as one of the most N-limited ecosystems (Vitousek et al. 2002; T Randerson et al. 2006), mainly because of its remoteness from N emission sources. In this context, increased N deposition on boreal forests is thought to act as a fertilizer (Flechard et al. 2010) that can stimulate tree growth (Pregitzer et al. 2010; Stuart et al. 2015). However, the evidence is lacking about the impact of increasing N deposition as well as of N accumulation in forest ecosystems over long-time scales (Bontemps et al. 2011).Therefore, it is of great significance to study the effects of nitrogen deposition on the main ecosystem processes of boreal forests, especially on the nutrient cycling processes below- and aboveground.

The Greater Khingan Mountains area is the only open coniferous forest area in the cold temperate zone in China, and *Larix gmelinii* is the main dominant tree species in the Greater Khingan Mountains forest community. To reveal the response of leaf nutrient uptake, root morphology and chemical characteristics to nitrogen deposition and their relationship with soil in a *Larix gmelinii* forest, a long-term nitrogen addition experiment was conducted in the Greater Khingan Mountains, Northeast China. The purpose of this study was to answer the following questions: (1) Does N addition alter the nutrient concentrations and stoichiometry in soil, fine roots, litter and needles? (2) Does N addition alter nutrient resorption by *Larix gmelinii*? (3) Does N addition alter various aspects of fine root morphology? We hypothesized that (1) nitrogen addition might reduce the nitrogen resorption efficiency (NRE) and phosphorus resorption efficiency (PRE); (2) TN in needles would show seasonal variation (3) The SRL of fine roots would be reduced by nitrogen addition, and the morphology of fine roots of different root orders would respond differently to different levels of nitrogen addition.

Materials and methods

Site description and experimental design

This study was carried out in a *Larix gmelinii* forest of the Nanwenghe National Natural Reserve in the Greater Khingan Mountains, Northeast China (51°05′-51°39′ N, 125°07′-125°50′ E). The climate in this area is a typical continental climate in the cold temperate zone. Affected by the Siberian cold current, the mean annual temperature is approximately −2.7 °C. The peak high temperature is 36 °C, and the minimum low temperature is −48 °C. The accumulated temperature above 10 °C is 1400–1600 °C, the annual sunshine time is approximately 2500 h, and the plant growth period is approximately 110 days. The mean annual precipitation is approximately 500 mm, mostly concentrated in July and August. The *Larix gmelinii* forest is the dominant plant community in the experimental area. The growth density of trees in the plot is 2852 (±99) trees/ha, with an average DBH of 8.98 (±0.32) cm. The main soil types in the experimental plot are sandy loam (0–20 cm) and gravel sand (20–40 cm).

To study the effect of nitrogen deposition, a nitrogen addition experiment was established. We randomly established 12 plots of 20 m × 20 m (Fig. 1). Based on the current nitrogen deposition rate (25 kg N ha^{-1} yr^{-1}) in northern China (Liu et al. 2013), a total of 4 treatments were set: control (0 kg N ha^{-1} yr^{-1}), low nitrogen (25 kg N ha^{-1} yr^{-1}), medium nitrogen (50 kg N ha^{-1} yr^{-1}) and high nitrogen (75 kg N ha^{-1} yr^{-1}) to simulate the response of plants to climate change against the backdrop of future atmospheric nitrogen deposition levels that are 1, 2 and 3 times the current rate, respectively, and three repetitions were set for each treatment. A 10-m-wide buffer belt was set up between the plots to prevent interference between the plots. The artificial application of nitrogen began in May 2011. Nitrogen was evenly sprayed once per month every year in the growing season of the local forest (May–September). Before each application, NH_4NO_3 was weighed according to the rate of nitrogen addition, mixed with 32 L water and then evenly sprayed with a sprayer on the forestland in each plot. To compensate water supply, the control plot was sprayed with the same amount of pure water.

Soil properties and plant nutrients

From May to September 2019, we used stainless steel samplers (5 cm in diameter and 20 cm in length) to take soil samples from five random locations in each plot once each month. Subsequently, each soil core was divided into 0–10 cm (surface soil layer) and 10–20 cm (deep soil layer) depth intervals. Representative soil samples were obtained from the different soil cores by combining and homogenizing the soil samples from the same soil layer. The soil samples were air-dried, and roots and other debris were removed. The pH value, total N, total C and total P of the soil were measured after grinding.

Five litter collectors (baskets made of PVC pipe and gauze, 1 m × 1 m × 1 m) were placed in each plot according to the five-point method, for a total of 60 litter collectors. The litter was collected once a month, and the litter from the five collectors in the same plot was combined evenly to obtain mixed samples. After being taken back to the laboratory, the litter samples were dried and crushed for analysis. The needles of *Larix gmelinii* were sampled monthly. Three healthy mature trees (with DBH and height similar to the average level) were randomly selected, and typical individual branches were collected from the upper two-thirds of the crown with a high pole pruner. The needles of three trees in each sample plot were mixed evenly, and a composite sample (approximately 300 g) was obtained. Once in the laboratory, the needles were dried and pulverized before analysis. This study excluded needles with any visible damage. We used the green leaves collected in summer and litter collected in autumn to calculate the nutrient reabsorption of leaves.

A stainless steel sampler was used to collect fine root samples within a 50-cm radius of *Larix gmelinii* (near the same trees that were selected for foliar sampling). The soil blocks were divided into the surface soil layer (0–10 cm) and the deep soil layer (10–20 cm). Living fine roots were extracted from soil blocks, washed with tap water on a 2-mm sieve cloth, washed with deionized water and stored at 4 °C. Fine root samples were scanned with a scanner (Expression 11000XL, Epson, NSW, Australia) at a resolution of 600 dpi. Based on a stream-order approach for the study of root branch orders (Pregitzer et al. 2002), the morphological changes in all fine root orders were studied. Distal roots were classified as first-order roots, while the joining of two first-order roots was classified as a second-order root. Third-, fourth- and fifth-order roots were defined in a similar manner. After scanning, the roots were dried and ground for further analysis.

The total N concentration in the soil, needles, litter and whole fine root samples was detected by a continuous flow analyzer (Skalar san^{+}, Netherlands). Total C (TC) was determined by an automatic TC/TN analyzer (Analytik Jena AG, multi N/C 3100, Germany). Total P was determined by an ultraviolet–visible spectrophotometer (SHIMADZU UV-1780, Japan), and soil pH was measured by a pH meter (SX7150, China) in a 1:2.5 (soil/water) suspension. WinRHIZO TronMF 2012 software (Regent Instrument Inc., Quebec, Canada) was used to analyze the roots in

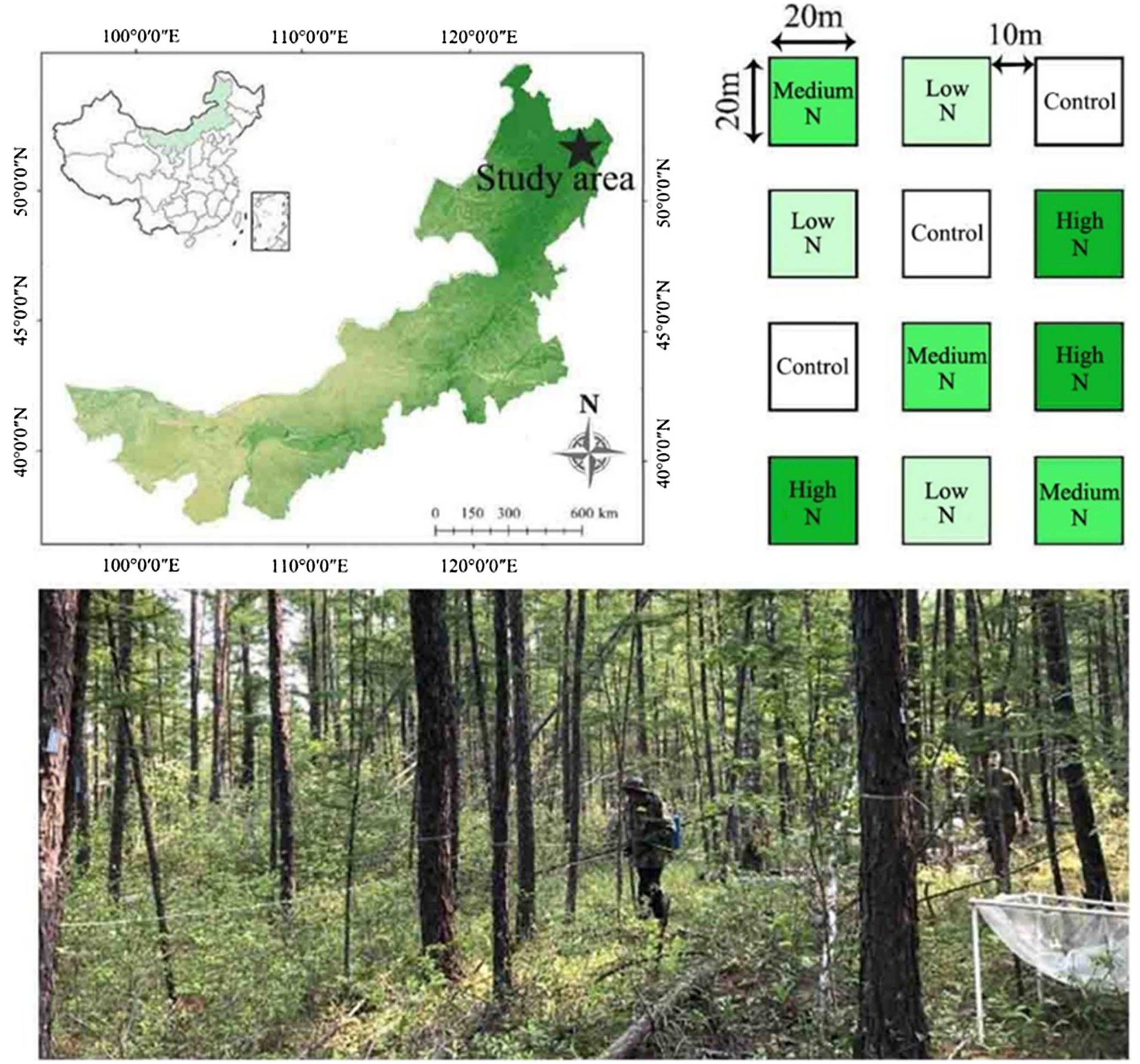

Fig. 1 Nitrogen addition sample plot and diagram of the experimental design in the boreal forest ecosystem in the Greater Khingan Mountains, northeastern China

the captured images and to perform fine root classification using a stream-order approach.

Data analysis

The nutrient resorption efficiency (RE) was calculated as [(NM—NS)/NM] × 100, where NM is the nutrient concentration of fresh leaves and NS is the nutrient concentration of senescent leaves. Specific root length (SRL) is the scanning root length divided by the mass after drying. The normal distribution of all the data was tested by the Kolmogorov–Smirnov test, and the homogeneity of variances was tested by Levene's test. We used one-way analysis of variance (ANOVA) to analyze the effects of nitrogen addition on the total C, total N and total P in the needles. We used two-way analysis of variance (ANOVA) to analyze the effects of N addition on soil and fine root TC, TN and TP at different soil depths, as well as the effect of fine roots length, diameter and surface area. General linear model-multivariate analysis of variance (ANOVA) was used to study the effects of months, treatments and their interactions on the physicochemical properties of *Larix gmelinii* needles. Pearson correlation was used to analyze the correlation between needles and soil and fine roots at different soil depths, and we performed regression analysis. All analyses were performed with SPSS 22.0 software package (SPSS, Inc., Chicago, Illinois, USA). Diagrams were drawn using Sigmaplot 13.0 software (Systat Software Inc., Chicago, IL, USA). Tukey's post hoc test was used to test differences between treatments. Statistically significant differences were accepted at $P < 0.05$.

Results

Response of soil stoichiometric characteristics to N addition

Compared with the control, nitrogen addition had no significant effect on the soil TC or TP concentrations in all treatments but significantly increased the soil TN concentration and soil N/P ratio and decreased the soil C/N ratio (Table 1). Nitrogen addition significantly reduced soil pH values (Table 1). High-N treatment significantly increased the C/P in 10–20 cm soil. Total N, TC, TP, C/N, N/P, pH in different soil layers had the same response to nitrogen addition (Table 1).

Effects of N addition on plant nutrient stoichiometry

Nitrogen addition significantly affected the N and P concentrations of needles compared to the control, but had a small effect on the C concentration, only the high-N treatment in July and August significantly increased the needle TC (Fig. 2a–c). The N and P concentrations in needles showed seasonal changes, and the values in July were higher compared to the rest of the period studied. The needle N concentration in September was the lowest compared with those in other months (Fig. 2b, c). Nitrogen addition (high- and medium-N) significantly increased TN, N/P and C/P and decreased TP and C/N in needles compared to the control treatment (Fig. 2b–f), and the needle N/P ratio under nitrogen addition was in the range of 7.76–13.08 (Fig. 2f). Nitrogen addition significantly increased TN and decreased TP in litter (Table 2). For the fine roots, N addition had no significant effect on TC, TP or the C/P ratio (Table 3). High-N treatment significantly increased the N concentration and N/P ratio and decreased the C/N ratio at both soil depths (Table 3). Moreover, the interaction of N addition and month had a significant impact on needle TN, C/N and N/P (Fig. 2b, d, f). High-N treatment significantly reduced the N resorption efficiency (NRE) (Fig. 3a). PRE was significantly higher in the medium-N treatment than in the control, but the PRE in the control treatment was very low, less than 10% (Fig. 3b).

Effects of N addition on fine root morphological traits

In this study, fine roots of *Larix gmelinii* were categorized into five root orders. High-N treatment significantly reduced the specific root length (SRL) of fine roots in the 0–10 cm soil layer (Table 3). Medium-N treatment significantly increased the mean diameter of the fourth- and fifth-order fine roots at both soil depths, and medium-N treatment significantly increased the mean diameter of the first- and third-order fine roots in the 0–10 cm soil layer but had no significant effect on the mean diameter of the fine roots in the 10–20 cm soil layer (Fig. 4). Medium-N treatment significantly increased the root length and surface area of fourth- and fifth-order transport fine roots but had no significant effect on lower-order fine roots (Fig. 4). The

Table 1 General characteristics of the soil

Soil depth	Treatment	Df	TC ($g\ kg^{-1}$)	TN ($g\ kg^{-1}$)	TP ($g\ kg^{-1}$)	C/N	C/P	N/P	pH
0–10 cm	Control	2	45.81 ± 6.89	2.00 ± 0.32c	0.83 ± 0.14	22.52 ± 1.08a	52.48 ± 2.6	2.41 ± 0.03b	5.52 ± 0.12a
	Low-N	2	45.25 ± 2.36	2.09 ± 0.17bc	0.79 ± 0.19	21.81 ± 0.36a	56.96 ± 4.74	2.77 ± 0.31b	5.41 ± 0.23ab
	Medium-N	2	45.80 ± 3.73	2.54 ± 0.22ab	0.81 ± 0.17	18.62 ± 0.31b	57.55 ± 5.00	3.30 ± 0.17a	5.29 ± 0.06ab
	High-N	2	48.61 ± 5.72	2.60 ± 0.27a	0.79 ± 0.11	18.36 ± 0.87b	62.29 ± 3.07	3.32 ± 0.21a	4.98 ± 0.05b
10–20 cm	Control	2	18.13 ± 2.37	0.87 ± 0.05b	0.73 ± 0.16	20.81 ± 1.48a	24.64 ± 0.93b	1.29 ± 0.24b	5.68 ± 0.15a
	Low-N	2	18.37 ± 0.31	1.02 ± 0.16ab	0.71 ± 0.11	17.57 ± 1.71ab	25.76 ± 1.45b	1.46 ± 0.06ab	5.53 ± 0.19ab
	Medium-N	2	19.85 ± 2.08	1.19 ± 0.27ab	0.71 ± 0.06	16.60 ± 1.18b	28.12 ± 1.68ab	1.68 ± 0.22a	5.42 ± 0.06ab
	High-N	2	20.99 ± 2.4	1.27 ± 0.23a	0.72 ± 0.09	16.49 ± 0.35b	30.70 ± 1.13a	1.73 ± 0.14a	5.22 ± 0.03b

Each value is the mean (SE) of three replications, two-way ANOVA was used to test N addition effects on soil at different soil depths; TC represents soil total carbon; TN represents soil total nitrogen; TP represents soil total phosphorous; C/N represents soil carbon–nitrogen ratio; C/P represents soil carbon-phosphorous ratio; N/P represents soil nitrogen-phosphorous ratio; Df represents degrees of freedom. Tukey's post hoc test was used to test differences among treatments. Different superscript letters within each column indicate significant differences ($P < 0.05$) among treatments

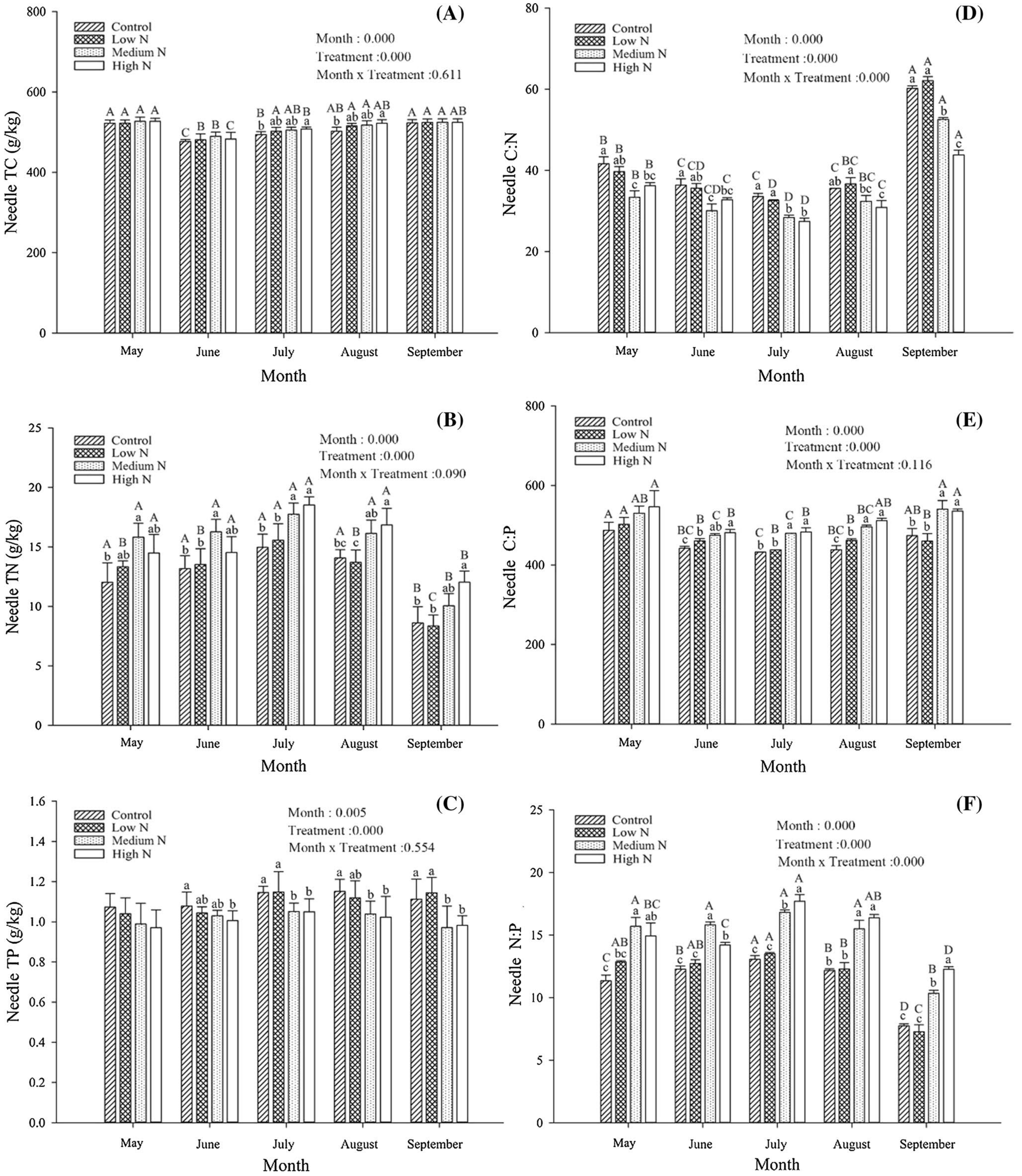

Fig. 2 Effects of N addition on C, N and P concentrations **(a–c)** and the C/N, C/P and N/P ratios **(d–f)** in fresh needles of *Larix gmelinii*. Bars with different letters are significantly different from each other ($P < 0.05$). Data are expressed as the mean ± standard error. Lowercase letters indicate the significance among different treatments, and uppercase letters indicate the significance among different months

Table 2 General characteristics of litter

Treatment	Df	TC (g kg^{-1})	TN (g kg^{-1})	TP (g kg^{-1})
Control	2	493.46 ± 32.83a	9.52 ± 0.34c	1.08 ± 0.01a
Low-N	2	491.30 ± 16.44a	9.23 ± 0.27c	0.98 ± 0.01b
Medium-N	2	486.46 ± 35.78a	10.82 ± 0.32b	1.00 ± 0.01b
High-N	2	488.96 ± 13.29a	13.87 ± 0.63a	0.98 ± 0.01b

Each value is the mean (SE) of three replications. One-way ANOVA was used to test N addition effects on litter TC, TN, TP. TC represents litter total carbon; TN represents litter total nitrogen; TP represents litter total phosphorous; Df represents degrees of freedom. Tukey's post hoc test was used to test differences among treatments. Different superscript letters within each column indicate significant differences ($P < 0.05$) among treatments

average diameter, length and surface area of fine roots were positively correlated with root order.

The relationships between soil and plant nutrients

There was a significant positive correlation between needle TN and soil TP concentration (Fig. 5b), and a negative correlation between needle TP and fine root TN concentration (Fig. 5a). There was a significant negative correlation between fine root TC and soil TP (Fig. 5c). There was no correlation between soil TP and fine root TN (Fig. 5d).

Table 3 General characteristics of fine roots

Soil depth	Treatment	Df	TC (g kg^{-1})	TN (g kg^{-1})	TP (g kg^{-1})	C/N	C/P	N/P	SRL(cm/g)
0–10 cm	Control	2	484.88 ± 10.57	13.03 ± 1.20b	4.10 ± 0.15	37.40 ± 1.69a	118.47 ± 4.24	3.17 ± 0.19b	6.19 ± 0.43a
	Low-N	2	493.83 ± 10.80	13.53 ± 1.35ab	4.02 ± 0.26	36.78 ± 2.25a	123.33 ± 6.27	3.37 ± 0.26ab	6.26 ± 0.22a
	Medium-N	2	499.37 ± 6.58	14.72 ± 1.34ab	4.09 ± 0.09	34.16 ± 2.57ab	121.99 ± 1.49	3.59 ± 0.28ab	6.06 ± 0.27a
	High-N	2	491.88 ± 9.74	16.20 ± 1.98a	3.93 ± 0.51	30.20 ± 1.99b	128.73 ± 6.18	4.13 ± 0.28a	4.53 ± 0.48b
10–20 cm	Control	2	471.39 ± 11.20	12.20 ± 0.88b	3.98 ± 0.43	38.84 ± 2.66a	118.92 ± 4.75	3.07 ± 0.11c	11.95 ± 0.74
	Low-N	2	475.79 ± 11.47	12.18 ± 1.05b	4.00 ± 0.49	39.33 ± 2.99a	119.20 ± 5.53	3.06 ± 0.15c	11.79 ± 0.61
	Medium-N	2	485.32 ± 11.27	13.57 ± 0.82ab	3.97 ± 0.29	35.88 ± 2.15ab	122.86 ± 7.24	3.43 ± 0.08b	11.54 ± 0.72
	High-N	2	474.91 ± 15.72	14.78 ± 1.34a	3.92 ± 0.46	32.36 ± 2.67b	121.83 ± 3.48	3.78 ± 0.16a	12.14 ± 0.48

Each value is the mean (SE) of three replications, two-way ANOVA was used to test N addition effects on fine roots at different soil depths; TC represents fine root total carbon; TN represents fine root total nitrogen; TP represents fine root total phosphorous; C/N represents fine root carbon–nitrogen ratio; C/P represents fine root carbon-phosphorous ratio; N/P represents fine root nitrogen-phosphorous ratio; SRL represents specific root length; Df represents degrees of freedom. Tukey's post hoc test was used to test differences among treatments. Different superscript letters within each column indicate significant differences ($P < 0.05$) among treatments

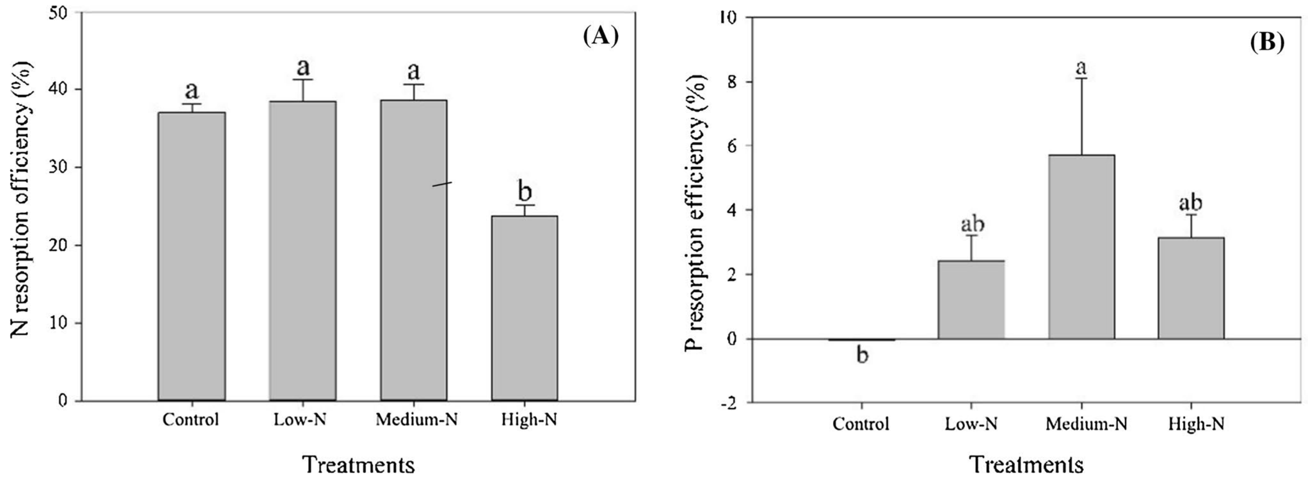

Fig. 3 Resorption efficiency of N and P in *Larix gmelinii* at different rates of N addition. Different lowercase letters indicate significant differences ($P < 0.05$)

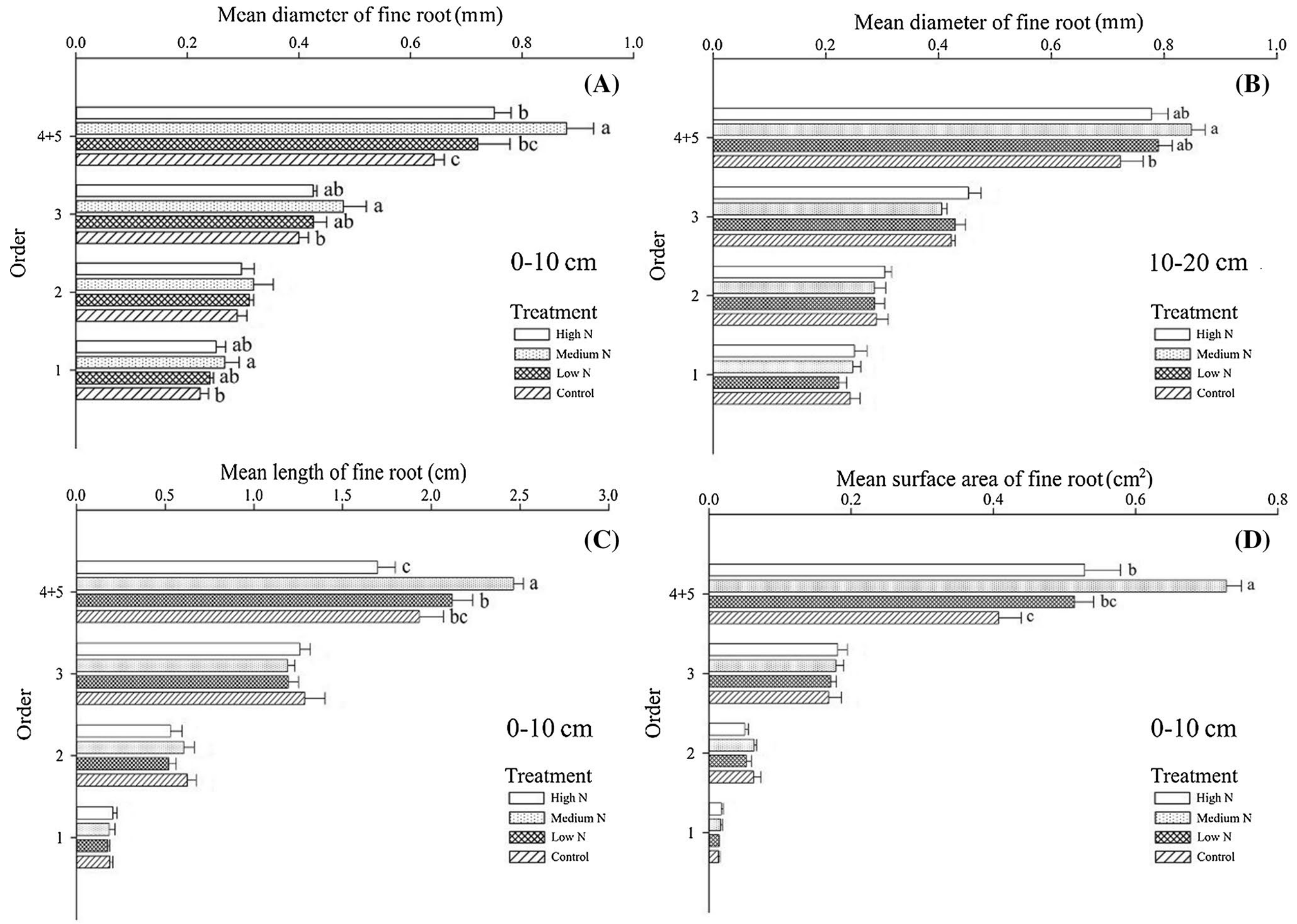

Fig. 4 Effect of N addition on fine root mean diameter (**a**: 0–10 cm soil; **b**: 10–20 cm soil), mean length (**c**: 0–10 cm soil) and mean surface area (**d**: 0–10 cm soil) of *Larix gmelinii* by root order (mean ± SE). Different letters indicate significant differences among N addition treatments ($P < 0.05$, Tukey's honestly significant difference test)

Discussion

Effect of N addition on elemental and nutrient stoichiometry in plant-soil systems

Forests in temperate regions are generally considered to be N-limited (Vitousek and Howarth 1991; Vitousek et al. 2010). Our results showed that the needle N/P ratio was in the range of 7.76–13.08 (Fig. 2f), which was slightly higher than the European coniferous forest of 9.76 (Kang et al. 2011) and slightly lower than the Chinese temperate *Larix gmelinii* of 8.08–13.81 (Li et al. 2017). This result seems to be similar to the global research of Peter et al. (2004) that as the environmental temperature increases and the latitude decreases, the N/P of plant leaves increases. Previous studies in our laboratory (Yan et al. 2018) found that N addition significantly increased the total biomass of *Larix gmelinii* trees, increasing also the rate of annual growth. The addition of nitrogen increased the total solid stock of carbon, but as the amount of N deposited increased, the net effect of N addition diminished, suggesting that N might be a limiting factor in boreal forests of *Larix gmelinii*. Our results showed that nitrogen deposition caused a nutrient imbalance in the *Larix gmelinii* forest ecosystem in the Greater Khingan Mountains, especially in the soil. Nitrogen deposition significantly increased the ratio of N/P in the soil and decreased the soil pH and soil C/N (Table 1). Soil acidification may lead to the degradation of root function, increasing the toxicity of Al^{3+} and affecting the resorption of nutrients by roots (Chen et al. 2017). A decrease in the soil C/N ratio may also be beneficial for plant growth and increase soil microbial biomass and activity (Li et al. 2016). Our results also showed that the response of C, N and P in different soil depths to N addition was consistent, which was different from the results of Park and Ro (2018). This may be related to the local soil that is very thin, only 20–30 cm thick, and the underlying layer is full of stones. In terrestrial ecosystems,

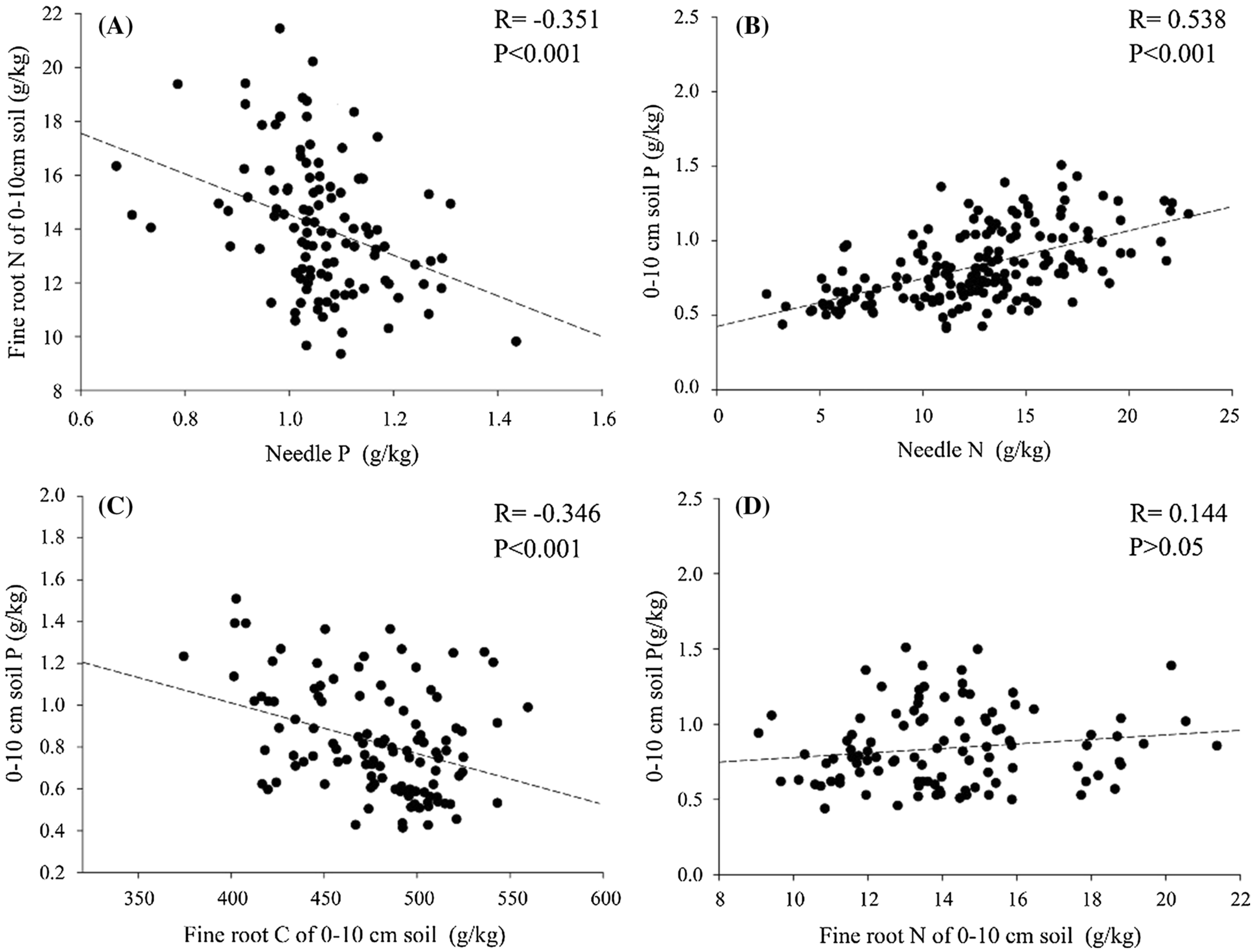

Fig. 5 **a**: The correlation analysis of needle P concentration and fine-root N concentration in 0–10 cm soil; **b**: the correlation analysis of needle N concentration and P concentration in 0–10 cm soil; **c**: the correlation analysis of fine-root C concentration in 0–10 cm soil and P concentration in 0–10 cm soil; **d**: the correlation analysis of P concentration in 0–10 cm soil and fine-root N concentration in 0–10 cm soil

N and P in plants were derived from soil pools, and the C, N and P concentration in the soil mainly depends on the release of C, N and P through litter decomposition by microbes (Luciola et al. 2012). However, litter is difficult to decompose by microbial action in soil with a C/N ratio > 25 (Tian et al. 2002). During the growing season of the study, the C/N ratio of *Larix gmelinii* leaves was greater than 25, which could affect the return of nutrients from litter degradation. This phenomenon may explain the N-limited growth pattern of *Larix gmelinii*. After 8 years of artificial nitrogen application, the needle N concentration increased significantly, while the needle P concentration decreased significantly in the growing season, which was consistent with the research results of Kou et al. (2017). Green leaf nutrient concentration can reflect soil fertility in some cases (Lambers et al. 2008), which indicates that N addition may change the availability of soil nutrients.

The TN and N/P of needles showed a seasonal pattern that increased in summer and then decreased in autumn, reaching its highest value in July, which was similar to the results of Li et al. (2017). The nitrogen concentration in the needles increased significantly in May and June. TN and N/P increased significantly under the high nitrogen treatment in July, August and September. Seasonal patterns in the nitrogen concentration and nitrogen/phosphorus ratio showed a strong effect of the needle development stage on the needle nutrient concentration (Fig. 2b, f). Under high-N treatment, needle TN increased significantly. With the rapid growth of needles, the accumulated nitrogen becomes diluted, resulting in a downward trend of total nitrogen. In July and August, the needles matured gradually, and the nutrient dilution process stopped. At the same time, the strong photosynthetic activity still requires a large amount of N to meet its own consumption needs. The growth slowed down or even stopped gradually after autumn, but the effect of nitrogen application on the nutrient resorption rate was still observable, and growth still showed an increasing trend under high nitrogen addition. The seasonal variation in needle N/P and the seasonal response of needle N to nitrogen addition indicate that the threshold for nutrient limitation in needles of *Larix gmelinii* varies with the season. This may be due to the differences in the nutrient requirements of plants in different seasons. At the same time, the cost of nutrient acquisition varies among the different growth periods.

We also found that there was a linear relationship between the needle N and the total P concentration in soil as well as a linear relationship between the fine root N and the needle P concentration (Fig. 5b, a). This indicates that the essential elements are not cycling independently. Nitrogen and P are closely linked through soil nutrient dynamics and cycling within plants (Sardans et al. 2012).

Effects of N addition on fine root morphology and stoichiometry

Plant roots have evolved to maximize the resource acquisition while minimizing the energy required for root tissue growth and maintenance. In this study, nearly all the morphological and chemical properties of *Larix gmelinii* roots exhibited trends similar to those reported in many other forest plant species (Pregitzer et al. 2002; Xiong et al. 2012). The experimental results showed that high-N addition significantly reduced the SRL (Table 3) of fine roots in the 0–10 cm soil layer. SRL is considered an indicator of the cost–benefit relationship in the root system (Fitter et al. 1991). Many studies have found that SRL is positively correlated with root respiration and negatively correlated with root longevity (Eissenstat et al. 2000; McCormack et al. 2012). Fine root turnover is an important way for plant C sinks to export C to the soil. The lower SRL value might indicate that high-N addition reduces the growth and metabolism of roots, thus prolonging the life of fine roots and slowing down the carbon input from fine roots to soil. Medium-N treatment significantly increased the root length and surface area of fourth- and fifth-order transport fine roots but had no significant effect on lower-order fine roots, which suggested that the N increase might have altered the exchange rates of resources across the plant-soil interface, resulting in an increase in the transport capacity of roots. Changes in root length and surface area can reflect the nutrient uptake efficiency of individual roots. This result indicates that plants prefer to invest more C in long-lived roots (i.e., higher-order roots) with the increase in nitrogen deposition to improve the C utilization efficiency.

Medium-N treatment significantly increased the fine roots diameter of 0–10 cm soil layer, significantly increased the fine root diameter of fourth- and fifth-order roots in 10–20 cm soil layer, but had no significant effect on first- and third-order roots (Fig. 4), which can be explained in two ways. First, plants can adjust and optimize their resource transportation strategies by increasing their fine root diameters. Nitrogen addition may lead to higher nitrogen uptake by roots and enhanced transport, especially in nitrogen-limited ecosystems. Second, previous studies have shown that soil acidification caused by N addition can aggravate soil aluminum release, and then may lead to an increase in root diameter (Zobel et al. 2007). The low-order roots diameter in deep soil did not respond to N addition, which may be due to the energy cost involved. Because the N concentration in deep soils is lower (Table 1), plants get nutrients at a lower cost from shallow soils, thus increasing investment in shallow fine roots.

Li et al. (2015) found that simulated nitrogen addition increased the availability of inorganic nitrogen absorbed by roots, which was consistent with our results. High-N treatment significantly increased the N concentration and N/P ratio of fine roots (Table 3). Significant positive correlations were observed between aboveground plant and root stoichiometry (Fig. 5), indicating that the nutrient concentrations in plants are closely related to the transport to aboveground plant parts and to fine roots. Freschet et al. (2010) reported that the nutritional concentrations of root tissue tended to be similar to those in leaves and stems. The above study further showed that the aboveground and fine root nitrogen and phosphorus concentrations and the ratio of nitrogen to phosphorus had a consistent correlation. Our results provide strong evidence that the internal specific changes in the main plant nutrient characteristics (N, P and N: P) are consistent not only at the level of a single plant organ but also the whole plant.

Effects of N addition on plant nutrient capture and resorption

Nutrient resorption mainly occurs during leaf senescence. Through this process, plants can reabsorb nutrients from senescing leaves and reduce their dependence on soil nutrient availability (Gonzales et al. 2019; Seidel et al. 2019). A previous meta-analysis (You et al. 2018) showed that the global average values of NRE and PRE under natural conditions were 47.4% and 53.6%, respectively. Nitrogen addition significantly reduced NRE by 13.3%, but had no significant effect on PRE globally. The NRE and PRE of temperate coniferous forests in China were 57% and 60% (Zheng et al. 2020); the NRE and PRE of European coniferous forests were 43% and 48%, respectively (Primicia et al. 2014). Our results showed that high nitrogen application significantly reduced the NRE of plant leaves by 35.7%, but the PRE was very low. Even at the medium nitrogen application level, PRE was only 5.7% (Fig. 3), which indicated that phosphorus resorption had little change under the condition of unbalanced nitrogen and phosphorus input. Nitrogen addition significantly reduced the concentration of needle P (Fig. 2c). For the phosphorus deficiency caused by nitrogen deposition, species with high stability can maintain their phosphorus supply by increasing plant phosphorus resorption and/or phosphorus uptake from soil. However, the PRE in our study is much lower than the global average PRE, 52.0%–46.9% (Aerts 1996; Vergutz et al. 2012; Yuan and Chen 2015), suggesting that *Larix gmelinii* might prefer to absorb phosphorus from the soils under nitrogen addition. When nitrogen deposition eases nitrogen limitations, plant growth depends more on whether the plant can maintain a balanced supply of phosphorus. Phosphatase activity can affect the release rate of phosphorus into soil. However, due to the high concentration of nitrogen in phosphatase, phosphatase activity is often limited by the nitrogen supply. Marklein and Houlton (2012) found that nitrogen addition increased phosphatase activity in soil. Fujita et al. (2010) showed that increased N stimulated phosphatase activity through the N/P stoichiometric effect, thereby increasing plant P uptake. Although nitrogen application did not significantly increase the P concentration in the soil in our experiment (Table 1), our study showed that the P concentration in the soil was significantly positively correlated with the N concentration in the needles (Fig. 5b). We believe that nitrogen addition may reduce the dependence of plants on internal P cycle to a certain extent. There is a balance between nutrients acquired by plants through nutrient resorption and nutrients acquired from soil, and this balance depends on the relative energy consumption of these two processes; plants tend to use the process that consumes less energy (Wright and Cannon 2001; Mao et al. 2013; Wang et al. 2014). Because *Larix gmelinii* can obtain more phosphorus from the outside environment and obtain more nutrients from its roots than from its needles, *Larix gmelinii* may be more likely to absorb nutrients from the soil.

We also found that nitrogen addition significantly increased the N/P ratio in needles and fine roots (Fig. 2, Table 3). To maintain their P supply, plants depend to a large extent on P uptake from soil and organic P mineralization. Nasto et al. (2014) found that plants can distribute more C to root production and/or root exudates, which can alleviate P limitation by increasing the mineralization and absorption of P in the rhizosphere. In our study, nitrogen addition significantly increased the investment of *Larix gmelinii* in their belowground parts, significantly reduced the SRL of fine roots, and increased the fine root diameter of fourth- and fifth-order fine roots (Table 3; Fig. 4), which was more conducive to the acquisition of nutrients in the soil of larch forests. Deng et al. (2016) also found that nitrogen addition significantly increased the ratio of arbuscular mycorrhizal (AM) to ectomycorrhizal in a young stand of *Larix principis-rupprechtii*, and soil acid phosphatase activity was positively correlated with the biomass of AM. Mycorrhizal fungi can mediate resorption and reduce dependence on absorption in aging plants, and arbuscular mycorrhizae are more important and effective than ectomycorrhizae in promoting plant P acquisition (Lambers et al. 2008). All this evidence suggests that *Larix gmelinii* may be more likely to consume nitrogen and adjust its C distribution to meet its phosphorus needs than to rely on internal nutrient cycling.

Under different nutrient constraints, the effect of N addition on NRE is greater than that of PRE (Fig. 3), which can be attributed to the enrichment of N in soil. Increasing the nitrogen input can reduce plant dependence on internal cycling because plants can obtain more nitrogen and phosphorus from the external environment than from resorption. In addition, the reduction in NRE and the increase in the nitrogen concentration in needles will increase the concentration of nitrogen returned to soil by plants, which will significantly affect the litter decomposition rate (Zhang et al. 2016). Numerous studies have shown that nitrogen addition can improve N use efficiency in the soil and litter layer, and high-quality litter has a higher decomposition rate than low-quality litter (Janssens et al. 2010; Lv et al. 2014; Gong et al. 2015); therefore, nitrogen deposition may accelerate the carbon and nitrogen cycles in *Larix gmelinii* forests.

Under N limitation, high-N addition significantly changed soil N availability, thereby reducing NRE (Mayor et al. 2014; Lü et al. 2016). To maintain a balance with NRE, PRE should decrease correspondingly when soil P availability is relatively high (Reed et al. 2012; Han et al. 2013). Although excessive nitrogen addition may stimulate phosphatase activity to increase the availability of soil phosphorus (Fujita et al. 2010), plants can also increase their PRE to rapidly compensate for phosphorus deficiency. Therefore, changes in soil nutrient status may affect plant nutrient use strategies. These adjustments substantially improve the plant nutrient balance and adaptability. These results may be further attributed to the changes in soil nutrient patterns, plant growth strategies and nutrient cycling in ecosystems caused by nitrogen addition.

Conclusions

In this study, we attempted to clarify the response of nutrient uptake strategies to N deposition in boreal forest ecosystems through long-term nitrogen addition field experiments. With the increase of N addition, plants tend to invest more C in long-lived roots (i.e. higher order roots) to improve C utilization efficiency. At the same time, increasing N input can reduce the dependence of *Larix gmelinii* on internal circulation, because plants get more nitrogen and phosphorus from external environment than from absorption. Nitrogen addition may change the availability of soil nitrogen and reduce NRE. Under different nutrient constraints, the effect of N application on NRE is greater than that of PRE. These results indicate that soil nutrient status affects the nutrient utilization strategy and uptake efficiency of *Larix gmelinii*, and improved our ability to predict *Larix gmelinii* growth with increase in N deposition in the future.

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