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ORIGINAL PAPER

Species-mixing alters root nutrient acquisition and leaf nutrient conservation strategies in plantation forests

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Abstract Leaf nutrient conservation and root nutrient acquisition from soils are two critical mechanisms by which plants sustain their nutrition. Species mixing may affect these two strategies; however, few studies have investigated the changes in both strategies simultaneously, and the less on their associations. Here, we determined leaf nitrogen (N) resorption efficiency (LNRE), leaf phosphorus (P) resorption efficiency (LPRE) and six absorptive root traits of Manchurian ash (*Fraxinus mandshurica*, a broad-leaved species) in the pure plantation and mixed-species plantations of Manchurian ash with coniferous species of Dahurian larch (*Larix gmelinii*), Korean pine (*Pinus koraiensis*) and Korean spruce (*Picea koraiensis*), respectively. Our aims were to explore leaf nutrient conservation and root nutrient acquisition strategies, as well as their associations. We found that the LNRE increased under mixing with coniferous species. However, the LPRE in mixed-species plantations was significantly lower than that of the pure Manchurian ash plantation, except when it was mixed with Korean spruce. Compared with the pure plantations, there were no significant differences in root diameter (RD), root tissue density (RTD), root N concentration (RN) and root P concentration (RP) in the mixed-species plantations, while root biomass (RB) and specific root length (SRL) varied with the mixed species. The simple and multiple regression analyses suggested that SRL was the best predictor for LNRE variation, and RTD for LPRE, respectively. The principal component analysis (PCA) showed a multi-dimensional root economic space across the pure and mixed-species plantations, where the root 'collaboration' dimension loaded at the first axis, characterized by a negative correlation between SRL and RD. Across the pure and mixed-species plantations, LNRE was not related to root nutrient acquisition strategy, while LPRE decreased with increased 'outsourcing' strategy along the 'collaboration' dimension of root economics space. Overall, our results suggest that mixing with coniferous species altered leaf nutrient conservation and root nutrient acquisition strategies of Manchurian ash. Specifically, ash tended to produce thicker, denser roots, and to rely more on 'outsourcing' nutrient foraging to mycorrhiza, while exhibiting reduced phosphorus resorption in leaves. These findings may deepen our understanding of the nutrient acquisition and conservation strategies of mixed-species plantations at the whole-plant level.

Keywords Broad-leaved species · Coniferous species · Mixed-species plantation · Leaf nutrient resorption · Root economics space

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Introduction

Forest ecosystems serve as significant carbon sinks, therefore playing a critical role in mitigating climate change (Bastin et al. 2019; Chen et al. 2025). Consequently, afforestation not only yields significant timber resources, but also greatly enhances carbon sequestration potential (Piao et al. 2009). Mixed-species plantations rather than monocultures are increasingly acknowledged as a superior strategy for afforestation (Richards et al. 2010). This is because, in comparison to monocultures, mixed-species plantations typically exhibit higher production and greater resilience to both biotic and abiotic stresses (Feng et al. 2022; Li et al. 2024; Xia et al. 2026). Niche complementarity may be an important mechanism for the enhanced productivity of mixed-species plantations, which allows different species to utilize various resources more efficiently while minimizing competition (Zheng et al. 2024). Nitrogen (N) and phosphorus (P) are the predominant limiting nutrients for terrestrial plant productivity (Du et al. 2020). Therefore, it is crucial to focus on tree N and P acquisition and utilization in the context of mixed-species interactions.

A variety of ecological strategies have been developed by plants to adjust to nutrient limitations (Freschet et al. 2010). One main strategy is the remobilization of nutrients from senescing leaves, that is, leaf nutrient resorption (i.e., aboveground nutrient conservation strategy) (Wright and Westoby 2003; Bu et al. 2019). Plants that grow in nutrient-poor habitats usually have higher leaf nutrient resorption (Yan et al. 2018; Yang et al. 2025), which is referred to as nutrient limitation control (Chen et al. 2021). Tree mixing can lead to substantial changes in soil nutrients (Gillespie et al. 2021; Guo et al. 2025), however, limited research has investigated whether and how tree mixing affects leaf nutrient resorption efficiency (Chen and Chen 2022; Lin et al. 2022). Moreover, except for the nutrient limitation control mentioned above, leaf nutrient resorption is also regulated by other regulatory strategies. One is the stoichiometry control strategy, where N and P are resorbed in direct proportion to the N:P ratio of green leaves (Chen et al. 2021; Sun et al. 2023). Another is nutrient concentration control, which is based on the nutrient concentration in green leaves, similar to soil nutrients, where a high green leaf nutrient concentration correlates with low leaf nutrient reabsorption (Chen et al. 2021). However, we still lack a basic understanding of which control strategy governs the changes in leaf nutrient resorption in mixed-species plantations.

Apart from the aboveground nutrient conservation, plants can also acquire nutrients from soil via their belowground compartments, i.e., absorptive fine roots. Different tree species may take various nutrient acquisition pathways, effectively characterized by the root economics space, informed by the analysis of root core functional traits (Bergmann et al. 2020). The classic root economics space has two orthogonal dimensions. One spans from a 'do-it-yourself' strategy, characterized by effective soil exploration using relatively cost-effective roots (higher specific root length (SRL)), to an 'outsourcing' strategy that involves investment in more enduring roots with a larger diameter, alongside collaboration with mycorrhizal fungi in exchange for soil nutrients, that is called the 'collaboration' gradient. The other is termed the 'conservation' gradient, ranging from high root N concentration (RN) to large root tissue density (RTD), representing a trade-off between 'fast' vs 'slow' nutrient uptake and return on investment (Reich 2014). Although some studies in the plantations have examined the impact of species mixing on root functional traits (Xiang et al. 2015; Germon et al. 2018), how root acquisition strategy changes based on the root economics space remains unclear.

The links between leaf nutrient conservation and root nutrient acquisition have recently garnered increasing attention. However, several studies based on interspecific variation have obtained conflicting results. For instance, Xiao et al (2025) found that as leaf N resorption efficiency (LNRE) decreased, species shifted from a 'slow' (high RTD) to a 'fast' (high RN) strategy along the 'conservation' dimension among eight temperate broadleaf species. Whereas, leaf P resorption efficiency (LPRE) was positively correlated with the 'do-it-yourself' (high SRL) strategy along the 'collaboration' dimension. However, there were no significant correlations between LNRE, LPRE and both dimensions of roots across 34 coexisting temperate woody species (Wang et al. 2025). Compared with studies focused on interspecific variation, few research has examined the relationship between intraspecific variation in leaf nutrient conservation and root nutrient acquisition strategies, especially regarding the effects of species mixing. Clarifying the effect of mixed-species on the relationship between leaf nutrient conservation and root nutrient acquisition in the plantations can enhance our understanding of trees' adaptability to species mixing from a whole-plant perspective, and further deepen the mechanisms for interspecific interaction within mixed-species plantations.

Manchurian ash (*Fraxinus mandshurica*, refer to ash below) is an important broad-leaved timber species in northeast China, which is often managed as mixed-species plantations with coniferous species for improving productivity (Zhang et al. 1999). Thus, we selected pure plantations of ash, and plantations of ash mixed with deciduous coniferous species of Dahurian larch (*Larix gmelinii*, refer to larch below), evergreen coniferous species of Korean pine (*Pinus koraiensis*, refer to pine below) and Korean spruce (*Picea koraiensis*, refer to spruce below). Specifically, Ash associates with arbuscular mycorrhiza (AM), and all three conifers associate with ectomycorrhiza (ECM). We determined LNRE, LPRE and six economic traits of ash (Table 1). Our

Table 1 Abbreviations for leaf and root traits, as well as soil properties in this study

Item	Abbreviation	Unit
Leaf nitrogen resorption efficiency	LNRE	%
Leaf phosphorus resorption efficiency	LPRE	%
Nitrogen concentration of mature leaf	LN_M	mg g^{-1}
Phosphorus concentration of mature leaf	LP_M	mg g^{-1}
Nitrogen concentration of senesced leaf	LN_S	mg g^{-1}
Phosphorus concentration of senesced leaf	LP_S	mg g^{-1}
Root biomass	RB	g m^{-2}
Root diameter	RD	mm
Specific root length	SRL	mg g^{-1}
Root tissue density	RTD	g cm^{-3}
Root nitrogen concentration	RN	mg g^{-1}
Root phosphorus concentration	RP	mg g^{-1}
Soil pH (water)	pH	-
Soil bulk density	SBD	g cm^{-3}
Soil moisture	SM	%
Soil total carbon concentration	STC	mg g^{-1}
Soil total nitrogen concentration	STN	mg g^{-1}
Soil total phosphorus concentration	STP	mg g^{-1}

"-": not applicable

aims were to examine the impacts of mixing ash with coniferous species on leaf nutrient conservation and root nutrient acquisition, as well as the relationships between these two strategies of the target species, i.e., ash. Here, we proposed three hypotheses as follows:

(1) Mixing with coniferous species alters leaf nutrient resorption efficiency of ash, as soil nutrient status can change after over 30 years of intercropping (Guo et al. 2025).
(2) Mixing with coniferous species increases the absorptive root biomass of ash due to the complementary utilization of space and resources (Wambsganss et al. 2021), and increases root diameter (RD) of ash, i.e., rely more on an 'outsourcing' strategy due to the mycorrhizal complementarity between AM and ECM (Ye et al. 2025);
(3) Ash with higher root nutrient foraging efficiency (i.e., higher RN) or tendency towards the 'outsourcing' strategy (i.e., higher RD) that are high carbon costs in nutrient acquisition and maintenance (Reich 2014; Raven et al. 2018), are likely to reduce their reliance on leaf nutrient resorption efficiency, so as to improve the whole-plant level nutrient-gain to carbon-cost ratio (Ding et al. 2023; Wang et al. 2025).

We also explored which classical control strategy of leaves (i.e., nutrient limitation control; stoichiometry control; nutrient concentration control) governs their nutrient resorption of ash in the context of mixed-species plantations.

Materials and methods

Site description and plot establishment

We conducted this study at the Jianlagou Experimental Station (45°21'–45°25' N, 127°30'–127°34' E) of Northeast Forestry University, Heilongjiang Province, China. The research region features a temperate continental monsoon climate with a mean annual temperature of 2.8 °C. The average daily air temperature varies from – 19.6 °C in January to 20.9 °C in July (Liu et al. 2024). The mean annual precipitation is 723 mm, with over 65% occurring from June to August. There are 120–140 d in the growth season. Soil is classified as Hap-Boric Luvisols, characterized by a high organic matter concentration and well-developed horizons with an average thickness of 40–50 cm (Ma et al. 2024).

In 1985, the secondary forests at this site underwent clear-cutting in > 30 m strips, leaving secondary forests intact between the clear-cutting areas. In 1986, pure ash plantations and mixed-species plantations of ash with three coniferous species (ash × larch, ash × pine, ash × spruce), a total of four plantation types, were established on a rather homogeneous slope of 450–500 m a.s.l. in different clear-cutting strips. Bare-root 2-year-old seedlings were planted utilizing a 1.5 × 2.0 m planting grid. The mixed-species plantations were mixed by strips with three rows of ash × five rows of larch, pine or spruce, respectively. We established three 20 × 30 m plots as independent repetitions in each plantation, and recorded the tree height and diameter at breast height (DBH) of ash (Table S1). The distance between every two plots was maintained at least 30 m to prevent spatial autocorrelation and neighboring effects. Therefore, there were 12 plots in total (four plantation types × three plots). It is worth nothing that these plots may still be pseudo-replicates, as the original design did not have repetitions for each forest type. However, given that the site conditions are quite homogeneous and each plantation covers more than 5 ha (Gu et al. 2017), the potential risk could be substantially reduced.

Leaf sampling

We randomly selected three average individuals of ash from each plot to collect mature leaf samples. In the mixed-species plantations, the selected individuals of ash were chosen in the mixed rows. In August 2022, we collected the representative twigs of sunlit branches from the middle to the upper canopy. Subsequently, the fully expanded mature leaves, free from insect damage, were promptly removed from the twigs. From mid- to late September, three litter

traps with 2-mm mesh size (1 × 1 m) were placed beneath each individual of ash to gather freshly fallen leaves in a manner similar to that of the mature leaves. Those sampled mature and senesced leaves were put in closed paper bags and brought to the laboratory for further processing.

Root and soil sampling

Six root samples (0–10 cm) were randomly taken from each plot using a soil auger (inner diameter = 6.2 cm) in August 2022. Therefore, there were 72 soil cores in total (four plantation types × three plots × six soil cores). In mixed-species plantations, soil cores were collected halfway between the rows of ash and coniferous species. Each soil core separated about 10.0 g of soil, combined to form a single composite sample of each plot, and then passed through a 2-mm sieve for further processing. The remaining soil and root composite sample in each soil core was placed on a 0.25-mm sieve (ensure no root loss during washing) and was washed using a gentle flow of water. By examining root color, architecture, elasticity and toughness, we could discern ash roots from those of other shrubs or herbs, as well as from coniferous species in the mixed-species plantations, and further discern living roots from dead roots of ash. Living ash roots and soil samples were stored in a cooler with ice (0–4 °C), and then transported to the laboratory for further processing in less than four hours.

Absorptive root morphological traits and biomass

In the laboratory, we washed ash roots with deionized water (1 °C) to get rid of adhering soil particles from the root surface. According to the root branch ordering method outlined by Pregitzer et al. (2002), we used forceps to dissect root samples into the distal three order roots for further analysis. This is because our previous study had shown that the absorptive roots of ash were mainly composed of the first three order roots (Gao et al. 2025). Post-dissection, absorptive root samples from each soil core were split into two subsamples: one subsample was directly dried in an oven to constant weight (65 °C) and subsequently weighed (nearest = 0.0001 g); the other one with 0.3–0.5 g fresh weight was scanned at 600 dpi using a flatbed scanner with backlighting (Epson Expression 12000XL; Epson Telford Ltd, Suwa Nagano, Japan), then over dried and weighed as mentioned above. Root system analysis software was used to determine RD (mm), root volume, and the total root length (WinRHIZO Pro 2016; Regent Instruments Inc., QC, Canada). Thus, SRL (m g^{-1}) was calculated by dividing total root length by the dry weight. RTD (g cm^{-3}) was calculated by dividing the dry weight by total volume (Chen et al. 2026). Root biomass of each soil core was summed from the total biomass of two subsamples, and was expressed as root biomass per square meter (RB; g m^{-2}).

Leaf and absorptive root N, P concentration

All mature and senesced leaf samples were washed using deionized water, and then oven dried to constant weight at 65 °C. The dried leaves and absorptive roots were ground to a fine powder with a micro ball mill (Scientz 48 L cryogenic high-throughput tissue grinder, China). N concentrations of leaves and absorptive roots were measured using a Macro Elemental Analyzer (vario MACRO, Elemental Co., Hanau, Germany). P concentrations of leaves and absorptive roots (using H_2SO_4-$HClO_4$ oxidation digestion method) were measured using a flow-injection autoanalyzer (Auto Analyzer 3, SEAL Analytical GmbH, Norderstedt, Germany).

Soil properties

For each composite soil sample, one subsample (10.0 g fresh weight) was used to estimate soil moisture (SM) content using mass loss methods after 48 h of drying at 105 °C. The remaining subsample was air-dried to determine soil pH, total carbon concentration (STC), total N concentration (STN) and total P concentration (STP). We determined soil pH using an acidometer (MT-5000, Shanghai, China) with a soil-to-water ratio of 1:2.5 (w/v). STC, STN and STP were measured with similar methods as used for leaves and absorptive roots.

Data analysis

Nutrient resorption efficiency is the proportionate removal of a nutrient during senescence (Vergutz et al. 2012). LNRE and LPRE were computed using the following equations:

$$LNRE\,(\%) = \frac{LN_M - LN_S \times MLCF}{LN_M} \times 100 \quad (1)$$

$$LPRE\,(\%) = \frac{LP_M - LP_S \times MLCF}{LP_M} \times 100 \quad (2)$$

where, LN_M and LP_M represent N and P concentrations of mature leaves, respectively; LN_S and LP_S represent N and P concentrations of senesced leaves, respectively; MLCF is the mass loss correction factor of leaves to make up for the loss of leaf mass loss during the senescence phase (van Heerwaarden et al. 2003), with a value of 0.888 for ash (Wang et al. 2020a).

LNRE, LPRE, leaf chemical traits and absorptive root traits were averaged at the plot level ($n = 3$), since we treated each plot as an independent repetition. Before statistical analysis, the Shapiro–Wilk test was used to check

for data normality, and Levene's test was used to check for variance homogeneity of data. A log-10 transformation was conducted when necessary. To test the first hypothesis, one-way ANOVA (analysis of variance) was first performed to test the differences in LNRE and LPRE of ash across different plantation types. The relationships between LNRE and LN_M STN, LPRE, as well as between LPRE and LP_M, STP were then assessed using simple linear regression, aiming to determine which control strategy governs leaf nutrient resorption variation with species mixing. To test the second hypothesis, we first used one-way ANOVA to test the intraspecific variation of absorptive root traits (RB, RD, SRL, RTD, root N concentration (RN), root P concentration (RP)) of ash across different plantation types, then performed the principal component analysis (PCA) on six absorptive root traits to identify the response of root acquisition strategy to various mixed-species. For the third hypothesis, the relationships between LNRE, LPRE and the scores of the first two axes (PC1 and PC2) of PCA on absorptive root traits were tested by simple linear regression analysis. The relationships between LNRE, LPRE and single or multiple absorptive root traits were tested by simple linear regression analysis and multiple regression analysis, respectively. All statistical analyses were conducted using SPSS19.0 (2010, SPSS Inc., Cary, NC, USA).

Results

Effect of species mixing on leaf nutrient resorption

LN_M of ash was lower in the pure plantation (24.06 ± 0.74 mg g^{-1}) than in three mixed-species plantations, but which was significant only in the ash × spruce plantation (29.80 ± 2.42 mg g^{-1}) (Fig. S1a). A similar pattern was found in LP_S of ash, which was lowest in pure plantation (1.66 ± 0.04 mg g^{-1}) and highest (2.03 ± 0.05 mg g^{-1}) in the ash × spruce plantation (Fig. S1d). By contrast, no significant difference in LN_S was found among various plantation types (Fig. S1b), nor did to LP_M of ash (Fig. S1c).

LNRE of ash in the three mixed-species plantations was significantly greater than in the pure plantation (Fig. 1a, $P < 0.05$). In contrast to LNRE, LPRE of ash in the pure plantation was significantly higher than that of ash × spruce plantation, but no significant differences were observed compared to the others (Fig. 1b). LNRE and LPRE were significantly increased with increased LN ($b = 1.17$, $R^2 = 0.50$, $P = 0.010$, Fig. 2a) and LP ($b = 7.37$, $R^2 = 0.41$, $P = 0.025$, Fig. 2b), respectively. Only LPRE had a significant relationship with STP ($b = -10.91$, $R^2 = 0.37$, $P = 0.037$, Fig. 2e), but no significant relationship was found between LNRE and STN (Fig. 2d). Moreover, LNRE did not show any relation with LPRE (Fig. 2c).

Effect of species mixing on absorptive root traits

Compared with the pure plantation, mixing with coniferous species increased RB of ash, but the increase was

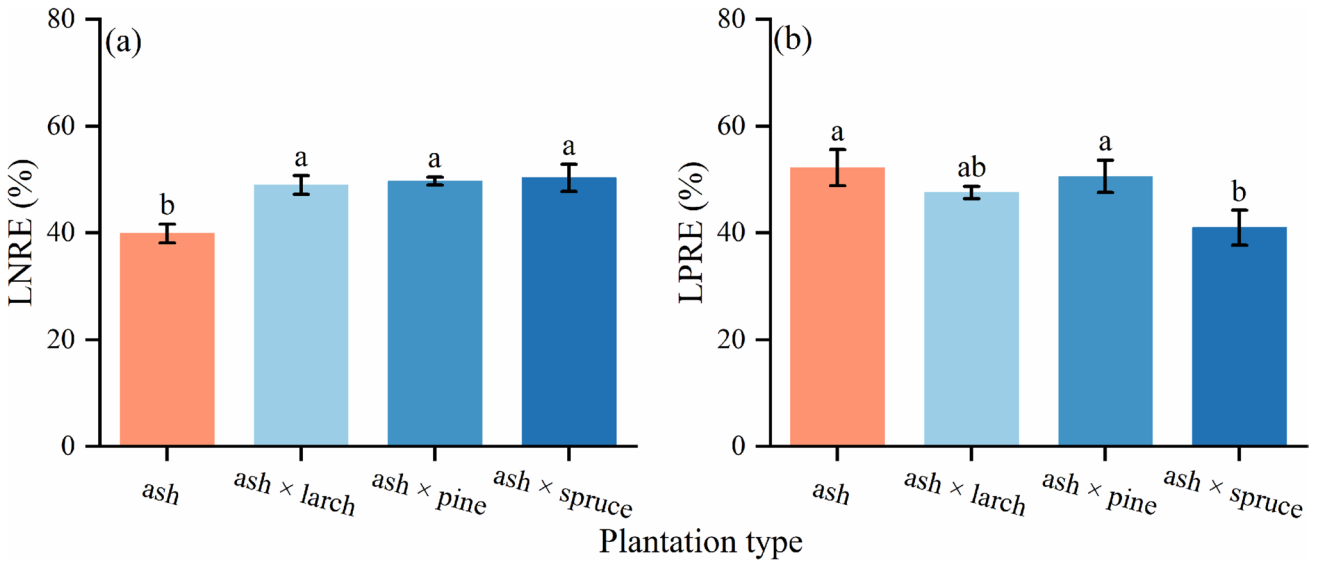


Fig. 1 Leaf N (a), P (b) resorption efficiency of *Fraxinus mandshurica* in different plantation types. Abbreviations were given in Table 1. Values are mean ± SE ($n = 3$). Significant differences between plantation types are indicated by different lowercase letters ($P < 0.05$). ash: Manchurian ash; larch: Dahurian larch; pine: Korean pine; spruce: Korean spruce

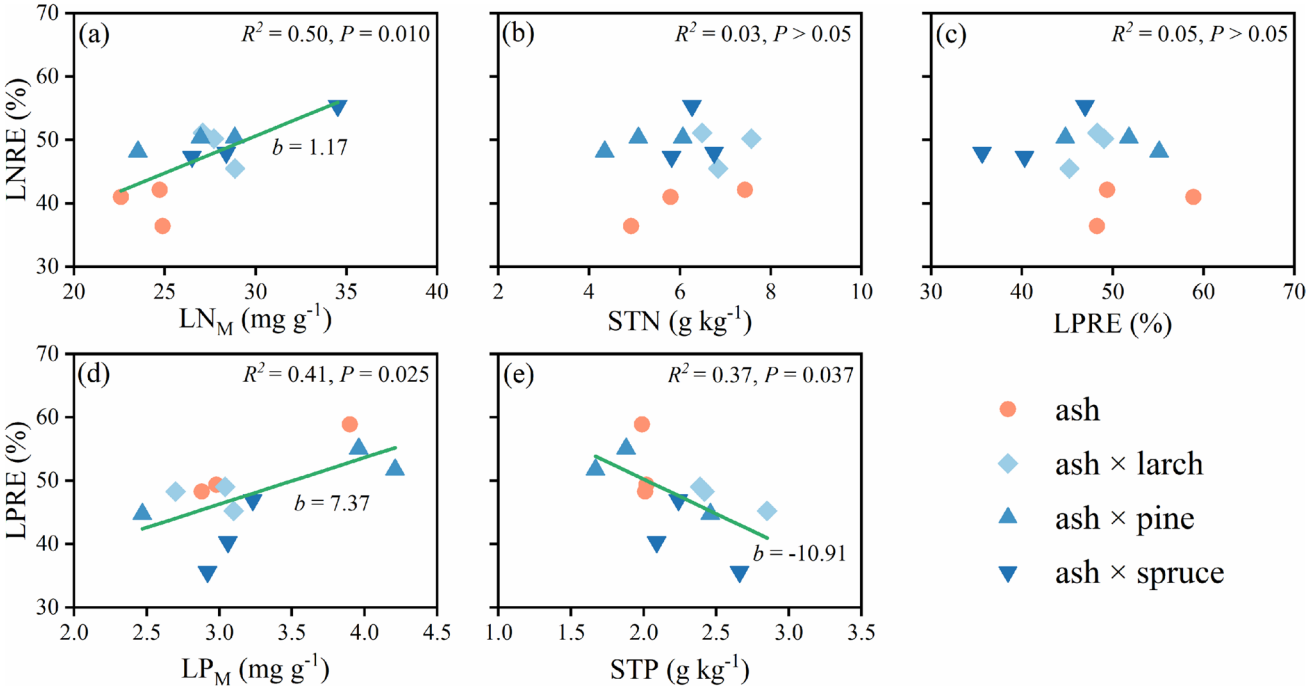


Fig. 2 Relationships between leaf N resorption efficiency and N concentration of mature leaf (a), soil total N concentration (b), and leaf P resorption efficiency (c), respectively; leaf P resorption efficiency and P concentration of mature leaf (d), soil total P concentration (e), respectively ($n = 12$). Abbreviations were given in Table 1. ash: Manchurian ash; larch: Dahurian larch; pine: Korean pine; spruce: Korean spruce

significant only in the ash × pine plantation (Fig. 3a). For SRL, only absorptive roots of ash × spruce was significantly lower (59.32 ± 4.58 m g^{-1}) than the pure plantation (73.83 ± 1.23 m g^{-1}, Fig. 3c). RTD and RN of ash did not show any significant effect of mixed-species, but roots of ash × spruce always exhibited the largest values of 0.30 ± 0.03 g cm^{-3} and 24.87 ± 0.15 mg g^{-1}, respectively (Fig. 3d, e). Moreover, RD and RP of ash did not significantly differ across different plantation types (Fig. 3b, f).

The PCA of six root traits showed a multi-dimensional space, where the first three axes (PC1, PC2 and PC3) explained 40.9%, 26.8% and 16.5% of the total variance, respectively (Fig. 4). RD occupied the positive end of the PC1, whereas SRL occupied the negative end (Fig. 4, Table S2). The PC2 was mainly composed of RB and RN in opposite directions (Fig. 4a, Table S2), while RP and RTD mainly occupied the PC3 (Fig. 4b, Table S2).

Relationships between leaf nutrient resorption efficiency and absorptive root traits

Simple linear regression analysis showed that there were only weak relationships between LNRE and single absorptive root trait (Fig. S2), except for a significant negative slope with SRL ($b = -0.41$, $R^2 = 0.35$, $P = 0.041$, Fig. S2c). Multiple regression analysis revealed that SRL ($b = -0.41$, $R^2 = 0.33$, $P = 0.041$) alone and the combination ($R^2 = 0.64$) of SRL ($b = -0.52$, $P = 0.006$) and RP ($b = -11.33$, $P = 0.027$) can explain variations in LNRE (Table S3). In comparison, simple linear regression analysis showed that LPRE significantly decreased with increased RTD ($b = -101.70$, $R^2 = 0.57$, $P = 0.005$) and RN ($b = -3.71$, $R^2 = 0.33$, $P = 0.049$) (Figs. S3d, e). Multiple regression analysis showed that only RTD was able to explain the variations in LPRE (Table S3). Furthermore, LNRE had no relationships with the PC1 or PC2 of absorptive root traits variation (Fig. 5a, b), nor with the PC3 (data not shown). By contrast, LPRE significantly decreased with the increased PC1 ($b = -4.65$, $R^2 = 0.57$, $P < 0.01$) (Fig. 5c), indicating that ash with thicker and denser roots for nutrient foraging in the case of mixing with coniferous species tends to reduce the leaf phosphorus resorption. However, there was no significant relationship between LPRE and the PC2 (Fig. 5d), nor was there with the PC3 (data not shown).

Discussion

Variation in leaf nutrient resorption

Our study found that LNRE and LPRE of ash responded differently when mixed with coniferous species (Fig. 1).

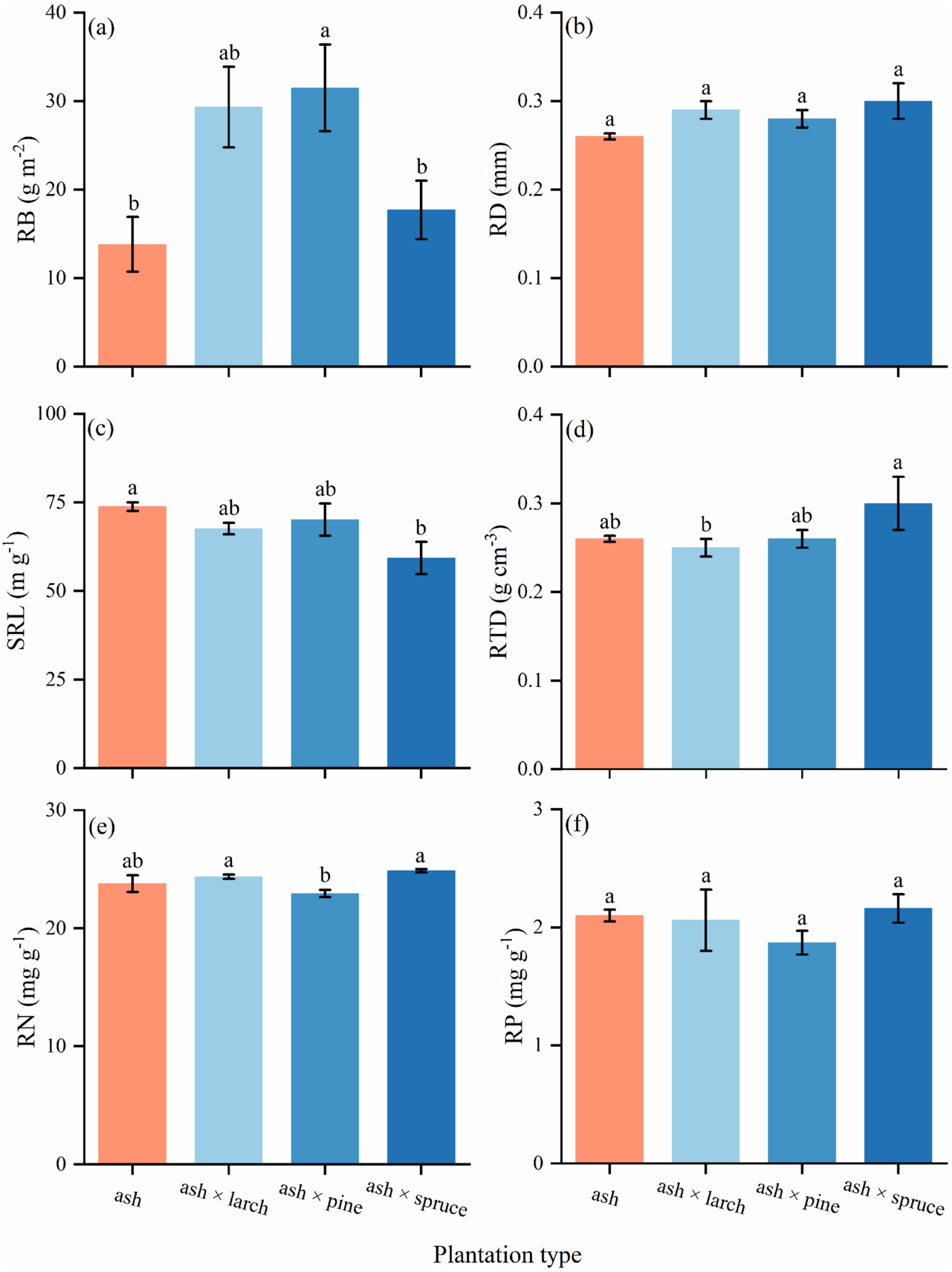
Specifically, LNRE of ash significantly increased in the mixed-species plantations relative to the pure plantation, which partially supports our first hypothesis. This result is in line with a previous study on Mongolian pine (*Pinus sylvestris* var. *mongolica*), which demonstrated significantly higher LNRE when mixed with Simon poplar (*Populus simonii*) than in the pure plantation (Li et al. 2025b). The LN_M: LP_M ratio ranges from 7.57 to 9.69 across all plantations, less than the typical threshold of 14 (Koerselman and Meuleman 1996), confirming the general N rather than P limitation in our study site, a common nature of soil in temperate forests (Du et al. 2020). Coniferous needle litters generally have slow decomposition and nutrient return rates, which may exacerbate the N limitation of soils to some degree, thus ash may increase LNRE in the mixed-species plantations. As such, mixed with coniferous species decreased LPRE of ash, as P seems not so limited compared with N. Actually, the shift of LPRE can be partially attributed to the change of STP (Fig. 2e, Table 2), despite not all STP being increased in the mixed-species plantations (Table 2). This might be primarily due to the available P in soils, as ectomycorrhiza in the mixed-species plantations may increase soil available P concentration (Zhang et al. 2023; Yuan et al. 2026), thereby enhancing the availability of P for roots and reducing dependence on LPRE. Thus, these results further demonstrate the control of leaf and soil nutrient limitations on leaf nutrient resorption efficiency during the shift of species composition associated with afforestation.

In addition, both LNRE and LPRE increased with increased LN_M and LP_M, respectively, which did not meet the criteria for the nutrient concentration control strategy (Chen et al. 2021). Also, we found no significant relationship between LNRE and LPRE of ash, failing to support the stoichiometry control strategy (Liu et al. 2025). One possible reason for the above phenomena is that the variations in LNRE and LPRE of ash after mixing with conifers were limited, and their trends were mixed-species dependent. A recent global meta-analysis found that LNRE and LPRE are decoupled under global change (warming, drought, increased rainfall, etc.), mainly affected by the shift in N and P limitation (Hong et al. 2025). Similarly, our findings indicate that LNRE and LPRE responses to species mixing are also not synergistic, varying with the specific conifers and the relative strength of N limitation. Overall, the control of nutrient limitation on leaf nutrient resorption is more prominent than the control of nutrient concentration and stoichiometry in our study (ref. Chen et al. 2021).

Variation in root nutrient acquisition strategy

Absorptive root traits of ash were modified by species mixing, depending on the specific root trait and the specific mixed species (Fig. 3). First, species mixing tended to increase RB of ash (Fig. 3a), with the values ranging from high to low: mixing with pine, larch and spruce, which is significant only when mixing with pine, supporting our second hypothesis. This may be caused by the morphological diversification of the first three order roots among these coniferous species. In our previous study, we found that RD is the thickest for pine, followed by larch, and the thinnest for spruce, compared with the thinnest roots of ash (Wang et al. 2019). Therefore, the likely strongest complementarity of root morphological traits occurs between ash and pine, resulting in the largest RB of ash in the ash × pine plantation. It is worth noting that the changes in RB we observed only represent the upper 10 cm of soil, and the vertical distribution of RB may be altered due to interactions with other tree species (Lei et al. 2012), which requires further research. Second, in opposition to our second hypothesis, we observed that species mixing did not influence RD of ash (Fig. 3b), and only significantly decreased SRL of ash in ash × spruce (Fig. 3c), largely differing from previous studies that tree mixing increased SRL but decreased RD (Bolte and Villanueva 2006; Shu et al. 2018). However, a global meta-analysis found that plant species mixtures had no significant effect on SRL (Peng and Chen 2021), which was comparable to our findings (Fig. 3c). Therefore, our study, in conjunction with previous research, suggests that the impacts of tree mixing on root biomass and morphology might be species-specific to some extent.

Root nutrient acquisition strategy can be depicted by the variation and association among root functional traits, which has been well represented by the root economics space (Bergmann et al. 2020). Our study showed that intraspecific covariation in absorptive ash root traits across the pure and mixed-species plantations formed two main dimensions (Fig. 4). Specifically, RD and SRL occupied the opposite directions along the PC1, which represented the 'collaboration' dimension of the root economics space (Bergmann et al. 2020). In contrast to the classic framework of root economics space, the PC2 did not conform to the 'conservation' dimension (i.e., a trade-off between RN and RTD), but consisted of a trade-off between RB and RN (Fig. 4). High N concentration in fine roots usually indicate increased metabolic activity and potentially faster rates of nutrient uptake (Reich et al. 2008; Ding et al. 2020). Therefore, the trade-off between RB and RN implies a trade-off between an 'amount' strategy of investing more biomass and an 'efficiency' strategy of being more active (Yi et al. 2023). Our findings align with earlier research on intraspecific covariation of root traits, which also only aligned with the 'collaboration' dimension (Isaac et al. 2017; Ren et al. 2023), indicating that the 'collaboration' dimension plays the primary role in both intraspecific and interspecific variations. Furthermore, we found ash roots in the pure and ash × pine plantations tend to have larger SRL, whereas those in the ash × spruce


(a)
RB (g m-2)
40
30
20
10
0
b
ab
a
b
(b)
RD (mm)
0.4
0.3
0.2
0.1
0.0
a
a
a
a
(c)
SRL (m g-1)
100
75
50
25
0
a
ab
ab
b
(d)
RTD (g cm-3)
0.4
0.3
0.2
0.1
0.0
ab
b
ab
a
(e)
RN (mg g-1)
30
20
10
0
ab
a
b
a
(f)
RP (mg g-1)
3
2
1
0
a
a
a
a
ash
ash × larch
ash × pine
ash × spruce
Plantation type

◂**Fig. 3** Absorptive root traits of *Fraxinus mandshurica* in different plantation types. RB (a), RD (b), SRL (c), RTD (d), RN (e), RP (f). Abbreviations were given in Table 1. Values are mean ± SE ($n = 3$). Significant differences between plantation types are indicated by different lowercase letters ($P < 0.05$). ash: Manchurian ash; larch: Dahurian larch; pine: Korean pine; spruce: Korean spruce

plantation possessed larger RD and RTD, indicating the substantial impact of mixed-species, as well as their species-specific adaption of ash roots. Based on the root economics space concept, when ash is grown in pure plantation, or mixed with thick-root species such as Korean pine (see the detailed discussion in the paragraph above), are more likely rely on themselves for nutrient acquisition, while shifting to an 'outsourcing" strategy when mixed with those species having more comparable traits such as diameter. However, as few studies to date have compared root nutrient acquisition strategies between pure and mixed-species plantations in the context of root economics space, our findings need to be validated across more forests in the future. Furthermore, although the positive correlation between RD and mycorrhizal colonization rate has been widely established for AM species (Kong et al. 2014; Lachaise et al. 2022; Guilbeault-Mayers and Laliberté 2024), future studies that directly measure mycorrhizal colonization, fungal community composition or functional type could better identify how roots adopt an 'outsourcing' strategy.

The relationship between leaf nutrient conservation and root nutrient acquisition

Contradicting our third hypothesis, LNRE of ash did not show any significant relationship with either dimension of the root economic space (Fig. 5a, b). Consistent with our results, Ding et al (2023) also found there was no significant correlation between LNRE and the 'collaboration' dimension of *Picea* species roots in alpine coniferous forests. However, they found LNRE was negatively correlated with the 'conservation' dimension (ranging from larger RTD to higher RP and RN), which was not found in our study. One possible reason for this discrepancy is that we added RB and RP into the framework of root economics space, resulting in the 'conservation' dimension not being typically constructed. Interestingly, we found there indeed was a positive but not significant relation ($R^2 = 0.33$, $P > 0.05$) between LNRE and the PC2 (mainly composed of RB and RN), implying ash roots in pure plantation tending to have lower biomass for foraging but higher potential for withdrawing N from senesced leaves. Additionally, for individual root traits, the single and multiple regressions both showed that LNRE significantly decreased with increased SRL (Fig. S2c, Table S3), indicating SRL is a factor that can reliably predict LNRE. The larger SRL could increase root exposure to soil N (Freschet et al. 2021), especially to the more mobile nitrate (Zhou et al. 2021), possibly reducing the need for leaf N resorption. In addition, the combination of SRL and RP showed a stronger association with LNRE, with both negative slopes (Table S3). Lower RP can lead to reduced ATP synthesis, thereby affecting N uptake and transformation (e.g., nitrate reduction) (Wang et al. 2020b), which in turn increases the demand for leaf N resorption. Overall, our results suggest that adjustments of ash root N acquisition strategy in responding to mixed-species likely operate relatively independently of leaf N conservation strategy.

Unlike LNRE, LPRE significantly decreased with increased 'collaboration' dimension (ranging from larger SRL to greater RD) of the root economics space (Fig. 5c). That is, ash with thicker roots in the context of mixed-species plantations expected to rely more on fungal hyphae for soil P uptake, was also more likely to resorb a smaller proportion of P from senescing leaves than in the pure plantation. As an AM species, thicker roots with potentially higher mycorrhizal infection may be less P-limited, which endows ash with higher efficiency to absorb P from soils, reducing the reliance on leaf P resorption. This finding is not consistent with our previous studies on 34 temperate coniferous and broadleaved species (Wang et al. 2025), in which no such pattern was found, but is supported by the findings on eight temperate broadleaved species (Xiao et al. 2025) that species with thicker roots for the 'outsourcing' strategy also have lower LPRE. Furthermore, both the single and multiple regressions revealed that LPRE significantly decreased with increased RTD (Fig. S3d, Table S3), suggesting that RTD is a reliable predictor of LPRE. RTD also exhibited high loadings on the 'outsourcing' side of PC1 (Fig. 4, Table S2), which may also play a role in the relationship between PC1 and LPRE. We also found LPRE of ash significantly decreased with increased RN (Fig. S3e). Consequently, these results of LPRE align with our expectation, which would decrease with a higher root acquisition efficiency (as indicated by a higher RN) or a more 'outsourcing' strategy (mainly reflected by a larger RD). However, leaf and root showed coordinated strategies for P acquisition and conservation, rather than the apparent limited element of N, the accurate reason for which is still not well clear and warrants further study. Moreover, many studies suggest that roots or mycorrhizal fungi also exude some organic acids and extracellular enzymes to mine nutrients in soil, representing another crucial strategy for nutrient acquisition (Lambers 2022; Wen et al. 2022; Li et al. 2025a). Therefore, in the future, nutrient mining via exudation should be integrated into the belowground nutrient acquisition strategy, which may deepen our understanding of the linkage between nutrient conservation and acquisition at the whole-plant level.

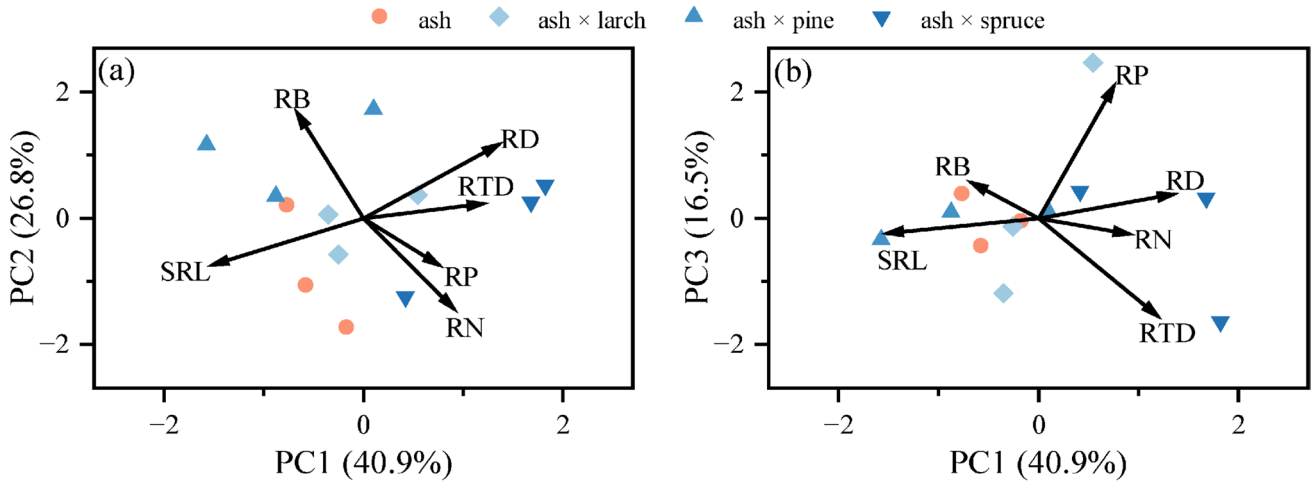


Fig. 4 Principal component analysis (PCA) for six absorptive root traits of *Fraxinus mandshurica* (a), the first axis and the second axis; (b), the first axis and the third axis ($n = 12$). Loading scores of each trait are shown in Table S2. Trait abbreviations were given in Table 1. ash: Manchurian ash; larch: Dahurian larch; pine: Korean pine; spruce: Korean spruce

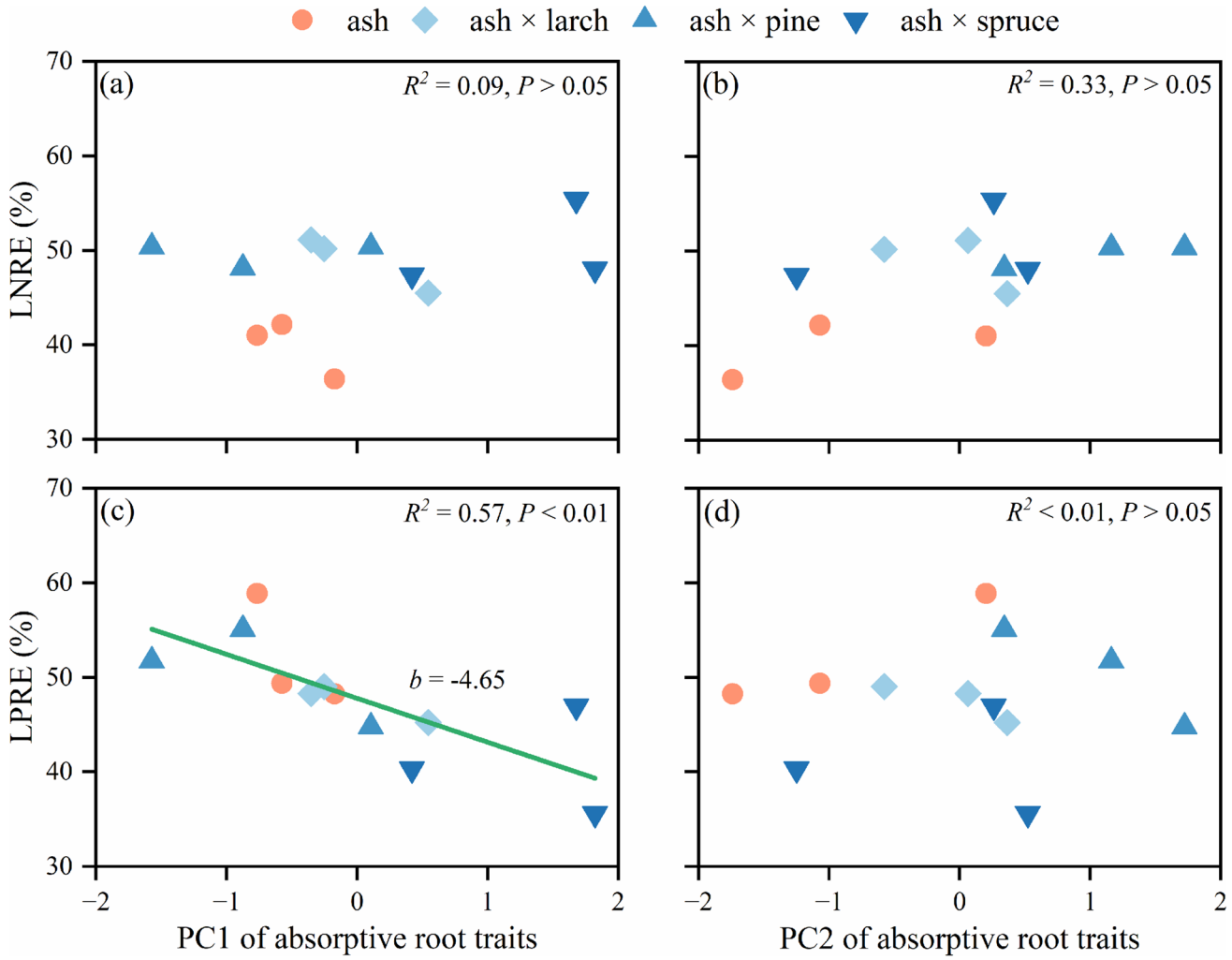


Fig. 5 Relationships between leaf N, P resorption efficiency and the first, second axis of PCA for absorptive root traits of *Fraxinus mandshurica* ($n = 12$). Abbreviations were given in Table 1. ash: Manchurian ash; larch: Dahurian larch; pine: Korean pine; spruce: Korean spruce

Table 2 Soil properties (0–10 cm depth) in different plantation types

Plantation types	pH	SBD (g cm^{-3})	SM (%)	STC (mg g^{-1})	STN (mg g^{-1})	STP (mg g^{-1})
ash	5.50 ± 0.04a	0.94 ± 0.03b	54.85 ± 4.20a	62.19 ± 1.54c	6.05 ± 0.73ab	2.01 ± 0.01b
ash × larch	5.27 ± 0.06a	1.01 ± 0.01ab	53.87 ± 2.91a	94.03 ± 4.49a	6.97 ± 0.32a	2.55 ± 0.15a
ash × pine	5.57 ± 0.14a	1.04 ± 0.05ab	61.20 ± 5.18a	57.58 ± 2.77c	5.16 ± 0.50b	2.00 ± 0.24b
ash × spruce	5.40 ± 0.08a	1.08 ± 0.03a	56.31 ± 3.81a	77.40 ± 3.77b	6.28 ± 0.27ab	2.33 ± 0.17ab

Abbreviations were given in Table 1. Values are mean ± SE ($n = 3$). Significant differences between plantation types are indicated by different lowercase letters ($P < 0.05$). ash: Manchurian ash; larch: Dahurian larch; pine: Korean pine; spruce: Korean spruce

Conclusion

Mixing with coniferous species increased LNRE but decreased LPRE of ash, which was confirmed by the nutrient limitation control strategy. Across the pure and mixed-species plantations, the intraspecific covariation in absorptive ash root traits formed two main dimensions, but only conformed to the 'collaboration' dimension of the root economics space. Compared with the pure plantations, species-mixing effects on the single root traits or root nutrient acquisition strategy of ash were species-specific, which may depend on the degree of complementary root morphology between mixed coniferous species and ash. LNRE of ash was not related to root nutrient acquisition strategy, indicating that leaf N conservation strategy is relatively independent of root nutrient acquisition strategy. By contrast, LPRE of ash significantly decreased with the increased 'outsourcing' strategy of the 'collaboration' dimension of the root economics space. Furthermore, SRL or SRL combined with RP served as a reliable indicator for LNRE, but RTD for LPRE, imply the importance of single root trait still needs to be considered when understanding the whole plant level resource utilization strategy. In general, our findings highlight that broad-leaved species exhibit high plasticity in leaf nutrient resorption and root nutrient acquisition strategies in response to mixing with different coniferous species, which deepens our understanding of trees' nutrient adaptation strategies in the context of species mixing from a whole-plant perspective.

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Data availability Data will be made available on request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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References

Bastin JF, Finegold Y, Garcia C, Mollicone D, Rezende M, Routh D, Zohner CM, Crowther TW (2019) The global tree restoration potential. Science 365(6448):76–79. https://doi.org/10.1126/science.aax0848

Bergmann J, Weigelt A, van der Plas F, Laughlin DC, Kuyper TW, Guerrero-Ramirez N, Valverde-Barrantes OJ, Bruelheide H, Freschet GT, Iversen CM, Kattge J, McCormack ML, Meier IC, Rillig MC, Roumet C, Semchenko M, Sweeney CJ, van Ruijven J, York LM, Mommer L (2020) The fungal collaboration gradient dominates the root economics space in plants. Sci Adv 6:eaba3756. https://doi.org/10.1126/sciadv.aba3756

Bolte A, Villanueva I (2006) Interspecific competition impacts on the morphology and distribution of fine roots in European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.). Eur J Forest Res 125(1):15–26. https://doi.org/10.1007/s10342-005-0075-5

Bu WS, Chen FS, Wang FC, Fang XM, Mao R, Wang HM (2019) The species-specific responses of nutrient resorption and carbohydrate accumulation in leaves and roots to nitrogen addition in a subtropical mixed plantation. Can J for Res 49(7):826–835. https://doi.org/10.1139/cjfr-2018-032

Chen XL, Chen HYH (2022) Foliar nutrient resorption dynamics of trembling aspen and white birch during secondary succession in the boreal forest of Central Canada. For Ecol Manage 505:119876. https://doi.org/10.1016/j.foreco.2021.119876

Chen H, Reed SC, Lv XT, Xiao KC, Wang KL, Li DJ (2021) Coexistence of multiple leaf nutrient resorption strategies in a single ecosystem. Sci Total Environ 772:144951. https://doi.org/10.1016/j.scitotenv.2021.144951

Chen WJ, Liu L, Penuelas J, Zhou GY, Hou LQ, Wu ZR (2025) Strategies of allocating root-shoot biomass in plantations and natural forests at various community stages and moisture levels. J for Res 36:126. https://doi.org/10.1007/s11676-025-01917-9

Chen SF, Gao M, Suo AL, Feng HY, Gong JW, Cheng DY, Chen F, Liu XD (2026) Effects of fire severity on the coupling relationship between fine root functional traits and soil physicochemical properties in *Pinus tabuliformis* forest. J for Res 37:13. https://doi.org/10.1007/s11676-025-01941-9

Ding JX, Kong DL, Zhang ZL, Cai Q, Xiao J, Liu Q, Yin HJ (2020) Climate and soil nutrients differentially drive multidimensional fine root traits in ectomycorrhizal-dominated alpine coniferous forests. J Ecol 108(6):2544–2556. https://doi.org/10.1111/1365-2745.13407

Ding JX, Ge WJ, Liu Q, Wang QT, Kong DL, Yin HJ (2023) Temperature drives the coordination between above-ground nutrient conservation and below-ground nutrient acquisition in alpine coniferous forests. Funct Ecol 37(6):1674–1687. https://doi.org/10.1111/1365-2435.14330

Du EZ, Terrer C, Pellegrini AFA, Ahlström A, van Lissa CJ, Zhao X, Xia N, Wu XH, Jackson RB (2020) Global patterns of terrestrial nitrogen and phosphorus limitation. Nat Geosci 13(3):221–226. https://doi.org/10.1038/s41561-019-0530-4

Feng YH, Schmid B, Loreau M, Forrester DI, Fei SL, Zhu JX, Tang ZY, Zhu JL, Hong PB, Ji CJ, Shi Y, Su HJ, Xiong XY, Xiao J, Wang SP, Fang JY (2022) Multispecies forest plantations outyield monocultures across a broad range of conditions. Science 376(6595):865–868. https://doi.org/10.1126/science.abm6363

Freschet GT, Cornelissen JHC, van Logtestijn RSP, Aerts R (2010) Substantial nutrient resorption from leaves, stems and roots in a subarctic flora: what is the link with other resource economics traits? New Phytol 186(4):879–889. https://doi.org/10.1111/j.1469-8137.2010.03228.x

Freschet GT, Roumet C, Comas LH, Weemstra M, Bengough AG, Rewald B, Bardgett RD, Deyn GBD, Johnson D, Klimešová J, Lukac M, McCormack ML, Meier IC, Pagès L, Poorter H, Prieto I, Wurzburger N, Zadworny M, Bagniewska-Zadworna A, Blancaflor EB, Brunner I, Gessler A, Hobbie SE, Iversen CM, Mommer L, Picon-Cochard C, Postma JA, Rose L, Ryser P, Scherer-Lorenzen M, Soudzilovskaia NA, Sun T, Valverde-Barrantes OJ, Weigelt A, York LM, Stokes A (2021) Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. New Phytol 232(3):1123–1158. https://doi.org/10.1111/nph.17072

Gao GQ, Ren H, Wang WN, Wang DN, Liu Z, Gu JC (2025) Anatomically defined absorptive fine roots are modulated by root-order architecture and morphology during tree ontogeny. Plant Soil 513(1–2):2887–2902. https://doi.org/10.1007/s11104-025-07355-0

Germon A, Guerrini IA, Bordon B, Bouillet JP, Nouvellon Y, de Moraes Goncalves JL, Jourdan C, Paula RR, Laclau JP (2017) Consequences of mixing *Acacia mangium* and *Eucalyptus grandis* trees on soil exploration by fine-roots down to a depth of 17 m. Plant Soil 424(1–2):203–220. https://doi.org/10.1007/s11104-017-3428-1

Gillespie LM, Hättenschwiler S, Milcu A, Wambsganss J, Shihan A, Fromin N (2021) Tree species mixing affects soil microbial functioning indirectly via root and litter traits and soil parameters in European forests. Funct Ecol 35(10):2190–2204. https://doi.org/10.1111/1365-2435.13877

Gu JC, Wang Y, Fahey TJ, Wang ZQ (2017) Effects of root diameter, branch order, soil depth and season of birth on fine root life span in five temperate tree species. Eur J for Res 136(4):727–738. https://doi.org/10.1007/s10342-017-1068-x

Guilbeault-Mayers X, Laliberté E (2024) Root phosphatase activity is coordinated with the root conservation gradient across a phosphorus gradient in a lowland tropical forest. New Phytol 243(2):636–647. https://doi.org/10.1111/nph.19567

Guo JH, Kneeshaw D, Peng CH, Wu YX, Feng L, Qu XJ, Wang WF, Pan C, Feng HL (2025) Positive effects of species mixing on biodiversity of understory plant communities and soil health in forest plantations. Proc Natl Acad Sci U S A 122(11):e2418090122. https://doi.org/10.1073/pnas.2418090122

Hong YX, Chen J, Lü XT, Li DJ, Sheteiwy MS, Maestre FT, Smith P, Ochoa-Hueso R, Sinsabaugh RL, Chen H (2025) Decoupling of plant nitrogen and phosphorus under global change over the last two decades. J Ecol 113(8):2120–2130. https://doi.org/10.1111/1365-2745.70081

Isaac ME, Martin AR, de Melo Virginio Filho E, Rapidel B, Roupsard O, van Den Meersche K (2017) Intraspecific trait variation and coordination: root and leaf economics spectra in coffee across environmental gradients. Front Plant Sci 8:1196. https://doi.org/10.3389/fpls.2017.01196

Koerselman W, Meuleman AFM (1996) The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. J Appl Ecol 33(6):1441–1450

Kong DL, Ma CG, Zhang Q, Li L, Chen XY, Zeng H, Guo DL (2014) Leading dimensions in absorptive root trait variation across 96 subtropical forest species. New Phytol 203(3):863–872. https://doi.org/10.1111/nph.12842

Lachaise T, Bergmann J, Hölzel N, Klaus VH, Kleinebecker T, Rillig MC, van Kleunen M (2022) Soil conditions drive belowground trait space in temperate agricultural grasslands. J Ecol 110(5):1189–1200. https://doi.org/10.1111/1365-2745.13862

Lambers H (2022) Phosphorus acquisition and utilization in plants. Annu Rev Plant Biol 73(1):17–42. https://doi.org/10.1146/annurev-arplant-102720-125738

Lei PF, Scherer-Lorenzen M, Bauhus J (2012) The effect of tree species diversity on fine-root production in a young temperate forest. Oecologia 169(4):1105–1115. https://doi.org/10.1007/s00442-012-2259-2

Li QC, Liu ZL, Jin GZ (2024) Mixed forests provide higher levels of growth and yield than monocultures across a broad range of conditions. For Ecol Manage 566:122083. https://doi.org/10.1016/j.foreco.2024.122083

Li X, Zeng DH, Zhang YS, Mao ZK, Sun YZ, Sheng ZM, Shi KL, Wang GR, Lin GG (2025a) Complementarity of fine roots and ectomycorrhizal fungi in nitrogen acquisition along a gradient of intraspecific competition intensity. Plant Cell Environ 48(7):4873–4885. https://doi.org/10.1111/pce.15487

Li X, Zeng DH, Sheng ZM, Sun YZ, Lin GG (2025b) Tree species mixing causes shifts in nitrogen acquisition and utilization strategies of Mongolian pine and Simon poplar. Ecol Process 14(1):16. https://doi.org/10.1186/s13717-025-00584-2

Lin Y, Xia CK, Wu GY, Wang FC, Wang SN, Liu YQ, Chen FS (2022) Replanting of broadleaved trees alters internal nutrient cycles of native and exotic pines in subtropical plantations of China. For Ecosyst 9:100067. https://doi.org/10.1016/j.fecs.2022.100067

Liu Z, Ren H, Zhang S, Ma YY, Gu JC (2024) Effects of long-term nitrogen addition on root nitrogen acquisition strategy: insights from a 19-year experiment in two temperate tree species. For Ecol Manage 570:122220. https://doi.org/10.1016/j.foreco.2024.122220

Liu Y, Sun W, Jia T, Su TH, Wu SS, Zhou CY, Mo YX, Qi JH, Lu ZY, Li S (2025) Leaf nutrient resorption of vascular epiphytes is regulated by stoichiometry and nutrient limitation control strategies. Plant Cell Environ 48(6):4550–4563. https://doi.org/10.1111/pce.15455

Ma YY, Yang N, Wang SY, Huo CF, Yu LZ, Gu JC (2024) Climatic and edaphic controls of root-tip production and mortality in five temperate tree species. J for Res 35:145. https://doi.org/10.1007/s11676-024-01797-5

Peng S, Chen HYH (2021) Global responses of fine root biomass and traits to plant species mixtures in terrestrial ecosystems. Glob Ecol Biogeogr 30(1):289–304. https://doi.org/10.1111/geb.13205

Piao SL, Fang JY, Ciais P, Peylin P, Huang Y, Sitch S, Wang T (2009) The carbon balance of terrestrial ecosystems in China. Nature 458(7241):1009–1013. https://doi.org/10.1038/nature07944

Pregitzer KS, Deforest JL, Burton AJ, Allen MF, Ruess RW, Hendrick RL (2002) Fine root architecture of nine North American trees. Ecol Monogr 72(2):293–309. https://doi.org/10.1890/0012-9615(2002)072[0293:FRAONN]2.0.CO;2

Raven JA, Lambers H, Smith SE, Westoby M (2018) Cost of acquiring phosphorus by vascular land plants: patterns and implications for plant coexistence. New Phytol 217(4):1420–1427. https://doi.org/10.1111/nph.14967

Reich PB (2014) The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. J Ecol 102(2):275–301. https://doi.org/10.1111/1365-2745.12211

Reich PB, Tjoelker MG, Pregitzer KS, Wright IJ, Oleksyn J, Machado J (2008) Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. Ecol Lett 11(8):793–801. https://doi.org/10.1111/j.1461-0248.2008.01185.x

Ren H, Gao GQ, Ma YY, Li ZW, Wang SY, Gu JC (2023) Shift of root nitrogen-acquisition strategy with tree age is mediated by root functional traits along the collaboration gradient of the root economics space. Tree Physiol 43(8):1341–1353. https://doi.org/10.1093/treephys/tpad047

Richards AE, Forrester DI, Bauhus J, Scherer-Lorenzen M (2010) The influence of mixed tree plantations on the nutrition of individual species: a review. Tree Physiol 30(9):1192–1208. https://doi.org/10.1093/treephys/tpq035

Shu WW, Shen XX, Lei PF, Xiang WH, Ouyang S, Yan WD (2018) Temporal changes of fine root overyielding and foraging strategies in planted monoculture and mixed forests. BMC Ecol 18(1):9. https://doi.org/10.1186/s12898-018-0166-z

Sun XB, Li DJ, Lv XT, Fang YT, Ma ZL, Wang ZC, Chu CJ, Li MM, Chen H (2023) Widespread controls of leaf nutrient resorption by nutrient limitation and stoichiometry. Funct Ecol 37(6):1653–1662. https://doi.org/10.1111/1365-2435.14318

van Heerwaarden LM, Toet S, Aerts R (2003) Current measures of nutrient resorption efficiency lead to a substantial underestimation of real resorption efficiency: facts and solution. Oikos 101(3):664–669. https://doi.org/10.1034/j.1600-0706.2003.12351.x

Vergutz L, Manzoni S, Porporato A, Novais RF, Jackson RB (2012) Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. Ecol Monogr 82(2):205–220. https://doi.org/10.1890/11-0416.1

Wambsganss J, Freschet GT, Beyer F, Goldmann K, Prada-Salcedo LD, Scherer-Lorenzen M, Bauhus J (2021) Tree species mixing causes a shift in fine-root soil exploitation strategies across European forests. Funct Ecol 35(9):1886–1902. https://doi.org/10.1111/1365-2435.13856

Wang YN, Gao GQ, Wang N, Wang ZQ, Gu JC (2019) Effects of morphology and stand structure on root biomass and length differed between absorptive and transport roots in temperate trees. Plant Soil 442(1–2):355–367. https://doi.org/10.1007/s11104-019-04206-7

Wang XC, Chen Y, Liu F, Zhao R, Quan XK, Wang CK (2020a) Nutrient resorption estimation compromised by leaf mass loss and area shrinkage: variations and solutions. For Ecol Manage 472:118232. https://doi.org/10.1016/j.foreco.2020.118232

Wang X, Wang HF, Chen Y, Sun MM, Wang Y, Chen YF (2020b) The transcription factor NIGT1.2 modulates both phosphate uptake and nitrate influx during phosphate starvation in Arabidopsis and maize. Plant Cell 32(11):3519–3534. https://doi.org/10.1105/tpc.20.00361

Wang DN, Freschet GT, McCormack ML, Lambers H, Gu JC (2025) Nutrient resorption of leaves and roots coordinates with root nutrient-acquisition strategies in a temperate forest. New Phytol 246(2):515–527. https://doi.org/10.1111/nph.70001

Wen ZH, White PJ, Shen JB, Lambers H (2022) Linking root exudation to belowground economic traits for resource acquisition. New Phytol 233(4):1620–1635. https://doi.org/10.1111/nph.17854

Wright IJ, Westoby M (2003) Nutrient concentration, resorption and lifespan: leaf traits of Australian sclerophyll species. Func Ecol 17(1):10–19. https://doi.org/10.1046/j.1365-2435.2003.00694.x

Xia Q, Liu SQ, Nie XQ, Chen YQ, Wang H, Niu BL, Ming AG (2026) Divergent factors shape the stability of *Pinus massoniana* rhizosphere organic carbon in subtropical mixed plantations. J for Res 37:67. https://doi.org/10.1007/s11676-026-02010-5

Xiang WH, Fan GW, Lei PF, Zeng YL, Tong J, Fang X, Deng XW, Peng CH (2015) Fine root interactions in subtropical mixed forests in China depend on tree species composition. Plant Soil 395(1–2):335–349. https://doi.org/10.1007/s11104-015-2573-7

Xiao Y, Pan L, Wang BR, Teng F, Wang XW (2025) Collaboration between leaf resorption and belowground nutrient acquisition in broadleaf species of temperate forest. Scand J for Res 40(3–4):1–9. https://doi.org/10.1007/s11104-015-2573-7

Yan T, Zhu JJ, Yang K (2018) Leaf nitrogen and phosphorus resorption of woody species in response to climatic conditions and soil nutrients: a meta-analysis. J for Res 29(4):905–913. https://doi.org/10.1007/s11676-017-0519-z

Yang H, Zhang PP, Wang GR, Wang QT, Wang DG, Wang RH, Zhang XJ, Yin HJ (2025) The synergistic strategy of leaf nitrogen conservation and root nitrogen acquisition in an alpine coniferous forest along an elevation gradient. Plant Soil 514(1–2):2067–2082. https://doi.org/10.1007/s11104-025-07514-3

Ye ZP, Ning C, Liu T, Yan MR, Cai WY, Xiao JY, Yan WD (2025) Impact of broadleaf tree introduction on rhizosphere fungal communities and root phosphorus-cycling genes in conifers of near-natural transformed plantation. For Ecosyst 14:100378. https://doi.org/10.1016/j.fecs.2025.100378

Yi RJ, Liu QY, Yang FT, Dai XQ, Meng SW, Fu XL, Li SG, Kou L, Wang HM (2023) Complementary belowground strategies underlie species coexistence in an early successional forest. New Phytol 238(2):612–623. https://doi.org/10.1111/nph.18736

Yuan J, Yan ZY, Wang YH, Fan SL, Chen JX, Ye KJ, Zheng GX, Wan SP, Zheng Y, Yu FQ, Wang YL, Lambers H, Kandeler E (2026) Oxalotrophic bacteria in the ectomycorrhizosphere play an essential role in phosphorus mobilization. Soil Biol Biochem 214:110077. https://doi.org/10.1016/j.soilbio.2025.110077

Zhang YD, Wang QC, Gu YH (1999) The relationship between growth and interspecific competition within the ash-larch mixed stand. J Northeast for Univ 27(2):6–9. https://doi.org/10.13759/j.cnki.dlxb.1999.02.002. ((**in Chinese**))

Zhang ZL, Guo WJ, Wang JP, Lambers H, Yin HJ (2023) Extraradical hyphae alleviate nitrogen deposition-induced phosphorus deficiency in ectomycorrhiza-dominated forests. New Phytol 239(5):1651–1664. https://doi.org/10.1111/nph.19078

Zheng L, Barry KE, Guerrero-Ramírez NR, Craven D, Reich PB, Verheyen K, Scherer-Lorenzen M, Eisenhauer N, Barsoum N, Bauhus J, Bruelheide H, Cavender-Bares J, Dolezal J, Auge H, Fagundes MV, Ferlian O, Fiedler S, Forrester DI, Ganade G, Gebauer T, Haase J, Hajek P, Hector A, Hérault B, Hölscher D, Hulvey KB, Irawan B, Jactel H, Koricheva J, Kreft H, Lanta V, Leps J, Mereu S, Messier C, Montagnini F, Mörsdorf M, Müller S, Muys B, Nock CA, Paquette A, Parker WC, Parker JD, Parrotta JA, Paterno GB, Perring MP, Piotto D, Polley HW, Ponette Q, Potvin C, Quosh J, Rewald B, Godbold DL, Van Ruijven J, Standish RJ, Stefanski A, Sundawati L, Urgoiti J, Williams LJ, Wilsey BJ, Yang B, Zhang L, Zhao Z, Yang

Y, Sandén H, Ebeling A, Schmid B, Fischer M, Kotowska MM, Palmborg C, Tilman D, Yan E, Hautier Y (2024) Effects of plant diversity on productivity strengthen over time due to trait-dependent shifts in species overyielding. Nat Commun 15:2078. https://doi.org/10.1038/s41467-024-46355-z

Zhou XL, Wang A, Hobbie EA, Zhu FF, Qu YY, Dai LM, Li DJ, Liu XY, Zhu WX, Koba K, Li YH, Fang YT (2021) Mature conifers assimilate nitrate as efficiently as ammonium from soils in four forest plantations. New Phytol 229(6):3184–3194. https://doi.org/10.1111/nph.17110

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