



Article Root Development in *Cunninghamia lanceolata* and *Schima superba* Seedlings Expresses Contrasting Preferences to Nitrogen Forms

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Abstract: The inorganic nitrogen (N) that can be absorbed and utilized by plants is mainly ammonium N (NH₄⁺-N) and nitrate N (NO₃⁻-N), which may affect seedlings' root morphology and growth through its heterogeneous distribution. Root morphology and seedling growth were investigated in a subtropical major conifer (Cunninghamia lanceolata) and a broadleaf tree species (Schima superba) under five different NH_4^+ -N to NO_3^- -N ratios (10:0, 0:10, 7:3, 3:7, 5:5). Results: (1) While both species developed thinner roots under the treatment with a high NO3⁻-N concentration, the roots of C. lanceolata were longer than those of S. superba. In contrast, the roots of both species were thicker under the treatment with a high NH_4^+ -N concentration, with those in S. superba being much longer than those in C. lanceolata. (2) The mixed NH_4^+ -N and NO_3^- -N treatments were more conducive to the aboveground growth and biomass accumulation of both tree species and the underground growth of S. superba. N sources with high NO_3^{-} -N concentrations were more suitable for underground growth in C. lanceolata seedlings and aboveground growth in S. superba seedlings. Under the N sources with high NH4⁺-N concentrations, C. lanceolata tended to develop aboveground parts and S. superba tended to develop underground parts. (3) The roots of the two tree species adopted the expansion strategy of increasing the specific root length and reducing the root tissue density under the N sources with high NO₃⁻-N concentrations but the opposite with high NH₄⁺-N concentrations. The root-to-shoot ratio of C. lanceolata increased under high NO₃⁻-N concentrations, while that of S. superba increased under high NO₃⁻-N concentrations. These results indicate that the responses of root morphology to different N forms are species-specific. Furthermore, according to the soil's N status, NH₄⁺-N can be appropriately applied to C. lanceolata and NO₃⁻-N to S. superba for cultivating seedlings.

Keywords: nitrogen forms; *Cunninghamia lanceolata; Schima superba;* morphological characteristics of root system

1. Introduction

Nitrogen (N) is an essential mineral element for plant growth. The inorganic nitrogen that can be absorbed and utilized by plants is mainly ammonium nitrogen (NH₄⁺-N) and nitrate nitrogen (NO₃⁻-N). The two forms of N in soils are not uniformly distributed but instead occur in different proportions and change with time, so they are distributed heterogeneously in time and space [1,2]. Studies have shown that the ratio of NH₄⁺-N and NO₃⁻-N in the soil ranges from 8:2 to 2:8 [3]. Heterogeneous environments with different ammonium and nitrate contents will have different effects on plant growth. In one study, mixed nitrogen culture was more conducive to the growth of the aboveground parts of *Citrus Sinensis* × *Poncirus trifoliata* seedlings than nitrogen alone, and the best effect was observed at an ammonium to nitrate ratio of 5 to 5 [4]. The growth of the aboveground and underground parts of *Pinus massoniana* seedlings cultured from tissue both reached the maximum value under the ammonium nitrogen-only treatment [5]. When plants grow in an environment with a heterogeneous distribution of different forms of N, especially



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). for a long time, they adopt different adaptation mechanisms for the underground and aboveground parts, and the roots' regulatory pathway is particularly important.

As the main nutrient-absorbing organ in plants, the root system carries out nutrient exchange and metabolism for the underground and aboveground parts of the plant. Under natural soil nutrient adversity, tree roots can explore, acquire and utilize limited soil nutrient resources through regulating their morphology, physiology and mycorrhizal plasticity [5,6]. With the intensification of global N deposition, the plastic response of plants' root morphology and structure [root length (RL), root surface area (RSA), root average diameter (RAD), root volume (RV), specific root length (SRL), etc.] to soil N is the most direct manifestation of plants' ability to adapt to environmental changes and seek nutrients [6,7]. Under different N forms, the root morphology of plants will show different nitrogen-seeking strategies [8]. Studies have shown that mixed nitrogen can increase the surface area of the root system and increase RL and the number of root tips, thereby increasing the absorption capacity of the root system and promoting aboveground growth [9]. When the supply ratio of NO_3^- -N was higher than 50%, the root quality of Larix gmelinii seedlings decreased significantly [10]. The biomass of shoots and lateral roots of *Cunninghamia lanceolata* seedlings was largest under NH_4^+ -N treatment [11]. However, compared with the NH_4^+ -N treatment, hybrid poplar plants under a NO_3^- -N treatment exhibited a higher proportion of fine roots, thicker roots and bigger SRL [12]. C. lanceolata roots also tend to grow in NO₃⁻-N patches, while Schima superba and P. massiniana tend to grow more and finer roots in NH_4^+ -N patches [8]. In an environment of nitrogen deficiency, plants will adjust their nitrogen-seeking strategies by increasing the SRL and root-toshoot ratio (RSR) [13,14]. Plants' biomass allocation can reflect the nutrient utilization of plant organs [15]. According to the optimal balance theory, plants tend to allocate resources to organs that can obtain restricted resources in order to obtain more restricted resources [16,17]. The SRL, root tissue density (RTD) and RSR can reflect the carbon allocation strategy of plants from different perspectives, which also conforms to the theory of root economics [18,19]. Therefore, studying the morphological characteristics of plant roots can intuitively reveal the nutrient uptake status of plants and their growth status.

C. lanceolata is an important fast-growing afforestation tree species in southern China. In recent decades, *C. lanceolata* forests have mostly been cultivated as artificial forests. The continuous planting of forest stands and soil acidification have led to the exhaustion of forestland, declines in the yield of forest stands, and reductions in the forests' ecological services [20,21]. Some studies have found that, in view of the problem of soil fertility declining after continuous planting of coniferous species, broadleaf tree species can effectively improve soil fertility and can thus be used as soil-improving tree species for mixed planting with conifers [22]. As an evergreen broadleaf tree species, *S. superba* produces a large amount of litter that decomposes quickly and contains high amounts of nutrients, which is conducive to water storage and fertilizer conservation. Therefore, *S. superba* is mostly used for mixing with coniferous species such as *C. lanceolata* to create a mixed coniferous and broadleaf forest. The resulting economic and ecological benefits have received widespread attention.

At present, research on the effects of different N forms on plant roots has mostly been conducted in crops, herbs and fruit trees, and research on the effects on roots of woody plants such as forest tree species is relatively limited and incomplete, especially regarding the coexistence mechanism of mixed *C. lanceolata* and *S. superba* forests. We hypothesized that the N uptake strategies of the roots of *C. lanceolata* and *S. superba* are different for different N forms. In view of this, in this experiment, the potted sand culture method was used to avoid the interference of soil N and to test the effects of different N forms on the morphological plasticity of *C. lanceolata* and *S. superba* roots' responses to N uptake and their differences.

2. Materials and Methods

2.1. Plant Materials

The test materials used in this study were selected from *C. lanceolata* and *S. superba*, the two main coniferous and broadleaf tree species occurring in mixed stands in the subtropical zone. One-year-old seedlings with uniform growth that were free from disease and insect pests and had a complete root system were selected as the test seedlings. Plastic pots (26 cm diameter \times 28 cm height) were used for cultivating the seedlings. The potting substrate selected was clean sand, which was repeatedly washed with distilled water until the N content in the sand was close to zero [23,24].

2.2. Experimental Setup

In April 2021, the sand culture experiments were conducted in a rainproof greenhouse with good ventilation and light transmission at Fujian Agriculture and Forestry University, China. The average temperature was 20.1 °C and the average relative humidity was about 77%. Each pot was filled with equal amount of clean sand. A matrix environment with different proportions of two N forms was constructed using different concentrations of NH₄⁺-N and NO₃⁻-N in the nutrient solution.

According to the research results of Zhang et al. [25] on the influence of fertilization on the soil nutrient content of *C. lanceolata* and the previous research results of Meng et al. [26] and Liu et al. [27], the total N concentration was set to 2 mmol·L⁻¹. In this study, we used five different ratios of NH₄⁺-N and NO₃⁻-N supplied as NH₄⁺-N:NO₃⁻-N = 10:0, 0:10, 7:3, 3:7 and 5:5 (Table 1). The 10:0 and 0:10 treatments had highly heterogeneous N, 7:3 and 3:7 had medium heterogeneous N, and 5:5 had homogeneous N. NH₄⁺-N was supplied as (NH₄)₂SO₄, while NO₃⁻-N was supplied as NaNO₃. In all treatments, while the concentration of the two forms of N were different, the content of the macronutrients (Hoagland formula) and micronutrients (Amon formula) remained the same. To prevent the conversion of ammonium to nitrate, the nitrification inhibitor dicyandiamide (7 µmol·L⁻¹) was added to the nutrient solution. The pH of the nutrient solution was adjusted to 5.8 with 2 mol·L⁻¹ NaOH or HCl. Each treatment had six replicates, and the total number of pots was 60. The nutrient solutions were added to the corresponding compartments at a rate of 50 mL every 5 days. Each pot was supplied with 150 mL of distilled water every 2–3 days. We did not water the pots for 24 h before and after pouring in the nutrient solution.

Treatment (NH ₄ ⁺ /NO ₃ ⁻)	Total N (mmol·L ⁻¹) $$	Different N Forms (mmol· L^{-1})	
		NH_4^+	NO ₃ -
10:0	2	2.0	0
0:10	2	0	2.0
7:3	2	1.4	0.6
3:7	2	0.6	1.4
5:5	2	1.0	1.0

Table 1. Treatments with different nitrogen forms.

2.3. Plant Harvesting and Data Collection

All the seedlings were harvested after 160 days of cultivation. The initial and final plant height and ground diameter of all seedlings were measured and recorded. Plants were separated into three parts: roots, stems and leaves. The fresh stems and leaves were oven-dried at 105 °C for half an hour to deactivate the enzymes and then at 65 °C to a constant weight.

The roots in each treatment were harvested carefully, cleaned with distilled water and dried with filter paper. We imaged all the roots using an Epson Expression 12,000XL scanner (Seiko Epson Corporation, Suwa, Nagano, Japan) and analyzed the images with WinRHIZO software (Pro2017a, Regent Instruments Inc., Quebec, Canada) to obtain the roots' morphological parameters, including the total root length (TRL, cm), total root surface area (TRSA, cm²), total root volume (TRV, cm³) and the roots' average diameter (RAD, mm). After scanning, all the roots were oven-dried at 105 °C for half an hour to deactivate the enzymes and then at 65 °C to a constant weight. The total seedling biomass (TSB, g) of the seedlings was the sum of the root, stem and leaf biomass in each treatment.

2.4. Data Analysis

All the data were processed and analyzed in Excel 2016 (Microsoft Office, Washington, Redmond, WA, USA). The increments in seedling height (Δ H, cm) and ground diameter (Δ GD, mm) were calculated by subtracting the seedlings' initial height and ground diameter from the final height and ground diameter, respectively. Specific root length (SRL, cm·g⁻¹) was calculated as total root length/total root biomass (TRB, g). Root tissue density (RTD, g·cm⁻³) was calculated by dividing the root biomass by the total root volume. The root-to-shoot ratio (RSR) was calculated as the ratio of root biomass to aboveground biomass.

Statistical analyses were conducted using SPSS 25.0 for Windows (SPSS Inc., Chicago, IL, USA). One-way ANOVA was conducted to evaluate the effect of nitrogen forms on the seedlings' Δ H, Δ GD, TRL, TRSA, TRV, RAD, TRB, TSB, SRL, RTD and RSR. Two-way ANOVA was performed on the effects of tree species and different N forms on the roots' morphological parameters, and plots were created using Origin 2018 (OriginLab, Northampton, USA). In this study, the ammonium and nitrate N concentrations were used as environmental factor variables, and the root and growth parameters of plants were used as biological factor variables to reflect the relationships among the parameters. The redundancy analysis (RDA) was conducted in Canoco 5.0 (Microcomputer Power, Ithaca, NY, USA).

3. Results

3.1. Significance Test of the Effects of Tree Species and Different Ratios of N Forms on the Seedlings' Growth and the Roots' Morphological Parameters

Table 2 shows that tree species and different N forms (a × b) had significant interaction effects on Δ H and Δ GD, TRL, TRSA, TRV, TRB, RTD and RSR (p < 0.05), while the interaction effect on RAD, TSB and SRL did not reach a significant level (p > 0.05). Separately, the effects of tree species (a) and different N forms (b) on all indicators reached the very significant level (p < 0.01), except for TRV under different ammonium to nitrate ratios, which reached the significant level (p < 0.05).

p-Value and Significance Level Factor Tree Species (a) NH_4^+/NO_3^- (b) $\mathbf{a} \times \mathbf{b}$ df 4 1 4 < 0.001 < 0.001 < 0.001 Seedling height increment (Δ H) Ground diameter increment (Δ GD) < 0.001< 0.001< 0.001Total root length (TRL) < 0.001 < 0.001 < 0.01 Total root surface area (TRSA) < 0.001< 0.001 < 0.01 Total root volume (TRV) < 0.001< 0.05< 0.05Roots' average diameter (RAD) < 0.001< 0.0010.835 Total root biomass (TRB) < 0.001< 0.01 < 0.001Total seedling biomass (TSB) < 0.001< 0.01 0.08 Specific root length (SRL) < 0.001< 0.01 0.113 Root tissue density (RTD) < 0.001< 0.01 < 0.05 Root-to-shoot ratio (RSR) < 0.001< 0.001 < 0.001

Table 2. Two-way ANOVA of the effects of tree species and different ratios of N forms on the seedlings' growth and the roots' morphological parameters.

3.2. Effects of Different N Forms on Root Morphology in the Two Tree Species

The roots' parameters were significantly influenced by the different N forms in each treatment (p < 0.05) (Figure 1). Under the five different ratios of the N forms, the TRL and

TRSA of *C. lanceolata* followed the order 10:0 < 7:3 < 3:7 < 5:5 < 0:10 (Figure 1a,c). Under the NO₃⁻-N-only treatment, the TRL and TRSA were 16.54–70.42% and 18.58–42.68% higher, respectively, than those under the other four treatments. The TRV followed the order 10:0 < 5:5 < 7:3 < 3:7 < 0:10 (Figure 1e). It was largest under the NO₃⁻-N-only treatment, which was 11.48–24.64% larger than that under the other four treatments. The RAD of *C. lanceolata* followed the order 5:5 < 0:10 < 7:3 < 3:7 < 10:0 (Figure 1g), and was significantly larger under the NH₄⁺-N-only treatment than under the other four treatments. In general, the roots of *C. lanceolata* preferred to grow under the treatments with higher NO₃⁻-N concentrations.



Figure 1. Effects of different NH_4^+ -N and NO_3^- -N ratios on the TRL (**a**,**b**), TRSA (**c**,**d**), TRV (**e**,**f**) and RAD (**g**,**h**) of the two tree species. Different lowercase letters indicate that the roots' morphological parameters were significantly different under different N forms (p < 0.05).

The TRL, TRSA and TRV of *S. superba* followed the order 3:7 < 10:0 < 0:10 < 7:3 < 5:5 (Figure 1b,d,f). The TRL, TRSA and TRV under the 5:5 ratio were 15.42-76.27%, 9.19-71.05%

and 7.97–72.24% larger, respectively, than those of the other four treatments. The RAD of *S. superba* followed the order 5:5 < 0:10 < 3:7 < 7:3 < 10:0 (Figure 1h). It showed the maximum value under the NH₄⁺-N-only treatment, which did not differ significantly from that under the 7:3 treatment but was significantly greater than that under the other three treatments, showing a minimum value at a ratio of 5:5. The morphological parameters of the root system of *S. superba* were superior in the treatments with higher NH₄⁺-N concentrations.

3.3. Effects of Different N Forms on Biomass in the Two Tree Species

The TRB of one-year-old seedlings of *C. lanceolata* ranged from 2.26 to 2.74 g·tree⁻¹ after 160 days of the experimental treatment (Figure 2a), and the TSB was 8.59–9.71 g·tree⁻¹ (Figure 2c). The TRB followed the order 3:7 > 0:10 > 5:5 > 7:3 > 10:0, and there were no significant differences among the 3:7, 0:10 and 5:5 ratios (p > 0.05). Conversely, the TSB was largest under the NH₄⁺-N-only treatment and followed the order 10:0 > 5:5 > 7:3 > 3:7 > 0:10. TRB accumulation was higher under the treatment with a high NO₃⁻-N concentration than that with a high NH₄⁺-N concentration. However, the TSB in *C. lanceolata* tended to accumulate at high NH₄⁺-N concentrations and homogeneous N supply.



Figure 2. Effects of different NH_4^+ -N and NO_3^- -N ratios on the TRB (**a**,**b**) and TSB (**c**,**d**) of the two tree species. Different lowercase letters indicate that TRB and TB were significantly different under different N forms (p < 0.05).

The TRB of *S. superba* seedlings ranged from 0.34 to 0.56 g·tree⁻¹ (Figure 2b) and the TSB was $3.12-4.10 \text{ g} \cdot \text{tree}^{-1}$ (Figure 2d). The TRB followed the order 7:3 > 5:5 > 10:0 > 0:10 > 3:7, while the TSB followed the order 5:5 > 3:7 > 7:3 > 0:10 > 10:0. The TRB accumulation in *S. superba* was higher under the treatment with a high NH₄⁺-N concentration and homogeneous N supply than under the treatment with a high NO₃⁻-N concentration, while the TSB tended to accumulate under the treatments with homogeneous and medium heterogeneous N supply. The environment with highly heterogeneous N supply was the most unfavorable for the accumulation of TSB in *S. superba*.

3.4. Effects of Different N Forms on Root Abundance in the Two Tree Species

The SRL of *C. lanceolata* followed the order 0:10 > 5:5 > 7:3 > 3:7 > 10:0 (Figure 3a) and was the highest under the NO₃⁻-N-only treatment, which was not significantly different from that under the control treatment (5:5) (p > 0.05) but was significantly higher than that

under the other three treatments (p < 0.05). The RTD of *C. lanceolata* followed the order 3:7 > 5:5 > 10:0 > 7:3 > 0:10 (Figure 3c). There were no significant differences between the 3:7 and 5:5 ratios, but both of these treatments resulted in a significantly higher RTD than the other three treatments. In contrast, the RSR followed the order 0:10 > 3:7 > 7:3 > 5:5 > 10:0 (Figure 3e), showing higher values under the treatment with a high NO₃⁻-N concentration.



Figure 3. Effects of different NH_4^+ -N and NO_3^- -N ratios on SRL (**a**,**b**), RTD (**c**,**d**) and RSR (**e**,**f**) between the two tree species. Different lowercase letters indicate that the SRL, RTD and RSR were significantly different under different N forms (p < 0.05).

The SRL of *S. superba* followed the order 5:5 > 0:10 > 3:7 > 10:0 > 7:3 (Figure 3b), showing a higher value under the treatment with a homogeneous N supply and a high NO₃⁻-N level. The difference between the 5:5 and 0:10 ratios was not significant, but both of them had a significantly higher SRL than the other three treatments. The RTD of *S. superba* followed the order of 10:0 > 7:3 > 3:7 > 0:10 > 5:5 (Figure 3d), showing that the heterogeneous N supply resulted in a higher RTD than the homogeneous N supply. Moreover, the treatments with a high NH₄⁺-N level resulted in a higher RTD than the treatments with a high NO₃⁻-N level. The RSR followed the order 7:3 > 10:0 > 0:10 > 5:5 > 3:7 (Figure 3f) and was highest under the treatments with high NH₄⁺-N.

3.5. Effects of Different N Forms on Aboveground Growth in the Two Tree Species

After 160 days of cultivation, the Δ H of *C. lanceolata* and *S. superba* seedlings was 10.2–17.7 cm and 7.0–10.5 cm (Figure 4a), respectively, and the Δ GD was 3.08–4.35 mm and



2.18–3.62 mm (Figure 4b), respectively. It can be seen that the Δ H and Δ GD of *C. lanceolata* were larger than those of *S. superba*.

Figure 4. Effects of different NH_4^+ -N and NO_3^- -N ratios on ΔH (**a**) and ΔGD (**b**). Data are expressed as the mean \pm standard error (SE). Different lowercase letters on the columns indicate significant differences among the treatments.

Under different N forms, the Δ H of *C. lanceolata* followed the order 5:5 > 7:3 > 3:7 > 10:0 > 0:10 and was largest under the control treatment (Figure 4a), which was 9.05–73.20% larger than that under the other treatments. The Δ H of *C. lanceolata* was greater under the homogeneous N supply than under the heterogeneous N supply, and it was smallest under the NH₄⁺-N-only and NO₃⁻-N-only treatments. The Δ H of *S. superba* followed the order 5:5 > 3:7 > 0:10 > 7:3 > 10:0 and was largest under the control treatment (Figure 4a), which was 12.93–49.05% larger than that under the other treatments. The Δ H of *S. superba* was greater under the homogeneous N supply than the heterogeneous N supply, and it was greater under the treatment with a high NO₃⁻-N concentration than under the treatment with a high NH₄⁺-N concentration. In the two tree species, seedling height initially increased and then decreased with the increase in NO₃⁻-N in the nutrients.

The Δ GD of *C. lanceolata* followed the order 7:3 > 5:5 > 10:0 > 0:10 > 3:7 and was largest at the ammonium to nitrate ratio of 7:3 (Figure 4b), which was 15.09–41.26% larger than that under the other treatments. The Δ GD of *S. superba* followed the order 0:10 > 3:7 > 7:3 > 5:5 > 10:0 (Figure 4b). It was largest at an ammonium to nitrate ratio of 0:10, which was 8.92–66.51% larger than that under the other treatments. Overall, *C. lanceolata* tended to increase the ground diameter of the seedlings under the treatment with a high NH₄⁺-N concentration and a homogeneous N supply, whereas *S. superba* preferred to increase the ground diameter under the treatment with a high NO₃⁻-N concentration.

3.6. Redundancy Analysis of Ammonium and Nitrate N Concentrations with Root and Growth Parameters

We used N forms as the environmental factor variables, and a redundancy analysis was performed on the roots' morphological and growth parameters of *C. lanceolata* (Figure 5a) and *S. superba* (Figure 5b). A smaller angle between them (close to 0°) indicated that the



positive correlation was significant, and a larger angle (close to 180°) indicated that the negative correlation was significant.

Figure 5. Redundancy analysis of the responses of roots' morphological and growth parameters to different ratios of the N forms. The proportions explained by Axis 1 and Axis 2 in (**a**) are 27.91% and 24.14% and those in (**b**) are 12.21% and 44.30%, respectively. Solid blue lines indicate the parameters. Solid red lines indicate NH_4^+ -N and NO_3^- -N. Abbreviations for the parameters are as follows: TRL, total root length; TRSA, total root surface area; TRV, total root volume; RAD, roots' average diameter; TRB, total root biomass; TSB, total seedling biomass; SRL, specific root length; RTD, root tissue density; RSR, root-to-shoot ratio; ΔH , height increment; ΔGD , ground diameter increment.

Figure 5a shows that the RAD, Δ GD and TSB of *C. lanceolata* had a positive correlation with NH₄⁺-N and a negative correlation with NO₃⁻-N. However, the Δ H and RTD decreased along the Y-axis, and the correlation with NH₄⁺-N was not significant. In contrast, the RSR, TRB, SRL, TRL, TRSA and TRV of *C. lanceolata* had a positive correlation with NO₃⁻-N and a negative correlation with NH₄⁺-N. Among these, the RSR had the strongest positive correlation with NO₃⁻-N. The RAD and RTD had a negative correlation with SRL.

Figure 5b shows that the RSR, RAD, TRB and RTD of *S. superba* had a positive correlation with NH₄⁺-N and a negative correlation with NO₃⁻-N. Conversely, the Δ GD, Δ H and TSB of *S. superba* had a positive correlation with NO₃⁻-N and a negative correlation with NH₄⁺-N. However, the correlations of TRSA, TRL and TRV with NH₄⁺-N and that of SRL with NO₃⁻-N were not significant. Among these, the Δ GD had the strongest positive correlation with NO₃⁻-N. The RAD and RTD had a negative correlation with SRL.

4. Discussion

4.1. Effects of Different N Forms on Root Morphology in Different Tree Species

When trees grow for a long period of time in a soil environment with a certain ratio of the N forms, they gradually form a growth pattern adapted to this soil environment, which is generally the coordinated effect of the aboveground and the underground parts. As the root is in direct contact with the soil for nutrient exchange, the change in root morphology is the intuitive embodiment of and basis for understanding the growth of forest trees. The results of this study showed that the TRL, TRSA and TRV of C. lanceolata were positively correlated with NO₃⁻-N (Figure 5a) and that the RAD was positively correlated with NH₄⁺-N. The TRL, TRSA, TRV and RAD of *S. superba* tended to be greater at high NH₄⁺-N concentrations, but the correlation was not significant (Figure 5b). Under a homogeneous N supply, the TRL, TRSA and TRV of *S. superba* were largest, while the RAD was smallest. *C. lanceolata* tended to grow more slender roots under the treatment with a high $NO_3^{-}-N$ concentration, while the roots of *S. superba* were extended under the treatment with a high NH₄⁺-N concentration and an ammonium to nitrate ratio of 5:5. This is consistent with the results showing that *C. lanceolata* grows more slender roots in NO₃⁻-N patches and *S.* superba grows more slender roots in NH_4^+ -N patches [8]. When C. lanceolata and S. superba were mixed in an environment with heterogenous nutrients, S. superba took advantage of

the compensatory strategy of a vertical growth direction in its fine roots, and alleviated the strong competition for nutrients because of the different level of soil colonization and the niche differentiation of fine roots of the two species [28,29], which was conducive to the coordination of the relationship between the two species [30]. We infer that this opposite root growth response resulted from complementary patterns in the absorption strategies of

different N forms in C. lanceolata and S. superba seedlings. The nitrogen-seeking strategy of tree roots will change with changes in the environment and in their adaptive mechanism. The environmental factors affecting the growth of forest roots mainly include the concentration of soil nutrients (such as N), the soil's pH value, and the soil's temperature and humidity. The strategies of forest trees for obtaining nitrogen also vary according to the forest's age, which will directly or indirectly affect the nitrogen uptake of trees [31]. For example, in an environment of mild nitrogen deficiency, the TRL of plants increased, while moderate nitrogen deficiency and excessive nitrogen supply inhibited the growth of the root system [32]. In acidic environments, NH_4^+ -N is the main N source for plants and is usually more readily available than NO₃⁻-N, especially in coniferous forests, where many conifers tend to absorb NH_4^+ -N [33]. Under drought stress, the uptake of NH₄⁺-N in different organs of *C. lanceolata* seedlings was significantly higher than that of NO_3^{-} -N, showing a preference for NH_4^{+} [34]. The growth and nutrient acquisition of plant roots are affected and restricted by many factors. When trees are under nutrient, water and other stress conditions, the root system will produce a series of adaptive changes in its morphological structure to obtain the limited resources and adapt to the ecological strategy of overcoming adversity through self-regulation [35]. Numerous studies have shown that in nutrient-limited environments, plants mainly use strategies such as increasing the roots' length and decreasing the roots' diameter, which expand the growth range of roots to obtain more nutrients for growth [36–38]. Nitrogen deposition causes the growth rate of the TRL and TRV of *C. lanceolata* to be faster than that of the RSA and RAD, in which the root system is elongated and dilated [39]. In another study, nitrogen deposition caused the root system of *S. superba* seedlings to show an increasing trend in the TRL, RAD, TRSA and TRV, and the root system was thick and dilated [40]. The results of this study showed that the roots of *C. lanceolata* seedlings were slender and dilated under the treatment with a high NO_3^{-} -N concentration, while the roots of *S. superba* seedlings were sturdy and dilated under the treatment with a high NH₄⁺-N concentration.

4.2. Effects of Different N Forms on Biomass and Root Abundance in Different Tree Species

The root biomass of plants is one of the manifestations of the amount of nutrients and water they absorb, and the allocation of aboveground and underground biomass also reflects the nutrient uptake and distribution in plants. The results of this study showed that in C. lanceolata, the accumulation of root biomass was higher under the treatment with a high $NO_3^{-}-N$ concentration and, the total accumulation of seedling biomass was higher under the treatment with a high NH_4^+ -N concentration (Figure 5a). However, the accumulation of root biomass in S. superba was higher under the treatment with a high NH₄⁺-N concentration. The total biomass was highest under the treatment with a homogeneous N supply, and accumulation was relatively high under the treatment with a high NO_3^{-} -N concentration (Figure 5b). In a limited-resource environment, when plants are limited by nutrients, they allocate biomass to the roots and reduce the allocation to aboveground biomass [41]. Under low nutrient conditions, C. lanceolata seedlings increased the amount of nutrient absorbed, mainly by altering the root structure rather than by allocating more nonstructural carbohydrates to the roots, while nutrient alleviation driven by nitrogen addition resulted in more carbohydrate being allocated to the aboveground organs, resulting in the accumulation of structural carbohydrates in the aboveground parts [42]. This means that the addition of nitrogen leads to a reduction in fine root biomass in *C. lanceolata* seedlings [43]. The same study found that there was a significant positive correlation between the biomass of fine roots and the content of NH_4^+ -N in a S. superba plantation [44]. The roots of S. superba from a heterogeneous N environment

showed greater dry biomass and N absorption efficiency than those from a homogeneous N environment [45]. This is contrary to the results of this study, which may be a result of the differences in the provenance of the *S. superba* specimens, as they may have differences in their N uptake.

As important indicators of roots' morphological characteristics, the SRL and RTD reflect the ability and efficiency of plants to allocate biomass to roots to absorb nutrients and water. In general, the larger the SRL and the smaller the root diameter, the stronger the ability of the root system to absorb nutrients and water [46]. To a certain extent, RTD can be considered a reflection of root tissue's stretching force. Generally, the greater the RTD, the greater the stretching force of the root tissue [47]. Numerous studies have shown that SRL has a negative correlation with RTD and RAD [18,48]. After N application, *Castanopsis fabri* adopted a rapid absorption strategy by increasing the SRL and the growth rate of roots, while *Castanopsis carlesii* adopted a relatively conservative resource absorption strategy by increasing the tissue density of fine roots [49]. The N deposition treatment significantly increased the fine root length of *S. superba* but had no significant effect on the tissue density [50]. In this study, we found that the SRL of *C. lanceolata* and *S. superba* were negatively correlated with RTD (Figure 5a,b). Therefore, we speculated that *C. lanceolata* and *S. superba* adopt an expansion strategy of increasing their SRL and reducing their RTD in an environment with a high NO₃⁻-N concentration.

The RSR is one of the indicators used to measure biomass allocation in plants. Numerous studies have shown that in a normal growth environment, the aboveground and underground parts of plants have synergistic growth, and biomass accumulation is also carried out synergistically [51]. Under stresses such as drought, plants allocate more biomass to the roots and increase the RSR to enhance the absorption capacity of water and other underground resources [41,52]. A previous study found that drought reduced fine root biomass and increased the RSR [53]. This study showed that the RSR of C. lanceolata was positively correlated with NO_3^{-} -N but negatively correlated with NH_4^{+} -N, which was consistent with the pattern shown by root biomass, and the RSR was largest under the treatments with NO₃⁻-N only and an ammonium to nitrate ratio of 3:7. The RSR of *S. superba* showed the opposite pattern and was consistent with the pattern shown by root biomass (Figure 5a,b), and the RSR was largest under the treatment with an ammonium to nitrate ratio of 7:3 and under the NH₄⁺-N-only treatment. Therefore, the results of this study showed that the allocation of biomass to aboveground and underground parts in C. lanceolata and S. superba seedlings responds differently to different N forms, and the N uptake strategy was adjusted by increasing or decreasing the RSR. Under the treatments with high NO₃⁻-N concentrations, C. lanceolata increased the RSR to obtain more N sources, while S. superba increased the aboveground biomass by reducing the RSR, but the opposite was true at high NH_4^+ -N concentrations. In a study of fine roots in hybrid poplar plantations, it was found that soil nutrient deficiencies caused by continuous cropping may lead to an increase in plants' carbon input to the roots [54]. Therefore, we inferred that a high $NO_3^{-}-N$ concentration may be a limiting nutrient for *C. lanceolata* seedlings. Correspondingly, N sources with high NH_4^+ -N concentrations are more suitable for the aboveground growth of *C. lanceolata* seedlings, and N sources with high NO₃⁻-N concentrations are more suitable for the development of aboveground parts in *S. superba*.

4.3. Effects of Different N Forms on the Growth of Different Tree Species

As one of the limiting elements of plant growth, N occurs in different forms in natural soil, and the different forms of N occur in different ratios, which will have different effects on plant growth. It is believed that the sole application of NH_4^+ -N is prone to inducing NH_4^+ toxicity, which restrains plant growth [55,56]. Moreover, many plants prefer mixed NH_4^+ -N and NO_3^- -N over a single N source [57]. In contrast, some studies have also found that the growth of the underground and aboveground parts of plant seedlings is positively correlated with treatments with NH_4^+ -N only [5]. The results of this study showed that the Δ H of *C. lanceolata* seedlings showed higher values under ammonium to nitrate ratios of 5:5

and 7:3, and Δ GD showed higher values under ammonium to nitrate ratios of 7:3 and 5:5. The Δ H of *S. superba* was larger under ammonium to nitrate ratios of 5:5 and 3:7, and the Δ GD was higher under ammonium to nitrate ratios of 0:10 and 3:7, which both had positive correlations with NO₃⁻-N and TSB (Figure 5b). Overall, our study supports the idea that *C. lanceolata* and *S. superba* seedlings prefer to develop aboveground parts under mixed NH₄⁺-N and NO₃⁻-N. Between the two, *C. lanceolata* seedlings are more inclined to absorb NH₄⁺-N for aboveground growth, which is more suitable for growth under ammonium to nitrate ratios of 5:5 and 7:3. Conversely, *S. superba* seedlings are more inclined to absorb NO₃⁻-N, which is more suitable for aboveground growth under ammonium nitrate ratios of 5:5, 3:7 and 0:10. The Δ GD of *S. superba* seedlings was largest under the ratio of 0:10, which may be because the application of NO₃⁻-N alone is beneficial for the growth in the woody diameter of *S. superba*.

Because they are timber species, it is also worth considering the aboveground growth of *C. lanceolata* and *S. superba*. Because of differences in their leaves, conifer and broadleaf species respond differently to different N forms [58]. Studies suggest that conifer species tend to absorb NH_4^+ -N, and broadleaf species tend to absorb NO_3^- -N [58,59]. This study supports this hypothesis, which proposes that *C. lanceolata* seedlings prefer NH_4^+ -N over NO_3^- -N for aboveground growth, while the opposite is true for *S. superba*. It is worth noting that TRL, TRSA, TRV, TSB, Δ H and SRL all showed maximum values in *S. superba* under an ammonium to nitrate ratio of 5:5. This means that both the aboveground and underground parts grow simultaneously under a homogeneous N supply. As a result, we speculate that the roots of *S. superba* seedlings may increase their length within the root system to obtain nutrients and use nutrients for seedlings' growth in terms of height and leaves to obtain more nutrients through photosynthesis under a homogeneous N supply [60].

5. Conclusions

In conclusion, the roots of *C. lanceolata* tended to be slender and accumulate more biomass under the treatment with a high NO_3^- -N concentration, while the opposite was true for *S. superba*. Under the high NO_3^- -N concentration, the roots of the two tree species adopted the expansion strategy of increasing the SRL and reducing the RTD. Moreover, *C. lanceolata* allocated more biomass to the root system at the high NO_3^- -N concentration, but *S. superba* allocated more biomass to the root system at the high NH_4^+ -N concentration. Compared with the treatments with a single N form, the mixed NH_4^+ -N and NO_3^- -N treatments were more conducive to the growth and biomass accumulation of the two tree species. *C. lanceolata* tends to grow under high NH_4^+ -N concentrations, while *S. superba* tends to grow under high NH_4^+ -N concentrations, while *S. superba* tends to grow under high NO_3^- -N concentrations. *C. lanceolata* grows better under NH_4^+ -N: NO_3^- -N ratios of 5:5 and 7:3, while *S. superba* grows better under NH_4^+ -N: NO_3^- -N ratios of 5:5 and 7:3, while *S. superba* for cultivating seedlings.

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