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Vertical dynamics in subterranean ecology: thinning and water-nitrogen additions drive multilayered responses in soil-fine root systems of Populus tomentosa plantations

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Abstract

Purpose

Fine roots and soil properties show distinct vertical patterns, reflecting their coupled responses to thinning and water-fertilizer management. This study aimed to elucidate soil-root interactions and provide insights for the sustainable management of plantations.

Methods

A split-plot design was established with three thinning intensities (no thinning, moderate, heavy) and three water-nitrogen treatments (control, irrigation, irrigation + nitrogen). Soil profiles (0–6 m) and fine roots were sampled to assess changes in soil moisture, nutrient dynamics, and fine root traits. Multivariate analyses were used to identify key regulatory drivers.

Results

Soil water content (SWC) peaked at 300–400 cm and was sensitive to management in the 20–500 cm layer. Thinning and irrigation increased SWC, whereas water-nitrogen input reduced it in mid-depth layers. Thinning enhanced nitrogen accumulation, while water-nitrogen input offset nitrogen loss but increased nitrate leaching risk. Fine root biomass density was highest in the 0–20 cm layer, with deeper layers remaining stable. Water-nitrogen addition increased specific root area, with SWC as the main determinant after thinning, and both phosphorus and SWC driving responses under fertilization.

Conclusion

Thinning improved water availability but constrained nutrients, while water-nitrogen input shifted fine roots toward an acquisitive strategy, highlighting management-specific soil-root interactions.

1. Introduction

Fine roots, as the primary organs responsible for water and nutrient acquisition, play a crucial role in tree growth and ecosystem productivity through their spatial distribution and morphological plasticity (Zou et al., 2022; Tan et al., 2023). Serving as the key interface between plants and soil, and as the primary conduits for soil resource uptake, fine roots are indispensable for resource acquisition within forest ecosystems (Xi et al. 2013; Kramer-Walter and Laughlin 2017). Their critical ecological functions have sustained long-standing research interest in belowground processes (Jackson et al. 1997; Gill and Jackson 2000; Reich et al. 2014; Bergmann et al. 2020; Kou et al. 2025). In arid and semi-arid regions, the exploitation of deep soil resources (> 1 m) is particularly crucial for tree survival (Laclau et al. 2001; Di et al. 2018; Germon et al. 2020; Henriksson et al. 2021; Zhu et al. 2023). Nevertheless, studies

examining deep soil characteristics and the vertical distribution of fine roots in plantations remain limited.

The spatial distribution and physiological functions of fine roots are strongly influenced by plantation management practices, such as thinning, irrigation, and nitrogen addition, which regulate belowground resource acquisition strategies by modifying stand structure and soil conditions (He et al. 2022; Pang et al. 2022; Yang et al. 2025b). Thinning reduces stand density and alleviates belowground competition, thereby improving the availability of light, water, and nutrients, which promotes the proliferation of fine roots in the surface soil (< 1 m) (Qin et al., 2024; Zhao et al., 2024). However, most existing studies have focused on soil layers within 1 m, leaving a knowledge gap regarding the spatial heterogeneity and functional adaptability of fine roots in deeper layers (Pang et al. 2022; Zhao et al. 2024). Similarly, water and nitrogen addition disrupt the original carbon-water-nitrogen balance, inducing phenotypic plasticity in fine roots (Pregitzer et al. 1993; Wang et al. 2021a; He et al. 2022). Therefore, elucidating the dynamics of fine root distribution down to 6 m under water and nitrogen addition is theoretically significant for understanding deep resource acquisition strategies and provides a scientific basis for optimizing water and fertilizer management in plantations.

Fine root plasticity represents a core adaptive strategy to environmental heterogeneity, manifested through coordinated adjustments in morphology, biomass, and physiological function (Kong et al. 2017; Zhang et al. 2024). This plasticity enables plants to optimize the cost-benefit balance of root system construction, thereby enhancing survival competitiveness (Lima et al. 2010), and can be conceptualized as an "investment-benefit" decision guided by ecological stoichiometry (Peng et al. 2017). Within plantation management contexts, thinning and water-nitrogen addition influence fine root plasticity via distinct pathways: thinning promotes the expression of fine root potential by reducing competition (Pang et al. 2022; Zhao et al. 2024), whereas water-nitrogen addition directly induces adaptation by modifying resource availability (Coleman 2007; Dou et al. 2022; Zhang et al. 2022). Consequently, fine roots adopt a gradient strategy along the soil profile, exhibiting a "foraging type" in topsoil (high specific root length, high root tip density) and a "conservative type" in deeper soil layers (larger diameter, reduced branching, extended lifespan) (Wang et al. 2016; Zhou et al. 2022). Although soil water and nutrient conditions are key drivers of fine root dynamics (Ellsworth and Sternberg 2019; Liu et al. 2024), management interventions can facilitate root penetration into deeper layers by improving subsurface conditions (Pang et al. 2022; He et al. 2022). However, a significant knowledge gap persists regarding the interactive network linking "management practices-soil environment-fine root plasticity," particularly in deep soil layers.

The North China Plain, one of the largest regions globally with concentrated artificial forest plantations, hosts over 3 million hectares of poplar plantations. Nevertheless, this region faces severe ecological challenges, including declining groundwater levels leading to the formation of dry soil layers (Liu et al. 2022), and progressive depletion of organic matter in surface soils, which reduces fertility (Zhang et al. 2018; He et al. 2021; Yang et al. 2025a). Investigating the effects of management practices on deep soil-root interactions is therefore of dual significance: theoretically, it advances understanding of deep

resource acquisition strategies in arid-region trees; practically, it provides a foundation for sustainable management models emphasizing water conservation, soil nourishment, and efficiency enhancement. In particular, elucidating the response patterns of the soil-root system in deep layers under short-term management interventions can directly inform precision water and fertilizer strategies and promote efficient use of belowground ecological space in *Populus plantations* on the North China Plain.

Populus tomentosa, a major native tree species widely cultivated in plantations on the North China Plain, delivers substantial ecological, economic, and social benefits (Zhu et al. 2024a; Wang et al. 2025). This study assessed *Populus tomentosa* plantations to evaluate the short-term impacts of different management practices on soil properties and fine root plasticity through varying thinning intensities and water-nitrogen addition treatments. The objectives were: (1) to assess the short-term effects of thinning and water-nitrogen addition on soil moisture and nutrient properties across the 0–6 m soil profile; (2) to elucidate the responses of fine root vertical distribution and morphological plasticity to management interventions; and (3) to investigate the interrelationships between soil properties and fine root traits. We hypothesized that: (1) thinning and water-nitrogen addition would significantly improve soil fertility, with effects exhibiting distinct vertical gradients (He et al. 2021; Liu et al. 2022); and (2) water-nitrogen addition would induce "foraging-type" plasticity in fine roots, whereas thinning would more likely trigger "conservative-type" plasticity, with this differential response positively associated with the degree of soil resource heterogeneity (Wang et al. 2016; Zhou et al. 2022; Pang et al. 2022; Zhao et al. 2024).

2. Materials and methods

2.1. Study site and experimental plantations

The research was conducted in 2023 at a state-owned forest farm located in Gaotang County, Liaocheng City, Shandong Province, China (36° 48'N, 116° 05'E; altitude of approximately 30 m). The area is part of the warm temperate semi-arid monsoon region of the northern hemisphere, characterized by four distinct seasons and abundant sunshine. Rainfall is concentrated in July and August, with an average annual precipitation of 553 mm and an average temperature of 13.9°C. The topography of the study site consists primarily of plains, with the water table located 6 to 9 meters below the surface (Liu et al. 2022). The soil is classified as sandy loam. Before afforestation, the soil contained 3.34 g·kg^{-1} organic matter, 0.23 g·kg^{-1} total nitrogen, and 4.92 mg·kg^{-1} available phosphorus (He et al. 2021).

The experimental plantation was established in the spring of 2016 using 2-year-old hybrid poplar saplings (*P. tomentosa* × *P. bolleana*) × (*P. alba* × *P. glandulosa*). The saplings had a breast height diameter of 2.12–3.51 cm (mean 2.68 cm) and a height of 2.60–3.62 m (mean 3.30 m). Trees were planted at 2 m× 3 m spacing, corresponding to a density of 1,666 trees ha^{-1}. Each tree received 70 g of basal fertilizer containing ≥ 31% N + P_2O_5 + K_2O (14-12-5) and ≥ 15% organic matter (OM).

2.2 Experimental design

A split-plot design was employed for the experiment. In April 2022, thinning was performed in the experimental forest with two intensities: alternate row thinning (50% thinning, spacing adjusted to 2 m × 6 m, T50) and alternate row and tree thinning (75% thinning, spacing adjusted to 4 m × 6 m, T75), along with an unthinned control plot. Within each thinning intensity, three water-nitrogen treatments were applied: irrigation with nitrogen (WN), irrigation only (W), and no irrigation or nitrogen addition (CK). Following thinning, drip irrigation systems (Netafim, Israel) were installed with drippers spaced 50 cm apart at a flow rate of 1.6 L h^{-1}, positioned 30 cm from both sides of the tree row. Irrigation scheduling was based on the quantitative relationship between *Populus tomentosa* growth and soil water availability (Xi et al. 2016), triggered when soil water potential at 20 cm below the dripper reached − 20 kPa (79% field capacity). Irrigation commenced in early April and ended before the rainy season in late June. Nitrogen was applied as urea (46% N) at 156 g $tree^{-1}$ $year^{-1}$ in six applications at 20-day intervals, corresponding to the species' growth rhythm (Wang et al. 2015). Routine weeding and pest control were conducted throughout the experimental period. To reduce the effects of light and soil heterogeneity, NT, T50, and T75 areas were divided into blocks along the north-south axis. Within each block, the three water-nitrogen treatments were randomly assigned, with plot sizes ranging from 16 to 64 trees, and protective rows established on the east and west sides.

2.3 Acquisition and measurement of soil and root samples

Fine roots were sampled using soil cores. In October 2023, five standard trees (n = 5) were selected per plot under five treatments: NT, T50, T75, T75W, and T75WN. Soil cores (0.0008836 m^3) were collected 30 cm east of each tree to a depth of 6 m, divided into 20 cm increments from 0-100 cm and 100 cm increments from 100–600 cm, yielding 10 layers. Each soil layer was weighed in the field to obtain fresh weight (W). Three root-free subsamples were taken: one dried at 105°C to determine moisture content (W1 and W2), while the remaining two were air-dried for nutrient analysis and stored at − 4°C for inorganic nitrogen measurements. Soil water content (SWC, %) was calculated as:

$$SWC = \frac{W_1 - W_2}{W_2} \times 100\%$$

1

All roots were washed via wet sieving to remove soil and organic material. Live roots were separated from dead roots based on color, flexibility, and breakage resistance, and only roots < 2 mm in diameter were considered fine roots (Zou et al. 2022; Tan et al. 2023). Roots were scanned (Epson Twain Pro, 400 dpi) without overlap, and diameter, surface area, volume, and length were measured using WinRHIZO (Regent Instruments Inc., Quebec, Canada). Fine roots were then dried at 75°C to constant weight to determine biomass (FRB). Morphological traits included mean root diameter (MRD), fine root biomass density (FRBD), fine root length density (FRLD), fine root tissue density (FRTD), specific root surface area (SRA), and specific root length (SRL), calculated as:

$$\mathrm{FRBD} = FRB/SV$$

2

$$\mathrm{FRLD} = FRL/SV$$

3

$$\mathrm{FRTD} = FRB/FRV$$

4

$$\mathrm{SRA} = FRA/FRB$$

5

$$\mathrm{SRL} = FRL/FRB$$

6

Where SV represents soil volume, FRL is root length, FRV is root volume, and FRA is root surface area.

Soil samples, after root and stone removal, were air-dried and sieved (100-mesh, 0.15 mm; 20-mesh, 0.85 mm) for nutrient analysis. Samples stored at − 4°C were used for NO_3^--N and NH_4^+-N determination. Organic carbon was measured by the potassium dichromate external heating method, available phosphorus (AP) via the molybdenum–antimony anti-colorimetric method, and total nitrogen (TN) and total phosphorus (TP) using concentrated H_2SO_4–$HClO_4$ digestion in a fully automated analyzer (SMARTCHEM 450, AMS Alliance, France). SOM was calculated as organic carbon × 1.724 (Zhang et al. 2022). NO_3^--N and NH_4^+-N were extracted with 1 M KCl and measured via UV spectrophotometry and indophenol blue colorimetry, respectively.

2.4 Data analysis

Data were organized in Excel 2016. Homogeneity of variance and normality were assessed using Levene's test and the Kolmogorov-Smirnov test, respectively. Non-normal data were transformed to meet ANOVA assumptions. Two-way ANOVA evaluated the effects of thinning (T), water and nitrogen addition (W), soil depth (D), and their interactions (T×D, W×D) on soil properties and fine root traits. One-way ANOVA tested differences among treatments within the same soil layer, with post hoc Tukey HSD comparisons (α = 0.05).

Pearson correlations were used to assess relationships among fine root traits (SPSS 25, IBM SPSS Statistics, IBM Corporation, Armonk, NY, USA). Redundancy analysis (RDA) was conducted in CANOCO 5 (Microcomputer Power, Ithaca, NY, USA) to evaluate the relative importance of soil properties on fine root variation. Based on the plant economics spectrum theory (Reich et al. 2014; Kong et al. 2017; Weigelt et al. 2023), MRD, FRBD, and FRTD were classified as "conservative" strategy indicators, reflecting substantial carbon allocation to robust tissues, whereas FRLD, SRA, and SRL represented the "acquisitive" strategy, reflecting minimal carbon investment for rapid resource uptake. Standardized data

were used to construct and analyze structural equation models (SEM) in AMOS 20.0 (IBM SPSS Amos, IBM Corporation, Armonk, NY, USA). Figures were generated in Origin 2023 (Origin Lab Corporation, Northampton, MA, USA).

3 Result

3.1 Soil moisture content

Soil water content (SWC) exhibited significant depth variability ($P < 0.05$) (Table S1), with peak SWC observed at depths of 300–400 cm across all treatment groups (Fig. 1). The vertical distribution of SWC showed sensitivity to silvicultural measures in the 20–500 cm soil layer, while the 0–20 cm and 500–600 cm layers remained relatively stable (Fig. 1). Two-way ANOVA revealed significant effects of thinning intensity and water-nitrogen addition on SWC ($P < 0.05$) (Table S1). Both thinning and water input significantly increased soil water content, with a particularly pronounced effect observed in the 80–400 cm soil layer (Fig. 1). However, the combined input of water and nitrogen resulted in a decrease in SWC, with this effect most pronounced in the 100–200 cm soil layer (Fig. 1).

3.2 Soil nutrients

Soil organic matter (SOM) was significantly influenced by thinning intensity, water-nitrogen addition, and soil depth ($P < 0.05$) (Table S1). Across the soil profile, SOM exhibited a nonlinear response to thinning intensity, with the highest values observed under moderate thinning (T50) followed by the unthinned control (NT), and the lowest in high-intensity thinning (T75) (Fig. 2). In low-density stands (T75), the application of water and nitrogen significantly enhanced SOM content, with values following the order T75WN > T75W > T75 (Fig. 2).

Soil total nitrogen (TN) content was significantly affected by thinning and water-nitrogen addition ($P < 0.05$) (Table S1). Thinning promoted TN accumulation, whereas water addition reduced TN content; the combined input of water and nitrogen mitigated this reduction. However, this mitigation was significant only in the 0–20 cm soil layer ($P < 0.05$) (Fig. 3). Ammonium nitrogen (NH_4^+-N) and nitrate nitrogen (NO_3^--N) contents were significantly affected by thinning intensity, water-nitrogen addition, and soil depth ($P < 0.05$). Among these, the interaction between water-nitrogen addition and soil depth significantly influenced inorganic nitrogen ($P < 0.05$), whereas the interaction between thinning intensity and soil depth was significant only for nitrate nitrogen ($P < 0.05$) (Table S1). Thinning significantly increased ammonium nitrogen contents in the 0–40 cm, 200–300 cm, and 500–600 cm soil layers (Fig. S1), and markedly increased nitrate nitrogen contents at 100–200 cm, 300–400 cm, and 500–600 cm (Fig. S2). Water addition promoted the leaching and downward movement of ammonium nitrogen, whereas combined water and nitrogen addition mitigated nitrogen loss and enhanced accumulation in deeper soil layers (300–600 cm) (Fig. S1). Nitrate nitrogen exhibited greater stability in the 0–60 cm surface layer, with no significant differences detected among the T75, T75W, and T75WN treatments. The combined addition of water and fertilizer (T75WN) promoted nitrate nitrogen accumulation in the 60–100 cm and 300–500 cm soil layers, thereby increasing the potential risk of leaching (Fig. S2).

Soil total phosphorus (TP) was significantly affected by thinning intensity, soil depth, and their interaction ($P < 0.05$), and was also significantly regulated by water-nitrogen addition ($P < 0.05$) (Table S1). In the 0–20 cm, 60–80 cm, and 100–200 cm soil layers, TP contents under the T75W and T75WN treatments were significantly higher than under T75, with the most pronounced increase occurring in the 100–200 cm layer, where TP increased by 196.82% and 59.23%, respectively, compared to T75 (Fig. 4). Soil available phosphorus (AP) contents were also significantly affected by thinning intensity, soil depth, and their interaction ($P < 0.05$) (Table S1). High-intensity thinning (T75) significantly reduced AP contents in the 0-400 cm soil layer, whereas in the 200–400 cm layer, AP contents followed the trend T50 > NT > T75 with increasing thinning intensity (Fig. 5).

3.3 Fine root plasticity

Thinning treatments were not found to significantly influence the short-term plasticity of most fine root traits. However, soil depth was observed to play a critical role in regulating fine root trait variation across experimental forests subjected to three thinning intensities. Analysis of variance indicated that soil depth significantly influenced several key metrics, including mean root diameter (MRD), fine root biomass density (FRBD), and fine root length density (FRLD) ($P < 0.05$). Peak values of FRBD and FRLD were recorded in the top 0–20 cm soil layer for all treatments, with mean values of 456.83 $g \cdot m^{-3}$ and 2,655,151.30 $cm \cdot m^{-3}$, respectively. In contrast, these indices remained relatively stable in the deeper 200–600 cm soil layer (Fig. S3). MRD initially increased with soil depth before declining, with peak depths for the T50 and T75 treatments occurring in shallower soil layers compared to the control (NT). Under the NT treatment, specific root area (SRA) and specific root length (SRL) attained their maximum values in the 60–80 cm soil layer, whereas the T50 and T75 treatments peaked in the 80–100 cm soil layer (Fig. 6). These results indicate that fine root distribution and morphology are strongly stratified along the soil profile and are influenced primarily by soil depth rather than short-term thinning intensity.

The water and nitrogen addition experiment conducted under T75 high-intensity thinning exhibited limited short-term effects on most fine root functional traits. A significant increase in specific root area (SRA) was the only notable change observed ($P < 0.05$). However, the interaction between water-nitrogen addition and soil depth was found to significantly affect the vertical distribution patterns of SRA and SRL ($P < 0.05$) (Fig. 6). Fine root morphological traits displayed distinct strategic differentiation under different management interventions. In the T75WN treatment, SRA and SRL remained stable within the 0-400 cm soil layer but increased sharply at 400–500 cm depth. In contrast, the T75W and T75 treatments primarily promoted increases in SRA and SRL at depths above 200 cm. Notably, the T75W treatment exhibited particularly significant increases in the 20–40 cm, 60–80 cm, and 80–100 cm soil layers (Fig. 6). These patterns suggest that water-nitrogen addition interacts with soil depth to modify fine root plasticity, with deeper soil layers responding more prominently under combined treatment, whereas single-factor interventions primarily affect upper soil horizons.

Pearson correlation analysis (Fig. S4) further supported these observations, revealing highly significant positive correlations ($P < 0.001$) between FRBD and FRLD across different experimental treatments and soil depths (0-600 cm, 0-100 cm, and 100–600 cm), indicating a strong consistency in the response of

these traits to environmental variation. However, negative correlations were detected between these traits and both SRA and SRL. Notably, correlations between MRD and other fine root traits displayed distinct vertical differentiation across soil layers. Within the 0-100 cm surface layer, MRD was negatively correlated with FRBD, FRLD, and fine root tissue density (FRTD), whereas in the 100–600 cm deeper layer, MRD was positively correlated with these traits. These results suggest that MRD may fulfill different ecological functions in distinct soil layers, reflecting the adaptive differentiation of fine root traits in response to soil environmental heterogeneity.

3.4 The relationship between fine root plasticity and soil properties

Following thinning, specific root area (SRA) and specific root length (SRL) were positively correlated with soil water content (SWC), total nitrogen (TN), and nitrate nitrogen (NO_3^--N), whereas fine root biomass density (FRBD) and fine root length density (FRLD) were predominantly negatively correlated. Soil water content (SWC) was identified as the primary factor influencing variation in fine root traits after thinning, accounting for 32.9% of the observed variance (Fig. 7a). Soil depth exerted a significant influence on the interactions between fine root traits and soil factors. In the surface soil layer (0-100 cm), available phosphorus (AP) and SWC were identified as the key regulatory factors, with their correlation patterns closely aligning with those observed across the entire 0-600 cm soil profile (Fig. 7c). In the deeper soil layers (100–600 cm), AP emerged as the primary factor regulating fine root development, explaining more than 38% of the observed variance (Fig. 7e).

The water-nitrogen addition experiment, conducted after thinning, further altered the interactions between soil properties and fine root traits. Fine root biomass density (FRBD) and fine root length density (FRLD) were positively correlated with total nitrogen (TN) and nitrate nitrogen (NO_3^--N), but negatively correlated with ammonium nitrogen (NH_4^+-N), soil organic matter (SOM), available phosphorus (AP), and SWC. AP and SWC were identified as the primary regulatory factors under the water-nitrogen addition treatments ($P < 0.05$) (Fig. 7b). In the shallow soil layer (0-100 cm), nitrate nitrogen (NO_3^--N) stimulated the development of FRBD and FRLD, whereas SWC predominantly regulated SRA and SRL, accounting for 48.9% of the observed variation (Fig. 7d). In the deeper soil layers, a distinctly different regulatory pattern was observed, with phosphorus (TP, AP) and soil moisture positively influencing FRBD and FRLD, whereas nitrogen (NO_3^--N, NH_4^+-N) and SOM served as the primary drivers of variations in SRA and SRL (Fig. 7f).

3.5 SEM under thinning and water-nitrogen addition experiments

Both the thinning and water-nitrogen addition models showed a good goodness-of-fit. The χ^2 value for the thinning model was 187.680 ($d_f = 69$), and for the water-nitrogen addition model, it was 216.398 ($d_f = 82$). The chi-square to degrees of freedom ratios (χ^2/d_f) for the two models were 2.720 and 2.639, respectively, both below the threshold of 3.000. Furthermore, the RMSEA values for both models were

0.051 and 0.057, respectively, both below the critical value of 0.100, suggesting a good fit to the data (Fig. 8).

Path analysis revealed that thinning and water-nitrogen addition had opposing regulatory effects on soil properties (Fig. 8). Thinning significantly increased soil moisture but inhibited soil nutrient availability (Fig. 8a). In contrast, water and nitrogen addition treatments significantly enhanced soil nutrient content ($P < 0.001$) (Fig. 8b). Thinning has a limited short-term impact on the investment and development of fine roots, without significant direct regulatory pathways. However, thinning promotes a conservative development strategy that negatively impacts soil nutrient availability, thus inhibiting fine root development (Fig. 8a). In contrast, water and nitrogen addition promote the acquisitive development of fine roots in *Populus tomentosa* and suppress the conservative development strategy (Fig. 8b). This shift is primarily mediated through changes in soil nutrient availability.

4. Discussions

4.1 Vertical stratification of soil water and nutrients under management practices

Soil moisture displayed a clear vertical stratification, with a pronounced peak at 300–400 cm across all treatments (Fig. 1). Deeper layers (> 200 cm) generally retained more water than the surface (0-100 cm), consistent with earlier studies on the hydrological characteristics of deep soil in the North China Plain (Liu et al. 2022; Zhu et al. 2023). This pattern was largely driven by the vertical distribution of poplar roots, where high root density in the topsoil enhanced water consumption, while reduced root activity at depth allowed moisture accumulation (Zou et al. 2022; Tan et al. 2023; Zhu et al. 2024b). Thinning significantly enhanced soil moisture in the 80–400 cm layer (Fig. 1), partially supporting Hypothesis 1. This effect can be attributed to reduced canopy interception, enhanced precipitation infiltration, decreased transpiration after tree removal, and diminished root competition (Molina et al. 2021; Liu et al. 2025). Water addition also promoted soil moisture replenishment, but a decline in water content was observed in the 100–200 cm layer under combined water-nitrogen input, likely due to a fertilization-transpiration feedback in which nitrogen addition stimulated plant growth and water consumption (Samuelson et al. 2008). Furthermore, the upward shift of root distribution under fertilization (Fig. S3) may have intensified water competition in the middle soil layers, underscoring the need for precise fertilization strategies in water-limited environments.

Soil nutrients exhibited complex vertical responses to management interventions. Under moderate thinning (T50), soil organic matter (SOM) reached its highest level (T50 > NT > T75) (Fig. 2), consistent with the Intermediate Disturbance Hypothesis (Fox 2013), suggesting that moderate thinning optimizes the balance between litter inputs and decomposition. Both irrigation and irrigation-fertilization treatments markedly increased total phosphorus (TP) in the 100–200 cm layer (up to 196.82%) (Fig. 4), largely through three mechanisms: transformation of Ca-bound P into more plant-available Fe/Al-bound P (Wolf et al. 2013); stimulation of phosphatase activity by fertilization, accelerating organic P

mineralization (Gao et al. 2020; Wang et al. 2021b); and secretion of root-derived organic acids (e.g., citric and oxalic acids), which chelated metal ions and enhanced P availability (Jiang et al. 2025). These processes acted synergistically, increasing phosphorus bioavailability following water and nitrogen inputs.

Water input alone reduced total nitrogen (TN), whereas the combined water-nitrogen treatment offset this decline (Fig. 3), reflecting a balance between water-driven nitrogen leaching and fertilization-driven replenishment. Water addition also facilitated nitrate (NO_3^-–N) migration into deeper layers (200–600 cm) (Fig. S2). Under drip fertigation, rapid urea hydrolysis, nitrification, and transport led to nitrate accumulation at varying depths, with the peak shifting downward under greater irrigation (Xu et al. 2020; He et al. 2021). In contrast, ammonium (NH_4^+–N), being strongly adsorbed to soil colloids, showed low mobility (Dai et al. 2015). Although nitrate accumulation in deeper layers (300–600 cm) increased nutrient reserves, it also raised the risk of leaching, requiring careful nutrient management in ecologically sensitive areas.

In summary, management practices that explicitly account for the vertical stratification of soil water and nutrients are essential to enhance both productivity and sustainability of poplar plantations in water-limited regions.

4.2 Fine root adaptations to vertical resource heterogeneity

Our results demonstrate that fine root distribution across the 0-600 cm soil profile follows a clear resource-gradient adaptation strategy, consistent with recent advances in fine root ecology (Lu et al. 2025). The highest FRBD and FRLD values occurred in the 0–20 cm topsoil layer, supporting the optimal resource allocation hypothesis, as plants preferentially invest in absorptive roots within resource-rich layers (Coleman 2007; Giehl and Von Wiren 2014; Coleman and Aubrey 2018).

Forest management practices significantly modified fine root traits. Thinning exhibited relatively limited short-term effects on SRL and SRA but altered MRD, with peaks shifting to shallower layers under high-intensity thinning. This indicates that adaptive trait adjustment requires longer response times, consistent with previous observations on the temporal dynamics of root plasticity (Shen et al. 2017). Water addition (T75W) strongly influenced fine root morphology, increasing SRA by up to 655% in the 20–100 cm layer, highlighting soil water availability as a major driver of morphological plasticity (Vanguelova et al. 2005; Li et al. 2022; Tan et al. 2023). In contrast, the combined water-nitrogen treatment (T75WN) enhanced SRA and SRL in the 400–600 cm layer, suggesting that water regulates root morphology directly via turgor-driven cell division (Spollen and Sharp 1991; Alrajhi et al. 2024), whereas nitrogen indirectly modulates root construction by altering carbon allocation and hormonal signaling (Jing and Strader 2019; Taleski et al. 2024). The synergistic effect of water and nitrogen may further involve the activation of specific gene expression pathways in poplar (Shen et al. 2024).

A clear structure-function trade-off was also observed, with conservative traits (MRD, FRBD, FRTD) negatively correlated with acquisitive traits (SRA, SRL) (Fig. S4). This finding not only confirms the

applicability of the root economic spectrum theory (Reich 2014; Reich et al. 2014) to deep soil systems but also extends its relevance. The trade-off reflects an adaptive balance between resource acquisition efficiency and construction costs: conservative strategies invest in thicker, denser roots with longer lifespans, whereas acquisitive strategies favor higher SRL and SRA, enhancing uptake efficiency but reducing stress tolerance (Kong et al. 2017; Weigelt et al. 2023).

Management practices were shown to regulate these trade-offs. Thinning promoted conservative trait expression by reducing nutrient availability, while water-fertilizer addition favored acquisitive strategies, enhancing carbon input and nutrient uptake under resource-limited conditions. These results suggest that plantation management can actively shift fine root strategies along the conservative-acquisitive spectrum, with direct implications for belowground carbon allocation and nutrient cycling.

4.3Trade-offs in fine root strategies under management regimes

After thinning, soil water content (SWC) and available phosphorus (AP) in the 0-100 cm surface layer jointly governed the variation in fine root traits (Fig. 7). This pattern highlights the strong regulation of shallow root growth by immediate resource availability (Guilbeault-Mayers et al. 2024). As the most dynamic zone for water and nutrient fluctuations, the surface soil is subject to frequent wet-dry cycles that directly influence phosphorus uptake efficiency. Under optimal moisture conditions, phosphorus diffusion rates increase (Shapiro et al. 1960; Sharpley and Ahuja 1983), thereby enhancing root nutrient acquisition. In addition, high microbial activity and organic matter turnover in surface soils maintain a continuous supply of AP (Hawkins et al. 2022; Sica et al. 2025), driving fine roots to develop densely branched structures in resource-rich environments to maximize absorptive surface area (Goebel et al. 2011; Du and Wei 2018). By contrast, in deeper layers (100–600 cm), the relationship between AP and fine root structural traits reversed (Fig. 7), reflecting the resource constraints typical of these strata. Deep soils are characterized by relatively stable moisture but limited phosphorus availability (Mao et al. 2024). Given the extremely low mobility of phosphorus, deep roots adapt through morphological adjustments—such as elongating axes and reducing branching—rather than relying on opportunistic uptake as in surface soils (Wang and Lambers 2020; Lambers 2022; Barrow and Lambers 2022). This adaptive strategy enabled AP to explain up to 38% of trait variation in deep layers of thinned forests, suggesting that phosphorus is a key limiting factor regulating deep root development in *Populus tomentosa* after thinning.

Irrigation and fertigation further increased surface soil water availability in thinned stands (Fig. 1), alleviating fine root water limitation during growth and development. Accordingly, SWC was the primary factor explaining root trait variation under different water and nitrogen treatments (Fig. 7). In deeper layers, however, water mobility is restricted and anaerobic conditions are common, reducing the explanatory power of SWC. Under such conditions, roots responded more strongly to leached nitrogen (Fig. 7), optimizing resource acquisition by enhancing inorganic nitrogen utilization. For instance, under the T75WN treatment, fine roots increased specific root area (SRA) and specific root length (SRL),

thereby improving nitrogen uptake efficiency in deep soil (Fig. 6). This vertical differentiation reflects the precise adaptive strategies of root systems to resource environments at contrasting soil depths.

The adaptive shift in fine root construction strategy exhibited significant treatment specificity, primarily driven by dynamic changes in the soil nutrient pool, in full support of Hypothesis 2. Thinning profoundly modified the root environment by improving soil moisture conditions (Fig. 8). Reduced stand density alleviated belowground competition, enabling plants to optimize spatial distribution patterns (Qin et al. 2024). Enhanced light penetration and ventilation accelerated litter decomposition (Henneron et al. 2018; Latterini et al. 2024), improved soil aggregate stability (Ma et al. 2022), and reduced transpiration losses, thereby increasing deep soil water availability (Molina et al. 2021). These synergistic improvements favored the allocation of resources toward persistent root structures, as indicated by the enhancement of conservative traits such as fine root biomass density (FRBD) and mean root diameter (MRD), whereas acquisitive traits (e.g., SRL) were comparatively reduced (Figs. 6 and S3). This conservative shift suggests an adaptive transition from short-term resource capture toward long-term survival under reduced competition (Giehl and Von Wiren 2014).

In contrast, water and nitrogen addition treatments primarily regulated root development through chemical pathways (Coleman 2007; He et al. 2022). By increasing soil nutrient availability, they lowered the metabolic cost of root exploration (Fig. 8) while simultaneously influencing moisture distribution and altering plant carbon-nitrogen allocation. Under such conditions, plants exhibited typical “resource enrichment” responses, favoring acquisitive root architectures with high SRL and SRA (Fig. 6), while reducing investment in persistent structures. This pattern reflects a precision foraging strategy that facilitates rapid adaptation to short-term enrichment environments, consistent with Hypothesis 2.

Overall, thinning demonstrated unique advantages in improving soil water conditions and promoting stable root system development, whereas water and nitrogen additions were more effective in enhancing short-term productivity. A rational integration of these management strategies is likely to achieve synergistic optimization of root structural and functional traits, thereby improving both resilience and productivity in *Populus tomentosa* plantations. Future research should focus on elucidating the physiological and ecological mechanisms underlying trade-offs in root development strategies under combined management regimes, which will provide critical foundations for precision forest management frameworks grounded in ecological processes.

5. Conclusions

Thinning and water-nitrogen addition treatments exerted significant effects on soil moisture, nutrient distribution, and fine root traits, exhibiting pronounced vertical differentiation. Thinning increased soil water content in the 80–400 cm layer, whereas the synergistic application of water and nitrogen reduced moisture in the 100–200 cm layer but enhanced total phosphorus by 59.23%. Soil organic matter and total nitrogen were most responsive to management in the surface layers, while inorganic nitrogen accumulation was more prominent in deeper layers (300–600 cm). Irrigation primarily increased specific

root length (SRL) in the middle soil layers, whereas combined water-nitrogen addition promoted specific root area (SRA) in the deep soil (400–500 cm). Thinning had limited short-term impacts on fine root strategy, whereas water-nitrogen addition shifted root development toward a more acquisitive strategy by improving nutrient availability. These results provide novel insights into plantation root system responses and offer a scientific basis for optimizing sustainable management practices in managed forests.

Abbreviations

AP
available phosphorus
FRBD
fine root biomass density
FRLD
fine root length density
FRTD
fine root tissue density
MRD
mean root diameter
NT
no thinning
NH_4^+-N
ammonium nitrogen
NO_3^--N
nitrate nitrogen
T50
50% tree removal
T75
75% tree removal
TN
total nitrogen
TP
total phosphorus
SOM
soil organic matter
SRA
specific root surface area
SRL
specific root length
SWC

soil water content
W
irrigation only
WN
irrigation with nitrogen application

Declarations

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author contributions

YFW conceived the ideas; YFW, BYX, and LMJ designed the methodology; YFW, XFD, and YZ collected the data; YFW, KW, and DNW analyzed the data; YFW, BYX, and LMJ led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Figures

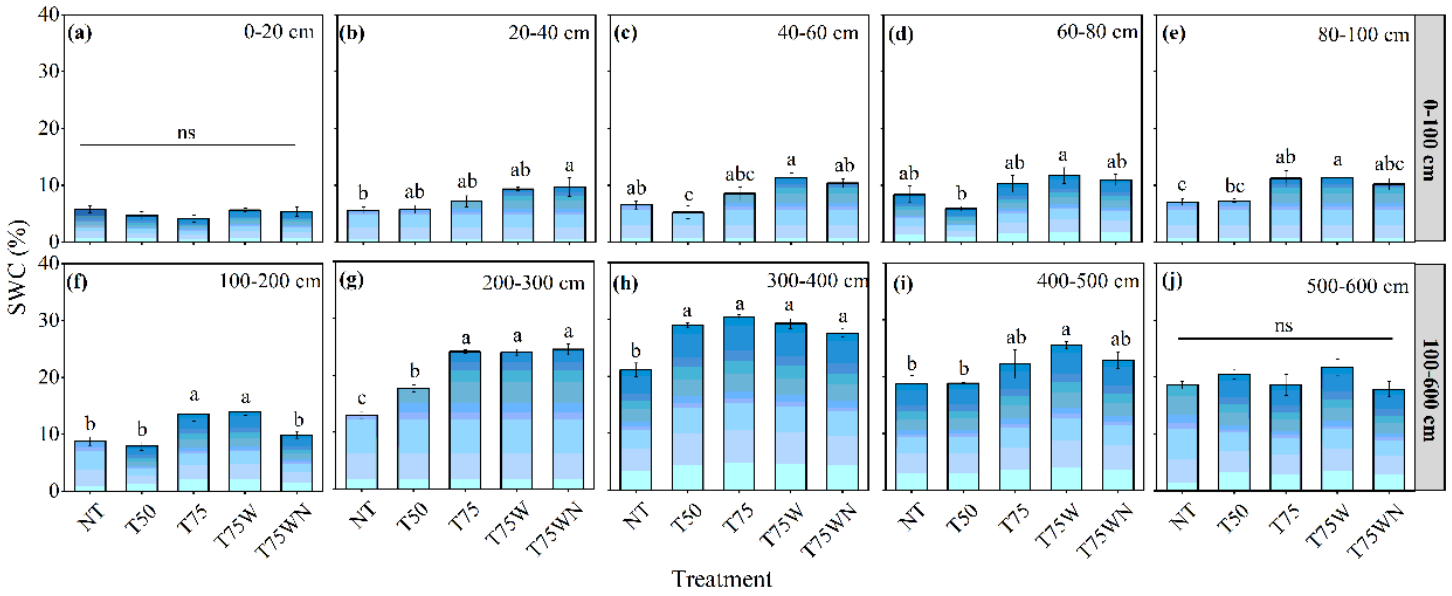


Figure 1

Variation patterns of soil moisture content (SWC) at 0-6 m depth under five treatments (n = 5). NT: No thinning; T50: 50% tree removal; T75: 75% tree removal; T75W: 75% tree removal with water addition; T75WN: 75% tree removal with water and nitrogen addition. Note: Different lowercase letters indicate significant differences among the five treatments (P<0.05), and ns indicates no significant differences among the five treatments.

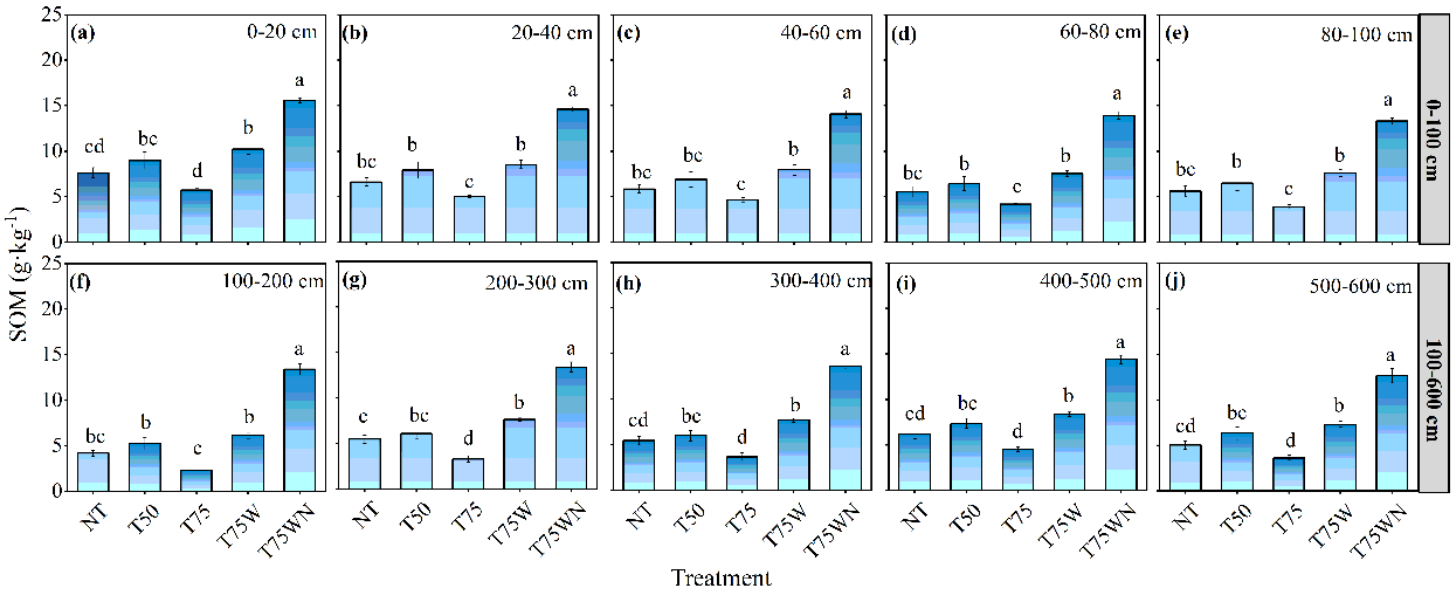


Figure 2

Variation patterns of soil organic matter (SOM) at 0-6 m depth under five treatments (*n* = 5). NT: No thinning; T50: 50% tree removal; T75: 75% tree removal; T75W: 75% tree removal with water addition; T75WN: 75% tree removal with water and nitrogen addition. Note: Different lowercase letters indicate significant differences among the five treatments (P<0.05), and ns indicates no significant differences among the five treatments.

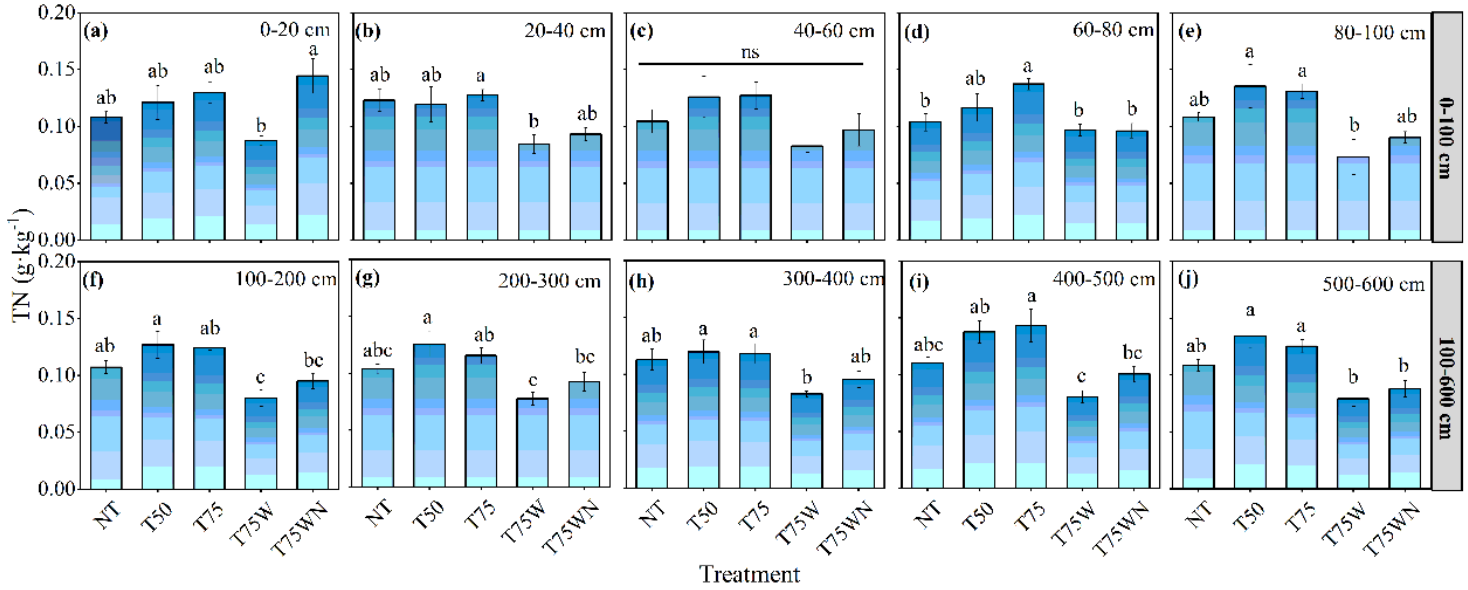


Figure 3

Variation patterns of soil total nitrogen (TN) at 0-6 m depth under five treatments (*n* = 5). NT: No thinning; T50: 50% tree removal; T75: 75% tree removal; T75W: 75% tree removal with water addition; T75WN: 75% tree removal with water and nitrogen addition. Note: Different lowercase letters indicate

significant differences among the five treatments (P<0.05), and ns indicates no significant differences among the five treatments.

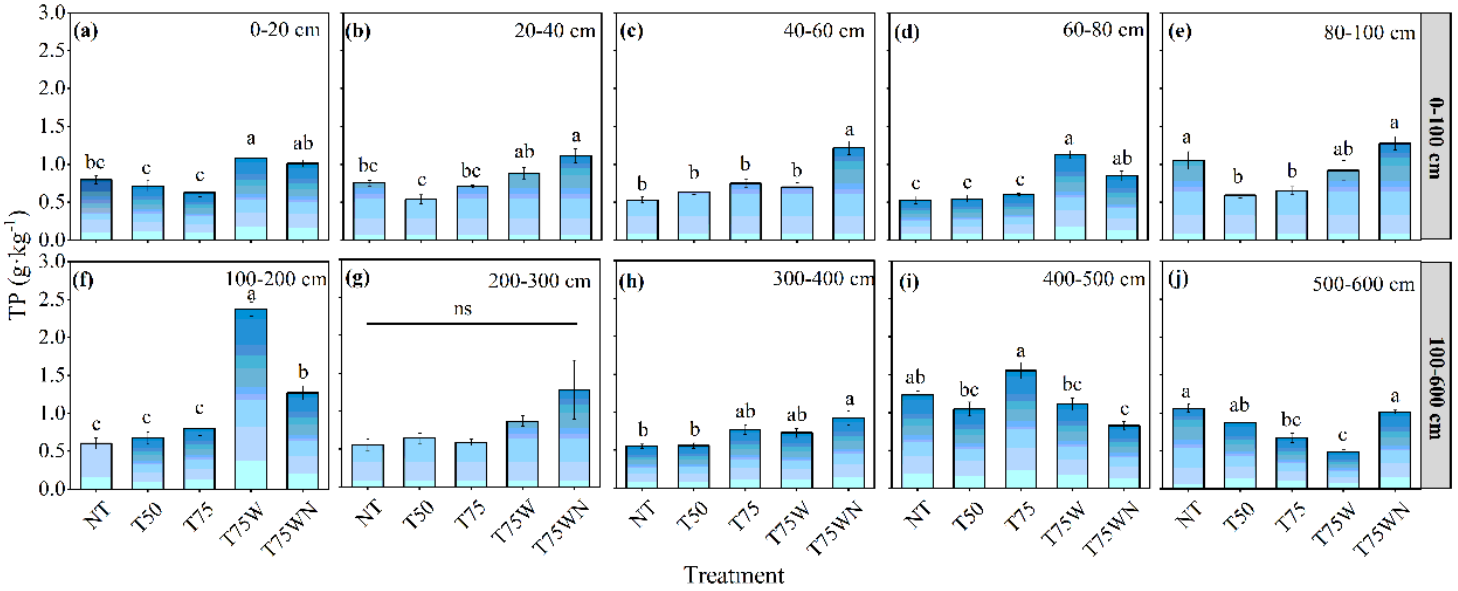


Figure 4

Variation patterns of soil total phosphorus (TP) at 0-6 m depth under five treatments (n = 5). NT: No thinning; T50: 50% tree removal; T75: 75% tree removal; T75W: 75% tree removal with water addition; T75WN: 75% tree removal with water and nitrogen addition. Note: Different lowercase letters indicate significant differences among the five treatments (P<0.05), and ns indicates no significant differences among the five treatments.

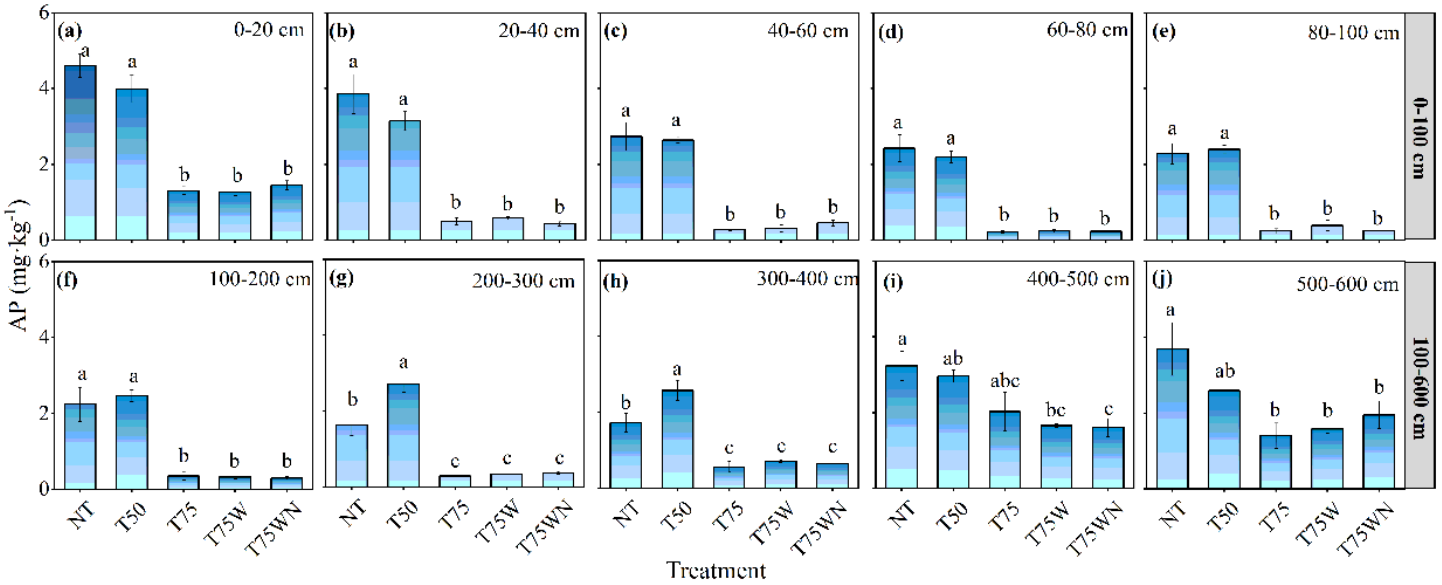


Figure 5

Variation patterns of soil available phosphorus (AP) at 0-6 m depth under five treatments (*n* = 5). NT: No thinning; T50: 50% tree removal; T75: 75% tree removal; T75W: 75% tree removal with water addition; T75WN: 75% tree removal with water and nitrogen addition. Note: Different lowercase letters indicate significant differences among the five treatments (P<0.05), and ns indicates no significant differences among the five treatments.

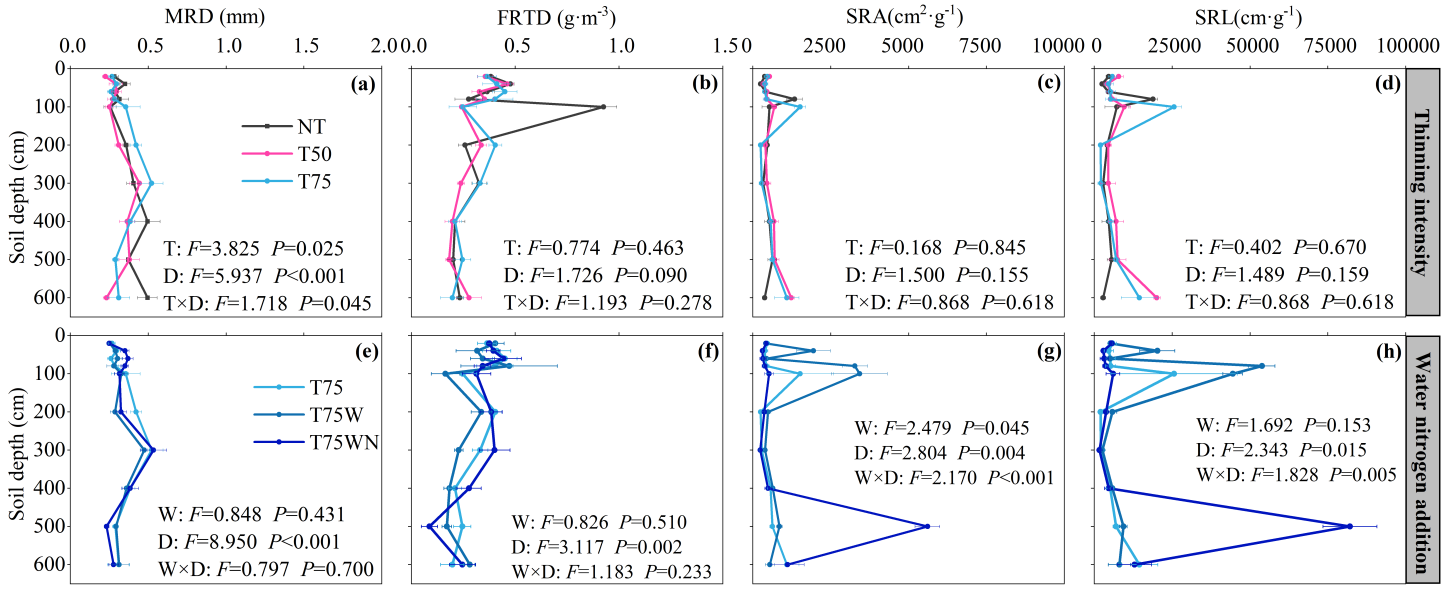


Figure 6

The plastic responses of mean fine root diameter (MRD, a, e), fine root tissue density (FRTD, b, f), specific root surface area (SRA, c, g), and specific root length (SRL, d, h) to different treatments within the 0-6 m soil depth (*n* = 5). NT: No thinning; T50: 50% tree removal; T75: 75% tree removal; T75W: 75% tree removal with water addition; T75WN: 75% tree removal with water and nitrogen addition. Note: T or W represents the main effect of thinning or water-nitrogen addition in the two-way ANOVA, D represents the main effect of soil depth, and T×D and W×D represent the interaction effect of the two. The analysis parameters displayed include the *F*-statistic (*F*) and *P*-values (*P*).

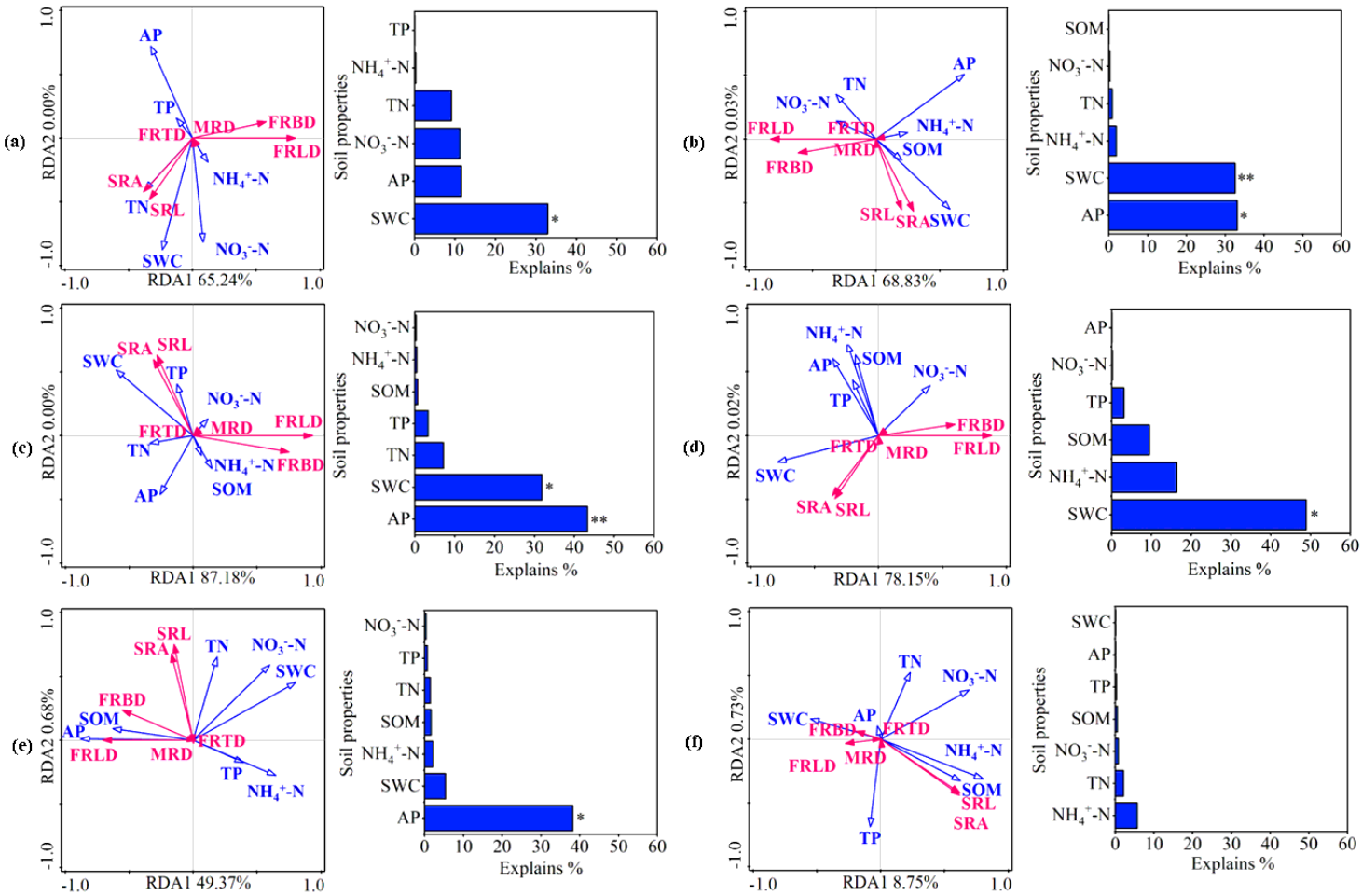


Figure 7

Redundancy analysis (RDA) of fine root plasticity and soil properties at different depths under thinning and water-nitrogen treatments. (a) Thinning at 0-600 cm; (b) Water-nitrogen addition at 0-600 cm; (c) Thinning at 0-100 cm; (d) Water-nitrogen addition at 0-100 cm; (e) Thinning at 100-600 cm; (f) Water-nitrogen addition at 100-600 cm. Note: SWC for soil water content, SOM for soil organic matter, TN for total nitrogen, TP for total phosphorus, AP for available phosphorus, NH4+-N for ammonium nitrogen, and NO3--N for nitrate nitrogen, MRD stands for mean fine root diameter, FRBD for fine root biomass density, FRLD for fine root length density, FRTD for fine root tissue density, SRA for specific root surface area, and SRL for specific root length.

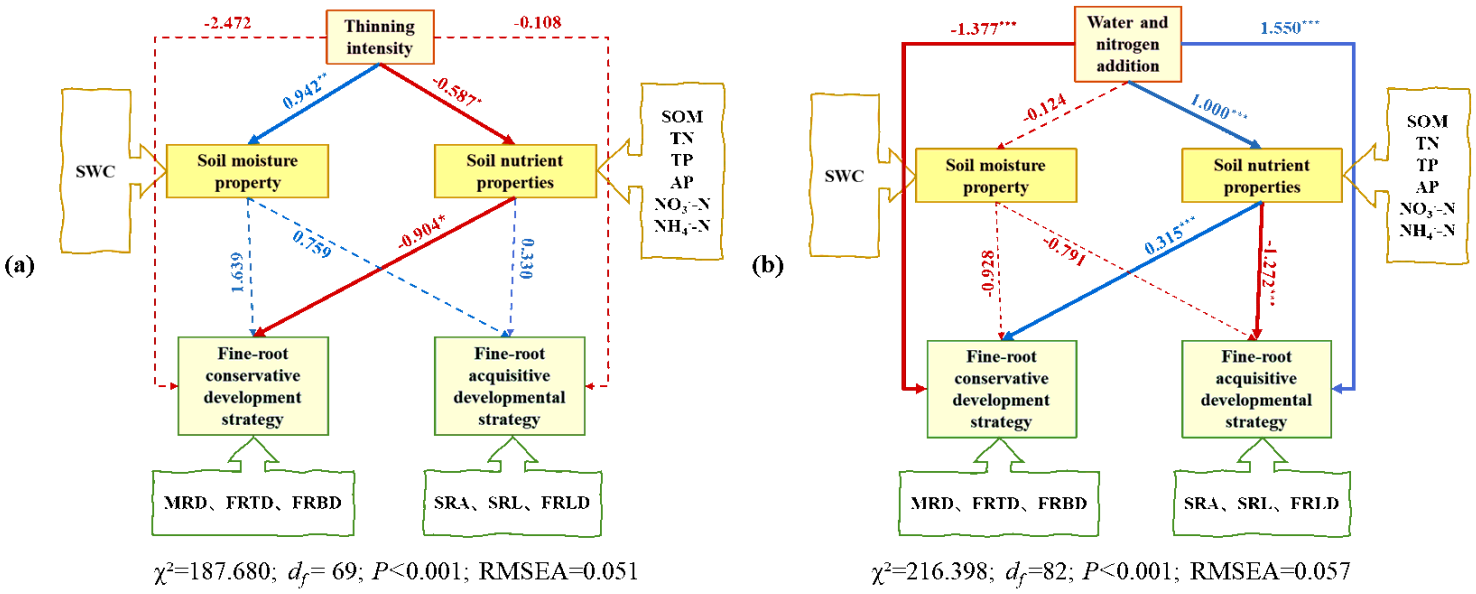


Figure 8

Structural equation models (SEM) of soil moisture and nutrient properties and fine root development strategies under thinning (a) and water-nitrogen addition (b). Boxes represent latent variables. Blue indicates positive effects, red indicates negative effects, solid lines indicate significant effects (P<0.05), dashed lines indicate non-significant effects (P>0.05), and numbers represent correlation coefficients. The goodness of fit of the SEM models was evaluated using the χ2 test and the root mean square error of approximation (RMSEA). Note: ***: P<0.001; **: P<0.01; *: P<0.05.

Supplementary Files

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- 3.Supplementalmaterials.docx