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Research Article

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Posted Date: November 20th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-11601262/v1

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Additional Declarations: No competing interests reported.

Root Morphological Traits and Growth Adaptation Strategies of Differently Graded *Pinus yunnanensis* Seedlings

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Abstract

Pinus yunnanensis is an important ecological and economic tree species in Southwest China; however, its natural forests are severely degraded, and seedling quality is critical for afforestation success and vegetation restoration. To clarify the regulatory patterns of seedling grade on root growth strategies and to reveal the adaptive mechanisms of *P. yunnanensis* seedlings to the environment, Two-year-old seedlings were classified into three grades (I, II, III) based on height using the mean ± 1/2 standard deviation method. Root morphology, biomass, and their correlations were analyzed. Results showed that total root length, root tip number, and root tissue density were conservative traits with no significant differences among grades. Root surface area, volume, average diameter, and biomass decreased with declining grade, while root-shoot ratio, specific root length, and specific root surface area increased. Grade III seedlings exhibited the greatest morphological differentiation. Across grades, morphological traits showed high plasticity, whereas structural traits were conservative. Grade III displayed higher functional trait plasticity for adaptation under resource limitation. Most root traits showed allometric relationships with biomass: lower-grade seedlings prioritized root expansion over biomass accumulation, while higher-grade favored aboveground growth. Principal component analysis revealed three adaptive strategies－Grade I: root system expansion; Grade II: intermediate transition; Grade III: resource-use efficiency. Different grades of *P. yunnanensis* seedlings formed differentiated growth adaptation strategies: Grade I adopted a stable expansion strategy, Grade II a flexible regulation strategy, and Grade III a fine root adaptation strategy.

Keywords: *Pinus yunnanensis*; seedling grade; root morphology; allometric growth; growth adaptation strategy

1.Introduction

Pinus yunnanensis, an indigenous tree species and pioneer species for afforestation of barren hills in southwest China, plays a vital role in soil and water conservation, water retention, and environmental amelioration (Deng et al., 2014; H. Li et al., 2024). Characterized by a broad ecological amplitude and superior wood quality, *P. yunnanensis* serves as an important economic and ecological tree species for afforestation and soil-water conservation (Chang et al., 2020; Shu, 1999).Despite its remarkable viability in natural habitats, natural forests of *P. yunnanensis* in Yunnan Province have undergone varying degrees of degradation in response to anthropogenic disturbances and climate change (Feng et al., 2023; Zhong , Zhou , Han , Feng , & Zheng 2011). Over two-thirds of the *P. yunnanensis* stands have exhibited stem distortion, with this

phenomenon being particularly pronounced in central Yunnan, where the affected stands are predominantly concentrated in hilly regions(C. He et al., 2021; Z. Li et al., 2024). This degradation has substantially diminished the economic value of *P. yunnanensis* timber(Xu et al., 2011).

Root systems represent a critical component of seedlings, and their morphological traits directly reflect seedling quality and environmental adaptability(Grossnickle, 2012). By comparing root morphological characteristics of two-year-old *P. yunnanensis* seedlings, we can evaluate seedling vigor, stress resistance, and growth potential. Root growth status exerts a direct influence on the development of above-ground vegetative organs(Poorter et al., 2012). Seedlings with favorable root traits generally exhibit stronger growth capacity and better adaptability, enabling them to maintain stable growth under diverse environmental conditions(Zhou et al., 2025). Root morphology can indicate the utilization efficiency of soil nutrients and water by plants, as well as the productivity of above-ground vegetative organs(Y. Liu, Duan, Wu, & Shi, 2025; Theodorou & Bowen, 1993). A well-developed and robust root system facilitates the regulation of water balance between above-ground and below-ground parts, thereby enhancing plant stress tolerance(Brunner, Herzog, Dawes, Arend, & Sperisen, 2015). As the primary organ for nutrient uptake, root morphological characteristics are not only core indicators for assessing seedling quality, but also profoundly reflect the survival strategies and long-term development potential of seedlings in complex environments(Feng , Zhang , & Ji 2016).

For *P. yunnanensis*, root systems are responsible for the transport of water and mineral nutrients, serving as the foundation for plant survival and growth(Fujii, 2024; Meng , Feng , Hu , Qin , & Yan 2017). By comparing root morphological characteristics of two-year-old *P. yunnanensis* seedlings, we can assess seedling vigor, stress resistance, and growth potential(Y. Liu et al., 2025; Pan et al., 2025). Root growth directly affects the development of above-ground vegetative organs(Gao, Cui, Zhang, & Kun, 2020; G. Tang et al., 2024). Seedlings with superior root traits typically possess stronger growth ability and better adaptability, maintaining stable growth under various environmental conditions(Poorter et al., 2012). Therefore, this study aims to elucidate plant adaptive capacity to environmental conditions and reveal the mechanisms underlying the interactions between soil environments and root systems by comparing root morphological characteristics of two-year-old *P. yunnanensis* seedlings under different conditions(Yan, Song, Jiang, & Wang, 2010).

2.Materials and Methods

2.1. Overview of the Study Area

The experiment was conducted at the nursery of Southwest Forestry University, Panlong District, Kunming City, Yunnan Province. Kunming featured a subtropical monsoon climate, located between 25°04′00″ N latitude and 102°45′41″ E longitude. It had a mild climate with warm winters and cool summers, where the four seasons resembled spring. The average annual temperature was approximately 15 °C, and the average annual sunshine duration reached around 2200 h, with a frost-free period of more than 240 days. Precipitation in Kunming showed distinct seasonality in temporal distribution; rainfall concentrated mostly in summer, while spring and winter were dry seasons with low precipitation.

2.2. Source of Experimental Materials

The seeds used in the experiment were collected as a mixed sample from a *P. yunnanensis* clone seed orchard in Midu County, Yunnan Province. The seeds were uniformly sterilized and

soaked before sowing. After the seeds germinated completely, the seedlings were transplanted into nursery pots (dimension: 18 cm in bottom diameter × 32 cm in height). The pots were filled with a substrate mixture consisting of humus soil and laterite at a ratio of 3:1. Regular seedling maintenance measures, including watering, fertilization, and pesticide spraying, were implemented during the seedling stage. All seedlings used in this study were nursery-grown from these seeds; no wild plants were collected from natural habitats.

2.3. Seedling Grading

A total of 185 two-year-old *P. yunnanensis* seedlings were graded from the nursery, and each seedling was labeled with a unique number. The ground diameter of each seedling was measured using a vernier caliper with an accuracy of 0.01 cm, and the seedling height was determined with a ruler with an accuracy of 0.1 cm (Y. He et al., 2023). Seedling height was used as the quality index for seedling grading, and the method of mean ± 1/2 standard deviation (SD) was adopted as the grading criterion. The seedlings were divided into three grades (Grade I, Grade II, and Grade III seedlings) (Figure 1). The value of M + 1/2 SD was set as the lower limit of Grade I seedlings, while M - 1/2 SD was defined as the upper limit (exclusive) of Grade III seedlings. Seedlings with values between M - 1/2 SD and M + 1/2 SD (exclusive) were classified as Grade II seedlings, where M represented the mean value and SD represented the standard deviation(Li et al., 2025).The sample sizes for each grade were: Grade I: n = 42, Grade II: n = 98, Grade III: n = 45.



Figure 1. Phenotypic observation of *P. yunnanensis* seedlings of Grade I, Grade II, and Grade III.

2.4. Determination of Indicators

Seedlings of different grades were brought to the laboratory, where the roots were rinsed with clean water to remove soil and then air-dried. Subsequently, the roots, stems, and leaves of the seedlings were separated using scissors, and the fresh weight of each organ was measured using an electronic balance. Subsequently, the root systems were scanned with a root scanner, and the scanned images were analyzed using plant image analysis software to obtain root morphological indicators (Figure 2), including total root length (cm), root surface area (cm^2), average root diameter (mm), root volume (cm^3), projected area (cm^2), and pixel area (cm^2). The separated organs were placed in labeled paper bags, deactivated in an oven at 105 C for 30 min, and then

dried at 80 C to a constant weight. The biomass of the related indicators was measured thereafter.

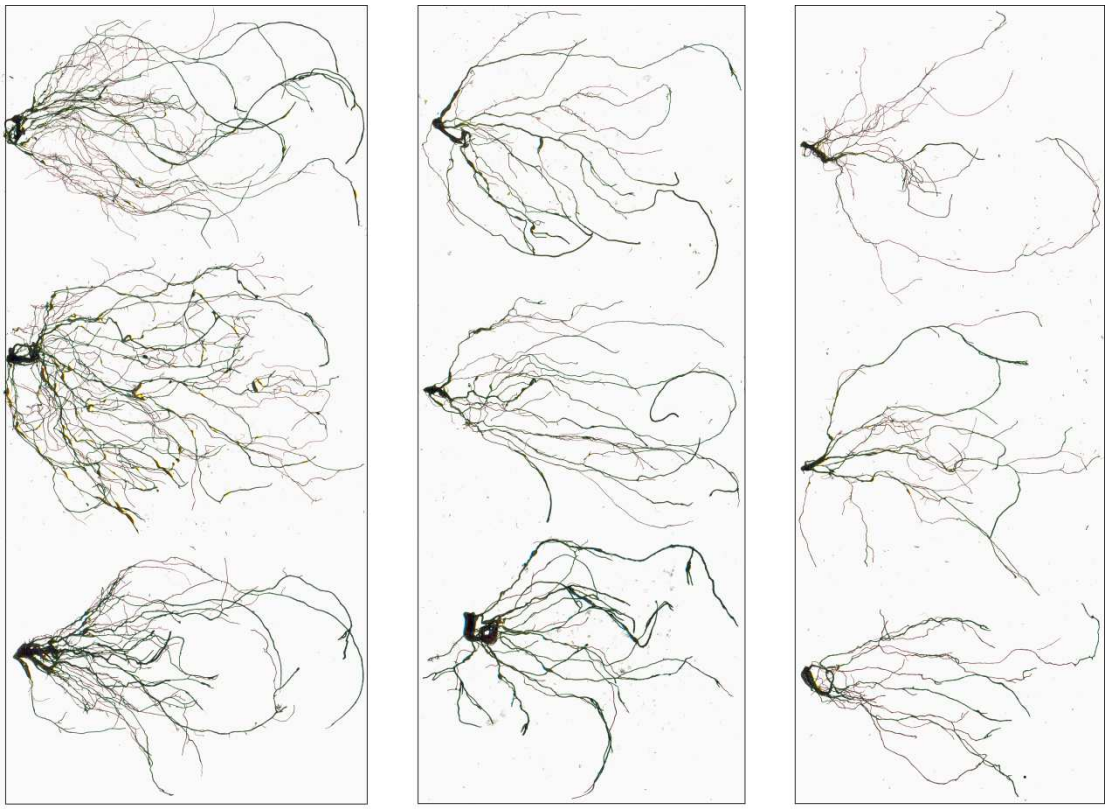

Figure 2. Root morphology of *P. yunnanensis* seedlings of Grade I, Grade II, and Grade III.

2.5. Data Processing

Excel was used for data collation and organization, and SPSS software was employed for descriptive statistics, one-way analysis of variance (ANOVA), and related calculations. Based on the obtained root morphological and biomass parameters, root architecture indices were calculated, including root-to-shoot ratio (root biomass / shoot biomass), specific root length (total root length / root biomass), root specific surface area (root surface area / root biomass), and root tissue density (root biomass / root volume).

Calculation of coefficient of variation (CV): The CV of each root trait in each seedling grade was calculated according to the following formula:

$$CV\ (\%) = (SD / Mean) \times 100$$

where CV is the coefficient of variation (expressed as a percentage), SD is the standard deviation of the root trait in the corresponding seedling grade, and Mean is the average value of the root trait in the same grade.

Phenotypic plasticity index (PI) is used to measure the degree of phenotypic change of organisms under different environmental conditions. PI = (Max - Min) / Max. The Max and Min refer to the maximum and the minimum mean value of a variable(Valladares, Sanchez‐Gomez, & Zavala, 2006). Allometric growth analysis allometric relationships were analyzed using Standardized Major Axis (SMA) regression on log10-transformed biomass data, following the model $\log10(Y) = a + b \cdot \log10(X)$. Slopes, 95% confidence intervals, coefficients of determination (R2), and tests of isometry (slope = 1) are reported(G. Tang et al., 2024). Graphical representations were generated using OriginPro 2024 software. All data are presented as mean ±

standard deviation.

3. Results

3.1. Analysis of Root Morphological Characteristics and Variation Patterns of P. yunnanensis Seedlings of Different Grades

The root system morphology of different grades of seedlings is shown in Figure 3. According to Figure 3, total root length, root tip number, and root tissue density showed no significant differences among the grades ($P > 0.05$) (Figure 3a, e, i), while the remaining indicators varied with grade across the three categories. Significant differences were observed in root surface area and average root diameter between Grade I and Grade III seedlings, with Grade I exhibiting the highest root surface area and Grade III the lowest (Figure 3b, d). For root volume, root biomass and aboveground biomass, Grade I seedlings had the highest values and Grade III the lowest, with no significant differences between Grade I and Grade II, but significant differences between Grade II and Grade III (Figure 3c, j、k). Overall, the trends in root surface area, root volume, average root diameter, and root biomass were relatively consistent, indicating that spatial expansion and biomass accumulation of the root system were restricted in Grade III seedlings, promoting the development of fine roots. In contrast, root-shoot ratio, specific root length, and specific root surface area exhibited opposite patterns. Specifically, significant differences in root-shoot ratio were found only between Grade I and Grade III seedlings, with no differences compared to Grade II (Figure 3f). Specific root length and specific root surface area showed no differences between Grade I and Grade II but significant differences with Grade III (Figure 3g, h), suggesting that Grade III seedlings balance growth and development by increasing root-shoot allocation and enhancing root resource absorption efficiency. Regarding the coefficient of variation, the coefficients for number of root tips, specific root surface area and aboveground biomass exhibited minor fluctuations across grades, indicating high phenotypic consistency. In contrast, the coefficients for total root length, root surface area, root volume, average root diameter, root biomass, root-shoot ratio, specific root length, and root tissue density varied with grade, with Grade III seedlings showing more pronounced individual differentiation in root morphology and resource allocation strategies (Figure 3a–k).

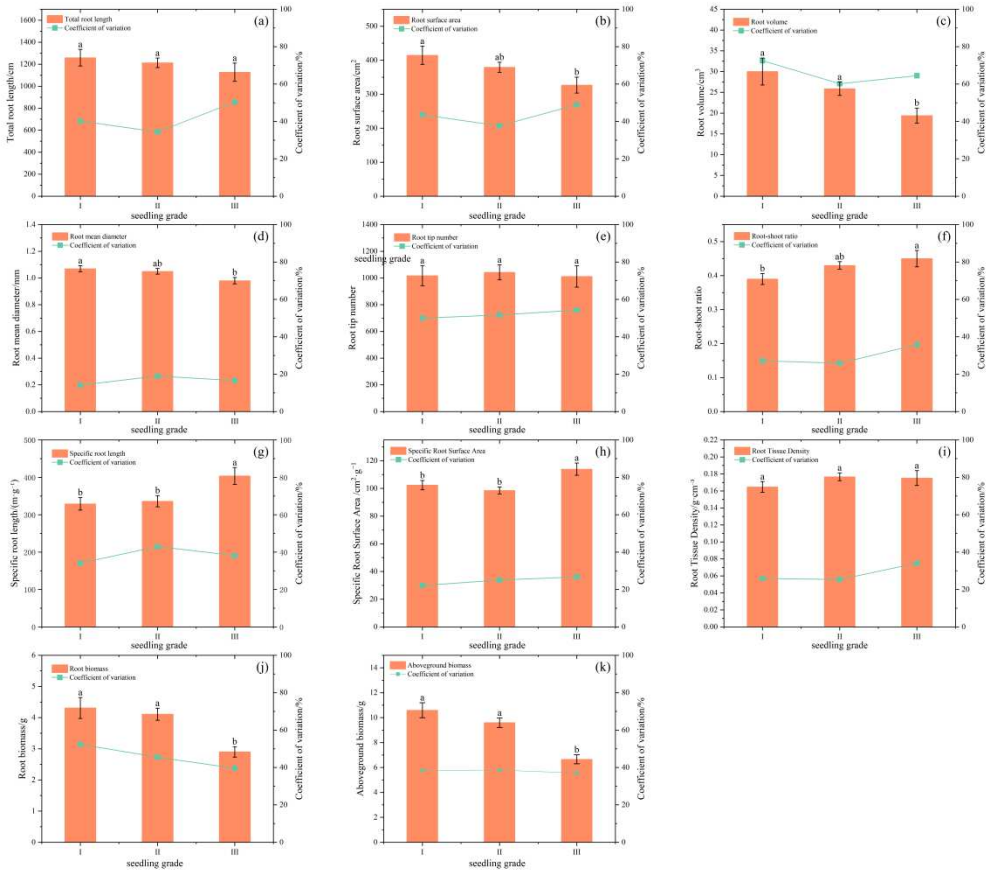

Figure 3: Root morphological traits, biomass and their coefficients of variation of different-grade *P. yunnanensis* seedlings

Note: (a) Total root length, (b) Root surface area, (c) Root volume, (d) Root mean diameter, (e) Root tip number, (f) Root-shoot ratio, (g) Specific root length, (h) Specific root surface area, (i) Root tissue density, (j) Root biomass, (k) Aboveground biomass. Values are mean ± standard error. Different treatments were regarded as significantly different when $P<0.05$. The green polyline indicates the coefficient of variation (CV) of each index. Grade I, II and III correspond to high, medium and low growth-grade seedlings, respectively.

3.2 Phenotypic Plasticity of Root Morphology in P. yunnanensis Seedlings Among Different Growth Grades

According to the phenotypic plasticity analysis shown in Figure 4, the ranking of root phenotypic plasticity among seedlings of different grades is generally consistent. For Grade I and Grade II seedlings, root volume exhibits the highest plasticity, followed by root surface area and total root length. Grade III seedlings also show relatively high plasticity in root volume, root surface area, and total root length, while root mean diameter maintains low plasticity. Meanwhile, Grade III seedlings display slightly higher phenotypic plasticity in root-shoot ratio, specific root length, and specific root area than Grade I and II seedlings, which aligns with their adaptive strategy of adjusting resource allocation under growth constraints. Root tissue density shows moderate plasticity across all grades, consistent with the observed morphological differences and variation patterns. Overall, the phenotypic plasticity patterns of root traits in different grades of *P. yunnanensis* seedlings are unified: morphological traits exhibit high plasticity, while structural traits show strong stability, which fully corresponds with the observed root morphology and variation characteristics. Grade I and II seedlings rely on highly plastic root systems to achieve spatial expansion and biomass accumulation, whereas Grade III seedlings enhance the plasticity of

functional traits to ensure resource uptake. Different grades of seedlings thus exhibit consistent and coordinated root adaptive strategies.

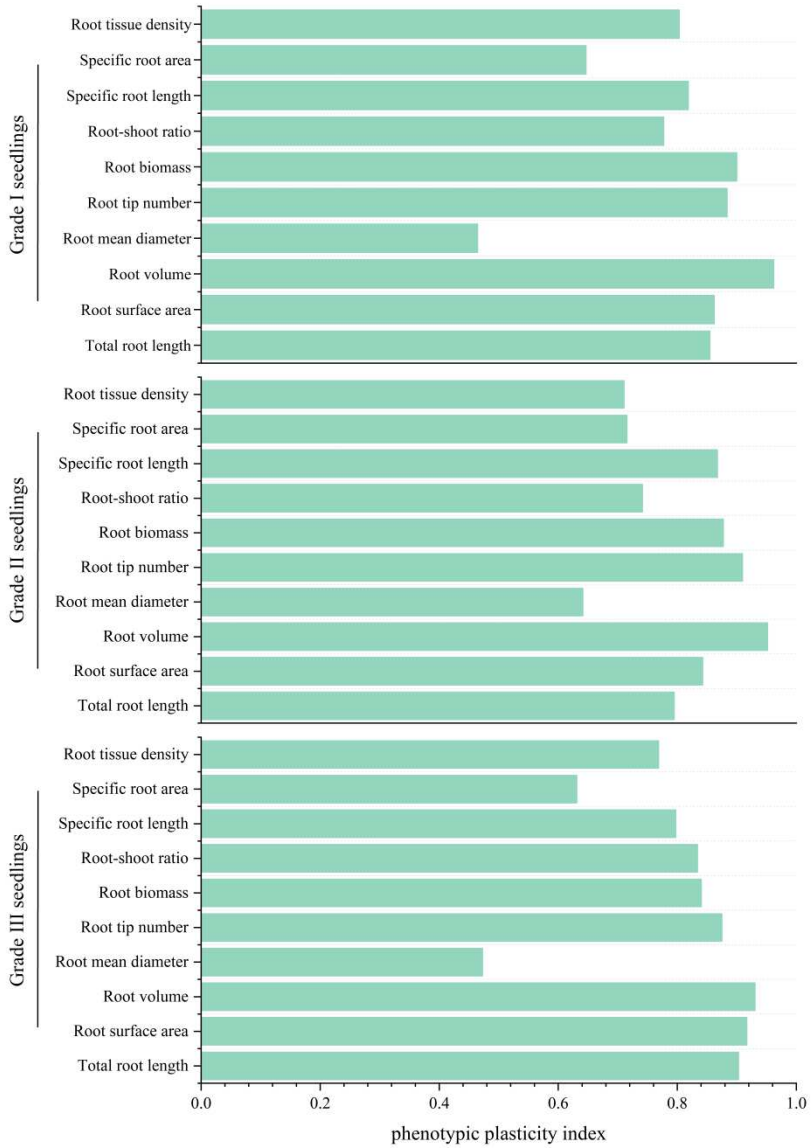

Figure 4: Phenotypic plasticity index of root traits in *P. yunnanensis* seedlings of different quality grades.

3.3 Analysis of Allometric Growth Relationships Between Root Morphology and Biomass of P. yunnanensis Seedlings of Different Grades

Significant differences existed in the relationships between various root growth traits and root biomass among seedlings of different grades. As shown in Figure 5, most of the relationships between root traits and root biomass across different grades were allometric. Specifically, regarding the allometric relationships between total root length, root surface area and root biomass, Grade I and Grade II seedlings exhibited allometric growth relationships, whereas Grade III seedlings showed isometric growth relationships. The slopes followed the order of Grade III > Grade I > Grade II, with the slopes of Grade III seedlings all greater than 1, indicating that the growth rates of total root length and root surface area were higher than the accumulation rate of root biomass; the opposite trend was observed in Grade I and Grade II seedlings (Figure 5a, b). The relationships between root volume, average root diameter, root-shoot ratio and root biomass were allometric across the three seedling grades, with the slopes increasing as the seedling grade

decreased (Figure 5c, d, f). In the allometric growth relationship between root volume and root biomass, the slopes of all three grades were greater than 1, which meant that the growth rate of root volume was faster than the accumulation rate of root biomass (Figure 5c). In contrast, for the relationship between average root diameter and root biomass, the slopes of all three grades were less than 1, implying that the accumulation rate of root biomass exceeded the growth rate of average root diameter (Figure 5d). The relationships between root-shoot ratio and root biomass were allometric in all three grades, with slopes increasing as the seedling grade decreased and all slopes being less than 1 (Figure 5f). The relationship between root tip number and root biomass was isometric in Grade I and Grade II seedlings but allometric in Grade III seedlings. The slopes of Grade II and Grade III seedlings were greater than 1, while that of Grade I seedlings was less than 1, with the slope decreasing as the seedling grade increased (Figure 5e). Specific root surface area, specific root length, and root tissue density exhibited allometric growth relationships with root biomass overall. The slopes were negative, indicating a negative correlation, and the slope values decreased as the seedling grade decreased (Figure 5g, h, i).

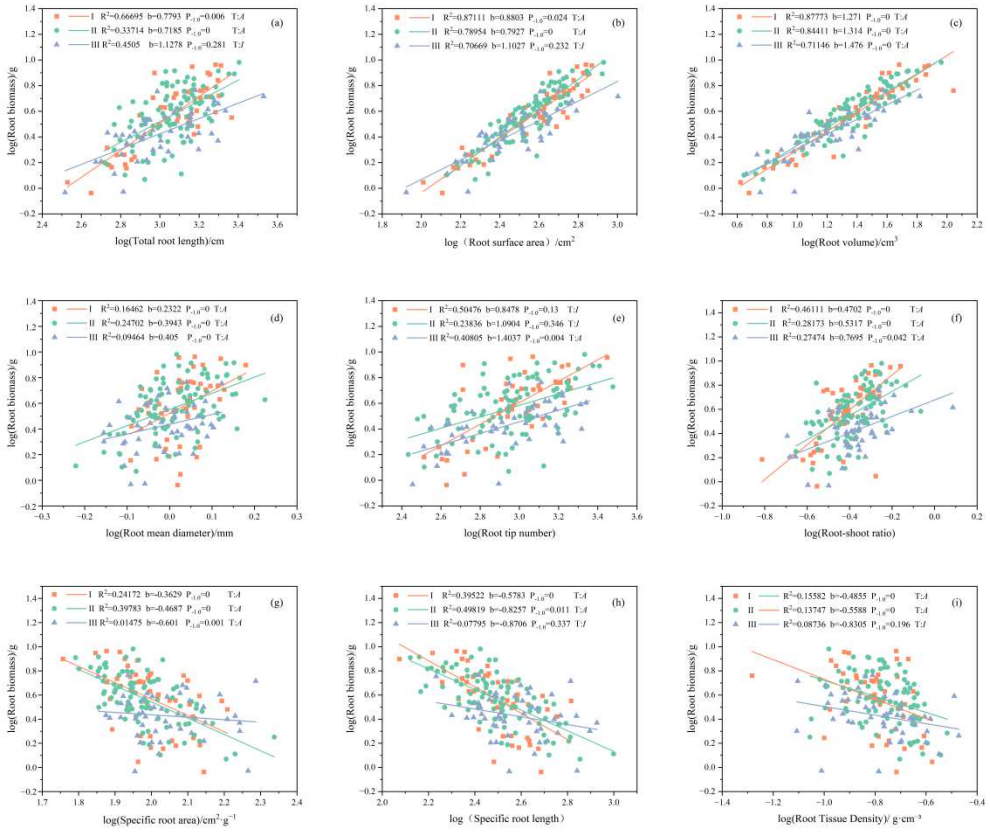

Figure 5： Allometric relationships between root biomass and root morphological traits in *P. yunnanensis* across different grades.

Note: (a) Total root length; (b) Root surface area; (c) Root volume; (d) Root mean diameter; (e) Root tip number; (f) Root-shoot ratio; (g) Specific root surface area; (h) Specific root length; (i) Root tissue density.

"b" = slope; $P_{-1.0}$: significance of slope difference from theoretical value 1.0; "A" = allometric relationship, "I" = isometric relationship (same below).

3.4 Allometric growth analysis of root morphology and biomass in different grades of P. yunnanensis seedlings

Significant differences exist in the allometric relationships between various root growth traits and aboveground biomass among different grades of *P. yunnanensis* seedlings. According to

Figure 6, for the allometric relationships of total root length and root surface area with aboveground biomass, Grade I, Grade II, and Grade III seedlings all exhibit isometric growth, with slopes decreasing as the grade level decreases, and all slopes are less than 1 (Figure 6a, b). Regarding the allometric relationship between root volume and aboveground biomass, all three grades show allometric growth. The regression slopes follow the order: Grade II > Grade I > Grade III, and all slopes are less than 1, indicating that the accumulation rate of aboveground biomass is faster than the growth rate of root volume (Figure 6c). For root mean diameter and specific root area in relation to aboveground biomass, all three grades display allometric growth. In the allometric relationship between root mean diameter and aboveground biomass, the slopes for Grade I and Grade II are greater than 1. For the relationship between specific root area and aboveground biomass, the slope for Grade II is greater than 1, indicating that in these grades, the accumulation rate of aboveground biomass is faster than the growth rate of root mean diameter and specific root area (Figure 6d, h). For root tip number in relation to aboveground biomass, Grade II and Grade III seedlings show allometric growth, while Grade I seedlings exhibit isometric growth. The slopes follow the order: Grade I > Grade III > Grade II (Figure 6e). For root-shoot ratio and root tissue density in relation to aboveground biomass, Grade I and Grade II seedlings show allometric growth, with all slopes less than 1. Moreover, the slopes for root tissue density versus aboveground biomass are negative across all three grades (Figure 6f, i). For specific root length in relation to aboveground biomass, Grade I seedlings show allometric growth, and the slopes are negative for all three grades (Figure 6g).

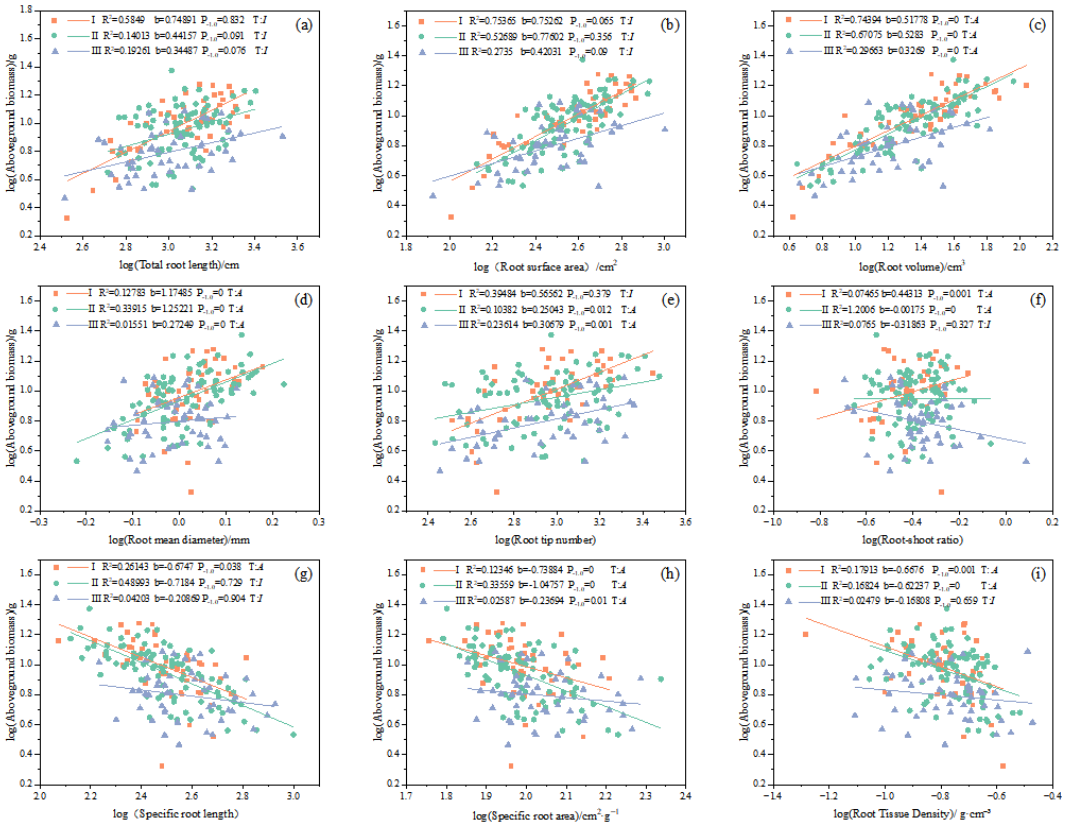

Figure 6: Allometric relationships between aboveground biomass and root morphological traits in *P. yunnanensis* across different grades. Note: (a) Total root length; (b) Root surface area; (c) Root volume; (d) Root mean diameter; (e) Root tip number; (f) Root-shoot ratio; (g) Specific root length; (h) Specific root surface area; (i) Root tissue density.

"b" = slope; P-1.0: significance of slope difference from theoretical value 1.0; "A" = allometric relationship, "I" = isometric relationship (same below).

3.5 Principal component analysis of root morphological traits in different grades of P. yunnanensis seedlings

As shown in Figure 7, on PC1, root biomass (0.20), root volume (0.15), root surface area (0.05), and root-shoot ratio (0.10) exhibit positive loadings, while seedling grade (Grade I: –0.25; Grade II: –0.20; Grade III: –0.15), specific root length (–0.10), and specific root area (–0.05) show negative loadings, indicating that PC1 primarily distinguishes the inverse relationship between root system size and seedling grade. PC2 mainly carries positive information from seedling grade (Grade I: 0.50; Grade II: 0.40; Grade III: 0.30), specific root length (0.20), and specific root area (0.10), reflecting the decisive role of absorption efficiency in seedling quality. Regarding the distribution of seedlings of different grades, Grade I seedlings are mainly concentrated on the positive side of the PC1 axis, closely aligning with the direction of traits such as total root length, root surface area, root volume, and root biomass. This indicates that the root morphology of Grade I seedlings is characterized by high total root length, high root surface area, high root volume, and high biomass accumulation. Grade II seedlings are relatively centrally distributed on both the PC1 and PC2 axes, showing a balanced performance across root traits. Grade III seedlings are mainly concentrated on the positive side of the PC2 axis, highly consistent with the distribution of specific root length, specific root area, and root tissue density, indicating that the root traits of Grade III seedlings are centered on high specific root length and high specific root area. The principal component analysis results clarify the differentiated root adaptation strategies of different grades of *P. yunnanensis* seedlings: Grade I seedlings rely on the expansion of root system size to achieve biomass accumulation, Grade III seedlings ensure resource uptake by optimizing root functional traits, and Grade II seedlings exhibit transitional root characteristics.

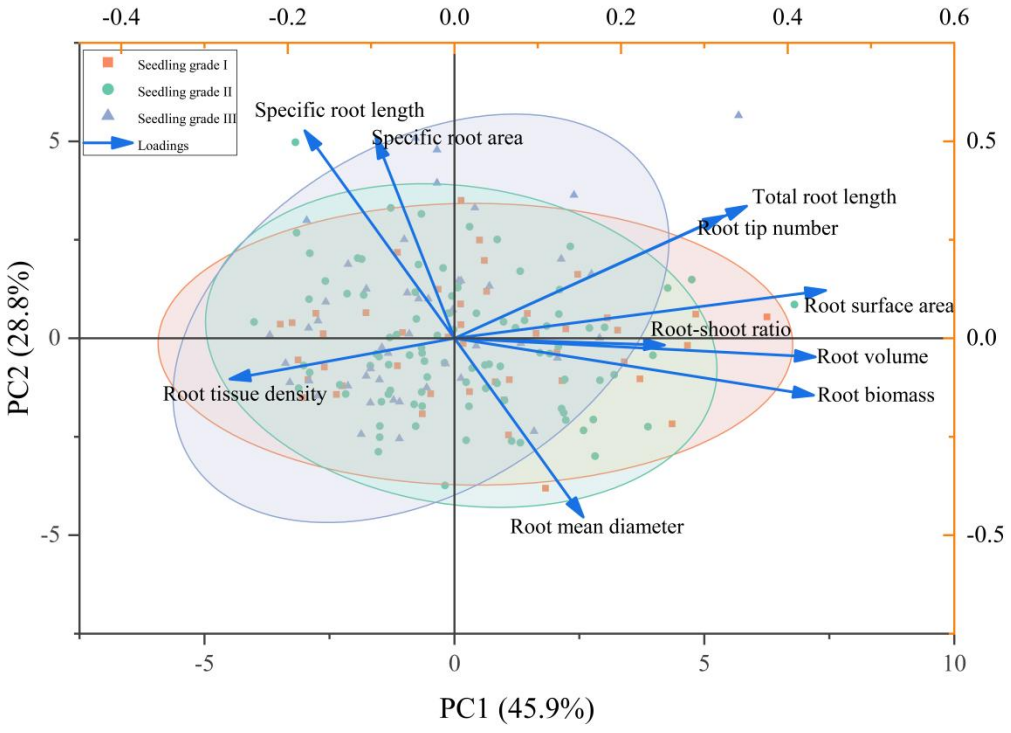

Figure 7: Principal component analysis (PCA) of root morphological traits of different grades of *P. yunnanensis* seedlings

Note: In the figure, Grade I seedlings (orange squares), Grade II seedlings (green dots), and Grade III seedlings (blue triangles) represent different growth grades of *P. yunnanensis* seedlings. Blue arrows indicate the loading vectors of each root morphological trait. PC1 is the first principal component (contributing 45.9% of the variance), and PC2 is the second principal component (contributing 28.8% of the variance). The ellipses of different colors represent the 95% confidence intervals for seedlings of each grade.

3.6 Analysis of Correlation Characteristics of Root Indicators of P. yunnanensis Seedlings of Different Grades

According to the correlation heatmap in Figure 8, Grade I seedlings exhibited significant positive correlations ($P < 0.05$) among total root length, root surface area, root volume, number of root tips, and root biomass, indicating a high degree of synergy between root morphological indicators and biomass in Grade I seedlings. In contrast, specific root length, specific root surface area, and root tissue density showed significant negative correlations ($P < 0.05$) with these traits. For Grade II seedlings, the positive correlations among total root length, root surface area, and root volume were slightly weaker than those in Grade I seedlings. The positive correlation between root biomass and root-shoot ratio was enhanced, while the negative correlations of specific root length, specific root surface area, and root tissue density with the aforementioned morphological and biomass indicators were significantly reduced. In Grade III seedlings, the positive correlations among total root length, root surface area, and root volume were further weakened. The association of average root diameter with other indicators such as total root length, root surface area, and root volume shifted from positive to negative. The negative correlations of specific root length, specific root surface area, and root tissue density were significantly strengthened, indicating a substantial reduction in the synergy among root system indicators in Grade III seedlings. Overall, most root morphological indicators across the three seedling grades showed strong correlations, suggesting that the root system development of two-year-old *P. yunnanensis* seedlings focuses on downward extension. Although positive trends were observed between root tissue density and specific root length, as well as between average root diameter and root-shoot ratio, these correlations were not statistically significant ($P > 0.05$).

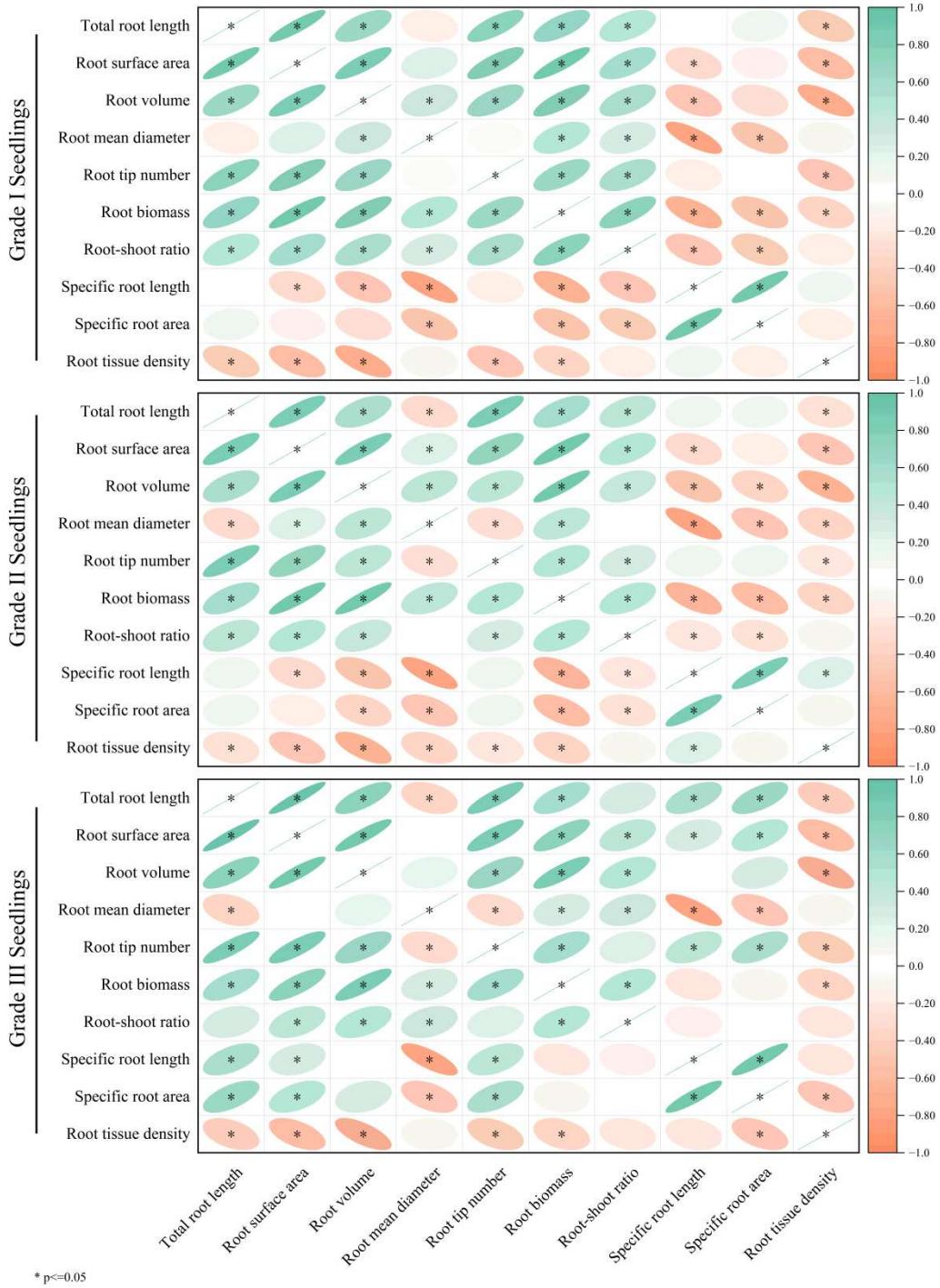

Figure 8: Correlation analysis of root morphological traits in *P. yunnanensis* seedlings across different grade classes.

Note: The color gradient of ellipses indicates the strength of Pearson correlation coefficients, with green representing positive correlations and red representing negative correlations (darker colors indicate stronger correlations). positive: bottom-left to top-right). Asterisks (*) denote significant correlations at the 0.05 level (*P < 0.05).

4. Discussion

4.1 Root Morphological Characteristics and Variation Patterns of P. yunnanensis Seedlings of

Different Grades

The root system is a crucial component of seedlings. Studying the morphological characteristics of the root system can reflect seedling quality and adaptability to the environment(Pan et al., 2025; Tang, Liao, Xu, & Cai, 2025). In this study, no significant differences were observed in total root length, number of root tips, and root tissue density among seedlings of different grades ($P > 0.05$), indicating that these parameters may be relatively conservative traits in the root system of *P. yunnanensis* seedlings, showing no response to variations in seedling grade(Pan et al., 2025). Root surface area, root volume, average root diameter, and root biomass exhibited a consistent variation pattern across different grades, following the order of Grade I > Grade II > Grade III(Chen et al., 2014). No significant difference was observed between Grade I and Grade II seedlings, while both grades showed significant differences from Grade III seedlings. From the perspective of growth strategies, the insufficient accumulation of root biomass in Grade III seedlings promoted the development of roots toward finer root morphology. Consistent with previous studies, low-grade seedlings optimize resource allocation by reducing average root diameter and shrinking root volume, thereby maximizing resource capture area with limited biomass investment(Larson & Funk, 2016). In contrast, the root-shoot ratio and specific root length showed an opposite grade differentiation pattern (Grade III > Grade II > Grade I), with significant differences among grades. Grade III seedlings balanced above-ground and below-ground growth and compensated for the deficiency of overall biomass by increasing the root-shoot ratio to raise the proportion of resource allocation to underground parts, and by enhancing specific root length to improve the resource absorption efficiency per unit root biomass. This finding is consistent with the theory proposed by Smith-Martin et al. that "plants in a low-growth state rely on root plasticity to regulate resource allocation"(Smith‐Martin, Xu, Medvigy, Schnitzer, & Powers, 2020; Tang et al., 2025).

The elevated root-shoot ratio and specific root length in Grade III seedlings may reflect a compensatory mechanism driven by limited aboveground photosynthetic capacity. Seedlings of lower grades had significantly smaller shoot size and fewer needles, which likely constrained their total photosynthetic area and carbon assimilation capacity. Under such carbon-limited conditions, optimal partitioning theory predicts that plants should allocate a greater proportion of assimilates to organs that acquire the most limiting resources. For Grade III seedlings, the limiting resource is likely soil nutrients and water, prompting increased investment in fine-root production (evidenced by higher SRL) rather than aboveground growth. This foraging response is consistent with the resource acquisition theory(Bloom, Chapin, & Mooney, 1985a), which states that plants preferentially invest in organs that acquire the most limiting resources. Notably, Norway spruce seedlings under low nutrient availability exhibited increased root growth and decreased shoot growth, leading to higher root-shoot ratios(Kaakinen, Jolkkonen, Iivonen, & Vapaavuori, 2004). Similar patterns have been observed in *Pinus contorta* and *Picea glauca* (Lieffers & Titus, 1989), where poor growing conditions consistently resulted in greater biomass allocation to roots. Thus, the root strategy of Grade III seedlings can be interpreted as an adaptive response to their intrinsically limited aboveground carbon gain: by constructing thin, high-SRL roots, they maximize the soil volume explored per unit carbon invested, thereby compensating for reduced photosynthetic capacity through enhanced belowground resource acquisition efficiency.

The results of coefficient of variation (CV) analysis further revealed the correlation between the phenotypic stability of each root index and grade adaptability(Pan et al., 2025). The CVs of

root tip number and specific root surface area showed small fluctuations among different grades, indicating high phenotypic consistency, which again confirmed their characteristics as conservative traits and highlighted their important role in maintaining the growth stability of seedling populations(Hogan, Valverde-Barrantes, Ding, Xu, & Baraloto, 2020). In contrast, the CVs of root surface area, root volume, average root diameter, root biomass, root-shoot ratio, and specific root length varied with seedling grades, and the degree of individual differentiation was more pronounced in Grade III seedlings(Aili et al., 2023). By means of differentiated adjustments of root morphology and resource allocation strategies among individuals, Grade III seedlings enhanced the environmental adaptability of some individuals(Y. Liu et al., 2025).

4.2 Changes in root phenotypic plasticity of different grades of P. yunnanensis seedlings

Phenotypic plasticity is an important survival strategy for plants to adapt to heterogeneous environments, balance resource allocation, and maintain population regeneration(Ghalambor, McKay, Carroll, & Reznick, 2007). Differences in the plasticity of seedling root traits directly determine their nutrient capture capacity, spatial expansion ability, and growth potential(Lynch, 2019). This study shows that the overall pattern of root trait phenotypic plasticity in different grades of *P. yunnanensis* seedlings is highly coordinated and consistent, but there are significant grade-dependent differences in functional trade-off strategies, which closely align with seedling grade differentiation and individual growth and development patterns(Y. Liu et al., 2025). Grade I and Grade II seedlings exhibit obvious advantages in root morphological growth, showing high phenotypic plasticity in expansion-related morphological traits such as root volume, root surface area, and total root length. These seedlings can rapidly regulate the development of root length, surface area, and volume to effectively expand underground space and improve water and mineral nutrient uptake efficiency, thereby supporting rapid aboveground biomass accumulation. At the same time, the plasticity of root mean diameter in these two grades remains consistently low, indicating that the root structure of vigorous seedlings is highly stable, which helps maintain nutrient transport efficiency in the roots(Moler, Toca, Jacobs, & Nelson, 2022). In contrast, Grade III seedlings experience growth constraints, and their root growth strategy shifts accordingly. On the one hand, they still maintain relatively high plasticity in root volume, root surface area, and total root length to sustain basic underground space expansion capacity; on the other hand, the plasticity of resource-use functional traits such as root-shoot ratio, specific root length, and specific root area is significantly higher than that in Grade I and Grade II seedlings(Van Der Bom, Williams, & Bell, 2020). Under limited growth conditions, low-grade seedlings actively adjust the root-shoot ratio, improve root nutrient use efficiency, and flexibly modify root morphology to adapt to the environment. This represents a compensatory adaptation mechanism for seedlings facing growth disadvantages(Toca, Moler, Nelson, & Jacobs, 2022). This clear pattern of plasticity differentiation elucidates the regeneration adaptation mechanism of *P. yunnanensis* seedlings and can provide a scientific basis for graded forest tending and seedling management in artificial afforestation.

4.3 Allometric Growth Mechanisms Between Root Morphology and Biomass of P. yunnanensis Seedlings of Different Grades

Allometric growth refers to the disproportionate growth relationship among different parts of an organism, which is determined by the genetic properties of the organism and influenced by environmental factors(Liao et al., 2025; Weiner, 2004). It serves as a crucial mechanism for organisms to adapt to the natural environment and optimize their external adaptability(Niklas &

Spatz, 2004). Significant differences existed in root growth and development among seedlings of different grades, and the variations in various root traits were distinct. This characteristic profoundly reflected the regulatory effect of seedling grades on root growth and allocation strategies(Pan et al., 2025). Regarding the relationships between total root length, root surface area and root biomass, Grade I and Grade II seedlings exhibited allometric growth relationships, whereas Grade III seedlings showed isometric growth relationships(Zhu et al., 2025). The slopes of Grade I and Grade II seedlings were both less than 1, while that of Grade III seedlings was greater than 1, indicating that the growth rates of root length and surface area were faster than the rate of biomass accumulation. To compensate for their growth deficiencies, low-grade seedlings prioritized root growth to promote the expansion of root surface area, thereby maximizing the resource capture range with limited biomass(Bloom, Chapin, & Mooney, 1985b). The relationships between average root diameter, root volume and root biomass were all allometric, with slopes increasing as seedling grades decreased(K. Tang et al., 2024). Among these, the slopes of root volume for all three grades were greater than 1, meaning that the growth rate of root volume was faster than the accumulation rate of root biomass. In contrast, the slopes of average root diameter were less than 1, indicating that the accumulation rate of root biomass exceeded the growth rate of average root diameter(Wang et al., 2020). Most of the other indicators showed allometric growth relationships with root biomass. Specifically, the relationship between root tip number and root biomass was isometric for Grade I and Grade II seedlings, but the slope of Grade I seedlings was less than 1 while that of Grade II seedlings was greater than 1, suggesting that despite the isometric growth pattern in both grades, inherent differences existed between them.

In the allometric relationships between root traits and aboveground biomass, total root length and root surface area exhibit isometric growth across all seedling grades, but the coordination between aboveground and belowground growth gradually weakens as seedling grade decreases. Core architectural traits such as root volume and root mean diameter show allometric growth in all grades, with Grade I and Grade II seedlings accumulating aboveground biomass significantly faster than root architecture is established, indicating that they prioritize aboveground photosynthetic growth advantages(Grotkopp, Rejmánek, & Rost, 2002; Tang et al., 2025). Root tip number, root-shoot ratio, and root structural functional traits display grade-dependent allometric differentiation: Grade I and Grade II seedlings show stronger coordination among traits, while Grade III seedlings flexibly adjust the allometric allocation of root functional traits to adapt to constrained growth environments. Specific root length and root tissue density exhibit negatively correlated allometric relationships across all grades, further indicating that lower-grade seedlings reduce investment in root structure and optimize resource allocation to maintain aboveground survival and growth(Wilson, 1988).

Overall, *P. yunnanensis* seedlings of different grades developed differentiated adaptive strategies by precisely regulating the allometric growth relationships between root systems and biomass: Grade I seedlings took biomass accumulation as the core and maintained coordinated allometric growth between root morphology and biomass; Grade II seedlings, as a transitional type, adapted to their own growth status by flexibly adjusting allometric slopes; Grade III seedlings coped with growth limitations by altering allometric types and enhancing the expansion of root morphology(Tang et al., 2025).

The contrasting root strategies of Grade I and Grade III seedlings can be further interpreted within the framework of the Root Economics Spectrum (RES). The RES describes a trade-off axis

from acquisitive to conservative strategies, where acquisitive roots are characterized by high specific root length (SRL), low root tissue density (RTD), and rapid resource uptake, whereas conservative roots exhibit the opposite syndrome. In the present study, Grade III seedlings exhibited significantly higher SRL and root-shoot ratio but lower root biomass and average diameter compared with Grade I seedlings, placing them closer to the acquisitive end of the RES. This pattern is consistent with the theoretical prediction that plants in resource-limited conditions prioritize traits that maximize resource capture per unit carbon invested. However, the RES in tree species is multidimensional rather than unidimensional. SRL is orthogonal to the main plant economic spectrum axis, meaning that high SRL can occur independently of RTD variation (Kramer‐Walter et al., 2016). In our study, Grade III seedlings showed high SRL but did not differ significantly in RTD from other grades, supporting the view that SRL and RTD represent separate functional dimensions in *P. yunnanensis* seedlings. The multidimensional nature of root traits(Weemstra et al., 2016), further suggests that Grade III's "fine-root strategy" is not simply a position shift along a single economics axis, but rather a coordinated reconfiguration across multiple functional dimensions—high SRL for resource acquisition, elevated root-shoot ratio for belowground investment, and reduced root diameter for construction economy.

4.4 Principal component analysis of root morphological traits of different grades of P. yunnanensis seedlings

Principal component analysis can reveal differences in root traits and growth strategies among different grades of *P. yunnanensis* seedlings(B. Liu et al., 2020). PC1 mainly reflects the overall growth status of the root system, with root biomass, root volume, and root surface area showing positive loadings, while seedling grade, specific root length, and specific root area show negative loadings, indicating that the larger the total root system size, the higher the seedling grade (closer to Grade I). PC2 primarily reflects root nutrient uptake efficiency and is closely associated with specific root length and specific root area. The results show that Grade I seedlings are mainly distributed on the positive side of the PC1 axis, possessing greater total root length, root surface area, root volume, and root biomass, and rely on expanding total root system volume to achieve biomass accumulation. In contrast, Grade III seedlings are concentrated on the positive side of the PC2 axis, relying on higher specific root length and specific root area to improve unit root absorption efficiency and compensate for growth disadvantages(G. Tang et al., 2024). Overall, *P. yunnanensis* seedlings exhibit a well-defined hierarchical root adaptation strategy: high-grade seedlings focus on root volume expansion, while low-grade seedlings enhance fine-root resource use efficiency to adapt and survive(Tang et al., 2025).

4.5 Correlations Among Root Indicators of P. yunnanensis Seedlings of Different Grades

Combined with the analysis of correlation heatmaps, significant differences were found in the correlations among root indicators of *P. yunnanensis* seedlings across different grades. Essentially, these differences in correlations directly reflected the differentiated growth strategies of seedlings at various grades(Li et al., 2025). In Grade I seedlings, total root length, root surface area, root volume, and root tip number showed significant positive correlations with root biomass, but exhibited negative correlations with specific root length , specific root surface area and root tissue density(Huaraca Huasco, 2021; Jin et al., 2023). Grade II seedlings represented a transitional type, where the positive correlations among core morphological indicators weakened, the positive correlation between root biomass and root-shoot ratio strengthened, and the negative correlations of fine root indicators diminished, thus achieving flexible regulatory effects(Gao et al., 2020). In

Grade III seedlings, the coordination among morphological indicators further decreased, and the correlation between average root diameter and other indicators shifted from positive to negative. These results indicated that synergistic growth effects existed among various plant indicators, and the root indicators interacted with one another(Fujii, 2024). Seedlings adjusted their root morphological structure to meet the demands of normal growth and development. This finding was correlated with the previous analyses of root morphology and allometric growth, which further enriched the theoretical system of grade-dependent regulation of root systems in *P. yunnanensis* seedlings. It also provided a scientific basis for accurately evaluating seedling growth status, optimizing cultivation measures in a targeted manner to enhance the synergistic growth capacity of root systems, and ultimately improving seedling quality(Sun, Wang, Chen, Cai, & Xu, 2025).

5. Conclusion

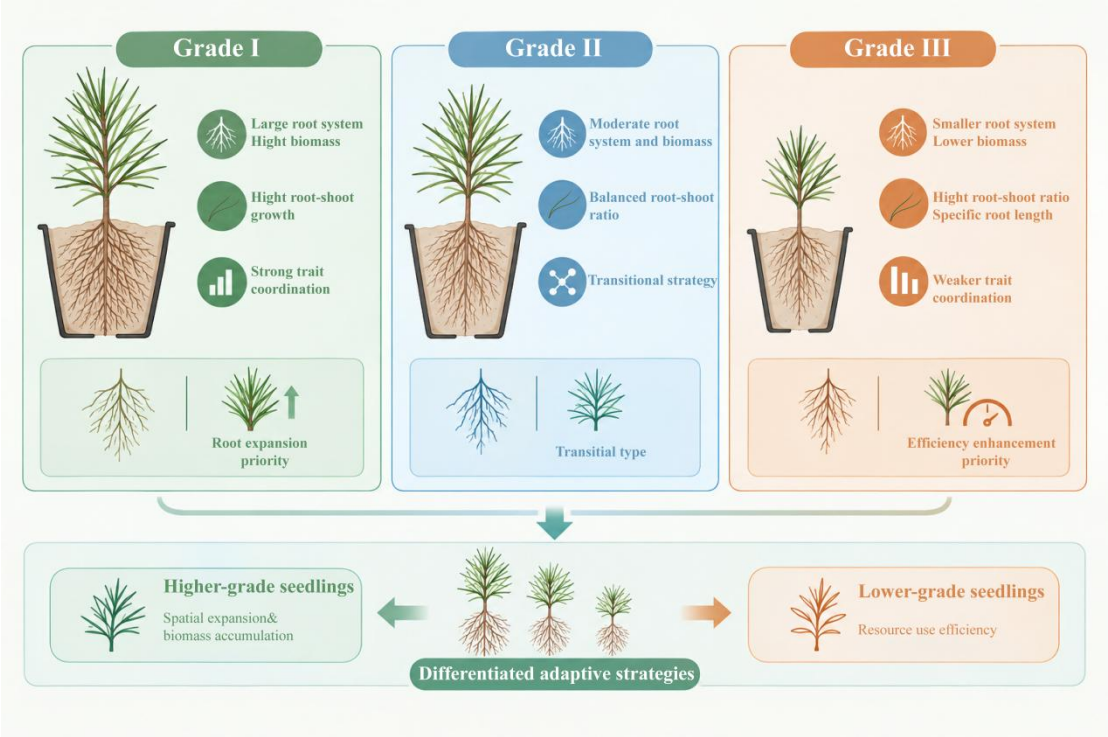

Figure 9: Root growth adaptation strategies of different diameter classes in *Pinus yunnanensis* seedlings

In this study, we investigated *P. yunnanensis* seedlings of different grades to analyze root morphology, biomass, phenotypic plasticity, allometric growth relationships, principal components, and trait correlations, aiming to reveal differences in root growth and adaptive strategies among seedling grades. The results showed significant differences in root morphology and biomass among grades. Grade I and II seedlings had large root system size and high biomass, while Grade III seedlings compensated for growth disadvantages by increasing root-shoot ratio and specific root length to optimize resource allocation. Lower-grade seedlings also exhibited greater trait variation. The overall pattern of root phenotypic plasticity was consistent across grades: morphological traits showed high plasticity, whereas structural traits were more stable. Grade III seedlings displayed higher plasticity in functional traits, allowing flexible adaptation to resource limitations. Most root traits showed allometric relationships with root biomass and aboveground biomass. Lower-grade seedlings had faster root expansion relative to biomass accumulation, while higher-grade seedlings showed a greater advantage in aboveground biomass accumulation;

functional traits were mostly negatively allometric. Principal component analysis indicated that Grade I seedlings prioritized root system expansion, Grade III seedlings focused on efficiency enhancement, and Grade II seedlings exhibited a transitional type, forming three differentiated adaptive strategies. Trait correlations weakened with decreasing seedling grade: Grade I seedlings had strong trait coordination, whereas Grade III seedlings showed reduced coordination. In summary, root growth strategies of *P. yunnanensis* seedlings are clearly differentiated across grades: higher-grade seedlings emphasize spatial expansion and biomass accumulation, while lower-grade seedlings focus on resource use efficiency（Figure 9）. These findings provide theoretical support for grade-based cultivation, growth status assessment, and optimization of management measures for this species.

Declarations

Abbreviations

Not applicable

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and materials

The data are available from the corresponding author.

Competing Interests

The authors declare no competing interests.

Funding

This research was supported by Yunnan Fundamental Research Projects (grant NO. 202401BD070001-023), the Project of Science and Technology Talent and Platform Program of Yunnan Provincial Department of Science and Technology (202605AF350003), the Yunnan Provincial First-Class Discipline Construction Fund for Forestry at Southwest Forestry University (LXXK-2025D01), Yunnan Graduate Tutor Team Building Project (2024-61).

Authors' contributions

Na Li: Writing – original draft, investigation, review & editing, Conceptualization. Xiaoyue Zhang: Investigation, Formal analysis, Data curation. Nianhui Cai: Investigation, review & editing. Yulan Xu: Writing – review & editing, supervision, Funding acquisition, Conceptualization.

Acknowledgements

Here, I would like to express my sincere gratitude to my supervisors Yulan Xu (Professor) for their guidance in my experimental work and article writing. Secondly, I would like to thank my research group partners.

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691