

Analysis of Phenotypic Plasticity and Growth Strategies of Multi-Generational Selected *Cunninghamia lanceolata* Varieties in Different Artificial Forest Soils

Wenyue Wang

wwy19970424@163.com

Chinese Academy of Forestry Research Institute of Subtropical Forestry <https://orcid.org/0000-0001-7826-010X>

Huimin Niu

Haobo Zhao

Zhen Zhang

Jingyong Ji

Guiping He

Zhichun Zhou

Research Article

Keywords: plant height, biomass, fine root functional traits, variation, phenotypic plasticity, genotype-environment interaction

Posted Date: May 15th, 2025

DOI: <https://doi.org/10.21203/rs.3.rs-6535533/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Abstract

Aims: Maximizing tree growth potential and effectively integrating with the growth environment are vital strategies for enhancing phenotypic plasticity. These approaches enable tree species to adapt to dynamic environmental conditions by leveraging the effects of the environment, genotype, and genotype-by-environment (G×E) interactions.

Methods: In this study, 25 improved *Cunninghamia lanceolata* varieties, developed through multiple generations of breeding, were transplanted into four artificial forest soils. We analyzed genotype, environment, and G×E interactions contributing to variations in growth, biomass, and root traits, identifying key factors driving phenotypic plasticity.

Results: The results show that soil environmental effects and G×E interactions are the dominant factors influencing trait variation, explaining 55.89% to 93.94% of the observed variation, while the varietal effect is relatively minor. Pronounced phenotypic plasticity drives divergent selection in aboveground and belowground growth strategies. Root average diameter (RAD), total root volume (TRV), and root-to-shoot ratio (R/S) are critical traits influencing root dry weight (RDW). Although RDW does not directly impact plant height, it significantly affects aboveground dry weight (ADW).

Conclusions: The above results emphasize that the changes in the aboveground-belowground growth strategies of Chinese fir during the seedling stage are related to the plasticity of root functional traits. For multi-generational genetically improved varieties, we explored how leveraging genetic effects (G), environmental effects (E), and genotype-by-environment interactions (G×E) in the selection of aboveground growth and root functional traits influences the driving processes of biomass accumulation. Our results provide actionable insights for selecting soil-specific genotypes in subtropical plantations, reducing dependency on chemical fertilizers.

1 Introduction

The availability of forest soil resources is gradually decreasing, while frequent extreme weather events—such as prolonged warming, droughts, and heavy rainfall—exacerbate nutrient depletion, severe soil erosion, and soil acidification. These factors create significant challenges in meeting the nutrient demands required for high-quality and high-yield timber production (Grierson et al., 2011; Wang et al., 2021). In the selection and promotion of afforestation species, the focus should be on harnessing their growth potential (genotype) and effectively integrating it with environmental factors (e.g., soil resources and climatic conditions), rather than relying heavily on excessive fertilization to boost productivity (Chen et al., 2023; Jie et al., 2024; Su et al., 2024). Consequently, identifying superior genotypes with strong growth potential and high phenotypic plasticity to enhance the productivity of artificial forests has emerged as a key research priority in the development of artificial forestry (Grierson et al., 2011).

Studies have demonstrated that plants adapt to variations in soil nutrient availability through biomass allocation and adjustments in functional traits, thereby altering their utilization of limited resources. The

growth potential of trees is determined by the genotypic response to variable growth environments, which leads to substantial phenotypic variation. This phenotypic variation, when sustained, provides a crucial foundation for selecting superior genotypes and evaluating their adaptability (Hendrik et al., 2012; Daniela. et al., 2014). Phenotypic evaluation trials involving multiple genotypes across diverse environments are a key step in identifying superior genetic materials in plant breeding (Miloš et al., 2015). Phenotypic traits are influenced not only by genotype but also by favorable environmental conditions, which can significantly shape an organism's phenotype. The impact of the environment on quantitative traits is considerably greater than on qualitative traits. Consequently, most genetic studies on quantitative traits must be grounded in phenotypic assessments conducted across multiple environments (Kramer-Walter et al., 2016; Boye et al., 2024; Guo et al., 2024).

Research has found that plant growth exhibits diverse responses to limited soil nutrients, with root systems, as vital resource-acquisition organs, determining the amount of water and nutrients absorbed for photosynthesis and growth (Bardgett et al., 2014; Chen, 2021; Zhao et al., 2024; Lu et al., 2024, Jin et al., 2024). The absorption function of roots is characterized by a series of traits, revealing the dimensions of root trait variation as a key step in understanding how roots and plants adapt to heterogeneous environments. The variation in root traits is extensive, with interspecific variation in absorption root diameter exceeding 100-fold and intraspecific variation exceeding 10-fold (Zhang et al., 2023). Therefore, understanding the range of root trait variation is crucial for comprehending root systems and plant adaptation to heterogeneity. However, many important root functions have been largely overlooked in modern plant breeding; thus, root functional traits should be a long-term focus for breeders (Chen et al., 2021; Han et al., 2022).

Within tree species, significant variations in root morphology and architecture exist among different genotypes. These differences are primarily reflected in the plasticity of traits such as root branching intensity, fine root length, root surface area, and root volume (Wang et al., 2006; Kong et al., 2014; Valverde-Barrantes., 2022). Plant roots have evolved various strategies for nutrient acquisition (e.g., phosphorus), including elongating and thinning to increase surface area and developing complex branching structures to explore larger soil volumes (Zemunik et al., 2015; McCormack et al., 2018; Wen et al., 2019; Messier et al., 2024). In adverse environments, plants may adapt by increasing root-to-shoot ratios or total root length, reducing root diameter and tissue density to lower construction costs, and expanding absorption areas to meet environmental challenges (Bennett et al., 2019; Kotula L et al., 2021; Franziska et al., 2024). The variations in plant responses to resource stress gradients are influenced by multiple factors, including genetic differences and ecological physiological adaptations (Valladares et al., 2007; Shipley et al., 2016; Freschet et al., 2019).

From a genetic perspective, leveraging the extent of genetic variation among individual genotypes can facilitate the selection of suitable genetic materials during plant adaptation to environmental conditions. From an ecological standpoint, phenotypic plasticity represents coordinated trait responses that occur across multiple environments. Under resource stress, any trait response can alter a plant's perception of resource limitations, reflecting substantial variability in root plasticity (Zhu et al., 2010; Freschet et al.,

2013; Guo et al., 2024). Furthermore, the high variation in specific root traits among genotypes is critical for developing nutrient foraging strategies. The joint variation of root morphological and functional traits provides valuable insights into the underground nutrient acquisition strategies of plants (Wen et al., 2020). For instance, plants with finer roots often rely more on morphological adaptations, such as increased specific root length, to expand soil exploration and enhance nutrient uptake, exemplifying a resource-acquisition strategy. In general, genotypes employing resource-conserving strategies are expected to exhibit stronger correlations among various root traits compared to those employing resource-acquisition strategies (Wen et al., 2019).

In practice, it is often observed that some genotypes are highly sensitive to environmental changes, while others exhibit a relatively sluggish response. Moreover, certain genotypes that perform well in specific environments may demonstrate poor phenotypes in other settings, whereas genotypes with suboptimal performance under one set of conditions may excel in others. This phenomenon is primarily driven by genotype-environment interaction effects (G×E) (Liu et al., 2021; Poupon et al., 2023). When analyzing the relationship between genotype and environment, the focus is typically on how an organism's genetic makeup interacts with external environmental factors to influence phenotype (Bennett et al., 2019; Franziska et al., 2024). However, most biological traits that directly affect tree growth are complex traits, controlled by numerous unknown genes and regulated through intricate signaling pathways. These traits often exhibit an "extended phenotype," which reflects underlying regulatory and physiological mechanisms guided by G×E interactions, serving as the direct mechanism maintaining such "hidden" variation (Lopez et al., 2023; Qin et al., 2024). The direct mechanism maintaining such "hidden" variability is the genotype-environment (G×E) interaction effect (Johnson et al., 2007; Michael et al., 2023; Li et al., 2017). Research on G×E effects has been conducted for numerous commercially important tree species worldwide, including *Pinus elliottii*, *Pinus taeda*, *Picea abies*, *Pinus radiata*, and *Larix kaempferi* (Braga et al., 2020; Rayssa et al., 2020; Poupon et al., 2023; Ling et al., 2021; Yuan et al., 2020). Most studies indicate that G×E effects are widespread in forestry, highlighting the importance of understanding the patterns and scales of these effects for accurate genetic gain assessments of tree traits. Leveraging genotype effects, G×E effects, and environmental effects to identify superior lines has proven effective in enhancing yields (Freschet et al., 2021). However, these studies predominantly focus on evaluating growth rates and wood properties using genetic population materials. There is limited research addressing the genetic effects, soil effects, and G×E effects on both aboveground growth potential and root development in trees. This gap in evaluation carries significant implications for the selection of superior genotypes and the quantitative assessment of soil resource utilization in forestry management.

To investigate how multi-generational, selected tree varieties sustain growth potential under changing soil environmental conditions, we focus on *Cunninghamia lanceolata* (Chinese fir), the most extensively planted tree species in China, widely distributed across southern provinces and primarily used for timber and construction materials (Liao et al., 2023). In this study, we transplanted 25 varieties, selected through three breeding generations, into four distinct artificial forest soils and measured their growth and root functional traits. The objectives were to: (1) elucidate the phenotypic basis underlying the

aboveground and belowground growth strategies of different *Cunninghamia lanceolata* varieties; (2) assess the relative contributions of genotype, environment, and their interactions to phenotypic variation in growth, biomass, and root functional traits; and (3) quantify the primary factors driving phenotypic plasticity. By examining the integrated phenotypic responses of *Cunninghamia lanceolata* varieties to soil environmental changes, this research aims to reveal how these varieties maintain high productivity while adapting to variable soil conditions. The findings provide valuable insights into the adaptation strategies of *Cunninghamia lanceolata* and offer a reference framework for its promotion and cultivation across diverse soil environments.

2 Materials and Methods

2.1 Experimental materials and design

The materials included 25 fir genotypes, which were derived from zygotic family lines (produced by free pollination) in the 3rd generation seed orchard, corresponding to parents with different genetic backgrounds, and were breeding materials selected by rotation (Supplementary Table 1). These lines were selected through rotational breeding for traits such as growth rate, wood density, and stress tolerance. Each genotype reflects unique combinations of alleles accumulated over three generations of selection, ensuring a broad genetic spectrum for evaluating plasticity. In November 2021, seeds were collected, and then uniformly sown and nursed in seedbeds to produce 1-year old seedlings, with seedling heights and diameters in the range of 21.15 ± 1.22 cm and 2.53 ± 0.19 mm, respectively. The container used for the controlled potting experiment was a non-woven bag with a height of 30 cm and a diameter of 20 cm.

The soils used for potting were obtained from a pure *Cunninghamia lanceolata* plantation (SS), a pure *Pinus massoniana* plantation (MS), a pure *Schima superba* plantation (KS), and a common red soil (RS) from an unplanted stand. The selection of these soils was based on the silvicultural needs of fir trees in production. The soils collected from plantation forests were 20–40 cm thick, and were sieved through a 5 mm sieve after removing debris such as plant residues, apoptosis, and gravel. The physicochemical properties of the soil from different plantation forests showed variability (Fig. 1). 2022 Seedlings of close plant size were selected in October, and the plants were transferred into pots, one plant per pot. A completely randomized block design was used, with three replicates set up for each treatment in each family line and 10 plants in each replicate, for a total of 3000 seedlings. Seedlings were watered thoroughly after transplanting and placed in a semi-controlled nursery with consistent management conditions such as temperature, light, moisture and humidity.

2.2 Growth Survey, Sample Harvesting and Indicator Measurement

2.2.1 Growth index survey

Seedling plant height (H) was measured regularly every month starting from April 1, 2023 with an accuracy of 0.01 cm. the last seedling plant height measurement was conducted on November 1, 2023. The growth curve of seedling plant height was obtained by using the fitting of plant height and planting days, and the optimized Logistic equation was as follows: $y = \frac{k}{1+ae^{-bt}}$, where t is the growth time, y is the growth of seedling height, k is the theoretical limit value of the upper limit value of the growth, and a and b are the coefficients to be determined, and the start and end time of the rapid growth period were calculated after deriving the fitted equation with the following formulas: the start time of the rapid growth period, $t_1 = (\ln a - 1.317) / b$, end of rapid growth period, $t_2 = (\ln a + 1.317) / b$ (Ge et al., 2020).

2.2.2 Determination of functional traits of root system

At the end of the survey, whole plant sampling was performed on the experimental seedlings using the destructive sampling method, and the root system was collected to ensure that it was intact and brought back to the laboratory. The underground part was cut from the root base, the root system was rinsed with deionized water and the surface water was dried, and the length, surface area and root volume data of the root system at each diameter level were determined using the image analysis software WinRHIZO Pro STD1600+ (Regent Instruments, Canada), and the diameter levels were in the order of the 1st diameter level (D1, 0 to 0.5 mm), the 2nd diameter level (D2, 0.5 to 1.0 mm), 3rd (D3, 1.0 to 1.5 mm), 4th (D4, 1.5 to 2.0 mm) and 5th (D5, > 2.0 mm). Parameters such as total root length (RL, cm), total root surface area (SA, cm²), total root volume (RV, cm³), mean root diameter (RAD, mm), number of bifurcations (RBN), and root conformation grading were obtained, which were then converted to obtain the specific root length (SRL, cm/g), specific root area (SRA, cm²/g), and branching strength (RBS) according to the following equation: SRL (cm/g) = RL/RDW, SRA (cm²/g) = SA/RDW, and RBS = RBN/RL. In addition, the root system with a diameter class ≤ 2.0 mm was referred to as fine roots, and the fine root length (TRL, cm), fine root surface area (TRA, cm²), and fine root volume (TRV, cm³) were calculated.

The aboveground part was divided into leaves, stems and branches, which were put into a constant temperature oven at 105°C for about 30 min, followed by baking at 80°C until constant weight, to obtain the leaf dry biomass (LDW, g), stem dry biomass (SDW, g), branch dry biomass (BDW, g), above-ground dry biomass (ADW, g), and root dry biomass (RDW, g), based on which the root-crown ratio was calculated (R/S) = RDW/ADW.

2.3 Data Statistics and Analysis

The GLM (Generalized Linear Model) procedure in SAS 9.4 software was employed to test the significance of Chinese fir's plant height and root functional traits among families, among soil environments, as well as the interaction effects between families and environments. The least significant difference multiple comparison method was used to analyze the difference levels (with a significance level of $\alpha = 0.05$). The TYPE1 method in the PROC VARCOMP program was adopted to calculate the variance components of each factor for the measured traits, and then the environment

variation coefficient (CV_e), genetic variation coefficient (CV_g), genetic correlation coefficient (CC_g) and family heritability (h_f^2) were calculated. For the estimation methods, please refer to the literature (Yuan et al., 2020). The breeding value prediction was based on the best linear unbiased prediction (BLUP) of the linear mixed-effects model. The analysis of GGE (Genotype main effects plus Genotype-by-Environment interaction) biplots was implemented using the R software package GGE - Biplot GUI. The biplot model equation is as follows: $\frac{Y_{ij} - \mu - \beta_j}{d_j} = \lambda_1 g_{i1} e_{1j} + \lambda_2 g_{i2} e_{2j} + \epsilon_{ij}$, where Y_{ij} represents the genetic value of genotype i combined with trait j , μ is the average value of all combinations of trait j , β_j is the main effect of trait j , g_{i1} and g_{i2} are the eigenvectors of genotype i on principal component PC1 and PC2 respectively, e_{1j} and e_{2j} are the eigenvectors of trait j on principal component PC1 and PC2 respectively, d_j is the phenotypic standard deviation, and ϵ_{ij} is the model residual resulting from the combination of genotype i and trait j .

To investigate the effects of genotype and environment on seedling growth, an initial structural equation model was developed based on regression analysis. Genotype and environment were used as exogenous variables, plant growth traits and biomass allocation as endogenous variables, and ADW and RDW as response variables. By running the “piecewiseSEM” package in R software, correlated variables with no significant path ($p > 0.05$) and high covariance were eliminated, and an information criterion (AIC) chi-square test $p > 0.05$, RMSEA < 0.05) and goodness-of-fit index (GFI) > 0.95 were obtained for the Model.

3 Result and analysis

3.1 Variation analysis

The genetic coefficient of variation (CV_g) for plant height and biomass of each organ ranged from 3.58–13.92%, while the environmental coefficient of variation (CV_e) ranged from 9.10–40.78%. The genetic variation coefficient for root phenotypic traits varied between 0.91% and 7.20%, with the environmental variation coefficient ranging from 15.50–25.87%. These findings indicate that the observed phenotypic trait variations are influenced by soil environmental effects, genotype effects, and G×E interactions (Table 1; Fig. 2).

Table 1
ANOVA tests for growth and root traits of *Cunninghamia lanceolata* seedlings.

Traits	Mean value	F value			Coefficient of variation (%)		h_f^2
		<i>G</i>	<i>E</i>	<i>G</i> × <i>E</i>	<i>CV_g</i>	<i>CV_e</i>	
H/cm	51.86	9.75**	144.99**	4.18**	3.58	9.10	0.57
ADW/g	9.57	4.79**	17.45**	1.91**	6.56	23.25	0.60
LDW/g	5.81	4.92**	13.16**	1.84**	6.91	23.61	0.63
BDW/g	0.99	5.90**	19.94**	1.66**	13.92	40.78	0.72
SDW/g	2.77	5.76**	21.77**	2.54**	6.66	22.11	0.56
RDW/g	2.47	1.27**	103.99**	2.22**	4.69	28.80	0.30
SRL/(cm/g)	1030.05	4.38**	30.54**	6.54**	5.85	23.90	0.25
SRA/(cm ² /g)	179.50	5.84**	23.90**	7.54**	3.87	17.81	0.18
RAD/mm	2.53	3.69**	37.35**	6.06**	2.73	16.15	0.11
RBS	8.75	21.68**	66.12**	29.46**	7.20	15.50	0.21
TRL/cm	2338.59	3.35**	63.00**	3.30**	0.91	24.69	0.10
TRA/cm ²	331.90	3.36**	80.14**	2.60**	3.60	24.86	0.23
TRV/cm ³	6.04	4.07**	80.57**	2.77**	4.91	25.87	0.32
R/S	0.26	3.75**	163.74**	4.82**	3.88	21.07	0.23
H, Plant Height; ADW, Aboveground dry weight; LDW, Leaf dry weight; BDW, Branch dry weight; SDW, Stem dry weight; RDW, Root dry weight; SRL, Specific root length; SRA, Specific root area; RAD, Root average diameter; RBS, Root branching strength; TRL, Fine root length; TRA, Fine root surface area; TRV, Fine root volume; R/S, Root to shoot ratio. <i>G</i> : Genotype; <i>E</i> : Environment; <i>G</i> × <i>E</i> : Genotype and environment interactions; <i>CV_g</i> : Genetic variation coefficient; <i>CV_e</i> : Environment variation coefficient; h_f^2 : Family heritability.							

The H, RDW, TRA, TRV, and R/S are significantly influenced by soil environmental effects, contribution rate of variance from 44.83–62.10%, branch biomass (LDW) is predominantly affected by genotype (44.11%) and other traits are largely influenced by the genotype × environment (*G*×*E*) interaction, which accounts for 45.23–74.69% of the variance, particularly in specific root length (SRL) and specific root area (SRA). Average root diameter (RAD) and branch strength (RBS) are also primarily affected by the *G*×*E* interaction, which contributes over 67.90% to their variation, indicating that genotype performance

varies significantly across different soil types. Both the G×E interaction and environmental effects are critical factors influencing the growth and root functional traits of fir during the seedling stage, contributing a cumulative 55.89–93.94% of the observed variation (Fig. 2).

3.2 Plasticity analysis

We focused on three key metrics: H, ADW, and RDW. The GGE-BLUP analysis results supported the rank effect of different genotypes among soil environments. PC1 and PC2 collectively account for 77.91% of the G + GE effect on H, 85.5% on ADW, and 86.19% on RDW. As shown in Fig. 3, respectively represent the adaptability of plant height, aboveground biomass and root biomass of each family. The results show that the more diverse the soil environment, the greater the change in the G×E effect. The optimal genotype at a location cannot appear in four soil environments at the same time, showing greater plasticity. Based on growth performance, genotypes with high production potential and relatively stable were selected. According to the selection rate of 10%, the average expected gain in plant height is 4.05%, and the average expected gain in aboveground biomass (ADW) The gain is 6.32%, and the average expected gain of root biomass (RDW) is 4.07% (Fig. 3).

3.3 Responses of growth and biomass to the environment

The growth rhythm of plant height (with $R^2 > 0.99$) demonstrates that diverse plantation soil conditions exert an impact on the duration of the rapid growth stage of seedlings, thereby further influencing the height growth during the seedling phase. The onset time of the plant height growth entering the rapid growth period is essentially consistent (around May 20th). Under KS soil, the growth increment of plant height is the maximum, and the duration of the rapid growth period is the longest (98 days). The growth amount under SS soil ranks second only to that under KS soil; nevertheless, the initiation time of the rapid growth period is the earliest, with a duration of 93 days. The growth amounts under MS soil and RS soil are relatively smaller, and the durations of their rapid growth periods are shorter, being 79 days and 75 days respectively. The duration of the rapid growth period of KS soil exceeds that of RS soil by 23 days, and the average growth amount is 17.43% higher (Fig. 4A).

Regarding the ADW, LDW, BDW, and SDW, the order among different plantation soils is as follows: KS > SS > MS > RS (Fig. 2). The ADW, LDW, BDW, and SDW of KS soil are respectively 15.87%, 13.36%, 20.09%, and 17.51% higher than those of RS soil. In terms of RDW, the order is: MS > KS > RS > SS. The MS soil, which exhibits the highest RDW, is 49.75% higher than SS soil (Fig. 4B).

3.4 Responses of above-ground and subsurface growth strategies

The Chinese firs in KS soil belong to the class with the H and ADW accumulation The RAD significantly increased, being 1.75–7.41% higher than in other soils. Additionally, the ability of RBS was the strongest, surpassing other soils by 10.29–20.52%. Comparatively, SS soils with the smallest root biomass had

higher SRL and SRA, finer RAD, and TRL, TRA, TRV and R/S than other soils. The RDW in MS soil was the highest, and the indexes of TRL, TRA, TRV and R/S were also the highest (Fig. 2).

The proportion of fine root length to total root length ranges from 97.83–98.03%, the proportion of fine root surface area to total root surface area is from 85.14–87.76%, and the proportion of fine root volume to total root volume is from 50.89–56.66%. Fine root phenotypic traits appear to be an important factor influencing the differences in underground biomass among different soils (Fig. 5). Among them, the length of fine roots in diameter class D1 accounts for 58.13–67.49% of the total root length, with the highest proportion in SS treatment (Fig. 5A), which is 7.43%, 7.37%, and 16.10% higher than that in MS soils, KS soils, and RS soils respectively. The fine root length proportions for the D2 and D3 diameter classes range from 23.62–32.06% and 5.31–6.02%, respectively, both with a high proportion in RS soil, while the proportion of fine root length in diameter classes D4 and D5 is the highest in KS soils (Fig. 5A). A similar phenomenon is presented in the proportion of root surface area of each diameter class in different soils (Fig. 5B, C). This indicates that seedlings in relatively barren soils rely more on the increase in the proportion of the length and surface area of fine roots in diameter classes D1, D2, and D3 to enhance the root's ability to absorb soil nutrients.

The R/S for each soil ranges from 0.2065 to 0.3237, with the R/S values in SS and RS soils being relatively lower. Specifically, the R/S of SS soil is 67.62% and 33.61% lower than those of MS and KS soils, respectively. This indicates that under nutrient-limited soil conditions, the accumulation and proportion of root biomass (RDW) are relatively low, which correlates with the resource utilization in line with the biomass allocation of aboveground leaf, branch, and stem parts (Fig. 4B). In terms of organ biomass proportion, LDW has the highest proportion, ranging from 45.80–50.61%, trailed by branch, root, and stem organs. SS soils exhibit the highest biomass proportion in leaf, branch, and stem organs and the lowest in root biomass. Compared with KS soil having the highest total biomass accumulation, the root biomass proportion in SS soils is 4.17% lower. These results suggest that different plantation soils impact the alteration of the aboveground - belowground growth pattern of Chinese fir seedlings. The combination of root traits adopts diverse strategies to modify its adaptability, and a trade-off mechanism exists between growth and nutrient acquisition (Fig. 4B and Fig. 6).

3.5 Analysis of character covariance and influencing factors

We tried to understand whether there was genetic covariance between plant traits in different soil environments, which was measured by genetic correlation coefficient (Fig. 7A), and the average correlation between traits was positive correlation (average genotype = 0.311), but the distribution of correlation coefficient was approximately normal distribution, where, Many pairwise correlations were statistically significant, suggesting that the growth of various genotypes and the high variability of specific root traits between different soil types may be the focus of plant adaptation strategies. Co-variability and plasticity caused the growth traits of Chinese fir at seedling stage to favor resource acquisition strategies (Fig. 6 and Fig. 7A). For example, in RS soil and SS soil with relatively poor

resources, the variation range of traits is greater, and the correlation between different traits is closer (Table 1).

The results of the structural equation model (SEM) indicate that RAD, TRV, R/S are key traits influencing the variation in RDW. The genetic effect (G) and the genotype-by-environment interaction (G×E) contribute to RDW through their impact on RAD, while the G and environmental effect (E) influence RDW through their effect on R/S. Furthermore, the E effect affects RDW by altering TRV. LDW and SDW are jointly influenced by G, E, and G×E interactions. The G and E effects impact ADW through their influence on H. Overall, RDW does not directly affect plant height, but it can directly influence ADW. When using G, E, and G×E effects to assist in selecting for aboveground growth and root functional traits, a clearer understanding of how these factors drive biomass accumulation can be achieved (Fig. 7B).

4 Discussion

4.1 Analysis of Variation Characteristics and Effects

We comprehensively quantified the responses of multiple aboveground and belowground traits to different soil environments. The results demonstrated that genotype effects, soil environment effects, and G × E interaction effects contributed to variations in the growth and root traits of Chinese fir to differing extents. Several traits exhibited substantial variation across transplantation environments, offering valuable insights into the strategies employed by this species to adapt to diverse soil conditions (Conti et al., 2018; Michael et al., 2023). These findings align with previous observations of rich phenotypic variation among different provenances, families, or clones of Chinese fir across forests of varying ages (Chen et al., 2021). However, unlike earlier studies, our research dissected the contributions of aboveground and belowground organs, enabling a more precise determination of variation sources. The analysis revealed that soil conditions and G × E interaction effects are the predominant factors influencing seedling growth, whereas genotype effects were comparatively less significant. This suggests that, after three generations of genetic selection, differences in growth among Chinese fir varieties have narrowed. The generalized heritability of test traits ranged from 0.10 to 0.72, with root functional traits generally showing values below 0.3 (Table 1). This highlights that for multi-generational improved varieties of Chinese fir, maintaining high growth should be coupled with greater emphasis on leveraging the synergistic benefits of genotype-environment interactions, particularly in terms of optimizing adaptation to varying soil conditions (Ren et al., 2023).

There are extensive variations in root morphology and configuration among forest genotypes, primarily reflected in the significant plasticity of traits such as fine root length, root surface area, and root volume. These variations serve as critical strategies for plants to acquire soil nutrients, with nutrient utilization efficiency being enhanced by expanding the root detection range within the soil (Zheng et al., 2024; Zhu et al., 2023). Previous studies have demonstrated substantial genotype and site-specific differences in Chinese fir, with the fine root-to-root length ratio and root surface area-to-root volume ratio differing by 2.79-fold and 1.72-fold, respectively. These findings indicate a trade-off between the multifunctional

traits of aboveground and belowground structures in the long-term adaptation to different soil environments (Chen et al., 2021).

4.2 Organ allocation and plasticity response

The plant height and aboveground biomass grown in KS soil are the highest, with strong root branching and larger average root diameters, indicating that in broadleaf artificial forest soil, increasing root density can expand the area of nutrient foraging in the soil. This enhances the ability of the root system to acquire water and nutrients and increases root thickness, allowing for greater nutrient storage. This is a key manifestation of phenotypic plasticity (Che et al., 2024; Maryam et al., 2024). Root morphology traits such as root diameter, specific root length, specific root area, and root dry matter content can comprehensively reflect the physiological status of roots and their responses to environmental changes (Kramer-Walter et al., 2016; Rathore et al., 2023). A high specific root length improves the efficiency of resource absorption relative to plant biomass investment, boosting the root's nutrient uptake capacity and reflecting the plant's allocation of matter and energy to the underground system. In nutrient-poor soils, plants typically increase investment in underground dry matter to enhance their adaptability to the environment (Hayashi et al., 2023; Turner et al., 2024). Our research shows that the root biomass in the four soils represents 17.10–24.08% of the total biomass (Fig. 4B). In both SS soils and RS soils, the expected increase in root dry matter content did not occur. Instead, these soils increased the SRL and SRA to a certain extent. Interestingly, the total length, surface area, and volume of fine roots in SS soils and RS soils were not the largest (Fig. 5D, E, F). However, when examining the proportion of fine roots across different diameter classes, the proportion of fine roots in the D1–D3 diameter range ($0\text{mm} < D \leq 1.5\text{mm}$) was higher, suggesting that the proportion of fine roots was not the largest overall (Fig. 5). These findings indicate that changes in root morphology may be more important than the allocation of root biomass (Li et al., 2021; Zhu et al., 2010). These results enhance our understanding of how plants respond to various environments and raise expectations for the plasticity of root functional traits (McCormack et al., 2017; Laliberté et al., 2017; Messier et al., 2024).

Recent studies have emphasized the importance of considering multiple trait responses simultaneously to better understand nutrient acquisition strategies in both aboveground and underground plant organs (Zhao et al., 2024). Plants do not respond to environmental changes by altering a single trait but rather by balancing a combination of traits to adapt to these changes. The interplay of multiple traits determines a plant's life history strategy (Bardgett et al., 2014; Shipley et al., 2016). In theory, there may also be trade-offs between the plasticity responses of various traits, influenced by genetic and ecological (physiological) factors (Murren et al., 2015). If we can reliably characterize plant plasticity through easily measurable fine root traits, we could more accurately simulate and predict plant behavior, especially in response to environmental changes (Wang et al., 2021; Carmona et al., 2021; Oscar, 2022). For instance, RAD is closely linked to SRA, SRL, and RDW, making it a good predictor of underground foraging strategies. In nutrient-poor soils, root systems tend to be thinner, and plants rely more on changes in root morphology (such as SRL and SRA) to enhance nutrient acquisition by expanding the soil exploration area—indicating a resource acquisition strategy. However, due to soil heterogeneity and limitations in

current technologies, research on root functional traits and their interrelationships lags research on aboveground functional traits (Michael et al., 2023).

4.3 Resource Acquisition Strategy

The strong correlation between traits with different functions reveals the trade-offs or synergistic effects that constrain and coordinate plant functions. In RS and SS soils, which are relatively nutrient-poor, trait variability is greater, and the correlations between different traits are more tightly linked (Fig. 7A). Through continuous cycle selection of genotypes, there is a gradual shift from a resource conservation strategy (in soils with relatively abundant nutrients) to a resource acquisition strategy (in soils with relatively poor nutrients), to maintain high growth potential (Liao et al., 2023). High SRA and SRL are typically negatively correlated with other traits that promote rapid growth, such as branch strength and root diameter. The "fast" traits may provide a competitive advantage in resource-rich environments, while "slow" traits, like high leaf dry matter content, may enable plants to thrive or dominate in resource-limited environments. Overall, most root morphological traits are strongly correlated, and variation in these traits is a key strategy for plants to acquire soil nutrients. This variation drives the differentiation of root architecture and morphological features. Given the multifaceted objectives of forestry production, when considering multi-trait selection and improvement from a breeding perspective, it is essential to account for the complex interactions introduced by genotype $\times$ environment ($G \times E$). Different traits may exhibit distinct $G \times E$ patterns. Therefore, studying $G \times E$ effects in multi-environment, multi-trait forest systems will likely become a major trend and research hotspot in the future.

5 Conclusion

This study highlights the growth plasticity of multi-generationally improved Chinese fir (*Cunninghamia lanceolata*) varieties across four soil environments. The primary factors influencing seedling-stage plant height, biomass, and root functional traits are soil environmental effects and genotype-by-environment ($G \times E$) interactions, while genotype effects have a relatively smaller impact. Plant height growth and biomass phenotypes exhibit considerable plasticity among different varieties, with a pronounced rank-order effect observed across plantation soils. Notably, plantation soils significantly influence the rapid growth phase of Chinese fir and alter the dynamics of aboveground–belowground growth. These changes are primarily driven by the adoption of distinct root trait strategies. The evident phenotypic plasticity causes aboveground–belowground growth strategies to diverge towards different adaptive directions. In resource-poor soils, plants tend to increase the proportion of fine root length and surface area within the first three diameter classes ($0 \text{ mm} < D < 1.5 \text{ mm}$), optimizing the trade-off between root functionality and soil nutrient acquisition. This leads to stronger correlations among various root traits. Overall, root diameter (RAD), total root volume (TRV), and root-to-shoot ratio (R/S) are the key traits influencing variations in root dry weight (RDW). While RDW does not directly affect plant height (H), it can directly influence aboveground dry weight (ADW). For multi-generational genetically improved varieties, we explored how leveraging genetic effects (G), environmental effects (E), and genotype-by-environment interactions ($G \times E$) can aid in the selection of aboveground growth and root functional traits,

providing a better understanding of their roles in driving biomass accumulation. These findings underscore the importance of integrating aboveground and belowground functional attributes in future breeding programs to develop environmentally stable and high-performing Chinese fir varieties. To achieve this, breeding efforts should assess the plasticity of Chinese fir across diverse environmental conditions and focus on cultivating varieties that align more effectively with specific target environments and management practices. consider the complex effects of G×E. As different traits may respond differently to G×E, future research on the G×E dynamics of forest trees across multiple environments and traits will be a key area of focus. Our results provide actionable insights for selecting soil-specific genotypes in subtropical plantations, reducing dependency on chemical fertilizers.

Declarations

CRedit authorship contribution statement:

The study was conceived and designed by Zhen Zhang, who was responsible for the overall project framework and methodology. Huimin Niu, Wenyue Wang, Haobo Zhao, Jingyong Ji and Guiping He contributed to the data collection and experimental setup, particularly in the field measurements of seedling growth and soil properties. Huimin Niu, Wenyue Wang and Zhen Zhang performed the statistical analysis and drafted the initial manuscript. Guiping He and Zhichun Zhou provided critical input on the interpretation of results and manuscript revision. All authors reviewed and approved the final version of the manuscript. Contributions from each author were essential to the successful completion of the research and manuscript.

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.

Acknowledgements and funding

This work was funded by the project "Breeding of New Varieties of Fast-growing Forest Trees in Southern China" of the National Key R & D Program during the 14th Five-Year Plan period (2022YFD2200201) and the topic of "Breeding of New Varieties of High Carbon Sink and High-quality Timber Tree Species" of the 14th Five-Year Plan for Forest Tree New Variety Breeding in Zhejiang Province (2021C02070-8). The authors are deeply grateful to the Research Group of Forest Tree Genetic Breeding and Cultivation of the Research Institute of Subtropical Forestry, Chinese Academy of Forestry for their great assistance in laboratory aspects.

References

1. Bardgett DR, Mommer L, De Vries FT (2014). Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology and Evolution*. 29, 692-699.

<https://doi.org/10.1016/j.tree.2014.10.006>.

2. Bennett JA, Klironomos J (2019). Mechanisms of plant-soil feedback: interactions among biotic and abiotic drivers. *New Phytologist* 222, 91–96. <https://doi.org/10.1111/nph.15603>.
3. Boye C, Nirmalan S, Ranjbaran A, Francesca L (2024). Genotype × environment interactions in gene regulation and complex traits. *Nature Genetics* 56, 1057–1068. <https://doi.org/10.1038/s41588-024-01776-w>.
4. Braga CR, Paludeto ZG, Souza MB, Aguiar VA, Pollnow MM, Carvalho MA, Tambarussi EV (2020). Genetic parameters and genotype × environment interaction in *Pinus taeda* clonal tests. *Forest Ecology and Management* 474, 118342. <https://doi.org/10.1016/j.foreco.2020.118342>.
5. Carmona CP, Bueno CG, Toussaint A (2021). Fine-root traits in the global spectrum of plant form and function. *Nature* 597, 683–687. <https://doi.org/10.1038/s41586-021-03871-y>.
6. Che JC, Wang Y, Dong A, Cao YG, Wu S, Wu RL (2024). A nested reciprocal experimental design to map the genetic architecture of transgenerational phenotypic plasticity. *Horticulture Research* 11, uhae172. <https://doi.org/10.1093/hr/uhae172>.
7. Chen HJ (2003). Phosphatase activity and P fractions in soils of an 18-year-old Chinese fir (*Cunninghamia lanceolata*) plantation. *Forest Ecology and Management* 178, 301–310. [https://doi.org/10.1016/S0378-1127\(02\)00478-4](https://doi.org/10.1016/S0378-1127(02)00478-4).
8. Chen WT, Zhou MY, Zhao MZ, Chen RH, Tigabu M, Wu PF, Li M, Ma XQ (2021). Transcriptome analysis provides insights into the root response of Chinese fir to phosphorus deficiency. *BMC Plant Biology* 21, 525. <https://doi.org/10.1186/s12870-021-03298-7>.
9. Chen X, Liu P, Zhao B, Zhang J, Ren B, Li Z, Wang Z (2021). Root physiological adaptations that enhance the grain yield and nutrient use efficiency of maize (*Zea mays* L.) and their dependency on phosphorus placement depth. *Field Crops Research* 276, 108378. <https://doi.org/10.1016/j.fcr.2021.108378>.
10. Conti L, Block S, Parepa M, Münkemüller T, Thuiller W, Acosta ATR, Kleunen M, Dullinger S, Essl F, Carboni M (2018). Functional trait differences and trait plasticity mediate biotic resistance to potential plant invaders. *Journal of Ecology* 106, 1607–1620. <https://doi.org/10.1111/1365-2745.13022>.
11. Daniela R, Wolfgang B (2014). Natural variation of root traits: from development to nutrient uptake. *Plant Physiology* 166, 518–527. <https://doi.org/10.1104/pp.114.244982>.
12. Franziska AS, Andreas JW, Nicolas T, Shu YT, Tina K, Franz B, Andrea C, Barbara E, Jennifer G, Benjamin DH. 2024. Rhizosheath drought responsiveness is variety-specific and a key component of belowground plant adaptation. *New Phytologist* 242, 479–492. <https://doi.org/10.1111/nph.19012>.
13. Freschet GT, Bellingham PJ, Lyver P, Bonner KI, Wardle DA (2013). Plasticity in above- and belowground resource acquisition traits in response to single and multiple environmental factors in three tree species. *Ecology and Evolution* 3, 1065–1078. <https://doi.org/10.1002/ece3.472>.
14. Freschet GT, Violle C, Bourget MY, Scherer LM, Fort F (2018). Allocation, morphology, physiology, architecture: the multiple facets of plant above- and below-ground responses to resource stress.

New Phytologist 219, 1338–1352<https://doi.org/10.1111/nph.15102>.

15. Ge HS, Song YP, Su XH, Zhang DQ, Zhang XY (2020). Optimal growth model of *Populus simonii* seedling combination based on Logistic and Gompertz models. Journal of Beijing Forestry University 42, 59–70. <https://doi.org/10.16075/j.bjfu.2020.005>.
16. Grierson CS, Barnes SR, Chase MW, Clarke M, Grierson D, Edwards KJ, Jellis GJ, Jones JD, Knapp S, Oldroyd G, Poppy G, Temple P, Williams R, Bastow R (2011). One hundred important questions facing plant science research. New Phytologist 192, 6–12. <https://doi.org/10.1111/j.1469-8137.2011.03766.x>.
17. Guo TT, Wei JL, Li XR, Yu JM (2024). Environmental context of phenotypic plasticity in flowering time in sorghum and rice. Journal of Experimental Botany 75, 1004–1015. <https://doi.org/10.1093/jxb/erac012>.
18. Han MG, Chen Y, Li R, Yu M, Fu LC, Li SF, Su JR, Zhu B (2022). Root phosphatase activity aligns with the collaboration gradient of the root economics space. New Phytologist 234, 837–849. <https://doi.org/10.1111/nph.20012>.
19. Hayashi R, Maie N, Wagai R, Hirano Y, Matsuda Y, Makita N, Mizoguchi T, Wada R, Tanikawa T (2023). An increase of fine-root biomass in nutrient-poor soils increases soil organic matter but not soil cation exchange capacity. Plant and Soil 482, 89–110. <https://doi.org/10.1007/s11104-022-05212-9>.
20. Hendrik P, Karl JN, Peter BR, Jacek O, Pieter P, Liesje M (2012). Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytologist 193, 30–50. <https://doi.org/10.1111/j.1469-8137.2011.03866.x>.
21. Jin X, Zhu J, Wei X, Xiao QR, Xiao QY, Jiang L, Xu DW, Shen CX, Lin JF, He ZS (2024). Adaptation strategies of seedling root response to nitrogen and phosphorus addition. Plants 13, 536. <https://doi.org/10.3390/plants13040536>.
22. Johnson MTJ (2007). Genotype-by-environment interactions leads to variable selection on life-history strategy in Common Evening Primrose (*Oenothera biennis*). Journal of Evolutionary Biology 20, 190–200. <https://doi.org/10.1111/j.1420-9101.2007.01290.x>.
23. Kong DL, Ma CG, Zhang Q, Li L, Chen XY, Zeng H, Guo DL (2014). Leading dimensions in absorptive root trait variation across 96 subtropical forest species. New Phytologist 203, 863–872. <https://doi.org/10.1111/nph.12856>.
24. Kotula L, Clode PL, Ranathunge K, Lambers H (2021). Role of roots in adaptation of soil-indifferent Proteaceae to calcareous soils in south-western Australia. Journal of Experimental Botany 72, 1490–1505. <https://doi.org/10.1093/jxb/eraa485>.
25. Kramer-Walter KR, Bellingham PJ, Millar TR, Smissen RD, Richardson SJ, Laughlin DC (2016). Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. Journal of Ecology 104, 1299–1310. <https://doi.org/10.1111/1365-2745.12617>.

26. Laliberté E (2017). Below-ground frontiers in trait-based plant ecology. *New Phytologist* 213, 1579–1603. <https://doi.org/10.1111/nph.14544>.
27. Li HF, Testerink C, Zhang Y (2021). How roots and shoots communicate through stressful times. *Trends in Plant Science* 26, 940–952. <https://doi.org/10.1016/j.tplants.2021.02.005>.
28. Li YJ, Mari S, Rowland B, Heidi D (2017). Genotype by environment interaction in the forest tree breeding: review methodology and perspectives on research and application. *Tree Genetics and Genomes* 13, 60. <https://doi.org/10.1007/s11295-017-1128-x>.
29. Liao YC, Fan HB, Wei XH, Wang HM, Shen FF, Hu L, Li YY, Fang HY, Huang RZ (2023). Shifting of the first-order root foraging strategies of Chinese fir (*Cunninghamia lanceolata*) under varied environmental conditions. *Trees* 37, 921–932. <https://doi.org/10.1007/s00468-023-02391-6>.
30. Ling JJ, Xiao Y, Hu JW, Ouyang FQ, Wang JH, Weng YH, Zhang HG (2021). Genotype by environment interaction analysis of growth of *Picea koraiensis* families at different sites using BLUP-GGE. *New Forests* 52, 113–127. <https://doi.org/10.1007/s11056-020-09824-1>.
31. Liu N, Ding CJ, Li B, Su XH, Huang QJ (2021). Analysis of the genotype interaction of four-year-old *Populus euramericana* using the BLUP-GGE technique. *Forests* 12, 1759. <https://doi.org/10.3390/f12091759>.
32. Lopez-Cruz M, Aguete FM, Washburn JD, Leon ND, Kaeppler SM, Lima DC, Tan RJ, Thompson A, Willard D, Campos G (2023). Leveraging data from the Genomes-to-Fields Initiative to investigate genotype-by-environment interactions in maize in North America. *Nature Communications* 14, 6904. <https://doi.org/10.1038/s41467-023-46904-2>.
33. Lu H, Ren MY, Lin RB, Jin KM, Mao CZ (2024). Developmental responses of roots to limited phosphate availability: Research progress and application in cereals. *Plant Physiology* 196, 2162–2174. <https://doi.org/10.1093/plphys/kiae026>.
34. Maryam NE, Sonnewald U (2024). Unlocking dynamic root phenotypes for simultaneous enhancement of water and phosphorus uptake. *Plant Physiology and Biochemistry* 207, 108386. <https://doi.org/10.1016/j.plphys.2024.108386>.
35. McCormack ML, Guo D, Iversen CM, Chen W, Eissenstat DM, Fernandez CW, Li L, Ma C, Ma Z, Poorter H, Reich PB, Zadworny M, Zanne A (2017). Building a better foundation: improving root-trait measurements to understand and model plant and ecosystem processes. *New Phytologist* 215, 27–37. <https://doi.org/10.1111/nph.14545>.
36. Messier J, Scarpitta AB, Li Y, Violle C, Vellend M (2024). Root and biomass allocation traits predict changes in plant species and communities over four decades of global change. *Ecology* 105, e4389. <https://doi.org/10.1002/ecy.4389>.
37. Michael HM, Clayton RF, Daniel R, Joseph XE, Alison MK (2023). Incorporating environmental covariates to explore genotype × environment × management (G × E × M) interactions: A one-stage predictive model. *Field Crops Research* 304, 109133. <https://doi.org/10.1016/j.fcr.2023.109133>.
38. Miloš I, Washington G, Yang H, Gregory D, Peter B, Harry W (2015). Pattern of genotype by environment interaction for radiata pine in southern Australia. *Annals of Forest Science* 72, 391–

401. <https://doi.org/10.1007/s13595-015-0461-2>.
39. Murren CJ, Auld JR, Callahan H, Ghalambor CK, Handelsman CA, Heskell MA, Kingsolver JG, Maclean HJ, Masel J, Maughan H (2015). Constraints on the evolution of phenotypic plasticity: limits and costs of phenotype and plasticity. *Heredity* 115, 293–301. <https://doi.org/10.1038/hdy.2015.25>.
40. Oscar V (2022). Dissecting how fine roots function. *New Phytologist* 233, 1539–1541. <https://doi.org/10.1111/nph.18256>.
41. Poupon V, Gezan SA, Schueler S, Lstibůrek M (2023). Genotype × environment interaction and climate sensitivity in growth and wood density of European larch. *Forest Ecology and Management* 545, 121259. <https://doi.org/10.1016/j.foreco.2023.121259>.
42. Qin YZ, Wang CG, Zhou TY, Fei YN, Xu YZ, Qiao XJ, Ming J (2024). Interactions between leaf traits and environmental factors help explain the growth of evergreen and deciduous species in a subtropical forest. *Forest Ecology and Management* 560, 121854. <https://doi.org/10.1016/j.foreco.2024.121854>.
43. Rathore N, Hanzelková V, Dostálek T, Semerád J, Schnablová R, Cajthaml T, Münzbergová Z (2023). Species phylogeny, ecology, and root traits as predictors of root exudate composition. *New Phytologist* 239, 1212–1224. <https://doi.org/10.1111/nph.18567>.
44. Ren KY, Xu M, Li R, Zheng L, Wang H, Liu S, Zhang W, Duan Y, Lu C (2023). Achieving high yield and nitrogen agronomic efficiency by coupling wheat varieties with soil fertility. *Science of The Total Environment* 881, 163531. <https://doi.org/10.1016/j.scitotenv.2023.163531>.
45. Shipley B, De BF, Cornelissen JHC, Laliberté E, Laughlin DC, Reich PB (2016). Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia* 180, 923–931. <https://doi.org/10.1007/s00442-015-3474-6>.
46. Su TH, Shen Y, Chiang YY, Liu YT, You HM, Lin HC, Kung KN, Huang YM, Lai CM (2024). Species selection as a key factor in the afforestation of coastal salt-affected lands: Insights from pot and field experiments. *Journal of Environmental Management* 360, 121126. <https://doi.org/10.1016/j.jenvman.2024.121126>.
47. Turner SC, Schweitzer JA (2024). Plant neighbors differentially alter a focal species' biotic interactions through changes to resource allocation. *Ecology* 105, e4395. <https://doi.org/10.1002/ecy.4395>.
48. Valverde-Barrantes OJ (2022). Dissecting how fine roots function. *New Phytologist* 233, 1539–1541. <https://doi.org/10.1111/nph.18256>.
49. Wang J, Defrenne C, McCormack ML, Yang L, Tian D, Luo Y, Hou E, Yan T, Li Z, Bu W, Chen Y, Niu S (2021). Fine-root functional trait responses to experimental warming: a global meta-analysis. *New Phytologist* 230, 1856–1867. <https://doi.org/10.1111/nph.17056>.
50. Wang JS, Defrenne C, McCormack ML, Yang L, Tian DS, Luo YQ, Hou EQ, Yan T, Li ZL, Bu WS, Chen Y, Niu SL (2021). Fine-root functional trait responses to experimental warming: a global meta-analysis. *New Phytologist* 230, 1856–1867. <https://doi.org/10.1111/nph.17056>.

51. Wang Z, Zhang X, Sophan C, Zhang J, Duan A (2021). Disentangling the effects of stand and climatic variables on forest productivity of Chinese fir plantations in subtropical China using a random forest algorithm. *Agricultural and Forest Meteorology* 304–305, 108386.
<https://doi.org/10.1016/j.agrformet.2021.108386>.
52. Wang ZQ, Guo DL, Wang XG, Gu JC, Mei L (2006). Fine root architecture, morphology, and biomass of different branch orders of two Chinese temperate tree species. *Plant and Soil* 288, 155–171.
<https://doi.org/10.1007/s11104-006-9119-0>.
53. Wen ZH, Li H, Shen Q, Tang X, Xiong C, Li H, Pang J, Ryan MH, Lambers H, Shen J (2019). Tradeoffs among root morphology, exudation and mycorrhizal symbioses for phosphorus-acquisition strategies of 16 crop species. *New Phytologist* 223, 882–895. <https://doi.org/10.1111/nph.15834>.
54. Wen ZH, Li HB, Shen Q, Tang XM, Xiong CY, Li HG, Pang JY, Ryan MH, Lambers H, Shen JB (2019). Tradeoffs among root morphology, exudation and mycorrhizal symbioses for phosphorus-acquisition strategies of 16 crop species. *New Phytologist* 223, 882–895.
<https://doi.org/10.1111/nph.15834>.
55. Wen ZH, Pang J, Tueux G, Liu F, Shen J, Ryan MH, Lambers H, Siddique KHM (2020). Contrasting patterns in biomass allocation, root morphology and mycorrhizal symbiosis for phosphorus acquisition among 20 chickpea genotypes with different amounts of rhizosheath carboxylates. *Functional Ecology* 34, 1311–1324. <https://doi.org/10.1111/1365-2435.13554>.
56. Yuan CZ, Zhang Z, Jin GQ, Zheng Y, Zhou ZZ, Sun LS, Tong H (2021). Genetic parameters and genotype by environment interactions influencing growth and productivity in Masson pine in east and central China. *Forest Ecology and Management* 487, 118991.
<https://doi.org/10.1016/j.foreco.2021.118991>.
57. Zemunik G, Turner B, Lambers H, Laliberté E (2015). Diversity of plant nutrient-acquisition strategies increases during long-term ecosystem development. *Nature Plants* 1, 15050.
<https://doi.org/10.1038/nplants.2015.50>.
58. Zhang Y, Cao JJ, Lu MZ, Kardol P, Wang JJ, Fan GQ, Kong DL (2023). The origin of bi-dimensionality in plant root traits. *Trends in Ecology and Evolution* 39, 78–88.
<https://doi.org/10.1016/j.tree.2023.01.006>.
59. Zhao JB, Guo BL, Hou YS, Yang QP, Feng ZP, Zhao YY, Yang XT, Fan GQ, Kong DL (2024). Multi-dimensionality in plant root traits: progress and challenges. *Journal of Plant Ecology* 17, rate 043.
<https://doi.org/10.1093/jpe/rtae043>.
60. Zheng GC, Su XP, Chen XL, Hu HY, Ju W, Zou BZ, Wang SR, Wang ZY, Hui DF, Guo JF, Chen GS (2024). Variations in fine root biomass, morphology, and vertical distribution in both trees and understory vegetation among Chinese fir plantations. *Forest Ecology and Management* 557, 121748.
<https://doi.org/10.1016/j.foreco.2024.121748>.
61. Zhu J, Zhang C, Lynch JP (2010). The utility of phenotypic plasticity of root hair length for phosphorus acquisition. *Functional Plant Biology* 37, 313–322. <https://doi.org/10.1071/FP09169>.

62. Zhu LQ, Yao XD, Chen WL, Robinson D, Wang XH, Chen TT, Jiang Q, Jia LQ, Fan A, Wu DM, Chen GS (2023). Plastic responses of below-ground foraging traits to soil phosphorus-rich patches across 17 coexisting AM tree species in a subtropical forest. *Journal of Ecology* 111, 830–844. <https://doi.org/10.1111/1365-2745.14012>.

Figures

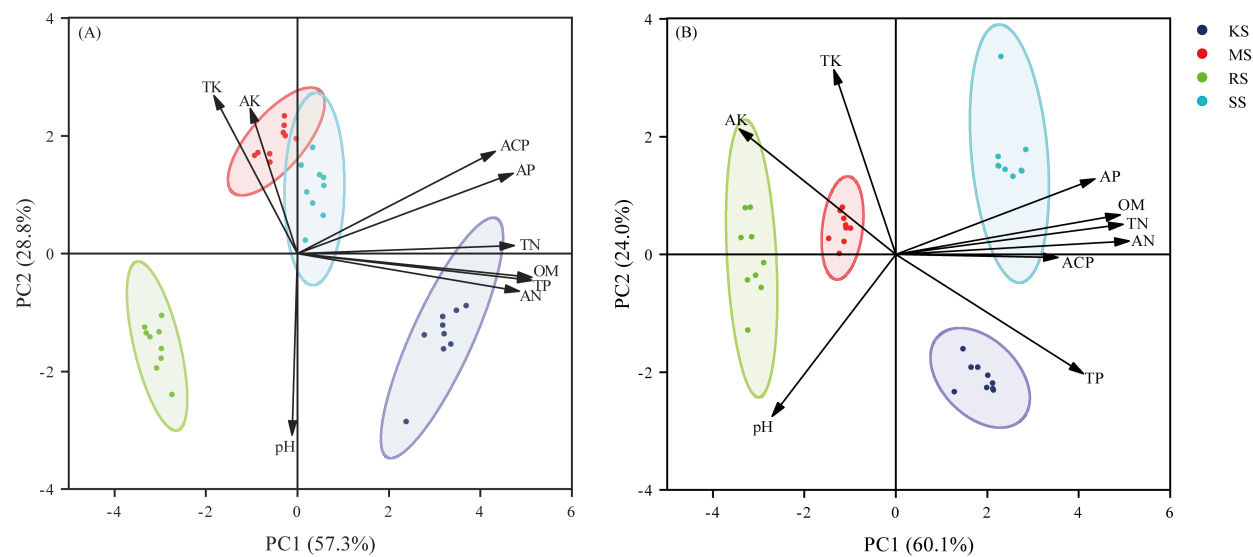


Figure 1

Diversity differences among four soil conditions. (A): pre-treatment; (B): post-treatment; The different colored circles in the diagram represent different soil types; TN, total nitrogen; TP, total phosphorus; TK, total potassium; AN, acute nitrogen; AP, available phosphorus; AK, acute potassium; OM, organic matter; ACP, acid phosphatase; pH, acidity and alkalinity.

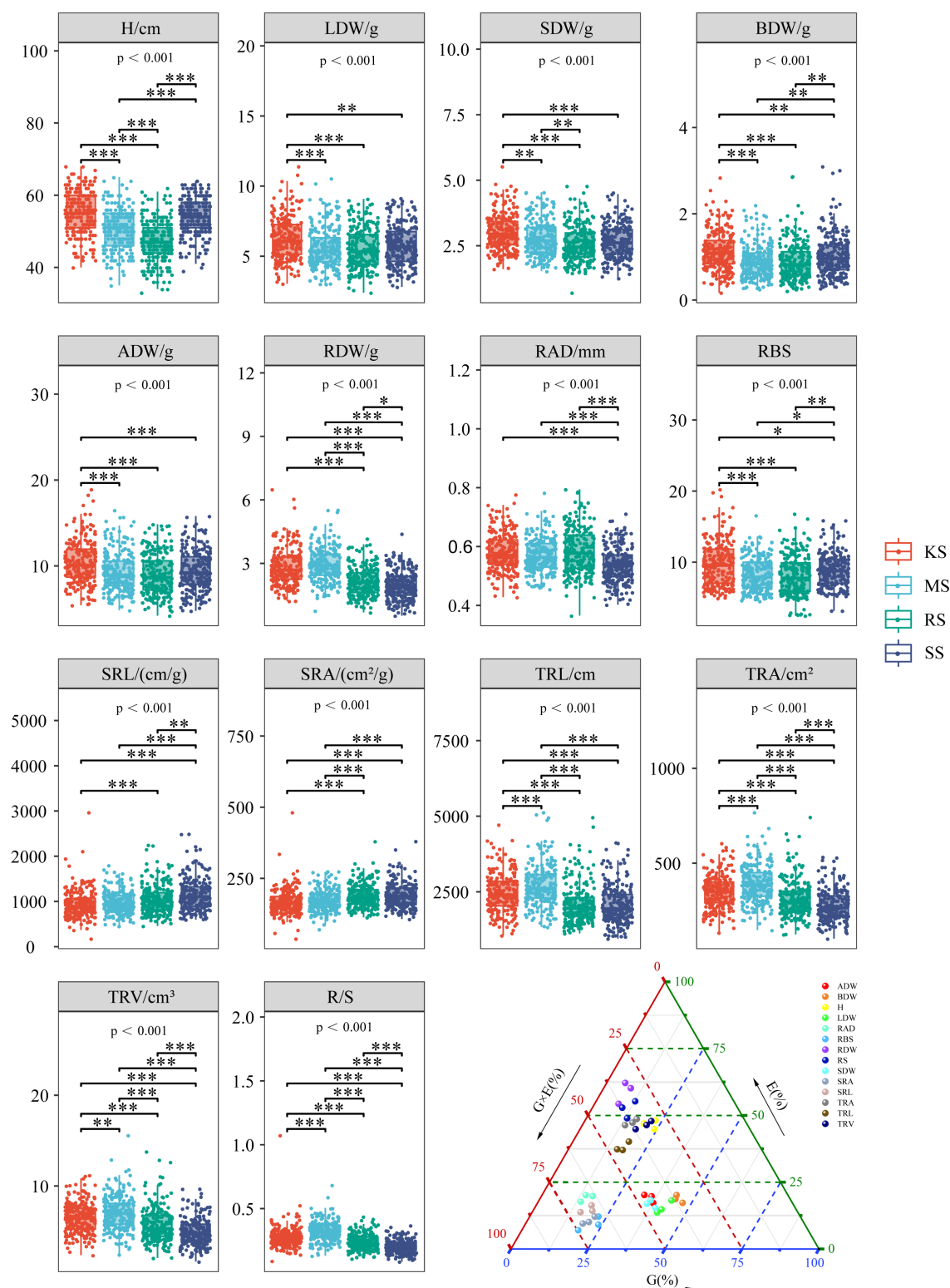


Figure 2

Expression values of traits and contribution rates of variation sources under various soil conditions. Bar graphs indicate variability in plant height, biomass, and root metrics, and dots indicate individual data, P values represent overall differences between groups, the horizontal lines represent comparisons between the two groups at either end of the scale, * indicates the level of significance of differences obtained by two-by-two comparisons; H, Plant Height; ADW, Aboveground dry weight; LDW, Leaf dry

weight; BDW, Branch dry weight; SDW, Stem dry weight; RDW, Root dry weight; SRL, Specific root length; SRA, Specific root area; RAD, Root average diameter; RBS, Root branching strength; TRL, Fine root length; TRA, Fine root surface area; TRV, Fine root volume; R/S, Root to shoot ratio; The ternary plot represents the share of genetic variance components, environmental variance components, and variance components of genotype-environment interactions for each of these metrics, with dots of the same color indicating replicate values for that metric. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

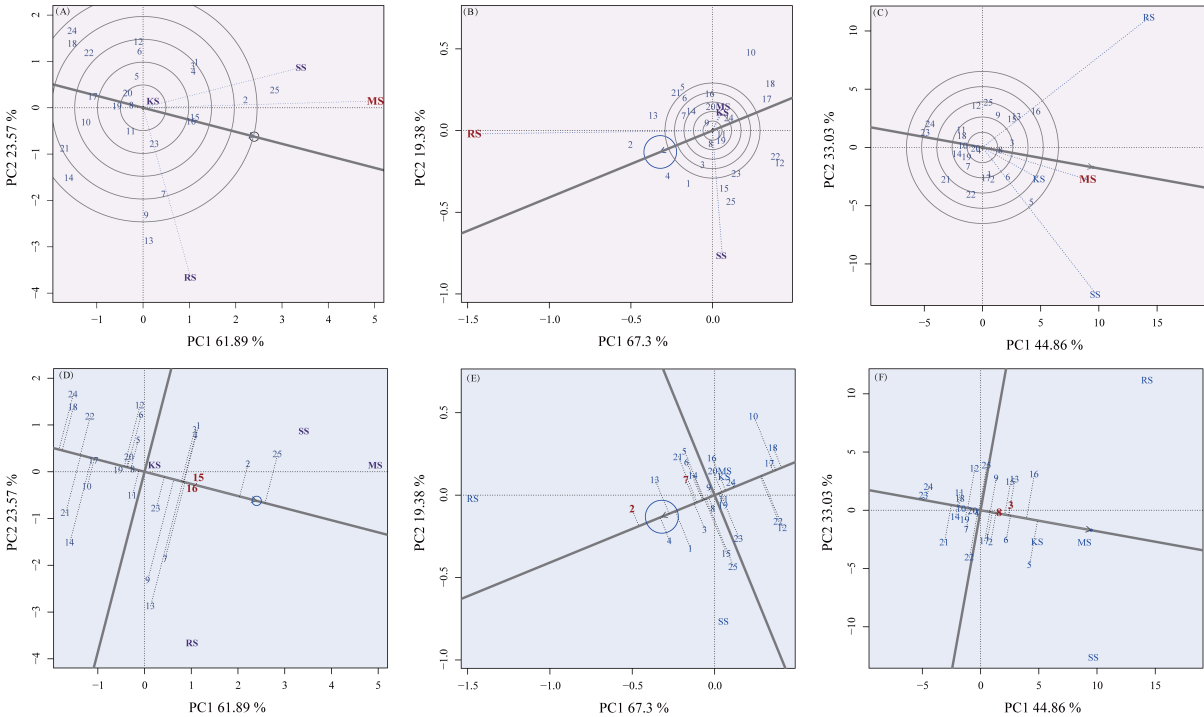


Figure 3

Plot of rank order effects of different genotypes among soil environments. (A), (B) and (C) represent differentiability and representativeness based on plant height, aboveground biomass and root biomass traits; Where the line with the arrow is the Average Environment Axis (AEA), through the connection between the average environment (the circle in front of the arrow) and the center point. The angle between the line segment of a test point and the Average Environment Axis is a measure of its representativeness of the target environment; the smaller the angle, the more representative it is, and the longer the line segment, the stronger the discriminatory power. If the angle between a test point and the mean environment axis is obtuse, it is not suitable as a test point. The direction of the arrow on the mean environmental axis is an evaluation of both the discriminatory power and representativeness of the test site. (D) (E) and (F) representative stable lineage ranking map based on plant height,

aboveground biomass and root biomass traits. The high-yield and stable-yield performance plot requires an Environmental Mean Axis (EMA) represented by a straight arrowed line, as well as Mean Environmental Values (MEV) indicated by circles on the EMA. Additionally, a perpendicular line passing through the origin and orthogonal to the EMA is included. Each variety point is projected onto the EMA using a perpendicular line. The direction of the EMA indicates the approximate average yield trend of the varieties across all environments. The perpendicular line passing through the origin and orthogonal to the EMA represents the tendency of genotype-by-environment interactions (G×E). The longer the perpendicular line between a variety point and the EMA, the less stable the variety is. The numbers in the plot represent different varieties.

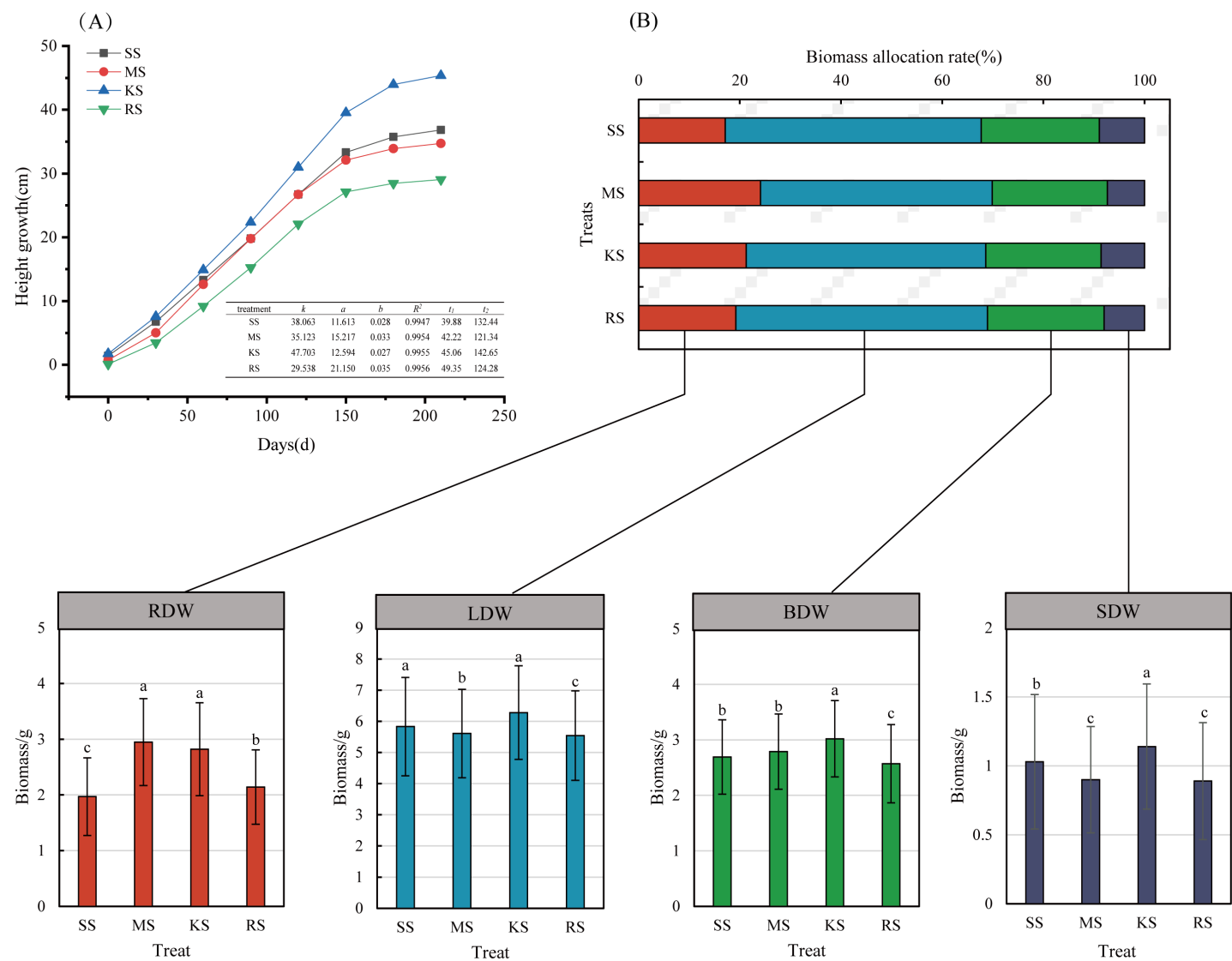


Figure 4

Plant height growth curve and biomass allocation of cedar under different soil treatments.

(A): Growth rhythm map, where k is the theoretical limit value of the upper limit value of the growth, and a and b are the coefficients to be determined, R^2 : coefficient of determination represents the goodness

of fit of the model, reflecting the extent to which the independent variable explains the variation in the dependent variable. t_1 : the start time of the rapid growth period; t_2 : end of rapid growth period. (B): Biomass distribution graph; The horizontally arranged bar chart represents the biomass allocation proportions among root, stem, trunk, and leaf organs, while the vertically arranged bar chart indicates the variation in biomass measurements of each organ across treatments; Different lowercase letters denote significant differences between treatments. ADW: Aboveground dry weight; LDW: Leaf dry weight; BDW: Branch dry weight; SDW: Stem dry weight; RDW: Root dry weigh.

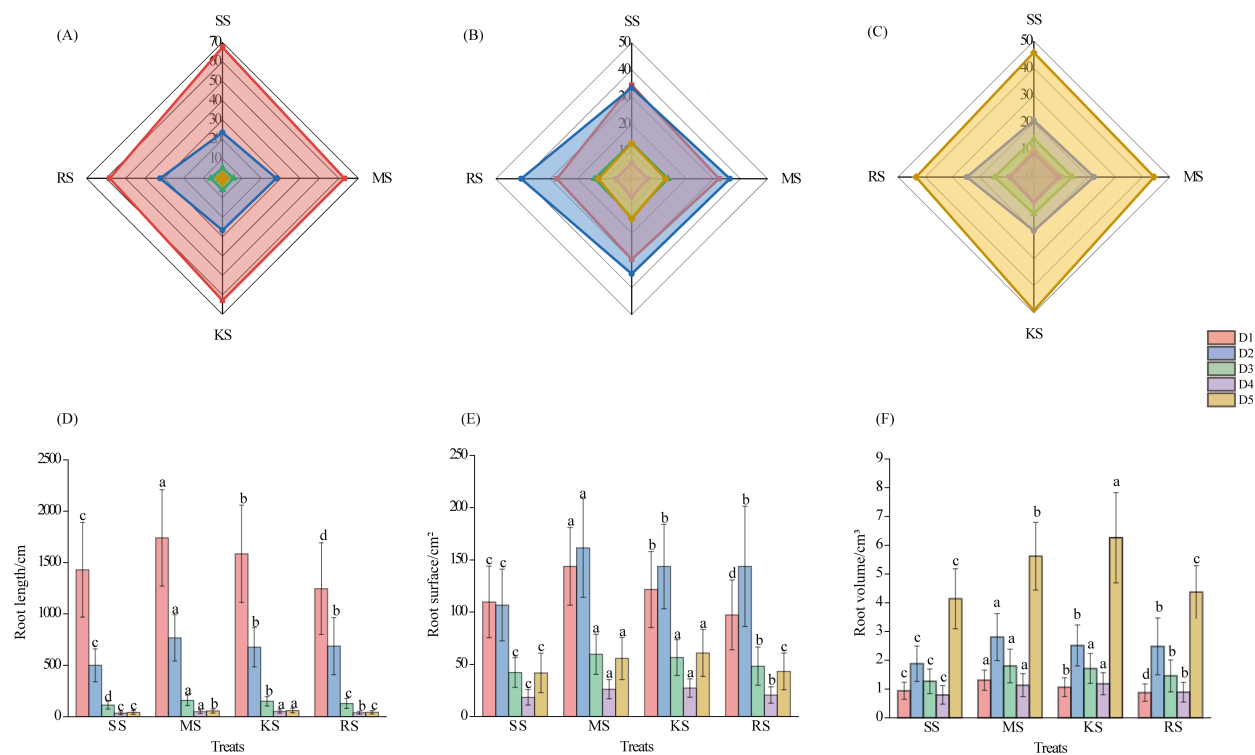


Figure 5

Distribution ratio and growth of D1-D5 radial root classes. (A): Proportion of root length grading (%); (B): Proportion of root surface area grading (%); (C) Proportion of root volume grading (%); (D): Root length; (E): Root surface; (F): Root volume; D1-D5 represent diameter levels, D1: 0 to 0.5 mm, D2: 0.5 to 1.0 mm, D3: 1.0 to 1.5 mm, D4: 1.5 to 2.0 mm, D5: >2.0 mm.

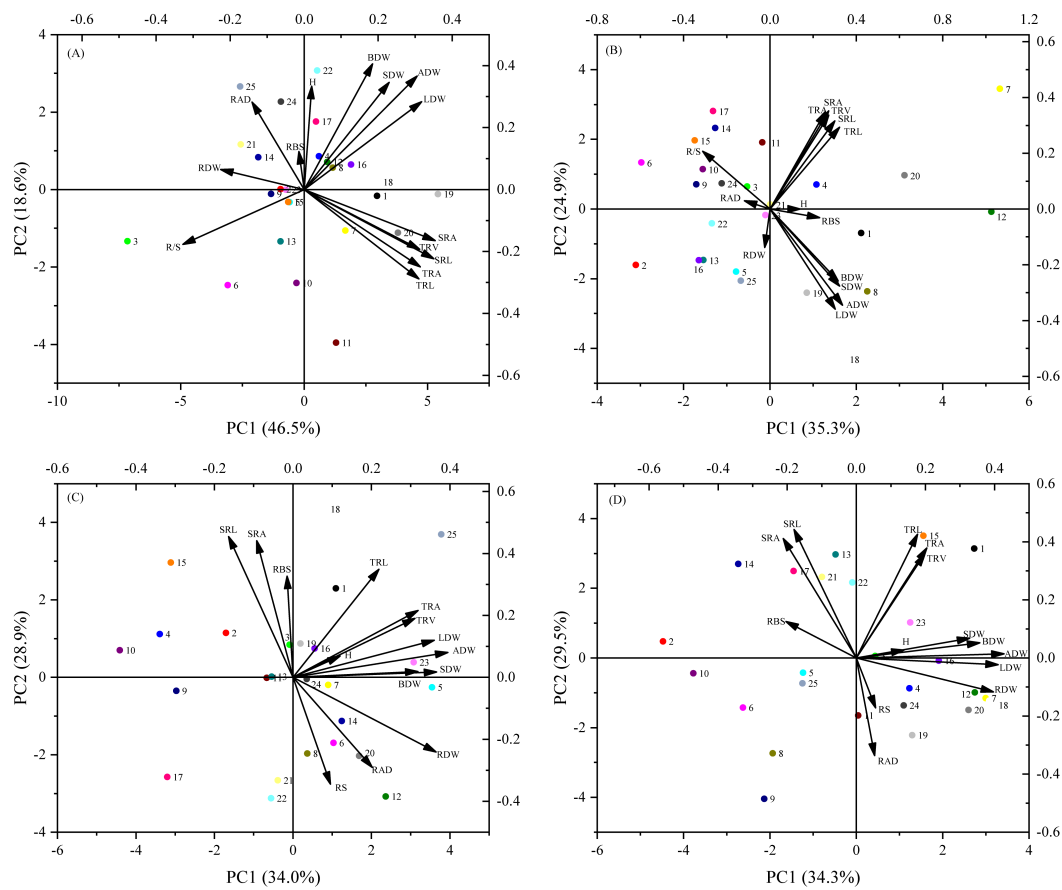
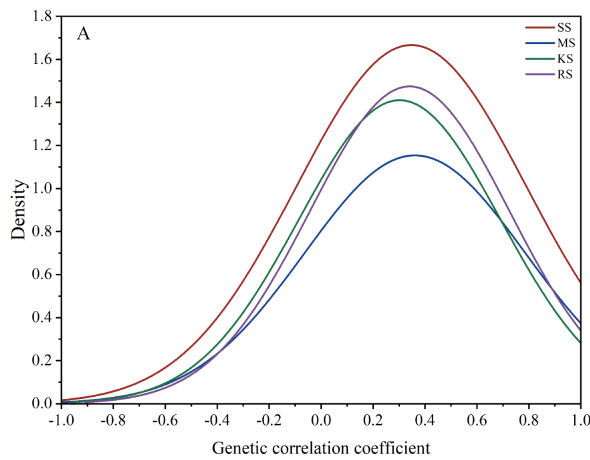


Figure 6

Selection of different genotypes for growth in each of the four soils. (A): KS Soil conditions;

(B): KS Soil conditions; (C): KS Soil conditions; (D): KS Soil conditions; The numbered dots in the figure represent the participating varieties; H, Plant Height; ADW, Aboveground dry weight; LDW, Leaf dry weight; BDW, Branch dry weight; SDW, Stem dry weight; RDW, Root dry weight; SRL, Specific root length; SRA, Specific root area; RAD, Root average diameter; RBS, Root branching strength; TRL, Fine root length; TRA, Fine root surface area; TRV, Fine root volume; R/S, Root to shoot ratio. Different colored circles represent different genotypes.



B

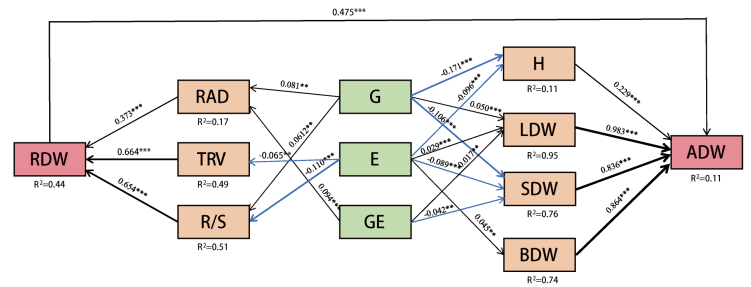


Figure 7

(A): Frequency distribution of genetic correlation indices between all traits. The frequency of distribution of correlation coefficients, measured as genetic correlation coefficients between two indices, was calculated 91 times using 14 traits. (B): Partial least squares structural equation modeling (PLS-SEM) reveals direct and indirect effects of genotype and environment on growth and root function traits. AIC =36.18, Fisher'C =41, $P=0.072$ in the model, Solid blue arrows indicate negative paths ($p < 0.05$), solid black arrows indicate positive paths ($p < 0.05$), and the width of the arrows indicates the strength of the causal relationship. Numbers on the line adjacent to the arrows are standardized path coefficients. R^2 indicates the total variance explained by the model. H, Plant Height; ADW, Aboveground dry weight; LDW, Leaf dry weight; BDW, Branch dry weight; SDW, Stem dry weight; RDW, Root dry weight; RAD, Root average diameter; TRV, Fine root volume; R/S, Root to shoot ratio; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Supplementarytable.docx](#)