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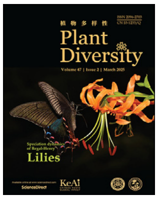

Research paper

Elevational variation in anatomical traits of the first-order roots and their adaptation mechanisms

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ABSTRACT

Root anatomical traits play an important role in understanding the link between root physiological function and ecological process. To determine how plants change root anatomical traits to adapt to distinct environments, we measured four key root anatomical traits—stele diameter (SD), cortex thickness (CT), root diameter (RD), and the stele to root diameter ratio (SDRD)—of first-order roots of 82 species collected from different vegetation zones along a 2000 m altitudinal gradient on the northern slope of Taibai Mountain. Compared with other altitudes, plants located in temperate birch and fir forests had thinner SD, CT, RD, and SDRD. We found that elevational variation in root anatomical traits could largely be explained by phylogenetic taxonomy (clade). In addition, changes in SD were driven by soil bulk density, whereas variations in CT and RD were influenced by soil available nitrogen. When phylogenetic factors were removed from our analysis, allometric relationships between RD and root anatomical traits (SD and CT) were observed across different altitudes. Our study reveals the influence of phylogeny and environment on the elevational variation in root anatomical traits and further supports the allometric relationship between root anatomical traits (SD and CT) and RD. These findings enhance our understanding of the evolutionary and adaptive mechanisms of root anatomical structures, providing a basis for predicting how root anatomical traits respond to global changes.

1. Introduction

Root functional traits play important roles in soil resource acquisition and the nutrient cycle (Violle et al., 2007; Bardgett et al., 2014). Root functional traits also help plants adapt to diverse environmental conditions by adjusting root morphology, chemistry, architecture, and anatomy (Pregitzer et al., 2002; Freschet et al., 2021). Root anatomical traits, such as cortex thickness (CT) and stele diameter (SD), are related closely to the physiological functions of roots, including acquisition and transportation functions, root respiration, and mycorrhizal colonization (Brundrett, 2002; Guo et al., 2008; Zhou et al., 2021; Betekhtina et al., 2023). Thus, determining how root anatomical structures adapt to distinct environments may provide important insights into the relationship between root form and function (Cao et al., 2023).

Previous studies have shown that root anatomical traits are influenced by environmental conditions. For example, root diameter (RD) has been shown to decrease gradually from tropical to temperate environments around the world (Chen et al., 2013; Ma et al., 2018) and in cold, drought environments or infertile soil (Freschet et al., 2017; Wang et al., 2018; Li et al., 2019; Ding et al., 2020; Laughlin et al., 2021). CT has been shown to increase in fertile soil, and SD to decrease in cold conditions (Qin et al., 2021; Li et al., 2022). In addition, plants produce thinner roots in infertile conditions (Li et al., 2022) and denser soils (Freschet et al., 2017). These findings suggest that one effective way for plants to survive

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in stressful conditions is to produce thinner rather than thicker roots (Pregitzer et al., 2002; Guo et al., 2008).

Recent studies have also revealed that variation in root anatomical traits (e.g., RD, CT, and SD) can be explained by phylogeny conservatism (Comas et al., 2012; Kong et al., 2014; Wang et al., 2018, 2024; Gu et al., 2014; Zheng et al., 2024a). These results indicate that evolutionary history plays a strong role in shaping root anatomical traits. For example, it has been reported that modern plants show thinner RD compared to plants from ancient lineages (Chen et al., 2013; Ma et al., 2018). However, little is known about how evolutionary history may have influenced other root traits such as SD and CT. Furthermore, few studies have examined how phylogeny and environment drive root anatomical traits in concert or which is more important.

One approach to quantifying the effects of phylogeny and environment on root anatomical traits is to examine how root anatomical traits change across an elevational gradient. Elevational gradients reflect the adaptive strategies of plants under suitable and stressful conditions as higher elevations have lower temperatures and higher soil heterogeneity compared to lower elevations (Körner, 2007). Root anatomical traits (i.e., RD, CT, and SD) will decrease across an elevational gradient according to the carbon supply-consumption balance theory (Kong et al., 2021). In this theory, CT, which has been positively correlated with root respiration and reflects carbon consumption (Chimungu et al., 2014; Lynch 2013; Zheng et al., 2024b), can be used as a proxy for carbon consumption. Thicker CT indicates higher carbon consumption, which is unfavorable for plant survival in stressful environments. Moreover, SD represents carbon supply because of its transportation function (Steudle and Peterson, 1998; Kong et al., 2021). In stressful environments, carbon consumption and supply can be balanced by thinner SD, which decreases carbon supply and limits carbon consumption. However, studies have reported that a large proportion of elevational variation in RD is influenced by phylogenetic factors (clade) (Wang et al., 2024), as in higher elevation habitats, the phylogenetic background shifts from ancient plant lineages to modern lineages (Körner, 2007; Chen et al., 2023; Bañares-de-Dios et al., 2024). Because other root anatomical traits are closely related to RD (Kong et al., 2014; Zheng et al., 2024a), it is possible that elevational variation in root anatomical traits can be mostly attributed to phylogenetic, rather than environmental, differences among species.

Plants adapt to the environment by adjusting a series of root traits, which contributes to coordinated changes among these traits. Recent studies have confirmed allometric relationships between RD and anatomical traits (SD and CT). Specifically, CT increases more in response to increases in RD than does SD (Gu et al., 2014; Kong et al., 2019; Zhou et al., 2022). These allometric relationships between root anatomical traits have been found across different plant types and environments (Zhang et al., 2023). However, these relationships may not occur in all habitats. For example, allometric relationships between anatomical traits were not found in plants on the Tibetan Plateau (average 3500 m) (Zheng et al., 2024a), indicating that allometric relationships among root anatomical traits may be somewhat dependent on elevation, although this hypothesis has yet to be validated.

Here, we test the following competing hypotheses: (1) root anatomical traits (SD, CT, RD, and SDRD) of plants become thinner at higher elevations to maintain the trade-off between the consumption and supply of carbon; (2) phylogeny rather than environmental factors accounts for a large proportion of the variation in root anatomical traits. We also examined how the allometric relationship between RD and root anatomical traits (SD and CT) changes at different elevations (Fig. 1). To test these hypotheses, we measured root anatomical traits of 82 species (belonging to 39 families and 63 genera) collected along an elevational gradient (1374 m–3375 m) of the northern slope of Taibai Mountain.

2. Materials and methods

2.1. Study area and root collection

The study area is located on the northern slope of Taibai Mountain in Shaanxi Province, China (33°49′N-34°10′N, 107°19′E–107°58′E), ranging in elevation from 1374 to 3375 m. The northern slope of Taibai Mountain has a mean annual temperature of 3.91 °C and a mean annual precipitation of 788 mm. Forest vegetation types vary at different elevations. For example, deciduous broadleaf and temperate birch forests occur at lower elevations (800 m–2800 m); fir and larch forests are located in middle elevations (2600 m–3350 m); and alpine shrubland is distributed in higher elevations (above 3350 m) (Tang and Fang, 2006).

Root samples were collected from July–August 2020. Three tree plots (20 m × 20 m) with similar slopes were set up randomly at each forest type for a quadrat survey; in addition, two shrub plots (5 m × 5 m) and five herb plots (1 m × 1 m) were established within each tree plot (Fig. S1). Details of sampling sites and the dominant species are described in Table S1. We then collected absorptive fine roots of common species at each forest type, including 82 species from 39 families and 63 genera. Species information and root anatomical traits of 82 species are shown in Table S2. For woody species, three mature plants of each species with similar diameter at breast height were selected in each forest type. We first searched taproots of each species and then traced lateral roots based on color and smell. For nonwoody species, the whole root system was excavated carefully. After removing soil adhering to roots, these samples (including the first five order roots) were placed immediately in reagent bottles filled with formalin-aceto-alcohol (FAA) solution and transported to the laboratory for measuring anatomical traits.

2.2. Root measurements

The first-order roots were chosen because they have complete cortical tissue (Guo et al., 2008). In the laboratory, 15 first-order roots of each species were picked out according to the procedure described by Pregitzer et al. (2002). These samples were washed gently in deionized water, dehydrated with a series of alcohol solutions, and embedded in paraffin. Root samples were then cut into 4-μm thickness sections and stained with safranin-fast green. The cortex and stele were stained green and red, respectively. SD, CT, and RD of sections were photographed using a light microscope and measured by the Motic Images Plus 3.0 before staining. Three images were taken for each species. Sections with complete tissues were then stained with safranin-fast green. Because many steles were incomplete, we measured 6 conduit diameters of each image including 3 bigger conduits and 3 smaller conduits, and calculated their mean values as the mean conduit diameter (CD). Because 1 or 2 images were obtained for each species, we only show the data of conduit diameter in Table S2. In total, SD, CT, and RD of 82 species and CD of 67 species were obtained (Table S2). The ratio of stele

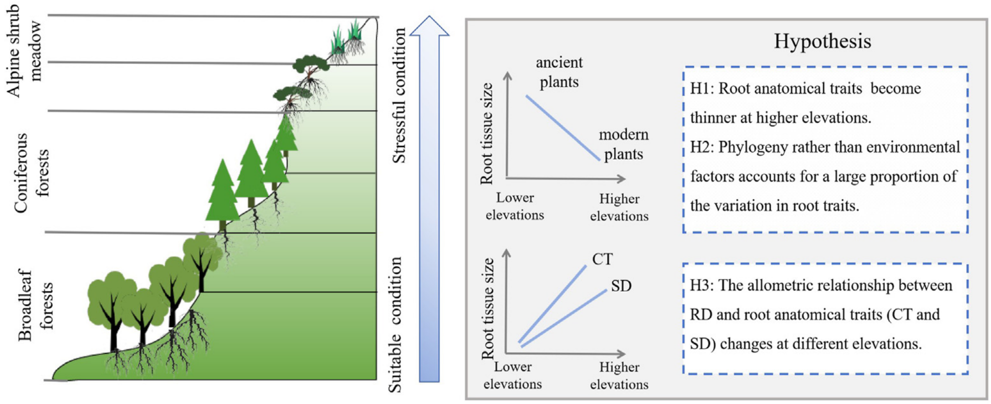

Fig. 1. The conceptual graph indicates changes in root anatomical traits and their allometric relationship along an elevational gradient and their driving factors. The figure on the left represents the dominant species along elevational gradients. Root anatomical traits (including SD, CT, RD, and SDRD) become thinner at higher elevations (Hypothesis 1). Phylogeny rather than environmental factors accounts for a large proportion of the variation in root traits (Hypothesis 2). We hypothesize that the allometric relationship between RD and root anatomical traits (SD and CT) changes at different elevations (Hypothesis 3). SD, stele diameter; CT, cortex thickness; RD, root diameter; SDRD, stele to root diameter ratio. Root tissue size includes SD and CT.

diameter to root diameter (SDRD) was calculated by the following equation:

$$\mathrm{SDRD} = \mathrm{SD}\ (\mathrm{mm}) / \mathrm{RD}\ (\mathrm{mm})$$

2.3. Environmental variables

Mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm) were downloaded from the WorldClim global database (1 km^2, http://www.worldclim.org). Aridity index (AI, mm mm^{-1}) was obtained from the Global Aridity Index and Potential Evapotranspiration (ET0) Climate Database v.2 (1 km^2, https://cgiarcsi.community).

Five soil samples at each plot were collected using an auger (6 cm) and mixed. In total, three soil samples were obtained in each forest type. These samples were used to determine soil organic concentration (SOC) and available N (AN) and P (AP), following detailed methods described by Wang et al. (2024). Soil bulk density (SBD) was determined using the ring knife method. Three soil samples were collected using a ring knife (a volume of 100 cm^{-3}) in each plot and then dried at 105 °C. SBD was calculated as the ratio of over-dried soil mass to the volume of the core.

2.4. Data analysis

One-way ANOVA tests were conducted to determine differences in root anatomical traits across different elevations.

Species names were confirmed on The Plant List (http://www.theplantlist.org/), and a species-level phylogenetic tree including 82 species was constructed using the U.PhyloMaker function based on the plant_megatree.tre reported by Jin and Qian (2022,2023). Blomberg's K value was calculated to assess the phylogenetic signals of each root trait. Larger values of Blomberg's K indicate higher phylogenetic conservatism (Blomberg et al., 2003).

Hierarchical and variation partitioning were used to evaluate the independent contribution of phylogenetic taxonomy (clade) and environment (climate and soil factors) on root anatomical traits with the *rdacca.hp* function (Lai et al., 2022a). In this analysis, clade was considered a phylogenetic factor due to the significant influence of clades on RD (Wang et al., 2024). Principal component analysis (PCA) was used to examine the covariation in root anatomical traits and reveal the adaptive strategies of root anatomical traits of each clade at different elevations with the factoextra package. For PCA, five elevations were categorized as lower (broadleaf forests, 1374–2440 m), middle (coniferous forest, 2934–3180 m), or higher elevations (alpine shrubland, 3375 m) according to leaf habit. One-way ANOVA tests were used to evaluate the difference in root anatomical traits among different clades. Then, linear mixed-effect models were performed to quantify the effects of environmental factors on root traits with the lme4 package. In these models, climatic and soil factors were treated as fixed factors, and the site was treated as a random factor. To avoid collinearity among explanatory variables, we calculated the variance inflation factor (VIF) of each variable and removed variables when VIF > 10. Marginal R^2 represents the variance explained by fixed factors, and conditional R^2 represents the total variance explained by both fixed and random factors. These indicators were calculated by using the glmm.hp function (Lai et al., 2022b). In addition, linear regression was used to examine the relationships between environmental variables and root traits.

Standardized major axis (SMA) was applied to fit regressions between RD and anatomical traits (SD and CT) at different elevations and compare differences in slopes by using the smatr package. We also analyzed this relationship when the influence of phylogeny was removed by using the phylogenetic independent contrast (PIC).

3. Results

3.1. Differences in root anatomical traits at different elevations

As elevation increased, four anatomical traits of first-order roots (SD, CT, RD, and SDRD) first decreased and then increased (Fig. 2a–d). Plants showed thinner SD, CT, and RD in temperate birch (2440 m) and fir forests (2934 m) (Fig. 2a–c), whereas SDRD reached a minimum in temperate birch forests (2440 m) (Fig. 2d).

3.2. The influence of phylogeny on root anatomical traits

SD and RD exhibited significant phylogenetic signals ($K = 0.17$–0.19, $P < 0.05$, Table 1). Phylogenetic taxonomy (clade) accounted for a large proportion of changes in CT, RD, and SDRD (Fig. 3b–d, 8.84%–10.78%). For all species, SD and RD were thicker in ancient plant lineages than modern plants (asterids) (Figs. S3a and c). For modern plants, there were significant differences in CT and SDRD (Figs. S3b and d). CT was thicker in eudicots than in

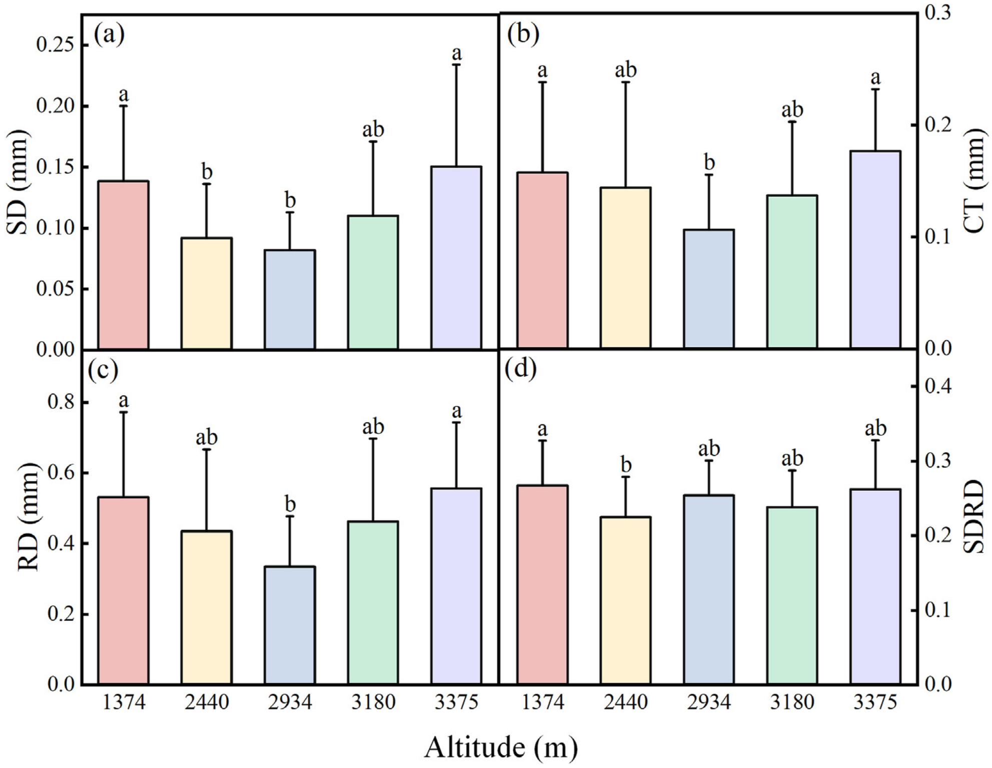

Fig. 2. Difference in root anatomical traits at different elevations. Different letters indicate a significant difference ($P < 0.05$). SD, stele diameter; CT, cortex thickness; RD, root diameter; SDRD, stele to root diameter ratio.

Table 1
Phylogenetic signals of root anatomical traits.

	SD	CT	RD	SDRD
K	0.19	0.15	0.17	0.13
P	< 0.05	0.08	< 0.05	0.07

K: Blomberg's *K* values. SD, stele diameter; CT, cortex thickness; RD, root diameter; SDRD, stele to root diameter ratio.

asterids (Fig. S3b); furthermore, SDRD was higher in asterids than in other modern plants (Fig. S3d).

Plants in different clades showed distinct adaptive strategies (Fig. 4b). Plants from ancient clades adopted thicker SD, CT, and RD at different elevations; whereas asterids exhibited the opposite strategy (thinner SD, CT, and RD). Root anatomical traits of clades other than ancient plants and asterids first decreased and then increased (Fig. 4b).

3.3. Environmental factors influence the changes in root anatomical traits

Except for SDRD, root anatomical traits (SD, CT, and RD) were driven by SBD and soil nutrients (AP and AN, Table 2). SD showed a positive relationship with SBD (Fig. 5a; $R^2 = 0.11$; $P < 0.01$). AN explained a large proportion of changes in CT and RD (Table 2) and was correlated negatively with them (Fig. 5b and c; $R^2 = 0.03–0.08$; $P < 0.05$). In contrast, SDRD was influenced greatly by phylogenetic taxonomy (clade) rather than by environmental factors (Fig. 3d).

3.4. Allometric relationships between root anatomical traits at different elevations

Four root anatomical traits were divided into two components (Fig. 4a). The first axis was related positively to SD, CT, and RD and accounted for 67.26% of the total variation. The second axis was related to SDRD and explained 32.01% of the total variation (Fig. 4a; Table S3). Similarly, SD and CT showed positive correlations with RD at different elevations (Fig. 6a–d). At lower and higher elevations, the slope of the relationship between CT and RD (Fig. 6b and d, slope = 1.01–1.16, $P < 0.01$) was higher than that between SD and RD (Fig. 6b and d, slope = 1.01–1.38, $P < 0.01$), consistent with the allometric relationship. At middle elevations, the difference between the slope of CT and SD with RD increases was not obvious but was significant after removing coniferous plants (Fig. 6c and e). This relationship still existed at different elevations when phylogeny was removed (Figs. S4a–d).

4. Discussion

4.1. Nonlinear relationship between elevation and root anatomical traits

The response of root traits to elevational gradients is a useful proxy for how these traits respond to stressful environments, as the environment becomes more severe at higher elevations (Körner, 2007). Global studies have revealed that plants in stressful conditions tend to produce thinner roots (Chen et al., 2013; Ma et al., 2018) to reduce carbon investment for survival (Eissenstat 1992). These findings also have been confirmed at the regional scale (Qin et al., 2021). Thus, we hypothesized that across the elevational gradient on the northern slope of Taibai Mountain, root anatomical traits would become thinner at higher elevations. However, as elevation increased, we found that root anatomical traits (SD, CT, RD, and SDRD) first decreased and then increased (Fig. 2a–d). This phenomenon may be attributed to the hasher environment at higher elevations, which enhances plants' dependence on mycorrhizae for acquiring water and nutrients. Plants located in alpine

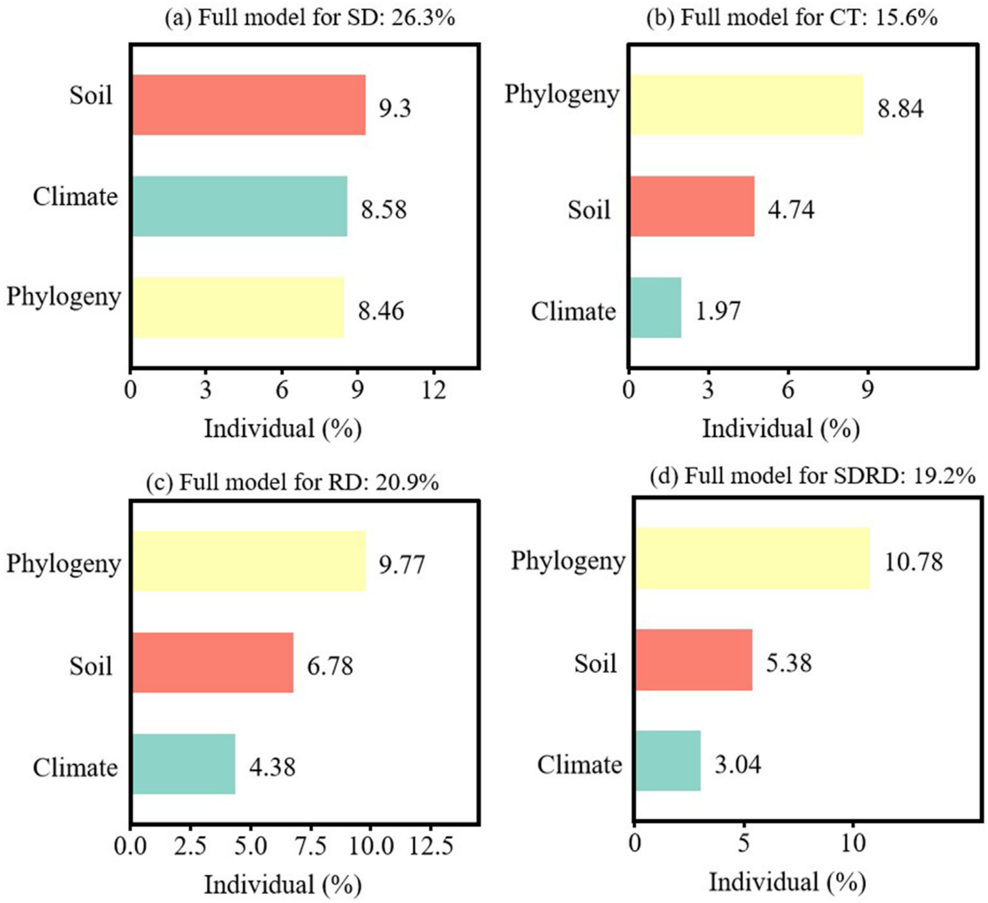

Fig. 3. Results of hierarchical and variance partitioning for the effects of phylogeny taxonomy (clade) and environment (soil and climate) on root anatomical traits. The title of each picture indicates the total variance explained by fixed factors. Each bar shows variance explained by the independent effects of each variable. Clade represents the influence of phylogeny. SD, stele diameter; CT, cortex thickness; RD, root diameter; SDRD, stele to root diameter ratio.

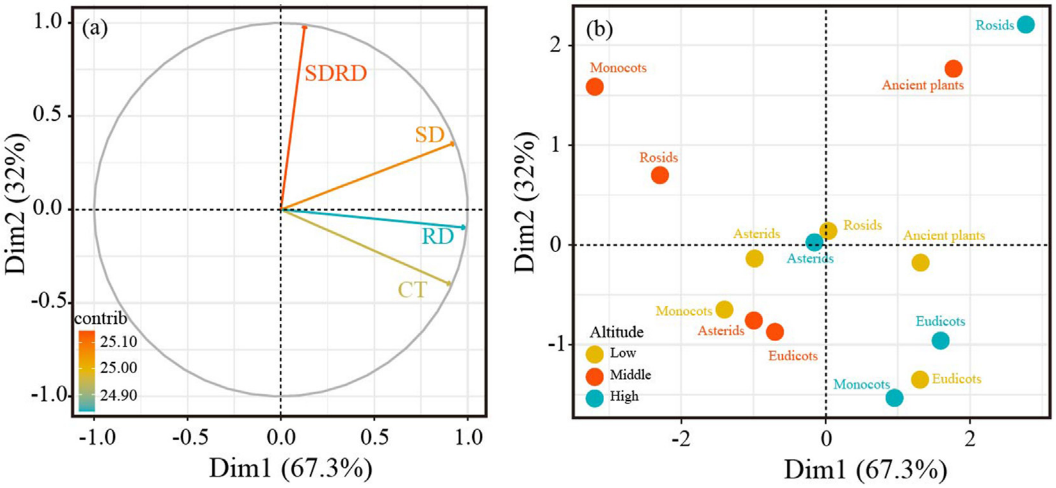

Fig. 4. Principal component analysis (PCA) of first-order root traits of all species. (a) Trait loadings biplot; (b) species distribution in the trait space. Plants from ancient lineages include conifers and magnoliids. SD, stele diameter; CT, cortex thickness; RD, root diameter; SDRD, stele to root diameter ratio; low, lower elevations (1374–2440 m); Middle, middle elevations (2934–3180 m); High, higher elevations (3375 m).

shrubland were colonized mainly by arbuscular mycorrhizal (AM) (Table S2). Increasing CT is beneficial for AM colonization and improves the absorptive capacity of plants to obtain soil resources, indicating an improvement in absorption function (Brundrett, 2002; Kong et al., 2017; Zhou et al., 2022). Therefore, plants may increase SD to enhance transportation function and achieve a balance between absorption and transportation functions (Kong et al., 2017). This finding demonstrates that plants at higher elevations adapt to stressful environments by investing C into the construction of structural tissues.

Table 2
Linear mixed-effect models showing the influence of environments on root anatomical traits.

Fixed effect	SD				CT			RD			SDRD		
	Df	Estimate	SS%	*P*	Estimate	SS%	*P*	Estimate	SS%	*P*	Estimate	SS%	*P*
Intercept	95	−0.10		0.20	0.22		< 0.01	0.80		< 0.01	0.15		0.40
AP	95	−0.005	**5.53**	0.02							−0.002	1.41	0.51
SBD	95	0.20	**10.50**	< 0.01							0.10	2.37	0.49
AI					−0.02	0.33	0.52	−0.10	1.27	0.19			
AN					−0.003	**4.42**	< 0.05	−0.01	**7.79**	< 0.01			
R^2_m			0.16			0.05			0.09			0.04	
R^2_c			0.16			0.05			0.09			0.04	

In each model, soil factors were set as fixed factors, and the site was treated as a random factor. AI, aridity index; SBD (g cm^{-3}), soil bulk density; AP (mg kg^{-1}), soil available phosphorus; AN (mg kg^{-1}), soil available nitrogen; R^2_m, marginal R^2; R^2_c, conditional R^2. Marginal R^2 represents the variance explained by fixed factors, while conditional R^2 indicates the variance explained by both fixed and random factors. SD, stele diameter; CT, cortex thickness; RD, root diameter; SDRD, stele to root diameter ratio.

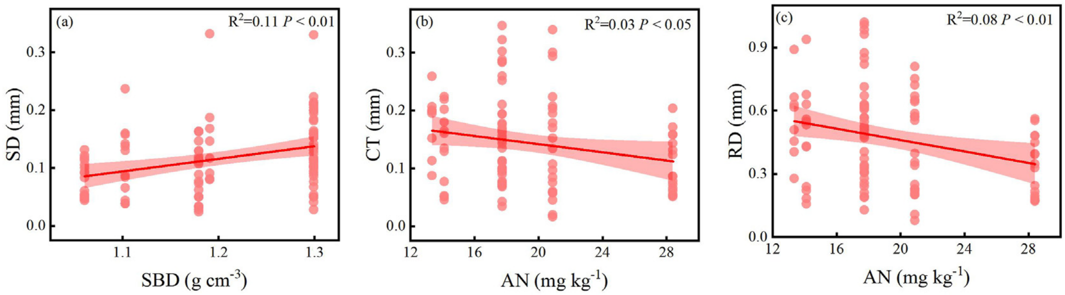

Fig. 5. Relationships between root traits and soil factors (a–c). R^2 and slope values were obtained by the linear regression (P < 0.05). SD, stele diameter; CT, cortex thickness; RD, root diameter; SBD (g cm^{-3}), soil bulk density; AN (mg kg^{-1}), soil available nitrogen.

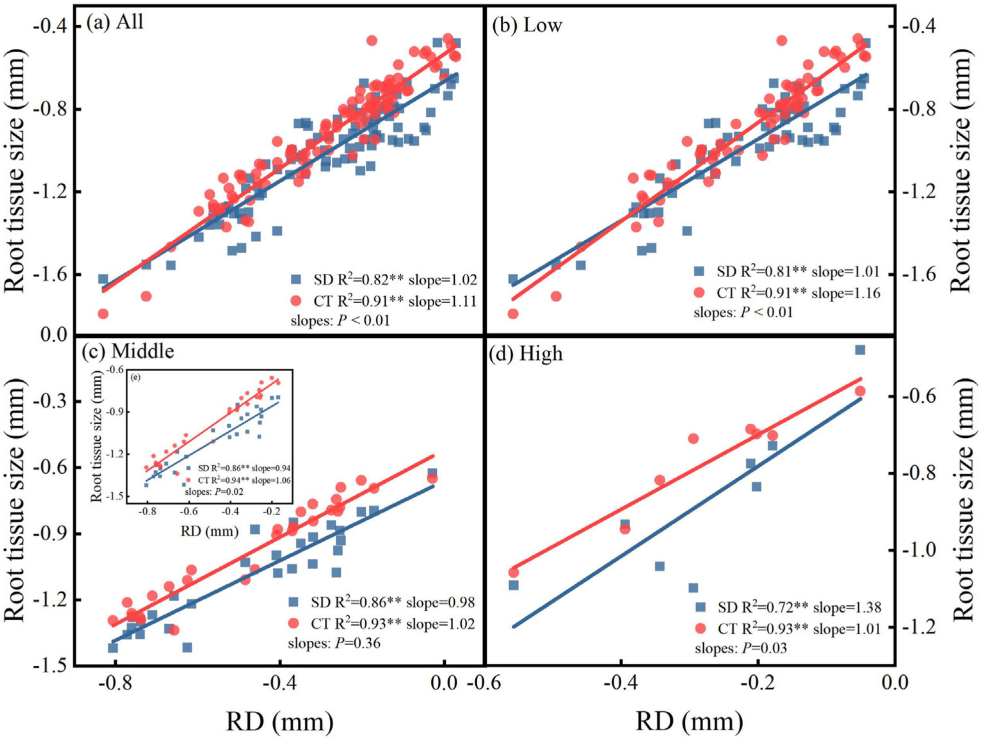

Fig. 6. Allometric relationships between root anatomical traits at different elevations (a–d). R^2 and slope values were obtained by the standardized major regression (P < 0.05). (e) allometric relationship between root anatomical traits (SD and CT) and RD after removing conifer plants. SD, stele diameter; CT, cortex thickness; RD, root diameter, Low, lower elevations (1374–2440 m); Middle, middle elevations (2934–3180 m); High, higher elevations (3375 m).

4.2. Phylogeny explains the elevational changes in the root anatomical traits

Except for CT and SDRD, root anatomical traits showed significant phylogenetic signals (Table 1). Similar results have been reported in woody and nonwoody species (Kong et al., 2014; Gu et al., 2014; Zhou et al., 2018; Wang et al., 2018). These results confirm that root anatomical traits are influenced significantly by phylogeny, indicating strong phylogenetic conservatism (Blomberg et al., 2003). Thus, it is crucial to consider the influence of phylogeny on root traits to increase our understanding of the correlation between plant evolutionary history and root anatomical traits.

In our study, phylogenetic taxonomy (clade) accounted for a large proportion of variation in root anatomical traits (Fig. 3a–e). Evolutionary background within forest communities differed greatly across different elevations (Fig. S2). In our study site, ancient plant lineages (i.e., the magnoliids and conifer) with thicker roots occur at lower and middle elevations (1374–3180 m); whereas modern species (i.e., asterids and rosids) with thinner roots occur at higher elevations (3375 m) (Comas and Eissenstat 2009; Chen et al., 2013; Valverde-Barrantes et al., 2020). Theoretically, root anatomical traits should be associated linearly with elevational gradients as roots are thicker in ancient plant lineages than in modern plants. Our finding that RD, SD, and CT first decreased and then increased across an elevational gradient (Fig. 2a–c) may be explained by clade-specific adaptive strategies. For example, ancient plant lineages (conifer and magnoliids) and asterids still adopted thicker and thinner roots at different elevations, respectively, but root anatomical traits of other clades, accounting for 61.20% of all species (Fig. S4), first decreased and then increased with elevation increases (Fig. 4b), further resulting in the nonlinear variation in root anatomical traits along the elevational gradients. Therefore, plant evolutionary background could explain the elevational variations in root anatomical traits, which may explain why plants are distributed in diverse environmental conditions. Nevertheless, few species of ancient plant lineages (i.e., conifers and magnoliids) are distributed on Taibai Mountain (Fig. S5). Future studies should explore changes in root traits of different clades along the environmental gradients at regional and global scales to improve our understanding of the vegetation distribution.

The adaptive strategies of plants have formed over long-term evolution under different environments (Comas et al., 2012; Valverde-Barrantes et al., 2020). During the Cretaceous period, plants needed to enhance the acquisition and transportation functions of their roots due to the lower temperature and soil availability (Fletcher et al., 2008; Comas et al., 2012). Several studies have demonstrated that RD decreases as divergence time decreases (Comas et al., 2012; Chen et al., 2013; Kong et al., 2014). Additionally, there is a positive correlation between CT and evolutionary time (Gu et al., 2014). We found similar patterns of variation, i.e., RD and SD were thinner in modern plant lineages than in ancient plant lineages (Figs. S3a and c). However, differences in CT and SDRD were found in modern plants. For example, compared to asterids species, eudicots had thicker CT. In addition, SDRD was thicker in rosids than in other clades except for ancient plants (Figs. S3b and d). These findings indicate that one important factor that influences SDRD is phylogenetic taxonomy, particularly clade.

4.3. Soil factors influence the variation in root anatomical traits along an elevational gradient

Soil factors also influenced the elevational variation in SD, CT, and RD. We also found that SBD accounted for large variations in SD (Table 2). SBD reflects soil compaction, which is known to have a significant influence on RD (Eissenstat et al., 2015), but few studies have considered the correlation between SBD and root anatomical traits. It has been reported that plants with thicker RD occur in denser soil due to their higher penetration capacity (Materechera et al., 1992; Freschet et al., 2017; Fort et al., 2020). SBD, thus, should relate positively to SD because of the positive relationship between RD and SD (Gu et al., 2014; Kong et al., 2014). Similar results also have been confirmed in our study (Fig. 4a). Thicker SD is associated with higher RTD and indicates denser roots, enabling them to absorb water and nutrients from deeper soils (Freschet et al., 2017; Ma et al., 2018). As elevation increases, we found that SBD first increased and then decreased (Table S1), thus, the positive correlation between SBD and SD may result in similar elevational patterns in SD.

Another major factor that influences the elevational variation in the CT and RD is AN (Table 2). Generally, thinner RD and CT reduce the investment of carbon and the metabolic cost of soil exploration in infertile soils (Jaramillo et al., 2013; Lynch et al., 2021). Several researchers have found that CT decreases as soil N content increases (Li et al., 2022). Analogously, we found that CT and RD decreased as AN increased (Fig. 5b and c). This is because CT is associated with the radial transportation of resources (Guo et al., 2008). Moreover, reducing CT in higher AN content can decrease radial transport resistance for water and nutrients to improve the transportation function of absorptive roots (Kong et al., 2017). Furthermore, increasing CT in lower AN content may enhance the absorption efficiency because CT provides a habitat for mycorrhizal fungi. Previous studies have argued that species with thicker roots have lower branch density and higher mycorrhizal colonization than species with thinner roots (Eissenstat et al., 2015; Liu et al., 2015). These results indicate that plants depend on root systems to acquire nutrients in fertile soil but on the mycorrhizal fungi in infertile soil. Thus, producing thinner roots is not a general pattern under adverse environments, which may be influenced by mycorrhizal fungi. Thus, it is necessary to explore the influence of mycorrhizal types and colonization on root anatomical traits in the future.

4.4. The allometric relationship between root traits depends on elevational gradients and phylogeny

Recent studies have demonstrated that there is an allometric relationship between root anatomical traits (Gu et al., 2014; Kong et al., 2014), i.e., the slope of the relationship between CT and RD is higher than that between SD and RD (Kong et al., 2019). Two hypotheses have been proposed to explain this phenomenon: the nutrient absorption transportation hypothesis and the carbon supply-consumption balance hypothesis (Kong et al., 2017, 2021). According to the Hagen–Poiseuille Law, the fluid flux in a pipe is proportional to the fourth power of the pipe radius (such as vessel and sieve tubes), and the absorption capacity of the cortex is proportional to the second power of the cortex radius (Jensen et al., 2016; Zhang et al., 2024). Therefore, the allometric relationships between CT and RD ensure the trade-off of the absorption and transportation functions as well as the carbon supply and consumption (Kong et al., 2017, 2021). Exploring the allometric relationship between root anatomical traits under diverse environments will enhance our comprehensive understanding of general patterns of this correlation and the multidimensional relationships between root anatomical traits.

Our findings indicated that the allometric relationship between root anatomical traits occurred at lower and higher elevations, but not at middle elevations (Fig. 6b and d). Similar results have been found at the global and regional scales (Gu et al., 2014; Li et al., 2023; Zhang et al., 2023). These findings demonstrate that such an allometric relationship is a potential mechanism for plants to adapt to different environments. The allometric relationship was obvious at different elevations when phylogeny was ignored (Figs. S4a–d). Thus, phylogeny can influence relationships between root anatomical traits. When we removed conifers from our analysis, allometric relationships between anatomical root traits were significant at middle elevations (Fig. 6c and e). This is because the slope between CT and RD of conifers is not higher than that between SD and RD (Zhang et al., 2023). Future research should explore the variation patterns of root anatomical traits of conifer plants to elucidate why they do not follow allometric relationships.

5. Conclusion

Our study showed that anatomical traits of the first-order roots (SD, CT, RD, and SDRD) first decreased and then increased along an elevational gradient. These changes were regulated mainly by phylogenetic factors. Various adaptive strategies of plants in different clades may cause the nonlinear relationship between root anatomical traits and elevation. For example, excluding plants from ancient lineages (e.g., conifer and magnoliids) and asterids, root anatomical traits of other clades, accounting for 61.20% of all species, first decreased and then increased along an elevation gradient. We also found that the elevational variation in SD, CT, and RD was influenced by soil factors (SBD and AN). In addition, we discovered the allometric relationship between root anatomical traits at different elevations is significant when the phylogenetic background is ignored, indicating that phylogeny influences allometric relationships. This finding suggests one mechanism plants use to adapt to new environments is to alter these allometric relationships between root anatomical traits. This study highlights the influence of phylogeny and environment on variation in root anatomical traits and their general allometric relationship, providing theoretical guidance for further exploring the response of root anatomical structures to global changes.

CRediT authorship contribution statement

Xue Wang: Writing – original draft, Investigation, Formal analysis. **Xinrui Liu:** Writing – review & editing, Investigation. **Shuang Chen:** Formal analysis. **Jiang Zhu:** Formal analysis. **Yanqi Yuan:** Writing – review & editing. **Rong Zhu:** Writing – review & editing. **Kaixi Chen:** Writing – review & editing. **Xue Yang:** Investigation. **Xiaochun Wang:** Investigation. **Weiyi Mo:** Investigation. **Ruili Wang:** Writing – review & editing, Funding acquisition, Conceptualization. **Shuoxin Zhang:** Writing – review & editing, Funding acquisition, Conceptualization.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2024.09.008.

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