



OPEN Mycorrhizal associations and root morphology shape mechanical performance in woody plants from cold regions

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Root mechanical traits, including load for failure in tension (F_r), tensile strength (T_r), tensile strain (ϵ_r), modulus of elasticity (E_r), and tensile toughness (W_r), are critical for plant anchorage and soil stability. These traits are shaped by root morphology, type (absorptive and transport roots), and mycorrhizal associations (arbuscular mycorrhizal and ectomycorrhizal fungi). This study investigates the relationships among these traits. We examined mechanical traits across eight woody species with different mycorrhizal associations, categorizing roots into absorptive and transport types. Root morphological traits - root diameter (RD), specific root length (SRL), root tissue density (RTD), and root biomass (RB) - were measured. Tensile tests were conducted to assess mechanical properties. Statistical analyses, including regression and principal component analysis (PCA), were used to elucidate trait relationships. Transport roots exhibited superior mechanical properties compared to absorptive roots, with RD and RB showing significant positive correlations with mechanical traits. AM roots demonstrated higher tensile strength, strain, and toughness than EM roots. PCA highlighted RD and SRL as dominant factors influencing root mechanical performance, while RB contributed significantly to transport roots' structural stability. This study underscores the critical role of root morphological traits and mycorrhizal associations in determining mechanical performance. These findings highlight the ecological trade-offs between mechanical stability and resource acquisition, offering novel insights into root functional strategies and their implications for ecosystem stability.

Keywords Root mechanical traits, Transport and absorptive roots, Mycorrhizal type, Root morphology

The mechanical properties of plant roots, including load for failure in tension (F_r), tensile strength (T_r), tensile strain (ϵ_r), modulus of elasticity (E_r), and tensile toughness (W_r) (Table S1), are critical for anchoring plants and stabilizing soils under environmental stress¹. These traits enable roots to resist mechanical forces such as wind, soil compaction, and erosion, directly influencing plant survival and ecosystem stability². Despite their importance, the mechanisms underlying variations in these traits remain poorly understood, particularly regarding how they are influenced by root anatomy, morphology, and ecological function³. This knowledge gap hinders our ability to predict plant responses to environmental challenges and design strategies for soil and vegetation management.

Transport and absorptive roots represent two major functional categories within root systems, each specialized for different roles⁴. Transport roots, characterized by larger diameters and higher lignification, are primarily responsible for anchorage and mechanical stability, while absorptive roots, with their finer structure, prioritize water and nutrient uptake⁵. Although previous studies have highlighted the mechanical superiority of transport roots over absorptive roots, the underlying structural and functional adaptations remain insufficiently explored⁶. Additionally, how the mechanical traits of these root types vary across species and environments, and the relationship between root mechanical properties and root morphology, require further investigation.

Mycorrhizal fungi play a crucial role in root colonization and adaptation, with both ectomycorrhizal (EM) and arbuscular mycorrhizal (AM) fungi forming symbiotic relationships with plant roots⁷. These associations can significantly influence root morphology, physiology, and mechanical traits⁸. In particular, both transport and absorptive roots exhibit distinct colonization patterns, with transport roots often showing higher colonization rates and stronger fungal networks compared to absorptive roots⁹. This difference in colonization can further contribute to the variability in mechanical properties between root types¹⁰. EM roots typically exhibit lower

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mechanical performance but enhanced nutrient exchange efficiency, while AM roots, characterized by higher lignification and greater cortical thickness, demonstrate superior mechanical stability¹¹. However, the variability in mechanical traits between EM and AM roots, and the ecological implications of these differences, remain unclear. Addressing this gap is essential to understand how mycorrhizal types shape root functions in diverse habitats.

Root morphology, including root diameter (RD), specific root length (SRL), root tissue density (RTD), and total fine root biomass (RB), plays a fundamental role in determining mechanical traits¹². Larger root diameters and higher tissue density are typically associated with greater tensile strength and modulus of elasticity, while higher SRL is linked to reduced mechanical performance¹³. However, the interactions between these morphological traits and root types or mycorrhizal associations have not been fully elucidated. This limits our understanding of how structural and functional traits combine to influence root mechanical properties and adapt to environmental pressures.

To address these, we propose two hypotheses: (1) Root morphological traits significantly influence root mechanical performance, with absorptive roots showing a more pronounced effect than transport roots. (2) Mycorrhizal type is a key factor influencing root mechanical performance, with AM fungi enhancing the mechanical properties of roots compared to EM fungi. By integrating biomechanical, morphological, and ecological perspectives, this study provides novel insights into the adaptive strategies of root systems, contributing to a deeper understanding of their role in plant resilience and ecosystem functioning.

Materials and methods

Species selection and experimental design

Eight dominant Woody plant species from the cold temperate forests of Heilongjiang Province, Northeast China, were selected for experimentation (Table S2). These species were categorized based on their mycorrhizal associations, encompassing both ectomycorrhizal and arbuscular mycorrhizal fungi. The EM group (*Picea asperata*, *Abies fabri*, *Quercus mongolica*, *Betula platyphylla*), the AM group (*Lespedeza bicolor*, *Aralia elata*, *Swida alba*, *Spiraea salicifolia*). The selection of species was based on three criteria: (1) they are commonly found in disturbed soils within the forests of Northeast China, (2) they are utilized by land managers for slope reinforcement, and (3) they exhibit various types of mycorrhizae, which are instrumental in studying ecological and soil stability dynamics.

One-year-old seedlings were purchased from a local nursery and planted at the experimental site located in the suburbs of Harbin, Heilongjiang Province, Northeast China (126°30'E, 45°54'N). Each species was planted in individual 3 m × 3 m plots, with three replicates per species, and a 2 m buffer zone was maintained between plots (Fig. 1). Planting commenced in April 2023 and continued until the plants were excavated for experimentation

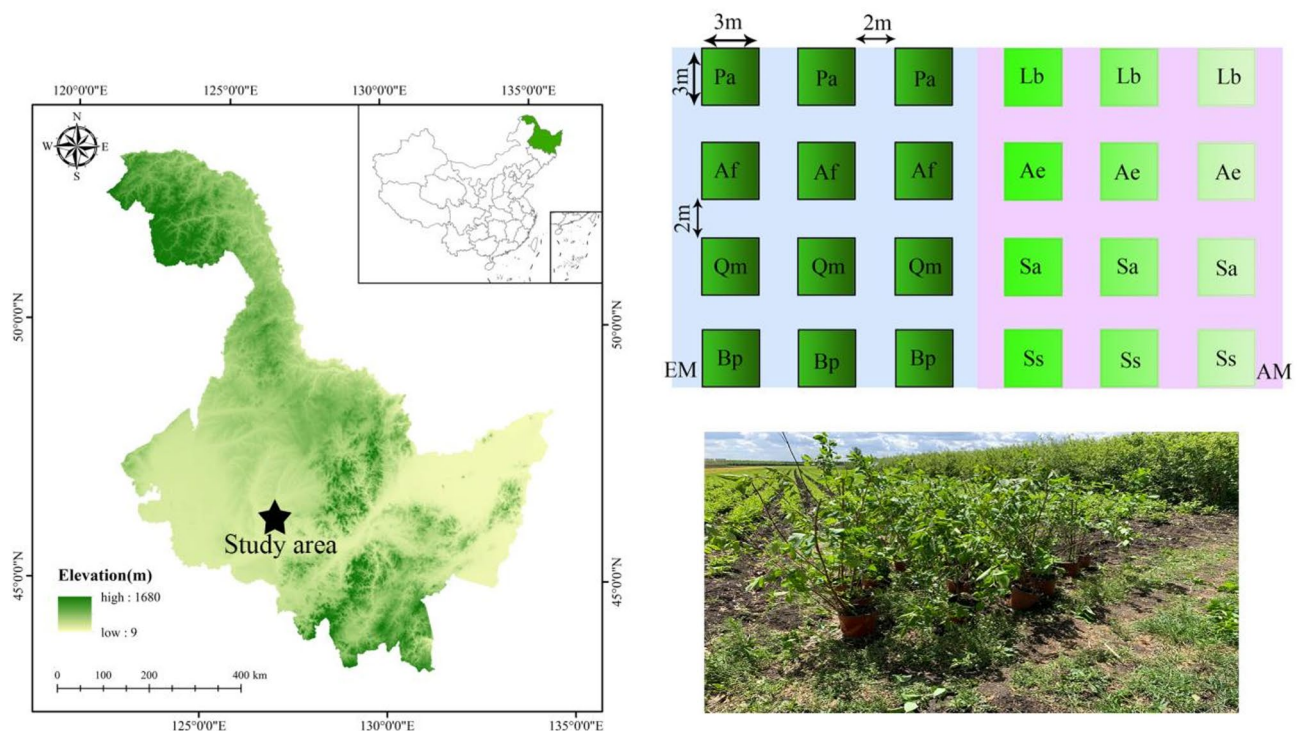


Fig. 1. Sample plot and diagram of the experimental design in Harbin, Heilongjiang Province, northeastern China. The map was created using ArcGIS software (version 10.8, <https://www.esri.com/>), and the experimental layout diagram was drawn using Adobe Illustrator (version 27.0, <https://www.adobe.com/>). The full names of the plant abbreviations in the figure can be found in Table S2.

in October 2023, coinciding with the peak growing season for woody plants in Northeast China. By October, it was considered that root traits had reached maturity. In the study area the average temperature from June to August was 19.1 °C, with a maximum temperature of 34.8 °C in July, based on data from 2017 to 2023. The average precipitation during this period was 135.6 mm. The soil in this region is classified as loamy clay, derived from glacial sedimentary deposits. The chemical properties of the surface soil are as follows: pH 6.2, total nitrogen content 2.1 g/kg, available potassium content 0.152 g/kg, available calcium content 2.05 g/kg, and available magnesium content 0.405 g/kg. All treatments, including soil preparation, daily irrigation of plants, weeding (manually every week), and pruning (every months), were conducted uniformly across all plots.

Sampling and measurement of root morphological traits

This study measured four morphological traits of fine roots (root morphological traits: average fine root diameter (RD), root tissue density (RTD), specific root length (SRL), total fine root biomass (RB). In October 2023, seedlings of each species were carefully excavated with shovels to avoid root damage, with three replicates per species. The roots were then washed under water and classified into two categories: absorptive roots, typically consisting of first, second, and third order roots; and transport roots, defined as higher order roots, all roots above the third order¹⁴. Root orders were determined according to the morphological root classification system¹⁵ (Fig. 2).

For each species, two subsamples of absorptive roots and transport roots were used to measure root morphology. This study included roots of orders 1 to 5 order, root samples from each species were scanned using a scanner with a resolution of 600 dpi (Expression 11000XL, Epson, NSW, Australia). The scanned images were analyzed using WinRHIZO Pro software to obtain root diameter (mm), length (cm) and root volume (cm³) across different diameter classes. The average root diameter (RD in mm) of absorptive roots and transport roots was calculated as the weighted average of the median root length for each diameter class. The specific root length (SRL in cm/g) was calculated as the ratio of total root length to root dry mass. The root tissue density (RTD in g/cm³) was calculated as the ratio of root dry mass to root volume. All fine roots from individual seedlings were dried at 70 °C for 48 h, then weighed to calculate total fine root biomass (RB in g).

Measurement of root diameter and mechanical traits

For mechanical performance testing of fine roots, plants were excavated from three replicate plots per species, ensuring the integrity of the root systems. The intact fine root structures were gently washed with water to remove soil particles and then preserved in a 15% alcohol solution to prevent decomposition. The samples were stored at 4 °C and transported to the laboratory for subsequent mechanical testing. During sampling, primarily intact and live roots were selected, with the assessment of live versus dead roots based on indicators such as color, epidermis, and flexibility. Additionally, efforts were made to minimize the loss of lower-order roots at the ends to ensure the integrity of the root system configuration. A pre-experiment was conducted to confirm

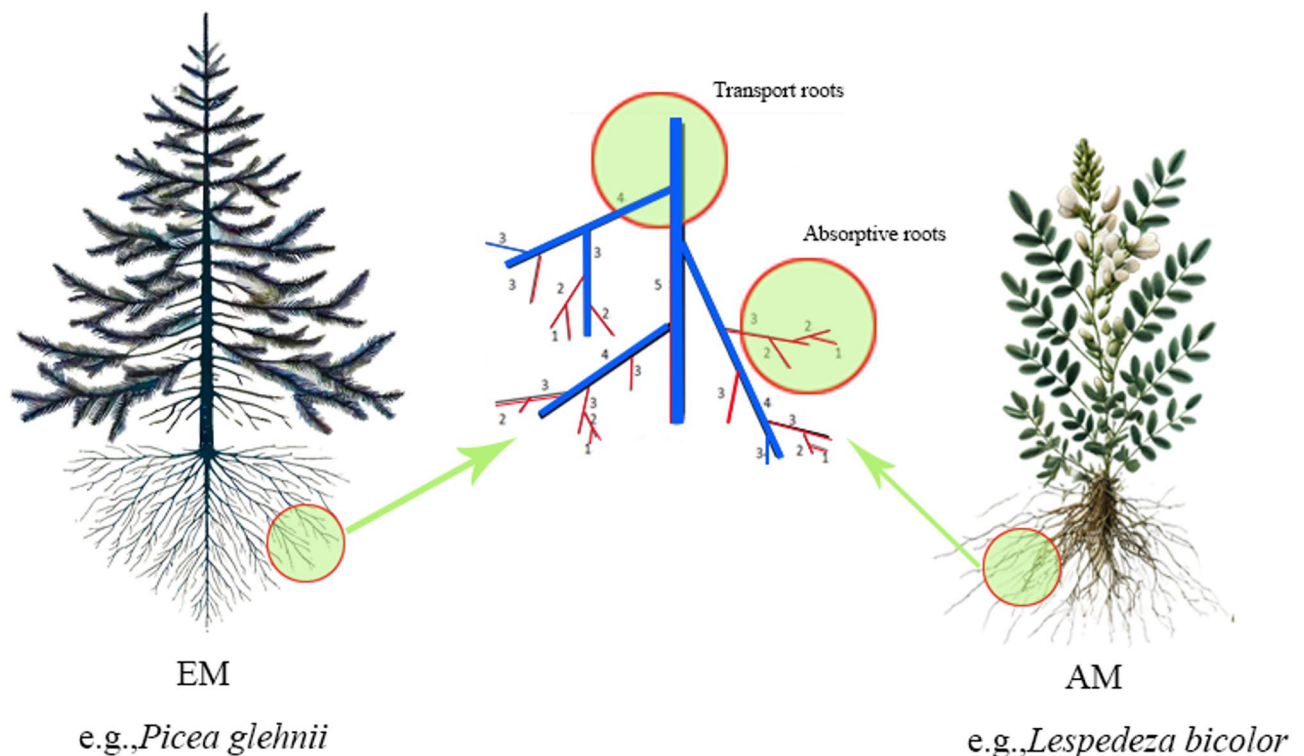


Fig. 2. Illustration of the root types and sampling locations in the root systems of EM and AM. This figure was created using Adobe Illustrator (version 27.0, <https://www.adobe.com/>).

mycorrhizal colonization in the selected species. Twenty absorptive roots and twenty transport roots from each species were randomly selected and stained with trypan blue. The roots were then examined under a microscope to observe the mycorrhizal fungal connections. This confirmed that the species studied indeed form mycorrhizal associations with either AM or EM fungi, depending on the species.

Root diameters were measured using a digital microscope (S8 APO, Leica, Germany; magnification $\times 8$) at a magnification level sufficient to capture fine structural details. Cleaned root samples were placed on a flat, transparent surface to ensure consistent focus, and images were taken at multiple points along each root segment. Diameter measurements were performed at the midpoint of each segment to minimize variability. The digital microscope software was calibrated prior to each session to ensure measurement accuracy.

We randomly selected 100 roots from EM and AM for tensile testing to measure the mechanical trait of the root system. The instrument used for measuring tensile mechanical properties was a microcomputer-controlled electronic universal testing machine (Zwick/Roell Z010, Germany, the maximum capacity of 125 N). Each root sample was clamped at both ends using a tensile testing apparatus, with a gauge length of 10 mm between the clamps. The roots were stretched at a constant speed of 50 mm/min until failure. The maximum force at breaking point was recorded. The success rate of the experiment was 78.2%. Through the control terminal, continuous measurements of tensile force, tensile strength, and other mechanical parameters were performed, and the deformation curves were recorded. When fixing the root samples, the two ends of each root segment were placed into the clamps, each end being clamped to about one-third of the root segment length, leaving the middle one-third exposed. During the tightening of the clamps, care was taken to ensure that the roots were perpendicular to the horizontal plane. In this study, it was considered that if a root broke in the middle or near the middle of the clamps, the breakage was due to tensile force rather than damage during other testing processes. The data recorded at this time were regarded as valid.

The load for failure in tension (F_r) was applied to each root until failure occurred, with the maximum load at the point of rupture recorded as the load for failure¹⁶. This load value was used to quantify the tensile strength of roots across different orders, providing data on the mechanical resistance of root structures under stress. All measurements were averaged to determine the characteristic load for failure in each root order.

The root tensile strength (T_r) was calculated using the formula¹⁷:

$$T_r = F / (\pi d^2 / 4)$$

Where F is load for failure in tension, d is root diameter.

The root tensile strain (ϵ_r) was measured during root tensile testing. Each root sample was aligned and mounted between grips, and a controlled tensile force was applied incrementally until root elongation occurred. Displacement was recorded in real time to measure the change in length under tension. Root tensile strain (ϵ_r) was calculated using the formula¹⁸:

$$\epsilon_r = \Delta L / L_0$$

where ΔL represents the change in length (elongation) and L_0 is the original length of the root segment. The calculated strain values were recorded and averaged across root samples from each root order, providing a quantitative assessment of the roots' elasticity under tensile stress.

Root modulus of elasticity (E_r) was calculated using the formula¹⁹:

$$E_r = \sigma / \epsilon_r$$

Where σ represents the stress (force per unit cross-sectional area) and ϵ_r represents the root tensile strain (relative elongation).

Root tensile toughness (W_r) can be calculated using the integral of the stress-strain curve from zero strain up to the strain at failure (ϵ_r)²⁰:

$$W_r = \int_0^{\epsilon_r} \sigma(\epsilon) d\epsilon$$

Where W_r is the root tensile toughness, indicating the energy absorbed per unit volume before failure. $\sigma(\epsilon)$ is the stress as a function of strain. ϵ_r is the strain at the point of failure.

Statistical analysis

All data were tested for normal distribution and homogeneity of variance using the Kolmogorov-Smirnov test and Levene's test, respectively. Regression analysis was used to investigate the relationships between root mechanical traits and root diameter. We conducted statistical adjustment through analysis of covariance to standardize the two sets of data to the same diameter level, and then compared the effects of mycorrhiza type (AM versus EM). The Tukey-Kramer HSD two-way ANOVA method was used to study the differences in root mechanical traits (F , T_r , E_r , ϵ_r , W_r), root diameter, root morphological traits (average fine root diameter (RD), root tissue density (RTD), specific root length (SRL), total fine root biomass (RB)) among different species. Multifactor ANOVA was used to evaluate the effects of different plant species, mycorrhizal types, root type (transport versus absorptive) on various parameters. We investigated relationships among multiple traits through principal component analysis (PCA). Prior to conducting the PCA, all traits were normalized to have a mean of zero. To explore the relationships between the measured variables, we generated a correlation matrix heatmap using

Pearson's correlation coefficient. All data were log-transformed to meet the normality assumption. All statistical analyses were performed using R 3.2.3.

Results

Correlations between root diameter and mechanical traits

The mechanical traits of roots showed significant correlations with root diameter across the studied species. For both AM (arbuscular mycorrhizal) and EM (ectomycorrhizal) root types, the load for failure in tension and root tensile strain exhibited significant positive correlations with root diameter (Fig. 3A and C), whereas root tensile strength showed a negative correlation with root diameter, with transport roots generally showing higher values compared to absorptive roots (Fig. 3B). The correlation was consistently stronger for transport roots, where the mechanical traits were significantly higher compared to absorptive roots, reflecting a general pattern across all species. In terms of root modulus of elasticity, there was a significant negative correlation with root diameter, with larger roots exhibiting lower values for modulus of elasticity, particularly in EM roots, where the decrease was more pronounced compared to AM roots (Fig. 3D). The root tensile toughness was significantly positively correlated with root diameter, with a clear trend showing that transport roots had significantly higher toughness than absorptive roots, especially in the AM group (Fig. 3E).

Moreover, the content of the table further confirms the differences between transport roots and absorptive roots within both AM and EM types (Table S3). Transport roots consistently exhibited significantly higher values for all mechanical traits, including load for failure in tension, root tensile strength, root tensile strain, and root tensile toughness, when compared to absorptive roots (Table S3). This trend was observed across both AM and EM root types. The root diameter of transport roots was found to have a stronger relationship with mechanical traits than absorptive roots, with transport roots demonstrating a more significant increase in mechanical strength, elasticity, and toughness (Table S3).

A: relationships between the load for failure in tension and root diameter of 8 species. B: relationships between the root tensile strength and root diameter of 8 species. C: relationships between the root tensile strain and root diameter of 8 species. D: relationships between the root modulus of elasticity and root diameter of 8 species. E: relationships between the root tensile toughness and root diameter of 8 species. Symbols: small pink symbols represent absorptive roots; large green symbols represent transport roots.

The influence of different mycorrhizal types on root mechanical traits

Table S4 presents the ANOVA results for the effects of species, mycorrhiza type, root type, and their interactions on root mechanical traits (Table S4). The analysis revealed that mycorrhiza type (AM versus EM) had a significant effect on most root mechanical traits, including load for failure in tension (F_r), root tensile strength (T_r), root tensile strain (ϵ_r), root modulus of elasticity (E_r), and root tensile toughness (W_r) (Table S4). Notably, significant differences were observed between AM and EM roots, particularly in terms of F_r , T_r , ϵ_r , E_r , and W_r . Additionally, the interaction between mycorrhiza type and root type ($M \times R$) was significant for several traits, indicating that the effect of mycorrhiza type on mechanical traits was influenced by the root type (absorptive versus transport) (Table S4).

Table S5 presents the ANCOVA results, showing the significant effect of mycorrhiza type on root mechanical traits, with the diameter of the roots controlled for in the analysis (Table S5). After adjusting for diameter, AM roots still exhibited significantly higher values in F_r , T_r , ϵ_r , E_r , and W_r compared to EM roots, demonstrating that mycorrhiza type (AM versus EM) plays a crucial role in modulating the mechanical performance of roots (Table S5).

In Fig. 4, the boxplots illustrate the differences in root mechanical traits between AM and EM roots, where AM roots consistently show significantly higher values for all traits (F_r , T_r , ϵ_r , E_r , and W_r) compared to EM roots (Fig. 4). These trends are most pronounced in the transport roots, which exhibit the highest values for all traits in AM roots (Fig. 4).

Error bars represent standard errors. Capital letters indicate different root type of the same mycorrhizal types, while lowercase letters indicate differences mycorrhizal types under the same root type. A significant difference is indicated when $P < 0.05$.

Relationships between mechanicals and morphological traits for absorptive and transport roots

The heatmap for absorptive roots shows significant negative correlations between root tensile strain (ϵ_r) and root tissue density (RTD), as well as between root tensile toughness (W_r) and specific root length (SRL) (Fig. 5a). These negative correlations suggest that as SRL and RTD increase, W_r and ϵ_r decrease. Furthermore, load for failure in tension (F_r) exhibited a significant positive correlation with both root tensile strength (T_r) and root modulus of elasticity (E_r), indicating that higher F_r values were associated with greater T_r and E_r values (Fig. 5a).

For transport roots, stronger positive correlations were observed between F_r , T_r , E_r , and root diameter (RD), with F_r also showing a significant positive correlation with root biomass (RB) (Fig. 5b). These results suggest that the mechanical traits of transport roots are more strongly linked to root diameter and biomass than those of absorptive roots (Fig. 5b).

The PCA for absorptive roots reveals that mechanical traits (red arrows), such as F_r , T_r , E_r , and W_r , were closely associated with morphological traits (black arrows), particularly SRL and RTD (Fig. 6a). This indicates that the mechanical traits of absorptive roots are influenced by root morphology. The PCA for transport roots demonstrates that F_r , T_r , and E_r were strongly correlated with root diameter (RD), suggesting that transport roots with larger diameters tend to exhibit higher mechanical strength, elasticity, and toughness (Fig. 6b).

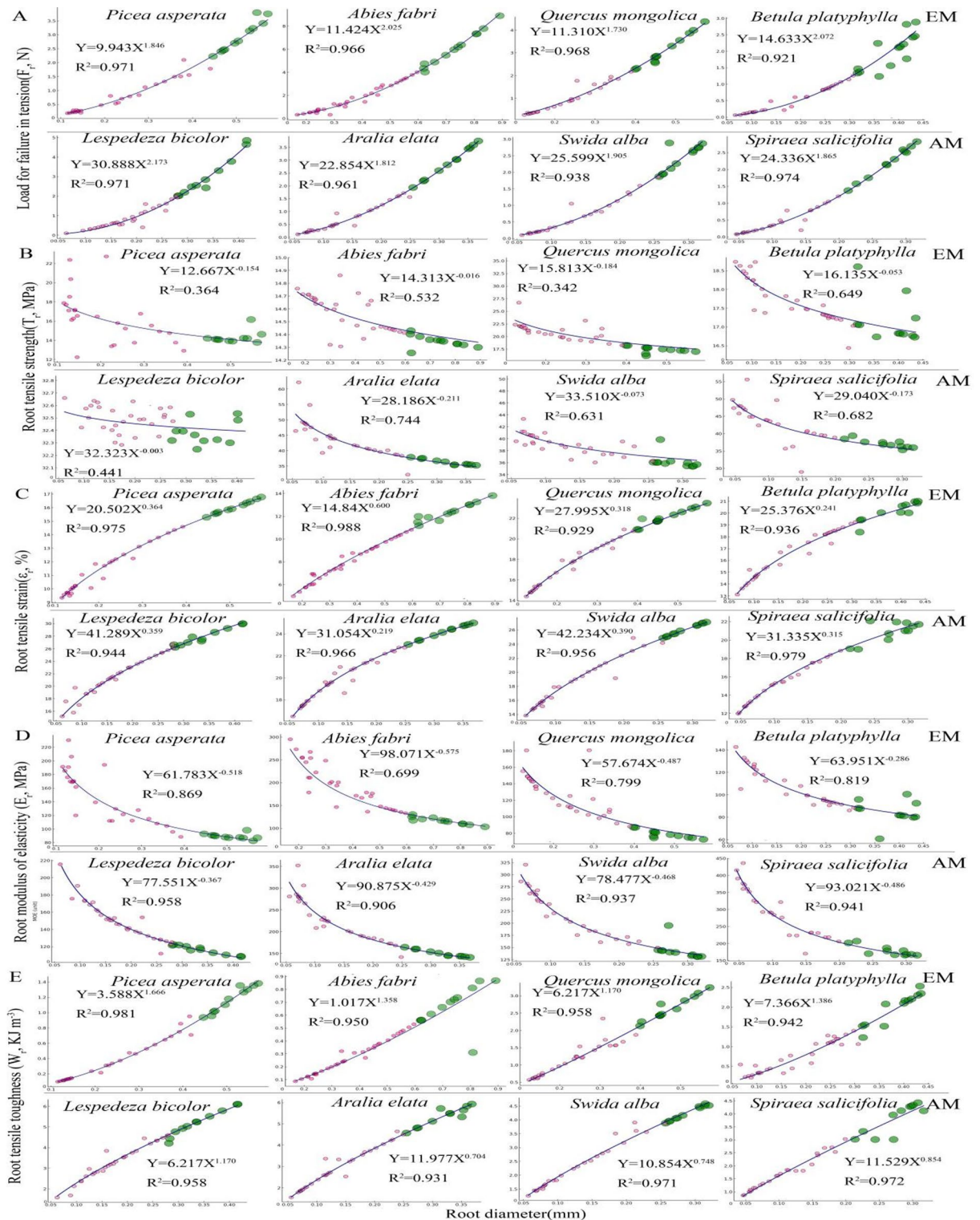


Fig. 3. Root diameter correlates with mechanical traits across species.

Discussion

Differential impact of root morphology on mechanical properties of absorptive and transport roots

The results from this study reveal significant correlations between root mechanical traits and root diameter, with transport roots generally exhibiting higher mechanical strength, elasticity, and toughness than absorptive roots across both AM and EM root types (Fig. 3, Table S3). Additionally, the correlation between root diameter and mechanical traits was consistently stronger for transport roots, indicating that larger root diameters contribute to

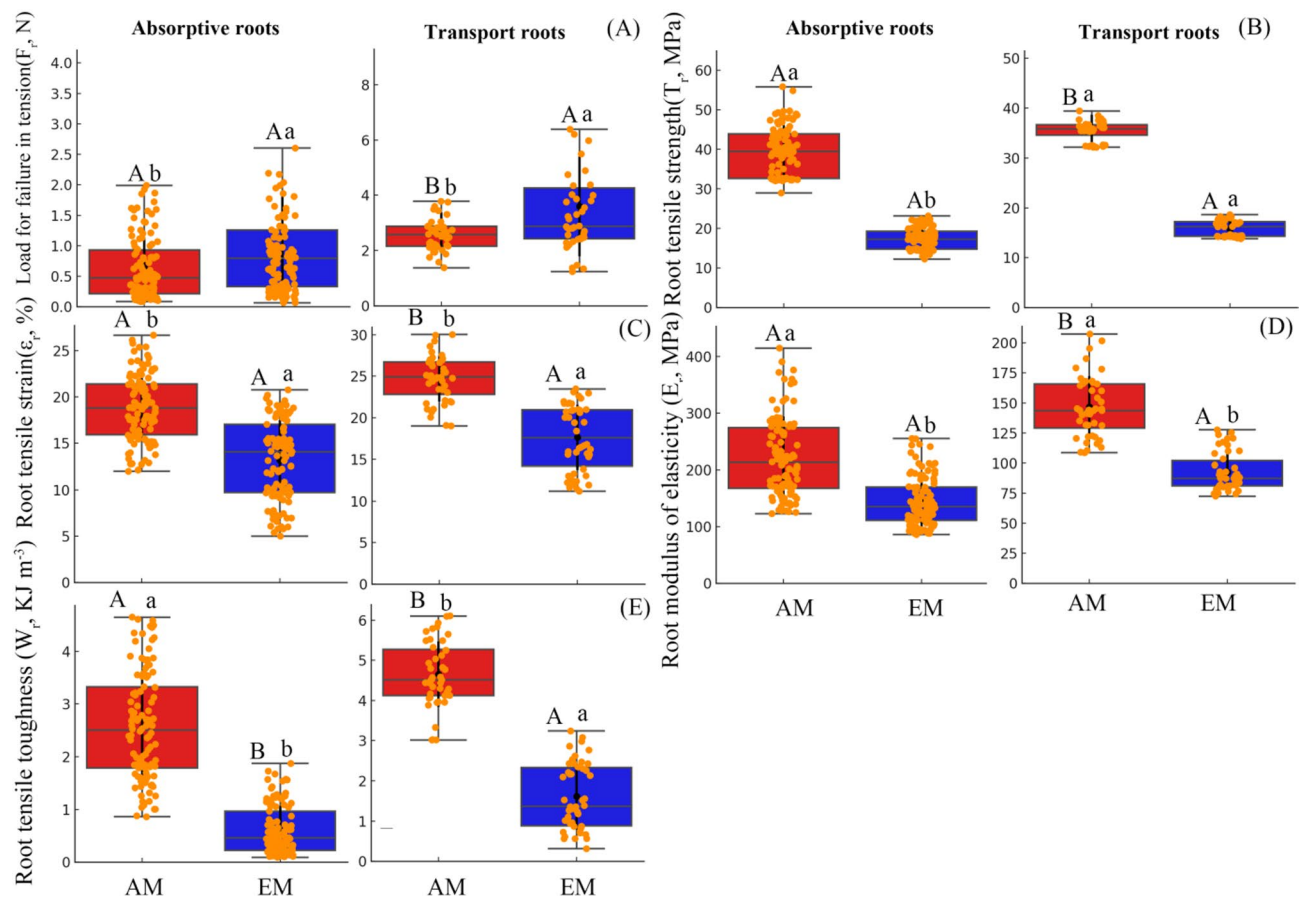


Fig. 4. AM roots show superior mechanical performance compared to EM roots.

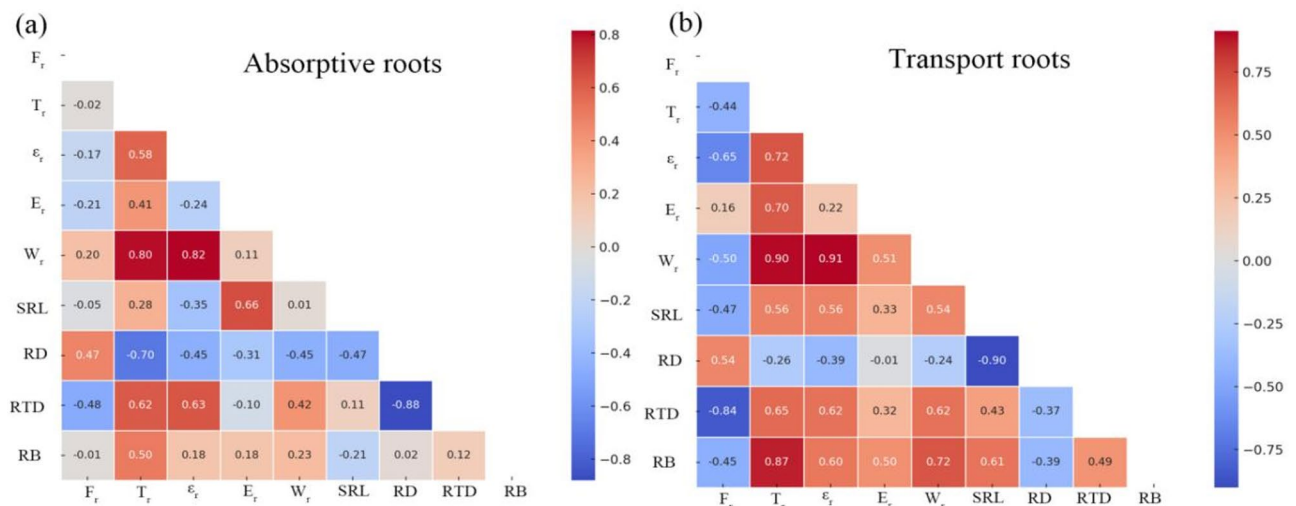


Fig. 5. Root traits heatmap analysis for absorptive (a) and transport roots (b). All data were log-transformed to meet the normality assumption. The color intensity in the heatmap represents the strength of the correlation, with the legend on the right displaying the corresponding correlation coefficient values. Strong positive correlations are shown in shades of red, while weaker correlations are shown in shades of blue. The closer the value is to 1 or -1, the stronger the linear relationship between the variables. Symbols and acronyms of traits: F_r - load for failure in tension, T_r - root tensile strength, E_r - root modulus of elasticity, ϵ_r - root tensile strain, W_r - root tensile toughness, RD - root diameter, SRL - specific root length, RTD - root tissue density, RB - root biomass.

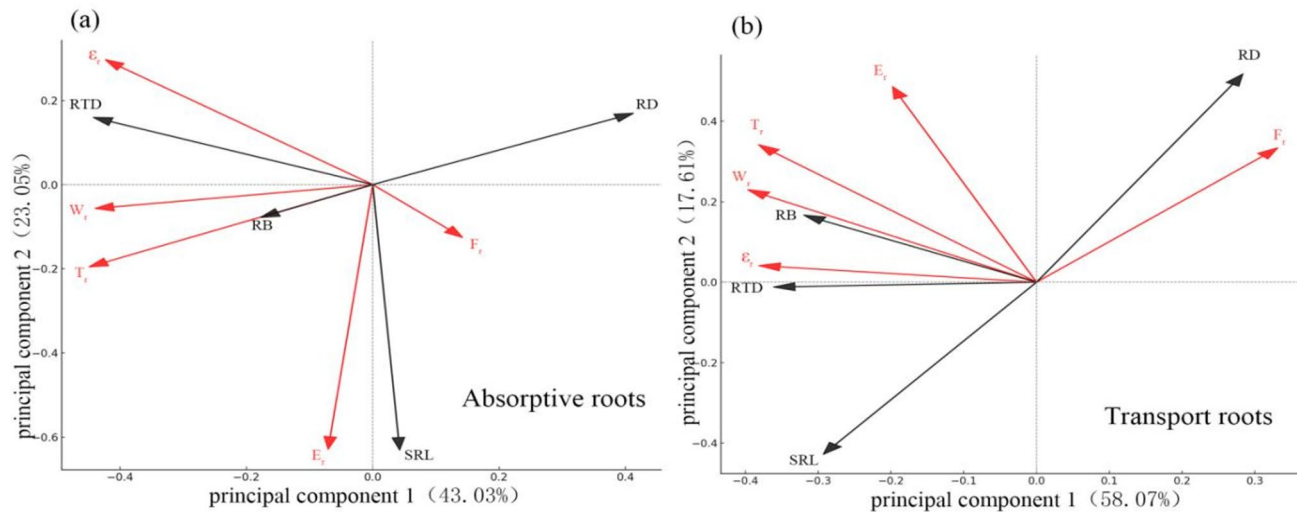


Fig. 6. Relationships between all root traits using principal component analysis for absorptive (a) and transport roots (b). Colours of arrows: red-root mechanical traits; black-root morphological or chemical traits. Symbols and acronyms of traits: F_r - load for failure in tension, T_r - root tensile strength, E_r - root modulus of elasticity, ϵ_r - root tensile strain, W_r - root tensile toughness, RD - root diameter, SRL - specific root length, RTD - root tissue density, RB - root biomass.

higher mechanical performance in these roots. The PCA analysis further supports this, showing that mechanical traits of transport roots are strongly associated with root diameter, while absorptive roots' mechanical traits are more closely linked to root morphology, such as specific root length (SRL) and root tissue density (RTD) (Fig. 6).

These findings suggest that root morphology plays a significant role in determining the mechanical traits of roots, with transport roots showing stronger correlations with mechanical properties than absorptive roots. This observation is consistent with previous studies, which have highlighted the functional differentiation between these two root types. Transport roots, being responsible for nutrient and water transport, tend to be thicker and more robust, enabling them to withstand greater mechanical stresses²¹. In contrast, absorptive roots are thinner and more flexible, optimizing them for nutrient uptake but sacrificing mechanical strength²². The significant influence of root morphology on the mechanical traits of absorptive roots, underscores the evolutionary trade-offs that shape the functional specialization of these roots, where mechanical performance is secondary to nutrient acquisition efficiency²³. This is in stark contrast to transport roots, where larger diameters and stronger mechanical traits are prioritized for structural support, reflecting the divergent ecological roles of these root types²⁴. Therefore, the results of this study align with these general ecological trends, confirming that transport roots are typically stronger, more elastic, and tougher than absorptive roots.

In comparison with earlier work, our results also support the hypothesis that the mechanical properties of roots are closely tied to their morphological characteristics, with a notable contrast in how these properties manifest across different root types. For instance, Bengough et al. (2011) found that root diameter significantly influences mechanical traits in several species, a pattern we observe in both AM and EM root types in this study²⁵. However, our study further emphasizes that the differences in mechanical properties between transport and absorptive roots are not just a function of diameter but also the underlying functional specialization of these roots. The significant negative correlation between modulus of elasticity and root diameter in EM roots, and the pronounced decrease compared to AM roots (Fig. 3), is particularly striking. This could be attributed to the distinct evolutionary pressures faced by these two types of mycorrhizal associations, with EM roots potentially being more adapted to environments requiring higher tensile strength and lower elasticity for better structural support²⁶.

The observed differences between the mechanical traits of transport and absorptive roots also lend support to the hypothesis that root morphology, particularly SRL and RTD, has a more pronounced impact on absorptive roots than on transport roots. This is consistent with findings by Balliu (2021), who suggested that absorptive roots are specialized for resource uptake rather than structural strength, leading to a greater sensitivity of their mechanical properties to variations in morphology²⁷. This could explain why absorptive roots exhibit significant negative correlations between root tensile strain and tissue density, as seen in our heatmap analysis (Fig. 5a), reflecting a trade-off between flexibility and strength. Additionally, the stronger positive correlations in transport roots between mechanical traits and root biomass (Fig. 5b) suggest that larger biomass contributes to enhanced mechanical performance, possibly due to a higher allocation of resources towards structural integrity²⁸.

In terms of our hypothesis, the results are consistent with the idea that root morphological characteristics significantly influence mechanical properties, and that the impact is more pronounced in absorptive roots. The greater variability in mechanical traits of absorptive roots, as opposed to transport roots, may be due to their functional role in nutrient acquisition, which necessitates a balance between flexibility and mechanical integrity²⁹. The evolutionary pressure for absorptive roots to optimize resource uptake likely leads to a greater

reliance on morphological traits like SRL and RTD, which in turn influence mechanical performance³⁰. On the other hand, transport roots, with their structural role in supporting nutrient and water transport, appear to have evolved to exhibit stronger mechanical properties regardless of the morphological traits like SRL and RTD³¹. This distinction in the functional roles of root types could explain the observed differences in their mechanical traits. Overall, this study adds to the growing body of literature on root mechanics by offering a detailed exploration of how different root types respond to variations in morphological traits, thereby advancing our understanding of root functional diversity and ecological adaptation.

The relationship between different mycorrhizal types and root mechanical traits

This study demonstrated significant variation in root mechanical traits between ectomycorrhizal (EM) and arbuscular mycorrhizal (AM) species (Table S3). Transport roots consistently exhibited higher mechanical properties, such as load for failure in tension (F_r), tensile strength (T_r), tensile strain (ϵ_r), modulus of elasticity (E_r), and tensile toughness (W_r), as well as larger diameters compared to absorptive roots (Table S3). AM species showed greater variability in mechanical traits than EM species, indicating their higher adaptability to diverse environments (Table S3). Among the traits analyzed, AM roots outperformed EM roots across root types, with AM transport roots displaying the most pronounced mechanical advantages, including enhanced tensile strength and toughness, emphasizing their superior mechanical stability and resistance (Fig. 4).

The superior mechanical traits of AM roots suggest a strong link between mycorrhizal type and root mechanical performance. The higher tensile strength, strain, and toughness observed in AM roots indicate their ability to endure greater mechanical stresses, which may stem from enhanced lignification, thicker cell walls, and increased biomass allocation to roots³². In contrast, EM roots, which exhibited lower mechanical performance, may prioritize resource exchange efficiency over structural reinforcement, reflecting a distinct ecological strategy³³.

These findings align with those of Danjon et al. (2008), who reported higher mechanical stability in AM roots due to robust anatomical structures and increased carbon allocation³⁴. Similarly, Wang et al. (2024) demonstrated that AM roots exhibit superior tensile properties due to their greater cortical thickness and vascular diameter, enhancing their resistance to mechanical stress³⁵. However, the greater variability in AM roots contrasts with the findings of Mao et al. (2023), who observed limited mechanical trait variability among AM species²⁰. This discrepancy may result from differences in species composition, environmental conditions, or measurement approaches³⁶. Variability in AM root mechanical traits could be influenced by factors such as soil type, fungal symbiosis, or growth conditions, which might affect root structure and lignification³⁷. Additionally, the selection of species with varying ecological strategies could also contribute to observed discrepancies³⁸.

The enhanced mechanical performance of AM roots is linked to their anatomical and physiological traits³⁹. AM roots have larger cortical areas, thicker steles, and increased lignification, which provide structural rigidity and enable them to withstand greater mechanical forces⁴⁰. Additionally, the larger vascular tissues in AM roots improve water and nutrient transport, indirectly enhancing mechanical stability by maintaining turgor pressure under stress⁴¹.

The greater variability in AM roots likely reflects their broader ecological adaptability⁴². AM fungi form associations with a wide range of plant species, leading to more diverse root structures and mechanical properties⁴³. This adaptability enables AM-associated plants to occupy heterogeneous environments where mechanical stability and resource acquisition are critical for survival⁴⁴. In contrast, the specialized nutrient exchange strategies of EM roots may limit their structural variability, as resources are primarily allocated to optimizing mycorrhizal efficiency rather than root mechanical reinforcement⁴⁵.

The observed differences in mechanical performance between AM and EM roots support the hypothesis that mycorrhizal type is a key factor influencing root mechanical traits. AM fungi, through their diverse ecological associations, enhance root mechanical properties by promoting increased lignification, thicker cell walls, and higher biomass allocation to roots⁴⁶. This strengthens root resistance to mechanical stress, particularly in transport roots. In contrast, EM roots prioritize efficient nutrient exchange over structural reinforcement, which may limit their mechanical performance⁴⁷. These contrasting strategies reflect the distinct ecological pressures faced by plants in nutrient-limited versus mechanically stressful environments⁴⁸.

The mechanical superiority of AM roots provides significant ecological advantages, particularly in environments with high mechanical stress. AM-associated plants, through enhanced structural reinforcement, may gain competitive advantages and higher survival rates in such conditions⁴⁹. Conversely, EM roots demonstrate a trade-off between mechanical performance and nutrient exchange efficiency, favoring success in nutrient-limited but mechanically stable habitats⁵⁰. These functional distinctions highlight the evolutionary strategies of plants in balancing mechanical performance and nutrient acquisition, shaping their ecological niches and adaptive potential⁵¹.

Conclusion

This study establishes that both root morphology and mycorrhizal type play critical roles in shaping root mechanical performance. Quantitative analyses revealed significant correlations between root diameter and mechanical traits, such as load for failure in tension, tensile strength, strain, and toughness. Transport roots consistently showed stronger mechanical properties than absorptive roots, with this trend being particularly pronounced in arbuscular mycorrhizal (AM) species. Furthermore, mycorrhizal type significantly influenced root mechanical traits, with AM roots outperforming ectomycorrhizal (EM) roots across all measured traits. The results support our hypothesis that root morphology, particularly diameter, influences mechanical performance more in transport roots, while mycorrhizal type is a dominant factor determining overall mechanical strength. This validates our initial hypothesis that AM fungi enhance root mechanical properties compared to EM fungi.

These findings emphasize the trade-offs between mechanical stability and resource acquisition across root types and mycorrhizal associations. Transport roots enhance anchorage and soil stability under stress, while mycorrhizal adaptations reflect distinct ecological strategies. Future studies should investigate the anatomical mechanisms underlying the mechanical advantages of AM roots, particularly lignification and cortical thickness. Expanding research to include diverse species and environmental conditions will deepen understanding of mycorrhizal influence on root mechanical traits.

Data availability

Data is provided within the manuscript or supplementary information files.

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References

- Jonasson, S. & Callaghan, T. V. Root mechanical properties related to disturbed and stressed habitats in the Arctic. *New Phytol.* **122**, 179–186. <https://doi.org/10.1111/j.1469-8137.1992.tb00064.x> (1992).
- Hudek, C. et al. Root morphology and biomechanical characteristics of high altitude alpine plant species and their potential application in soil stabilization. *Ecol. Eng.* **109**, 228–239. <https://doi.org/10.1016/j.ecoleng.2017.05.048> (2017).
- Freschet, G. T. et al. Root traits as drivers of plant and ecosystem functioning: Current understanding, pitfalls and future research needs. *New Phytol.* **232**(3), 1123–1158. <https://doi.org/10.1111/nph.17072> (2021).
- Wang, H., Inukai, Y. & Yamauchi, A. Root development and nutrient uptake. *Crit. Rev. Plant Sci.* **25**(3), 279–301. <https://doi.org/10.1080/07352680600709917> (2006).
- Stokes, A. et al. Desirable plant root traits for protecting natural and engineered slopes against landslides. *Plant Soil* **324**, 1–30. <https://doi.org/10.1007/s11104-009-0159-y> (2009).
- Lynch, J. P. et al. Root anatomy and soil resource capture. *Plant Soil* **466**, 21–63. <https://doi.org/10.1007/s11104-021-05010-y> (2021).
- Willis, A., Rodrigues, B. F. & Harris, P. J. C. The ecology of arbuscular mycorrhizal fungi. *CRC Crit. Rev. Plant Sci.* **32**(1), 1–20. <https://doi.org/10.1080/07352689.2012.683375> (2013).
- Mao, Z. et al. Mechanical traits of fine roots as a function of topology and anatomy. *Ann. Bot.* **122**(7), 1103–1116. <https://doi.org/10.1093/aob/mcy076> (2018).
- Zadworny, M. & Eissenstat, D. M. Contrasting the morphology, anatomy and fungal colonization of new pioneer and fibrous roots. *New Phytol.* **190**(1), 213–221. <https://doi.org/10.1111/j.1469-8137.2010.03598.x> (2011).
- Roumet, C., Urcelay, C. & Díaz, S. Suites of root traits differ between annual and perennial species growing in the field. *New Phytol.* **170**(2), 357–368. <https://doi.org/10.1111/j.1469-8137.2006.01667.x> (2006).
- Ali, F. et al. Functional and structural roles of wiry and sturdy rooted emerged macrophytes root functional traits in the abatement of nutrients and metals. *J. Environ. Manag.* **249**, 109330. <https://doi.org/10.1016/j.jenvman.2019.109330> (2019).
- Lu, B. et al. The role of fine root morphology in nitrogen uptake by riparian plants. *Plant Soil* **472**(1), 527–542. <https://doi.org/10.1007/s11104-021-05270-8> (2022).
- Boldrin, D., Leung, A. K. & Bengough, A. G. Root biomechanical properties during establishment of woody perennials. *Ecol. Eng.* **109**, 196–206. <https://doi.org/10.1016/j.ecoleng.2017.05.002> (2017).
- Rewald, B., Ephraïm, J. E. & Rachmilevitch, S. A root is a root is a root? Water uptake rates of Citrus root orders, plant. *Cell. Environ.* **34**(1), 33–42. <https://doi.org/10.1111/j.1365-3040.2010.02223.x> (2011).
- Liu, Y. et al. A new method to optimize root order classification based on the diameter interval of fine root. *Sci. Rep.* **8**(1), 2960. <https://doi.org/10.1038/s41598-018-21248-6> (2018).
- Yang, M. et al. Tree stability under wind: Simulating uprooting with root breakage using a finite element method. *Ann. Bot.* **114**(4), 695–709. <https://doi.org/10.1093/aob/mcu122> (2014).
- Melese, D. T. Effect of diameter, root moisture content, gauge length and loading rate on tensile strength of plant roots and their contribution to slope stability. *Lowland Technol. Int.* **22**, 4. https://doi.org/10.0001/ialt_jti.v22i4.749 (2021).
- Fu, J. et al. Biomechanical behavior of grass roots at different gauge lengths. *J. Mt. Sci.* **21**(9), 3201–3214. <https://doi.org/10.1007/s11629-023-8474-y> (2024).
- Whiteley, G. M. & Dexter, A. R. Elastic response of the roots of field crops. *Physiol. Plant.* **51**(4), 407–417. <https://doi.org/10.1111/j.1399-3054.1981.tb05578.x> (1981).
- Mao, Z. et al. Intra- and inter-specific variation in root mechanical traits for twelve herbaceous plants and their link with the root economics space. *Oikos* **2023**(1), e09032. <https://doi.org/10.1111/oik.09032> (2023).
- Correa, J. et al. Soil compaction and the architectural plasticity of root systems. *J. Exp. Bot.* **70**, 6019–6034. <https://doi.org/10.1093/jxb/erz383> (2019).
- Read, J. & Stokes, A. Plant biomechanics in an ecological context. *Am. J. Bot.* **93**(10), 1546–1565. <https://doi.org/10.3732/ajb.93.10.1546> (2006).
- Chen, Z., Zhu, L. T. & Luo, Z. H. Characterizing flow and transport in biological vascular systems: A review from physiological and chemical engineering perspectives. *Ind. Eng. Chem. Res.* **63**(1), 4–36. <https://doi.org/10.1021/acs.iecr.3c02463> (2023).
- Stachew, E., Houette, T. & Gruber, P. Root systems research for bioinspired resilient design: A concept framework for foundation and coastal engineering. *Front. Rob. AI* **8**, 548444. <https://doi.org/10.3389/frobt.2021.548444> (2021).
- Bengough, A. G. et al. Root elongation, water stress, and mechanical impedance: A review of limiting stresses and beneficial root tip traits. *J. Exp. Bot.* **62**(1), 59–68. <https://doi.org/10.1093/jxb/erq350> (2011).
- Barley, K. P. & Greacen, E. L. Mechanical resistance as a soil factor influencing the growth of roots and underground shoots. *Adv. Agron.* **19**, 1–43. [https://doi.org/10.1016/S0065-2113\(08\)60731-2](https://doi.org/10.1016/S0065-2113(08)60731-2) (1967).
- Balliu, A. et al. Environmental and cultivation factors affect the morphology, architecture and performance of root systems in soilless grown plants. *Horticulturae* **7**(8), 243. <https://doi.org/10.3390/horticulturae7080243> (2021).
- Stelte, W. et al. A study of bonding and failure mechanisms in fuel pellets from different biomass resources. *Biomass Bioenerg.* **35**(2), 910–918. <https://doi.org/10.1016/j.biombioe.2010.11.003> (2011).
- Fromm, H. Root plasticity in the pursuit of water. *Plants* **8**(7), 236 (2019). <https://doi.org/10.3390/plants8070236>
- Zhao, Q. et al. The interrelationship between the economic traits and hydraulic traits of leaves and roots: An integrated perspective in changing environments—a case study of cotton. *ESS Open. Archive Eprints* **410**, 41043900. <https://doi.org/10.22541/au.172115084.41043900/v1> (2024).
- Wang, Y. et al. Effects of morphology and stand structure on root biomass and length differed between absorptive and transport roots in temperate trees. *Plant Soil* **442**, 355–367. <https://doi.org/10.1007/s11104-019-04206-7> (2019).
- Shah, D. U., Reynolds, T. P. S. & Ramage, M. H. The strength of plants: Theory and experimental methods to measure the mechanical properties of stems. *J. Exp. Bot.* **68**(16), 4497–4516. <https://doi.org/10.1093/jxb/erx245> (2017).

33. Masi, E. B., Segoni, S. & Tofani, V. Root reinforcement in slope stability models: A review. *Geosciences* **11**(5), 212. <https://doi.org/10.3390/geosciences11050212> (2012).
34. Danjon, F. & Reubens, B. Assessing and analyzing 3D architecture of woody root systems, a review of methods and applications in tree and soil stability, resource acquisition and allocation. *Plant Soil* **303**, 1–34. <https://doi.org/10.1007/s11104-007-9470-7> (2008).
35. Wang, S. et al. Determination of biomechanical parameters and development of an improved FEM model for perennial alfalfa (*Medicago sativa* L.) roots. *Agronomy* **14**(12), 3033. <https://doi.org/10.3390/agronomy14123033> (2024).
36. Chao, A. et al. A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecol. Lett.* **8**(2), 148–159. <https://doi.org/10.1111/j.1461-0248.2004.00707.x> (2005).
37. Basyal, B. & Emery, S. M. An arbuscular mycorrhizal fungus alters Switchgrass growth, root architecture, and cell wall chemistry across a soil moisture gradient. *Mycorrhiza* **31**(2), 251–258. <https://doi.org/10.1007/s00572-020-00992-6> (2021).
38. Westoby, M. et al. Plant ecological strategies: Some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.* **33**(1), 125–159. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150452> (2002).
39. Galindo-Castañeda, T. et al. Improving soil resource uptake by plants through capitalizing on synergies between root architecture and anatomy and root-associated microorganisms. *Front. Plant Sci.* **13**, 827369. <https://doi.org/10.3389/fpls.2022.827369> (2022).
40. Kolb, E., Legué, V. & Bogeat-Triboulot, M. B. Physical root–soil interactions. *Phys. Biol.* **14**(6), 065004. <https://doi.org/10.1088/1478-3975/aa90dd> (2017).
41. Qaderi, M. M., Martel, A. B. & Dixon, S. L. Environmental factors influence plant vascular system and water regulation. *Plants* **8**(3), 65. <https://doi.org/10.3390/plants8030065> (2019).
42. Poorter, H. et al. Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. *New Phytol.* **193**(1), 30–50. <https://doi.org/10.1111/j.1469-8137.2011.03952.x> (2012).
43. Powell, J. R. & Rillig, M. C. Biodiversity of arbuscular mycorrhizal fungi and ecosystem function. *New Phytol.* **220**(4), 1059–1075. <https://doi.org/10.1111/nph.15119> (2018).
44. Bellgard, S. E. & Williams, S. E. Response of mycorrhizal diversity to current climatic changes. *Diversity* **3**(1), 8–90. <https://doi.org/10.3390/d3010008> (2011).
45. Liese, R. et al. The mycorrhizal type governs root exudation and nitrogen uptake of temperate tree species. *Tree Physiol.* **38**(1), 83–95. <https://doi.org/10.1093/treephys/tpx131> (2018).
46. Xia, M. et al. Coordination between compound-specific chemistry and morphology in plant roots aligns with ancestral mycorrhizal association in Woody angiosperms. *New Phytol.* **232**(3), 1259–1271. <https://doi.org/10.1111/nph.17561> (2021).
47. Jandyal, T. & Shah, M. Y. An experimental investigation on the effect of vetiver grass root system on the engineering properties of soil. *Life Cycle Reliab. Saf. Eng.* 1–16. <https://doi.org/10.1007/s41872-024-00257-7> (2024).
48. Brooker, R. W. et al. Facilitation and biodiversity–ecosystem function relationships in crop production systems and their role in sustainable farming. *J. Ecol.* **109**(5), 2054–2067. <https://doi.org/10.1111/1365-2745.13592> (2021).
49. Allsup, C. M., George, I. & Lankau, R. A. Shifting microbial communities can enhance tree tolerance to changing climates. *Science* **380**, 835–840. <https://doi.org/10.1126/science.adf2027> (2023).
50. Levine, J. I. et al. Competition for water and species coexistence in phenologically structured annual plant communities. *Ecol. Lett.* **25**(5), 1110–1125. <https://doi.org/10.1111/ele.13990> (2022).
51. Reich, P. B. et al. The evolution of plant functional variation: Traits, spectra, and strategies. *Int. J. Plant Sci.* **164**, S143–S164. <https://doi.org/10.1086/374368> (2003).

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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