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Changes in the root system architecture of Agriophyllum squarrosum and soil-driven mechanisms along the sand fixation gradient on the southeastern edge of the Tengger Desert

Keer Lou

keerlou@163.com

Ningxia University

Wenjie Qu

Lin Chen

Yinglong Chen

Xinguo Yang

https://orcid.org/0000-0002-7100-3992

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Abstract

Aims The root system architecture (RSA) of desert pioneer plants is crucial for establishment and survival during sand fixation; however, how RSA changes along the sand fixation gradient and how soil factors drive these changes remain unclear. We characterized the responses of the RSA of the desert pioneer species *Agriophyllum squarrosum*to increasing sand fixation and identified the underlying soil-driving mechanisms.

Methods Mobile, semi-fixed, and fixed dunes were selected. Eight RSA traits and six soil properties were measured on 90 plants and analyzed using analysis of variance, principal component analysis, redundancy analysis, linear mixed-effects models with variance decomposition, and linear fitting.

Results Sand fixation significantly altered most RSA traits ($P < 0.05$). With increasing sand fixation, root depth, root diameter, root tissue density, topological index, and fractal abundance decreased by 73.09%, 41.63%, 59.83%, 14.31%, and 7.14%, respectively, whereas specific root length, specific root surface area, and fractal dimension increased by 212.30%, 102.51%, and 10.26%, respectively. The root system shifted from coarse, dense, deep roots to fine, complex, shallow roots. Soil moisture content correlated positively with root depth ($P < 0.01$), and soil organic carbon, total nitrogen, and total phosphorus explained most of the variation in resource - related traits (first principal component; $R^2 = 0.83$, 0.75, and 0.68).

Conclusions Sand fixation drives the adaptive adjustment of the root system of *Agriophyllum squarrosum* by altering soil nutrient supply, moisture conditions, and physical structure, providing a reference for desert vegetation restoration.

Introduction

Desert ecosystems are primarily characterized by extreme aridity, intense wind and sand activity, and poorly developed soils. Their ecological processes are highly sensitive to precipitation pulses, surface stability, and vegetation changes, making them one of the most vulnerable terrestrial ecosystems in the context of global change (Fernandes et al. 2022; Vojdani et al. 2024; Zhang et al. 2023). In desert environments, vegetation establishment is typically constrained by a combination of shifting sand disturbances, soil infertility, and spatiotemporal heterogeneity of water availability. Consequently, pioneer plants—which are the first to colonize these unstable habitats — play a critical role in dune stabilization and early community succession (Hou et al. 2025; Zhong et al. 2024). Pioneer plants not only influence surface roughness and wind-blown sediment transport but also alter the soil environment for subsequent plant establishment by promoting the accumulation of fine-grained material and organic residues (Jiang et al. 2024). Therefore, elucidating the adaptive mechanisms of pioneer plants at different stages of desert succession is a crucial starting point for understanding desert vegetation restoration and succession processes.

Agriophyllum squarrosum is a typical annual pioneer plant in the deserts and sandy lands of northern China. Commonly found in shifting and semi-shifting sand dunes, it is characterized by rapid germination, rapid growth, and strong reproductive capacity, enabling it to rapidly establish populations in habitats with intense wind erosion and unstable substrates (Guo et al. 2025; Zhao et al. 2026). Due to its sensitivity to the initial desert fixation process, *Agriophyllum squarrosum* has become an important subject for studying the ecological adaptations of desert pioneer plants (Zhao et al. 2022). However, as desert stabilization progresses, vegetation cover increases, and community succession advances, the dominant status of *Agriophyllum squarrosum* diminishes, exhibiting distinct habitat-dependent phases (Ma et al. 2021). These phasic changes are often attributed to increased aboveground competition (Luo et al. 2020), while analyses of underground root systems and changes in the soil environment remain scarce.

The root system is the core organ through which plants acquire water and nutrients and adapt to heterogeneous soil environments; its environmental responses are directly reflected in root system architecture (Lesmes-Vesga et al. 2023). Among these, specific root length and specific root surface area typically characterize a plant's ability to form absorption interfaces per unit of biomass, while root diameter and root tissue density reflect root thickness, tissue compactness, and structural characteristics. Together, these traits influence a plant's strategic allocation between resource acquisition and structural maintenance (Ge et al. 2023; Wen et al. 2022). In addition to these morphological traits, topological and fractal traits can reveal, at a holistic level, the arrangement, complexity, and spatial occupancy capacity of root systems in soil (Gong et al. 2025). Relying on a single root trait alone is insufficient to fully explain the underground adaptation process of plants to changes in sandy soil environments; a combined analysis of structural traits—such as root morphology, topology, and configuration—is more helpful in identifying the direction of adjustments in root structure combinations across different habitats and their ecological significance (De La Peña et al. 2024).

Existing research on *Agriophyllum squarrosum* has primarily focused on seed germination, population characteristics, and aboveground traits (Ma et al. 2021; Zhao et al. 2022); however, there remains a lack of systematic understanding regarding how its root system responds to desert succession, and the role of soil physicochemical factors in this process remains unclear. Based on this, this study took *Agriophyllum squarrosum* from areas with varying degrees of sand fixation along the southeastern margin of the *Tengger Desert* as the research subject. It conducted a comprehensive analysis of its root structural traits while simultaneously measuring soil factors such as soil organic carbon, total nitrogen, total phosphorus, moisture content, bulk density, and porosity, aiming to answer the following three questions: (1) As a pioneer plant, does the root system architecture of *Agriophyllum squarrosum* change as the degree of sand fixation increases? (2) Do synergies and trade-offs exist among the structural traits of the *Agriophyllum squarrosum*'s root system? (3) How do soil physicochemical factors drive changes in the root system architecture of the *Agriophyllum squarrosum*? We hypothesize that as sand fixation increases, various root structural traits of *Agriophyllum squarrosum* will undergo changes to varying degrees, and that synergistic relationships exist among these traits; furthermore, soil physicochemical properties are likely the primary factors driving adjustments in root system

architecture. By elucidating the changes in *Agriophyllum squarrosum* root system architecture and the underlying soil-driven mechanisms, this study aims to provide a theoretical foundation for understanding the underground adaptation strategies of desert pioneer plants and plant–soil interactions.

Materials and Methods

Study area

The study area is located in the Shapotou region of Zhongwei City, Ningxia Hui Autonomous Region (37°30' N, 105°2' E, elevation 1,310–1,330 m; Fig. 1), on the southeastern edge of the *Tengger Desert*. The region has a temperate arid and semi-arid continental climate, characterized by scarce precipitation, intense evaporation, large diurnal temperature fluctuations, and frequent wind and sand activity. The long-term average temperature in the study area ranges from 7.3 to 9.5°C, with extreme minimum temperatures reaching − 25.1°C and extreme maximum temperatures reaching 38.1°C; the annual frost-free period is approximately 160–170 days. The long-term average annual precipitation is approximately 200 mm, with an uneven seasonal distribution; it is primarily concentrated from July to September, accounting for the majority of the annual precipitation. Annual sunshine hours total approximately 2,800 h, and annual evaporation is about 2,400 mm. The significant water deficit is a key factor limiting vegetation growth and ecosystem restoration in the region. The vegetation composition in the study area is dominated by xerophytic and sand-adapted plants, with a relatively simple community structure. Major shrubs include *Caragana korshinskii*, *Corethrodendron scoparium*, *Artemisia desertorum*, and *Corethrodendron fruticosum*; annual herbs include *Agriophyllum squarrosum* (L.) Moq., *Bassia dasyphylla*, *Corispermum hyssopifolium*, and *Stilpnolepis centiflora*; Perennial herbaceous plants include *Cleistogenes songorica*, *Allium mongolicum*, *Stipa caucasica*, and *Astragalus alaschanensis*.

Experimental design and sample collection

Field surveys and sample collection were conducted in August 2025, during the peak vegetation growth period, at the southeastern edge of the *Tengger Desert*. Based on multiple prior field surveys of areas within the study region exhibiting varying degrees of sand fixation, mobile dunes, semi-fixed dunes, and fixed dunes were selected to represent a sand fixation gradient. To minimize the influence of community composition and topographic conditions on the root system architecture of *Agriophyllum squarrosum*, typical sites within each area were selected as study plots—areas where only *Agriophyllum squarrosum* was present, with no significant interference from other plant species and relatively flat terrain.

Three 10 m × 10 m plots were established within each sand fixation zone, spaced approximately 100 m apart, for a total of nine plots. Within each plot, 10 well-growing *Agriophyllum squarrosum* individuals without obvious mechanical damage or pest and disease infestations were selected for population surveys, totaling 90 plants. The survey included population characteristics such as plant height, crown spread, stem diameter, and aboveground biomass (Table. S1). After measuring plant morphology and population characteristics, the aboveground parts were cut at the base of each plant and placed separately into numbered paper envelopes for subsequent biomass determination. Subsequently, the

root systems of the corresponding plants were collected. The trench method was used to excavate soil profiles around the plants to preliminarily assess the spatial distribution and vertical depth of the *Agriophyllum squarrosum* root systems; based on this, the complete root excavation method was employed to excavate the root system of each *Agriophyllum squarrosum* as completely as possible, thereby maximizing the preservation of root system integrity. After excavation, soil particles adhering to the root surfaces were carefully removed using soft-bristled brushes to avoid damaging fine roots and lateral roots. The cleaned root samples were placed in corresponding numbered envelopes for storage; a total of 90 complete *Agriophyllum squarrosum* plant samples were collected. Based on the actual vertical distribution of the root systems, soil samples were collected near each root sampling point within each plot using the ring cutter method. Specifically, a ring cutter with a diameter of 5 cm and a volume of 100 cm^3 was used to collect soil samples in layers from the soil surface downward at 10-cm intervals across the 0–50 cm soil profile, namely the 0–10, 10–20, 20–30, 30–40, and 40–50 cm. Three replicate samples were collected from each soil layer to determine soil physicochemical properties (Fig. S1 and S2). During sampling, obvious root systems, gravel, and areas disturbed by animals were avoided as much as possible to ensure the representativeness of the soil samples. After all plant and soil samples were collected, they were uniformly numbered and recorded, then transported back to the laboratory within 48 hours for subsequent processing and analysis.

Measurement of root structural traits

In the laboratory, the collected *Agriophyllum squarrosum* root samples were gently rinsed in clean water to remove adhering soil particles and impurities, while taking care to preserve the integrity of the root structure as much as possible. Subsequently, using tweezers, the washed root samples were evenly distributed across the transparent tray of a root scanner to prevent overlapping or tangling. The root samples were scanned using a root scanner (Epson Scan 2, Japan) at 300 dpi, and the scanned images were saved on a computer in TIFF format. The resulting root images were analyzed using WinRHIZO Pro software (Regent Instruments Inc., Canada) to obtain root diameter (RD), root length (TRL), root surface area (RSA), root volume (RV), root depth (RDepth), as well as the topological index (TI), fractal dimension (FD), and fractal abundance (FA). After the scanning analysis was completed, each root sample was placed in a numbered paper envelope and dried in an oven at 80°C for 48 hours until constant weight was reached; the root dry weight (RDW) was then determined. Based on the root morphological parameters and root dry weight, the specific root length, specific root surface area, and root tissue density were further calculated. The relevant calculation formulas are as follows:

$SRL = TRL/RDW$ (1)

$SRA = RA/RDW$ (2)

$RTD = RDW/RV$ (3)

$TI = log(A)/log(M)$ (4)

$lgNr = -FDlgr + lgK$ (5)

In the equation, SRL represents specific root length, in units of $cm \cdot g^{-1}$; SRA represents specific root area, in units of $cm^2 \cdot g^{-1}$; and RTD represents root tissue density, in units of $g \cdot cm^{-3}$. TI represents the root system topological index, where A denotes the number of connections along the longest path in the root system's topological structure, and M denotes the total number of external connections in the root system. In fractal analysis, Nr represents the number of grid cells required to cover the root system image at scale r; FD is the fractal dimension, which is the negative of the slope of the regression line; and lgK is the regression intercept, which reflects fractal abundance (FA).

Determination of soil physicochemical properties

At each sampling site, five soil layer samples were collected from top to bottom along the soil profile, with each layer 10 cm thick; three replicates were taken for each layer. Visible plant debris, roots, and stones were removed from the freshly collected soil samples, which were then thoroughly mixed and divided into aliquots for subsequent physicochemical analysis. Soil moisture content (SMC) was determined using the oven-drying method. Total nitrogen (TN) in soil was determined using the Kjeldahl method. Total phosphorus (TP) in soil was determined using the acid digestion–molybdenum-antimony colorimetric method. Soil organic carbon (TOC) was determined using the external heating oxidation method with potassium dichromate. Soil bulk density (BD) was determined using the ring-knife method and calculated based on the ring-knife volume and the mass of the oven-dried soil. Soil porosity (SP) was calculated based on soil bulk density and particle density (PD) using the following formula:

$SP=(1 - BD/PD) * 100\%$ (6)

In this equation, SP represents soil porosity, BD represents bulk density, and PD represents particle density, which is typically taken as 2.65 $g \cdot cm^{-3}$.

Data analysis

Microsoft Excel 2019 was used to organize and summarize the raw experimental data. All statistical analyses were performed in the R 4.5.2 environment. The "agricolae" package was used to perform one-way analysis of variance (ANOVA) on soil properties and root system indices from different regions after normalizing the data, and the LSD method was used for post-hoc multiple comparisons when significant differences were found ($P < 0.05$). The "FactoMineR" package was used to perform principal component analysis (PCA) on root traits, and the "corrplot" package was used to analyze correlations among root traits. The "vegan" package was used to conduct redundancy analysis (RDA) of the relationships between root traits and soil factors. The "lme4" package was used to construct linear mixed-effects models, and variance decomposition analysis was performed based on changes in the model's marginal R^2 to determine the relative contributions of soil factors to root traits. Linear models were fitted using the "lm" function from the "stats" package to relate PCA axis scores to soil indicators, and the results were visualized using the "ggplot2" package.

Results

Root structural traits of *Agriophyllum squarrosum* in areas with varying degrees of sand fixation

The results indicate that the root structural traits of *Agriophyllum squarrosum* vary to varying degrees. Root depth was highest in mobile dunes, at 45.55 cm, while it decreased significantly by 48.73% and 73.09% in semi-fixed and fixed dunes, respectively ($P < 0.01$). Specific root length in fixed dunes reached 294.20 $m \cdot g^{-1}$, showing a significant increase compared to semi-fixed and mobile dunes ($P < 0.01$); the specific root surface area also increased from 32.23 $cm^2 \cdot g^{-1}$ in mobile dunes to 65.27 $cm^2 \cdot g^{-1}$ in fixed dunes ($P < 0.01$). Root diameter decreased from 1.08 mm in mobile dunes to 0.63 mm in fixed dunes ($P < 0.01$); RTD decreased from 0.32 $g \cdot cm^{-3}$ to 0.13 $g \cdot cm^{-3}$ ($P < 0.01$). TI was highest in the mobile dune plots (0.75), while in the fixed dunes it was 14.31% lower ($P < 0.01$). The fractal dimension was highest in the fixed dunes (1.29), representing a 10.26% increase compared to the mobile dunes plots; fractal abundance, however, decreased by 7.14% relative to the mobile dunes.

Trade-offs among root system architecture of *Agriophyllum squarrosum*

The PCA biplot (Fig. 3a) illustrates the multivariate relationships among the eight root structural traits. The first two principal components collectively explained 62.2% of the total variance, with PC1 and PC2 contributing 49.4% and 12.8%, respectively. PC1 was primarily associated with resource-related traits, showing significant negative correlations with specific root length and specific root surface area ($P < 0.01$), while exhibiting significant positive correlations with root tissue density, root depth, root diameter, and topological index ($P < 0.01$). PC2 was primarily associated with spatial traits, showing a negative correlation with fractal abundance ($P < 0.01$) and a positive correlation with fractal dimension ($P < 0.01$). Consistent with the PCA results, correlation analysis (Fig. 3b) showed that root depth had the highest correlation coefficient (0.83) with RTD, exhibiting a highly significant positive correlation ($P < 0.001$), and was also highly significantly positively correlated with root diameter ($P < 0.001$). It also showed a weak positive correlation with TI ($P < 0.05$), and exhibited significant and highly significant negative correlations with specific root length and specific root surface area ($P < 0.001$), at -0.79 and − 0.69, respectively; specific root length showed a highly significant positive correlation with specific surface area ($P < 0.001$) and highly significant negative correlations with root diameter and RTD ($P < 0.001$). Furthermore, fractal dimension and fractal abundance were significantly correlated with root depth, specific root length, and root tissue density ($P < 0.05$).

Effects of soil factors on root structural traits

The RDA plot shows that RDA1 and RDA2 together explained 82.6% of the total variation (Fig. 4a), with RDA1, as the core axis, exhibiting greater explanatory power (81.5%). SMC and TOC were the main correlated variables in RDA1 ($P < 0.01$); SMC was consistent with the root depth direction, indicating that deep soil moisture content influences the vertical distribution of the *Agriophyllum squarrosum* root system. Meanwhile, TOC, TP, and TN were the main positively correlated variables in RDA1 ($P < 0.01$) and

were consistent with the specific root length direction, suggesting that soil nutrient factors are related to the root system's ability to acquire resources.

The linear mixed model indicated that soil factors strongly explain the variation in root traits, while the contribution of plot-level random effects was generally small (Fig. S3). Fixed-effects analysis (Fig. 4b - h) showed that TOC is an important factor influencing RTD variation and exhibits a significant negative correlation ($P < 0.01$); TN and TOC have significant positive effects on SRL ($P < 0.05$); TN and TP significantly promoted SRA ($P < 0.05$), while BD had a significant negative effect on SRA ($P < 0.05$); both TP and TOC significantly reduced RD ($P < 0.05$); SMC had a highly significant positive effect on RDepth ($P < 0.001$). The relationships between TI, FD, and FA and the various soil factors were relatively weak.

Effects of soil factors on the principal component of root structural traits

The results of the linear fitting (Fig. 5) show that there is a significant linear relationship ($P < 0.01$) between the principal component (PC1) of root structural traits and each soil factor. Specifically, TN, TP, and TOC were all significantly negatively correlated with PC1 ($P < 0.01$), with determination coefficients of $R^2 = 0.75$, 0.68, and 0.83, respectively, while SMC was significantly positively correlated with the root trait PC1 ($R^2 = 0.56$, $P < 0.01$). Soil bulk density was significantly negatively correlated with PC1 ($R^2 = 0.23$, $P < 0.01$), and porosity was significantly positively correlated with PC1 ($R^2 = 0.23$, $P < 0.01$); the coefficients of determination for both were relatively low. In contrast, PC2 did not show a significant linear relationship with any of the soil factors ($P > 0.05$). Overall, the soil variables exhibited a significant linear relationship primarily along PC1 ($P < 0.01$), while the linear explanation for PC2 was not significant ($P > 0.05$).

Discussion

Variations in the root structural traits of *Agriophyllum squarrosum* according to the degree of sand fixation

This study indicates that the root system architecture of *Agriophyllum squarrosum* varies significantly across areas with different degrees of sand fixation, suggesting that the sand fixation process can simultaneously reshape the vertical distribution, morphogenesis, tissue structure, and spatial configuration of the root system (Fujii et al. 2021). As the landscape transitions from mobile to fixed dunes, the root depth of *Agriophyllum squarrosum* gradually decreases, indicating that the vertical extent of its root system diminishes as sand fixation intensifies, and its distribution pattern gradually shifts from deep-reaching to shallow-rooted (Zhu et al. 2018). Root depth is typically influenced by a combination of factors, including the vertical distribution of soil moisture, mechanical resistance, and surface stability, and serves as a key indicator of the reorganization of root spatial configuration (Yang et al. 2016). Concurrently, significant increases in specific root length and specific root surface area indicate that the root length and surface area per unit of root biomass have increased, suggesting that the root system exhibits greater refinement and extension, reflecting a marked adjustment in its morphogenesis (Lozano et al. 2020; Lu et al. 2022; Zhou et al. 2020). The sustained decline in root

diameter and root tissue density further indicates that, as sand fixation increases, the root systems of *Agriophyllum squarrosum* gradually shift from a high-input, relatively dense structure to a low-input, relatively loose structure. As key traits in the root economy spectrum, root diameter and root tissue density collectively characterize the cost of root tissue construction and structural density; their decline suggests that the root system is more inclined to achieve a larger soil contact area at a lower construction cost (Kong et al. 2019). The decrease in the topological index with increasing sand fixation indicates a weakening of the dominant taproot and an increase in branching, reflecting a shift in the allocation of underground space from a relatively concentrated, extended structure to a more complex branched network (Chen et al. 2023). At the same time, the increase in fractal dimension indicates an increase in the spatial complexity of the root system, with the root network shifting from a relatively simple taproot-dominant structure to a more refined, multi-level network structure (Vorsatz et al. 2021); whereas the decrease in fractal abundance suggests an adjustment in the root system's spatial occupation pattern, with its extent of expansion likely tending to contract while the complexity of its local structure simultaneously increases (Li et al. 2020). Overall, as sand fixation increases, the root system of *Agriophyllum squarrosum* transitions from a robust, dense, and deep-reaching configuration to a more refined, low-density, and shallow complex network structure. This combination of trait changes indicates that the sand fixation process does not act on a single root system indicator alone, but rather reshapes the root system architecture of *Agriophyllum squarrosum* holistically by altering root depth distribution, the degree of fine-rooting, tissue density, and structural complexity (Ryalls et al. 2018). This is also consistent with the view emphasized in recent studies on root structural traits, which stress "multi-trait integration" rather than relying on a single indicator to explain changes in underground structure (Marcellus et al. 2024).

Characteristics of synergistic strategies in the root system traits of *Agriophyllum squarrosum*

In this study, the specific root length (SRL), root tissue density (RTD), and root diameter (RD) of *Agriophyllum squarrosum* exhibited synergistic changes across regions with varying degrees of sand fixation, indicating that its root morphology and tissue structure undergo coordinated adjustments along the sand fixation gradient (Kramer-Walter et al. 2016). As sand fixation increases, the root system of *Agriophyllum squarrosum* gradually shifts from a combination of high RTD and high RD to a combination of high SRL, low RTD, and low RD. This trend aligns with the continuous shift from a conservative to an acquisitive type described by the root economy spectrum, suggesting that plants may respond to habitat changes by regulating root construction costs, morphological extensibility, and tissue density (Ding et al. 2020). In mobile dunes, the higher RTD and RD of the *Agriophyllum squarrosum* root system may help enhance root mechanical strength and structural stability, thereby improving its resistance to disturbance in loose substrates and maintaining the continuity of water transport pathways. Coarser and denser root systems typically possess stronger supporting functions and stress tolerance, which helps the root system maintain an intact spatial structure in unstable sandy soil environments (Jia et al. 2024). Conversely, in fixed dunes, *Agriophyllum squarrosum* exhibits a higher SRL as well as lower RTD and RD, indicating that its root system tends to become finer and lighter. This allows a unit of biomass to form more and longer root branches, thereby enhancing its extent and contact area within the surface soil.

This trait shift is consistent with the root plasticity exhibited by plants under conditions of spatial heterogeneity in resource availability (Li et al. 2024). Furthermore, this study also found that the root system of *Agriophyllum squarrosum* undergoes significant spatial configuration adjustments. The fractal dimension (FD) and fractal abundance (FA), which reflect the complexity and spatial occupancy characteristics of the root network, respectively, exhibit different patterns of change along the sand fixation gradient. This indicates that *Agriophyllum squarrosum* does not simply expand or contract its underground distribution range, but rather reshapes the balance among branching complexity, spatial filling patterns, and root connectivity structures (Li et al. 2022). In mobile dune areas, higher spatial occupancy characteristics help the root system form a continuous distribution over a larger underground area, which is consistent with its adaptive trait of deep extension (Qiao et al. 2024). In contrast, the higher FD observed in stabilized sandy areas indicates a more complex root branching network, with the structure shifting from relatively axial and concentrated extension toward a finer, multilevel branching network — a pattern that typically enhances the efficiency of utilizing surface resources (Zhu et al. 2019). Therefore, the changes in FD and FA exhibited by *Agriophyllum squarrosum* across different stages of sand fixation are more likely to reflect a synergistic reshaping of its spatial expansion patterns and structural complexity, rather than a simple structural trade-off. Overall, these results suggest that pioneer plants do not rely solely on a single trait dimension to adapt to sandy environments, but rather respond to environmental changes during the sand fixation process through comprehensive adjustments in resource acquisition, spatial occupancy, and structural organization.

Effects of the soil environment on root system architecture

This study indicates that soil physicochemical factors are important background factors driving the differentiation of the root system architecture of *Agriophyllum squarrosum* (Ji et al. 2021). Linear fitting results show that the composite root resource trait (PC1) is significantly correlated with soil organic carbon, total nitrogen, total phosphorus, soil moisture, bulk density, and porosity, indicating that changes in the root system architecture of *Agriophyllum squarrosum* are not controlled by a single soil factor but are jointly regulated by nutrients, moisture, and soil physical properties (Morris et al. 2017). Among these, soil organic carbon, total nitrogen, and total phosphorus showed the strongest associations with PC1, suggesting that nutrient accumulation and increased soil fertility may be key factors influencing shifts in the resource acquisition strategies of *Agriophyllum squarrosum* root systems (Zhi et al. 2025). In semi-fixed and fixed dunes, higher levels of organic carbon and nutrients corresponded to greater specific root length, higher topological indices, and more complex root structures. This indicates that in relatively resource-rich environments, *Agriophyllum squarrosum* tends to enhance nutrient absorption efficiency by increasing fine root branching and spatial complexity, which is consistent with the understanding in the root economy spectrum that fine roots tend toward refinement and higher efficiency (Torres et al. 2026). Redundancy analysis results indicate a significant positive correlation between soil moisture and root depth, suggesting that moisture conditions primarily influence the vertical distribution of *Agriophyllum squarrosum* roots (Maan et al. 2023). Spatial heterogeneity in soil moisture directly alters the costs and benefits of water acquisition for plants, thereby driving root extension into deeper soil layers to enhance the utilization of deep-seated moisture (Li and Sawada

2022). At the same time, the significant relationship between soil physical properties—such as bulk density and porosity—and PC1 suggests that soil structure indirectly influences root morphological development by altering root penetration resistance and expansion space (De Moraes et al. 2018). It is worth noting that the composite spatial trait of the root system (PC2) did not exhibit a significant linear relationship with any of the soil variables. This may imply that the spatial configuration of the root system is also jointly influenced by microtopographic differences, individual developmental stages, and unmeasured soil factors, suggesting a more complex response mechanism (Qiao et al. 2024). Overall, the root system architecture of *Agriophyllum squarrosum* responds distinctly to changes in the soil environment: nutrient factors primarily promote root refinement and complexity; soil moisture primarily regulates vertical root distribution; while physical properties play a secondary regulatory role by constraining root penetration and extension processes. These differentiated responses collectively drive the remodeling of *Agriophyllum squarrosum* root system architecture during sand fixation and suggest that desert ecological restoration requires simultaneous attention to the synergistic improvement of soil nutrient, moisture, and structural conditions.

Conclusions

As a typical annual pioneer plant, the root system of *Agriophyllum squarrosum* undergoes systematic adjustments in response to changes in sand fixation. In mobile dunes, the plant's root system tends toward coarse, dense, and simple deep roots to adapt to an environment characterized by unstable substrate, high moisture heterogeneity, and frequent wind and sand disturbances; in fixed dunes, the roots of *Agriophyllum squarrosum* exhibit a refined, complex shallow root system, reflecting its fine-root acquisition strategy in response to a relatively stable and resource-rich soil environment. Soil nutrient factors are closely related to resource-related traits such as specific root length, while soil moisture is strongly associated with spatially distributed traits such as root depth; soil bulk density and porosity, in turn, participate in regulating root system adaptation by altering root penetration resistance and pore connectivity. This study elucidates the underground response mechanisms of *Agriophyllum squarrosum* to the sand fixation gradient from the perspectives of root system architecture and soil environment, providing a basis for understanding the adaptive strategies of desert pioneer plants, the succession processes of sandy land vegetation, and plant–soil feedback relationships. However, certain limitations remain. Since this study employed a spatial sequence design rather than a temporal sequence, it is difficult to completely rule out the influence of differences in initial topography, soil background, and historical disturbances among plot sites. Additionally, as sampling was conducted over a single year, the results primarily reflect root structure characteristics during the mid-to-late growing season of that year and do not fully account for the effects of interannual precipitation fluctuations and seasonal dynamics. Furthermore, this study focused exclusively on *Agriophyllum squarrosum*; the relevant conclusions require further validation across a broader range of desert pioneer plants. Future research should combine long-term fixed-point monitoring, repeated sampling across multiple years, and multi-species comparisons to further clarify the universality of root system architecture adjustments in pioneer plants during the sand fixation process and the underlying soil-driven mechanisms.

Declarations

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Competing Interests

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.

Data availability

Data will be made available on request.

References

1. Chen X, Chen Y, Zhang W et al (2023) Response characteristics of root to moisture change at seedling stage of *Kengyilia hirsuta*. Front Plant Sci 13:1052791. https://doi.org/10.3389/fpls.2022.1052791
2. De La Peña M, Ruiz-Romero R, Castro-Arza LI, Romero HM (2024) Changes in the Root Architecture of Oil Palm Seedlings in Response to Nitrogen Starvation. Agronomy 14:409. https://doi.org/10.3390/agronomy14030409
3. De Moraes MT, Bengough AG, Debiasi H et al (2018) Mechanistic framework to link root growth models with weather and soil physical properties, including example applications to soybean growth in Brazil. Plant Soil 428:67–92. https://doi.org/10.1007/s11104-018-3656-z
4. Ding J, Kong D, Zhang Z et al (2020) Climate and soil nutrients differentially drive multidimensional fine root traits in ectomycorrhizal-dominated alpine coniferous forests. J Ecol 108:2544–2556. https://doi.org/10.1111/1365-2745.13407
5. Fernandes VMC, Rudgers JA, Collins SL, Garcia-Pichel F (2022) Rainfall pulse regime drives biomass and community composition in biological soil crusts. Ecology 103:e3744. https://doi.org/10.1002/ecy.3744
6. Fujii K, Makita N, Kamara M et al (2021) Plasticity of pine tree roots to podzolization of boreal sandy soils. Plant Soil 464:209–222. https://doi.org/10.1007/s11104-021-04928-7
7. Ge L, Chen C, Li T et al (2023) Contrasting effects of nitrogen and phosphorus additions on fine root production and morphological traits of different plant functional types in an ombrotrophic peatland. Plant Soil 490:451–467. https://doi.org/10.1007/s11104-023-06087-3

8. Gong P, Li Y, Liu H et al (2025) Root zone infiltration irrigation affects plastic root developmental traits of fruit trees and root zone habitat in saline-alkali soil. Agric Water Manage 319:109802. https://doi.org/10.1016/j.agwat.2025.109802
9. Guo R, Baskin CC, Baskin JM et al (2025) Differences in life history and trait plasticities of short- and long-lived summer annuals in a Chinese desert. Plant Soil 516:1031–1049. https://doi.org/10.1007/s11104-025-07785-w
10. Hou Q, Hu W, Sun Y et al (2025) Active restoration efforts drive community succession and assembly in a desert during the past 53 years. Ecol Appl 35:e3068. https://doi.org/10.1002/eap.3068
11. Ji L, Liu Y, Wang J et al (2021) Differential Variation in Non-structural Carbohydrates in Root Branch Orders of *Fraxinus mandshurica* Rupr. Seedlings Across Different Drought Intensities and Soil Substrates. Front Plant Sci 12:692715. https://doi.org/10.3389/fpls.2021.692715
12. Jia L, Jiang Q, Sun J et al (2024) Contrasting depth-related fine root plastic responses to soil warming in a subtropical Chinese fir plantation. J Ecol 112:1058–1073. https://doi.org/10.1111/1365-2745.14286
13. Jiang X, Lin M, Zhang X et al (2024) Pioneer plants promote soil formation in a mixture of bauxite tailings and red mud. J Environ Manage 370:122590. https://doi.org/10.1016/j.jenvman.2024.122590
14. Kong D, Wang J, Wu H et al (2019) Nonlinearity of root trait relationships and the root economics spectrum. Nat Commun 10:2203. https://doi.org/10.1038/s41467-019-10245-6
15. Kramer-Walter KR, Bellingham PJ, Millar TR et al (2016) Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. J Ecol 104:1299–1310. https://doi.org/10.1111/1365-2745.12562
16. Lesmes-Vesga RA, Cano LM, Ritenour MA et al (2023) Variation in the Root System Architecture of Peach × (Peach × Almond) Backcrosses. Plants 12:1874. https://doi.org/10.3390/plants12091874
17. Li J, Le X, Chen X et al (2024) Divergent intra- and interspecific root order variability identifies a two-dimensional root economics spectrum. Plant Soil 499:473–490. https://doi.org/10.1007/s11104-023-06473-x
18. Li Q, Zhao C-Z, Wen J et al (2022) Fractal analysis of root architecture responses of *Saussurea salsa* to a gradient of flooding intensity and salinity. Plant Soil 471:669–683. https://doi.org/10.1007/s11104-021-05259-3
19. Li S, Sawada Y (2022) Soil moisture-vegetation interaction from near-global in-situ soil moisture measurements. Environ Res Lett 17:114028. https://doi.org/10.1088/1748-9326/ac9c1f
20. Li S, Wan L, Nie Z, Li X (2020) Fractal and Topological Analyses and Antioxidant Defense Systems of Alfalfa (*Medicago sativa* L.) Root System under Drought and Rehydration Regimes. Agronomy 10:805. https://doi.org/10.3390/agronomy10060805
21. Lozano YM, Aguilar-Trigueros CA, Flaig IC, Rillig MC (2020) Root trait responses to drought are more heterogeneous than leaf trait responses. Funct Ecol 34:2224–2235. https://doi.org/10.1111/1365-

2435.13656

22. Lu B, Qian J, Hu J et al (2022) The role of fine root morphology in nitrogen uptake by riparian plants. Plant Soil 472:527–542. https://doi.org/10.1007/s11104-021-05270-8
23. Luo Y, Du Z, Yan Z et al (2020) *Artemisia halodendron* Litters Have Strong Negative Allelopathic Effects on Earlier Successional Plants in a Semi-Arid Sandy Dune Region in China. Front Plant Sci 11:961. https://doi.org/10.3389/fpls.2020.00961
24. Ma Q, Wei L, Chen F et al (2021) Population dynamics of *Agriophyllum squarrosum* along an ecosystem restoration chronosequence in the *Tengger Desert*, China: Indication implications for desertification combating. Global Ecol Conserv 30:e01746. https://doi.org/10.1016/j.gecco.2021.e01746
25. Maan C, Ten Veldhuis M-C, Van De Wiel BJH (2023) Dynamic root growth in response to depth-varying soil moisture availability: a rhizobox study. Hydrol Earth Syst Sci 27:2341–2355. https://doi.org/10.5194/hess-27-2341-2023
26. Marcellus M, Goud EM, Swartz N et al (2024) Evolutionary history and root trait coordination predict nutrient strategy in tropical legume trees. New Phytol 243:1711–1723. https://doi.org/10.1111/nph.19962
27. Morris EC, Griffiths M, Golebiowska A et al (2017) Shaping 3D Root System Architecture. Curr Biol 27:R919–R930. https://doi.org/10.1016/j.cub.2017.06.043
28. Qiao J, Chen X, Chang SX et al (2024) Grazing intensity changes root traits and resource utilization strategies of *Stipa breviflora* in a desert steppe. Plant Soil. https://doi.org/10.1007/s11104-024-06597-8
29. Ryalls JMW, Moore BD, Johnson SN et al (2018) Root responses to domestication, precipitation and silicification: weeping meadow grass simplifies and alters toughness. Plant Soil 427:291–304. https://doi.org/10.1007/s11104-018-3650-5
30. Torres CD, López-Alaniz P, Magnin A, Puntieri JG (2026) Root architecture and fine-root economic traits in tap- and adventitious-rooted perennial herbs. New Phytol 250:2149–2162. https://doi.org/10.1111/nph.71079
31. Vojdani A, Baur LE, Rudgers JA, Collins SL (2024) Sensitivity of root production to long-term aridity under environmental perturbations in Chihuahuan Desert ecosystems. J Ecol 112:1487–1500. https://doi.org/10.1111/1365-2745.14319
32. Vorsatz LD, Pattrick P, Porri F (2021) Quantifying the in situ 3-dimensional structural complexity of mangrove tree root systems: Biotic and abiotic implications at the microhabitat scale. Ecol Ind 121:107154. https://doi.org/10.1016/j.ecolind.2020.107154
33. Wen X, Wang X, Ye M et al (2022) Response strategies of fine root morphology of *Cupressus funebris* to the different soil environment. Front Plant Sci 13:1077090. https://doi.org/10.3389/fpls.2022.1077090
34. Yang Y, Donohue RJ, McVicar TR (2016) Global estimation of effective plant rooting depth: Implications for hydrological modeling: GLOBAL HYDROLOGICAL EFFECTIVE ROOTING DEPTH.

Water Resour Res 52:8260–8276. https://doi.org/10.1002/2016WR019392

35. Zhang T, Chen Y, Ali S (2023) Abiotic stress and human activities reduce plant diversity in desert riparian forests. Ecol Ind 152:110340. https://doi.org/10.1016/j.ecolind.2023.110340
36. Zhao P, Li X, Ran R et al (2022) Precipitation and local environment shape the geographic variation of seed size across natural populations of sand rice (*Agriophyllum squarrosum*). J Exp Bot 73:5682–5697. https://doi.org/10.1093/jxb/erac231
37. Zhao P, Liu Y, Li X et al (2026) Seed Germination and Seedling Emergence of Sand Rice (*Agriophyllum squarrosum*) and the Environmental Effects. J Plant Growth Regul 45:4327–4338. https://doi.org/10.1007/s00344-026-12162-7
38. Zhi X, Bian X, Huang F et al (2025) Differential effects of non-structural carbohydrate allocation and C:N:P:K stoichiometry of rapeseed roots in diverse soil environments. Ind Crops Prod 225:120542. https://doi.org/10.1016/j.indcrop.2025.120542
39. Zhong L, Feng X, Zhao W (2024) Fixing active sand dune by native grasses in the desert of Northwest China. Ecol Process 13:77. https://doi.org/10.1186/s13717-024-00556-y
40. Zhou S-X, Walker RR, Edwards E (2020) Decoupled drought responses of fine-root versus leaf acquisitive traits among six Prunus hybrids. J Plant Ecol 13:304–312. https://doi.org/10.1093/jpe/rtaa015
41. Zhu H, Zhang LM, Garg A (2018) Investigating plant transpiration-induced soil suction affected by root morphology and root depth. Comput Geotech 103:26–31. https://doi.org/10.1016/j.compgeo.2018.06.019
42. Zhu Y, Weiner J, Yu M, Li F (2019) Evolutionary agroecology: Trends in root architecture during wheat breeding. Evol Appl 12:733–743. https://doi.org/10.1111/eva.12749

Figures

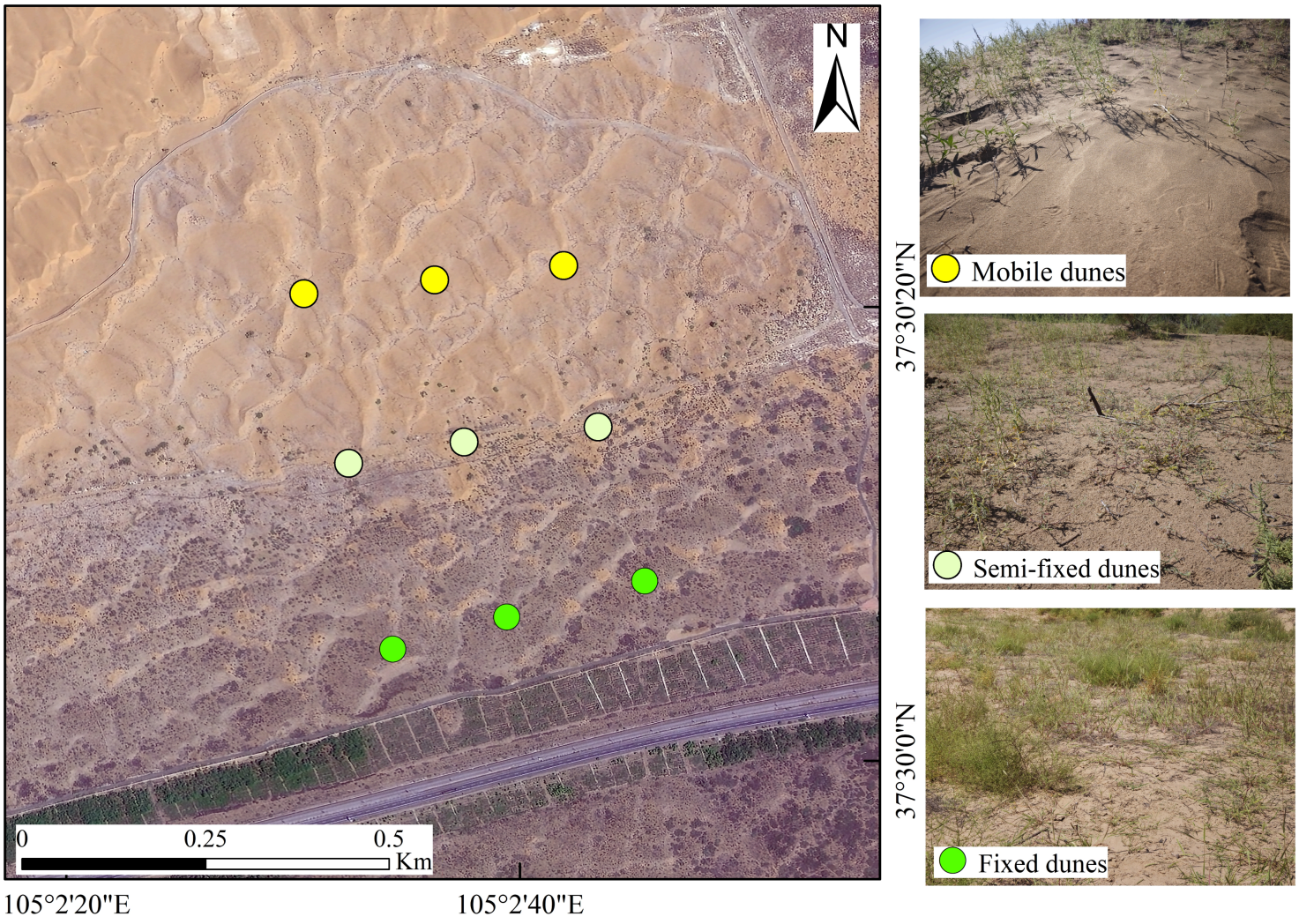


Figure 1

Location of the study area and distribution of sampling sites

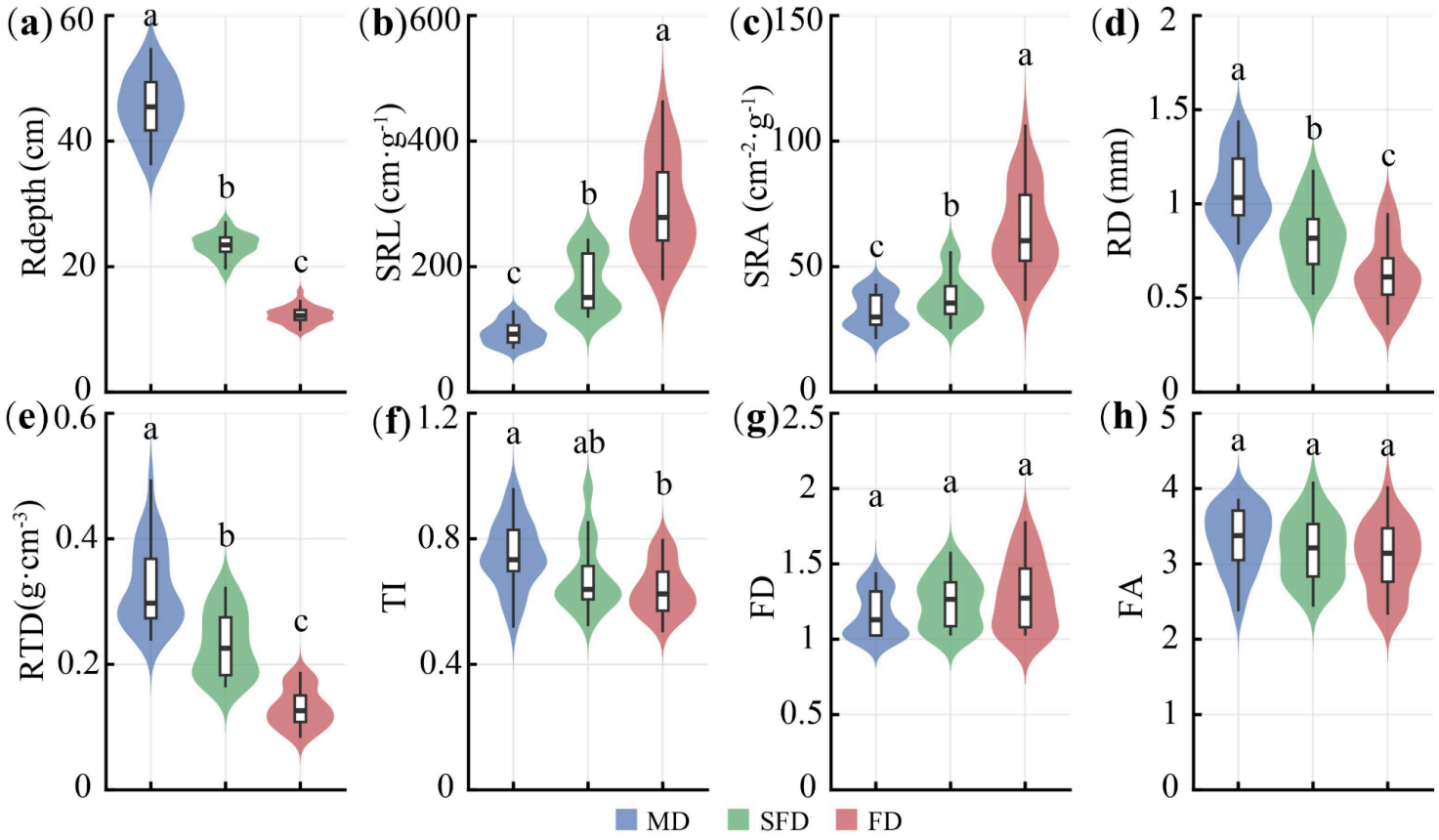


Figure 2

Distribution of root structural traits of *Agriophyllum squarrosum* under different levels of sand fixation. (a) root depth (b) specific root length (c) specific root surface area (d) root diameter (e) root tissue density (f) root system topological index (g) fractal dimension (h) fractal abundance. MD, SFD, and FD represent mobile dunes, semi-fixed dunes, and fixed dunes, respectively. Different lowercase letters indicate significant differences among sand fixation levels ($P < 0.05$)

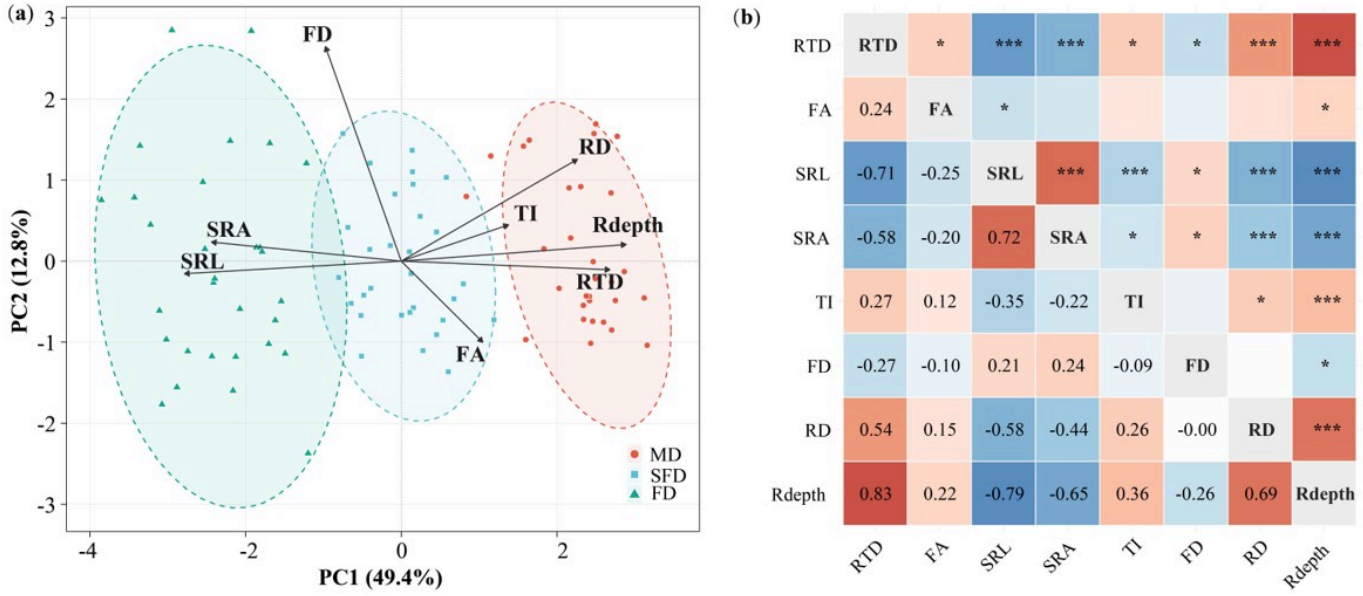


Figure 3

Principal component analysis of root structural traits in *Agriophyllum squarrosum* and correlation analysis among traits. (a) Biplot of principal component analysis (PCA) based on root structural traits. (b) Heatmap of Pearson correlations among root structural traits of *Agriophyllum squarrosum*. The color of the correlations indicates the direction and strength of the correlation; red indicates a positive correlation, blue indicates a negative correlation, and darker colors indicate a stronger correlation. The size of the circles indicates the absolute value of the correlation coefficient. Asterisks indicate the significance level: * P <0.05, ** P < 0.01, *** P < 0.001.Abbreviations are shown in Fig. 2

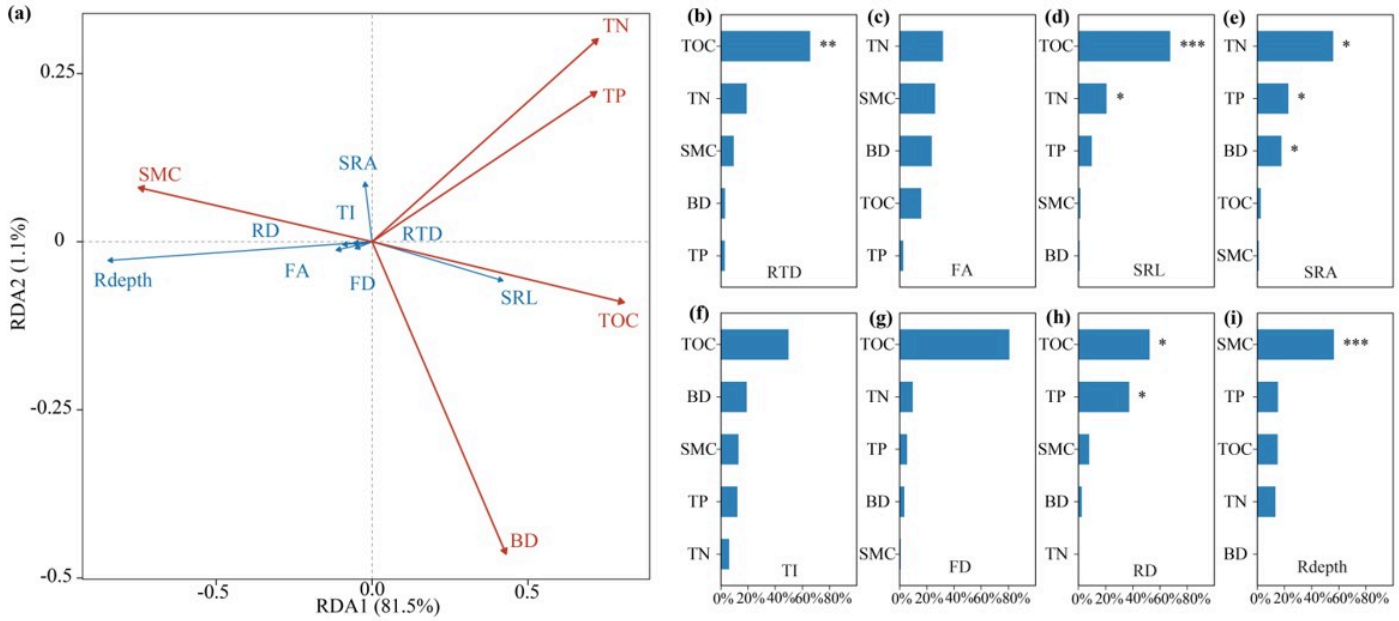


Figure 4

Comprehensive analysis of the effects of soil factors on root structural traits under sand fixation gradients. (a) Redundancy analysis (RDA) ordination plot showing the relationships between root traits and soil factors; red arrows indicate soil factors, blue arrows indicate root traits, and the percentages following RDA1 and RDA2 represent the proportion of variance explained by the corresponding ordination axes. (b - h) Relative contributions of soil factors to RTD, FA, SRL, SRA, TI, FD, RD, and RDepth. Asterisks indicate the significance level: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Abbreviations are shown in Fig. 2

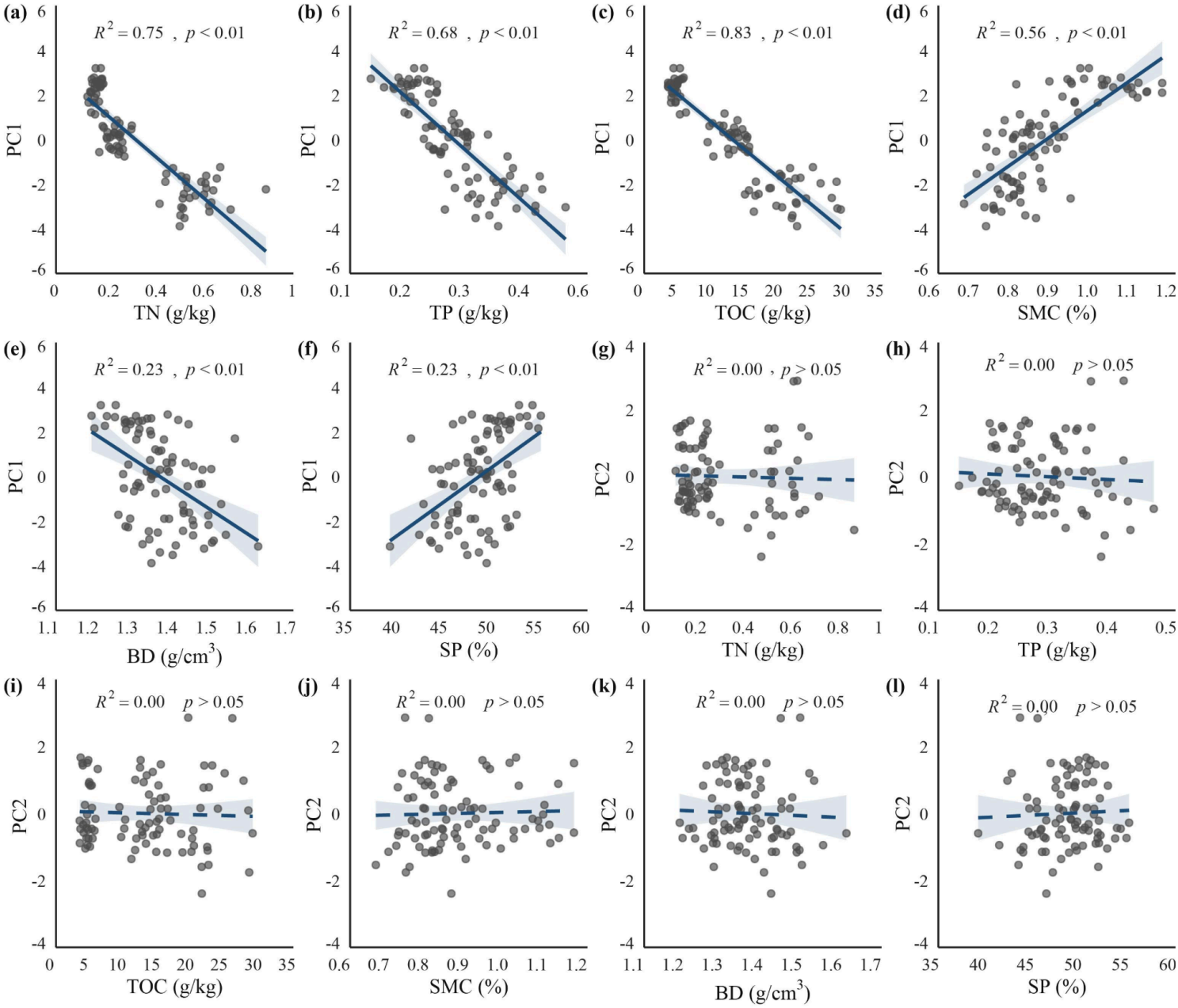


Figure 5

Variations in composite root structural traits as a function of soil factors. TN denotes total nitrogen in soil, TP denotes total phosphorus in soil, TOC denotes total organic carbon in soil, SMC denotes soil moisture content, BD denotes soil bulk density, and SP denotes soil porosity

Supplementary Files

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