Root system architecture and its scaling relationships of Reaumuria soongorica in Alxa steppe desert, Northwest China (Postprint)

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Abstract

Root system architecture has often been overlooked in plant research despite its critical role in plant adaptation to environmental conditions. This study focused on the root system architecture of the desert shrub Reaumuria soongorica in the Alxa steppe desert, Northwest China. Plant samples were collected during May–September 2019. Using excavation methods, in situ measurements, and root scanning techniques, we analyzed the root distribution, topology, and branching patterns of R. soongorica across an age sequence of 7–51 a. Additionally, we investigated the allometric relationships of root collar diameter with total coarse root length, biomass, and topological parameters. The results showed that the roots of R. soongorica were predominantly concentrated in shallow soil layers (10–50 cm), with lateral root branching and biomass allocation increasing with shrub age. The root topology exhibited a herringbone-like structure, with average topological and modified topological indices of 0.89 and 0.96, respectively, both of which adjusted with shrub age. The root system displayed a self-similar branching pattern, maintaining a constant cross-sectional area ratio of 1.13 before and after branching, deviating from the area-preserving rule. These adaptive traits allow R. soongorica to efficiently expand its nutrient acquisition zone, minimize internal competition, and optimize resource uptake from the upper soil layers. Furthermore, significant linear relationships were observed between log10-transformed root collar diameter and log10-transformed total coarse root length, biomass, and topological parameters. These findings advance non-destructive approaches for studying root characteristics and contribute to the development of root-related models. Besides, this study provides new insights into the adaptive strategies of R. soongorica under extreme drought conditions, offering valuable guidance for species selection and cultivation in desert restoration efforts.

Full Text

Preamble

Root system architecture and its scaling relationships of *Reaumuria soongorica* in Alxa steppe desert, Northwest China

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Abstract: Root system architecture has often been overlooked in plant research despite its critical role in plant adaptation to environmental conditions. This study focused on the root system architecture of the desert shrub *Reaumuria soongorica* in the Alxa steppe desert, Northwest China. Plant samples were collected during May–September 2019. Using excavation methods, in situ measurements, and root scanning techniques, we analyzed the root distribution, topology, and branching patterns of *R. soongorica* across an age sequence of 7–51 years. Additionally, we investigated the allometric relationships of root collar diameter with total coarse root length, biomass, and topological parameters. The results showed that the roots of *R. soongorica* were predominantly concentrated in shallow soil layers (10–50 cm), with lateral root branching and biomass allocation increasing with shrub age. The root topology exhibited a herringbone-like structure, with average topological and modified topological indices of 0.89 and 0.96, respectively, both of which adjusted with shrub age. The root system displayed a self-similar branching pattern, maintaining a constant cross-sectional area ratio of 1.13 before and after branching, deviating from the area-preserving rule. These adaptive traits allow *R. soongorica* to efficiently expand its nutrient acquisition zone, minimize internal competition, and optimize resource uptake from the upper soil layers. Furthermore, significant linear relationships were observed between $\log_{10}$-transformed root collar diameter and $\log_{10}$-transformed total coarse root length, biomass, and topological parameters. These findings advance non-destructive approaches for studying root characteristics and contribute to the development of root-related models. Besides, this study provides new insights into the adaptive strategies of *R. soongorica* under extreme drought conditions, offering valuable guidance for species selection and cultivation in desert restoration efforts.

Keywords: *Reaumuria soongorica*; root system architecture; root topology; root branching pattern; area-preserving rule; Alxa steppe desert

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Introduction

Roots are essential for the exchange of nutrients, water, and energy between plants and their soil environment [?]. Root system architecture (RSA), defined as the spatial distribution and arrangement of roots within the soil, is critical for plant adaptation to environmental conditions [?]. RSA demonstrates significant plasticity, varying both among species and within species across diverse habitats [?, ?]. This plasticity has been harnessed in advanced breeding techniques to produce stress-tolerant plants that can maintain biomass stability under adverse environmental conditions [?, ?]. Additionally, adaptations in RSA provide insights for replanting strategies to combat soil degradation and support ecological succession [?].

Research has shown that desert plants adapt to arid, nutrient-poor soils by altering aspects of RSA—including root distribution [?], topology [?], and morphology [?]—to enhance water and nutrient uptake [?, ?]. Kirschner et al. [?] reviewed that some desert plants can survive by developing deep taproots to access groundwater, while others produce shallow roots and take advantage of short rainy seasons and irregular rainfall. Fitter [?] identified two extreme root branching patterns: dichotomous and herringbone (Fig. 1 [Figure 1: see original paper]). Dichotomous systems, characterized by dense secondary branches and high internal competition, cover a smaller area than herringbone systems given the same carbon investment, making them less effective for exploring nutrient-rich soil. In contrast, the herringbone pattern, with sparser branching, is better adapted for water and nutrient acquisition in arid, nutrient-limited environments [?]. Root branching strategies play a critical role in plant adaptation to various environments [?].

Richter [?] proposed that the cross-sectional area (CSA) of a tree trunk or branch is equal to the combined CSA of its higher-level branches, a concept known as the area-preserving rule. Numerous models of root growth and function have applied this rule [?, ?], generally supporting its validity, though some exceptions exist [?]. Desert plants thrive in arid environments and their root branching strategies are closely linked to the hydraulic structure of their root systems and other key adaptive mechanisms [?]. However, our understanding of these strategies remains limited, including whether the root systems of typical desert species adhere to the area-preserving rule.

Due to the significant difficulty in excavating the root system of adult plants, most studies on RSA primarily focus on seedlings [?, ?], even though RSA is not constant throughout the plant life cycle [?]. For example, Li et al. [?] studied the desert shrub *Nitraria tangutorum* in the West Ordos National Nature Reserve, China and demonstrated that as the shrub grew, root diameter (RD) increased, branching patterns became more intricate, and the range of nutrient utilization expanded. Bai et al. [?] found that the root depth, branching number, specific root length, specific surface area, and RD of *Tamarix ramosissima* increased, while root branch angle and root-shoot ratio decreased with increasing shrub age in the oasis of Jinta County, Gansu Province, China. Understanding the dynamic changes in RSA—particularly in root distribution, topology, and branching patterns—across the life cycle of desert plants is essential for deciphering their drought adaptation strategies and for developing accurate root system models. In addition, some scaling relationships and allometries of whole plants or plant organs have been extensively discussed in the literature [**?**, **?**]. Understanding these scaling relationships for specific species is crucial for advancing non-destructive methods to investigate plant root characteristics.

Reaumuria soongorica is a small perennial shrub in the Tamaricaceae, widely distributed across the deserts of Central Asia and serving as one of the dominant species in the Alxa steppe desert of Northwest China. The belowground RSA of this shrub species provides critical insights into plant adaptive strategies under extreme drought conditions. We hypothesize that the RSA of *R. soongorica* (including root distribution, topology, and branching patterns) changes with shrub age to adapt to environmental stress, aiming to address three main questions: (1) how does the RSA of *R. soongorica* vary with age in an extremely arid habitat? (2) what branching strategies does *R. soongorica* employ to survive in such environments? and (3) how can key root system parameters be efficiently obtained through simple and measurable indicators?

2.1 Study Area

The study area (37°25 N–42°47 N, 97°10 E–106°54 E; Fig. 2a [Figure 2: see original paper]) is located on the southwestern edge of the Alxa Plateau in Northwest China. The region experiences a typical continental arid climate, with mean annual temperature of 9.4°C and annual precipitation of 119.5 mm during 1999-2018 [**?**]. The natural vegetation primarily comprises shrub species, including *R. soongarica*, *Salsola passerine*, *Nitraria sibirica*, *Sarcozygium xanthoxylon*, and *Kalidium foliatum*. Total vegetation coverage in the study area is 18.6%, with *R. soongarica* accounting for 61.8% of this coverage, making it the most widely distributed desert shrub in the region (Fig. 2b). The soil is classified as grey-brown desert soil, composed of 62.0% sand, 20.0% silt, and 18.0% clay (Fig. 2c). Groundwater levels are over 40 m below the surface, as determined by local well measurements, making precipitation the sole source of soil moisture replenishment.

2.2 Data Collection

From May to September in 2019, we selected a naturally flat area with uniform vegetation distribution and consistent soil nutrient and moisture levels as the sampling plot within the study area to conduct the sample collection (Fig. 2b–e). The plot size was 500 m\$$\times 500m.Atotalof66 * R.soongorica *$ $shrubswithvaryingsizeswererandomlyselected, ensuringaminimumdistanceof10mbetweeneachshrub.Thesh$

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mm) have high turnover rates and are difficult to collect completely [?], only coarse roots (diameter>2.0 mm) were included in the topological modeling.

The coarse roots of each shrub were carefully excavated intact with a shovel by digging outward from the shrub base until the entire coarse root system was unearthed. The roots were then manually cleaned with a brush, transported to the laboratory, and mapped onto grid paper for precise measurements [?]. For each shrub, we recorded the number of taproot nodes (Ntn), lateral roots per taproot node (Nlr), total number of nodes (N; including lateral root nodes), the number of external links (v_0) and interior links, total number of links (v; sum of interior and external links), and the maximal horizontal and vertical extensions of coarse roots (mm). External links refer to links at the terminal ends of the root system, reflecting the interconnected relationships among the plant root system, its surrounding environment, and other organisms. Interior links represent internal connections within the root system, facilitating the effective allocation of resources among different root parts (Fig. 3 [Figure 3: see original paper]). The interior and external link lengths (mm) were measured using a measuring tape. The root collar diameters (RCD; mm) of each shrub and the RD before branching (d_0; mm) and after branching (d ; mm) at each node were measured using an electronic digital caliper [?]. The coarse roots were sorted into taproot and lateral roots, oven-dried at 65.0°C to a constant weight, cooled for 4-6 h, and weighed using an electronic balance (range: 0.01-500.00 g; resolution: 0.01 g) to determine the biomass of taproot (Bt; g) and lateral coarse roots (Blcr; g) per shrub. A total of 66 *R. soongorica* shrubs were collected, ranging in age from 7 to 51 years. Based on age distribution, the shrubs were grouped into three age classes: 0-19 years (25 shrubs), 20-29 years (25 shrubs), and $ $30 years (16 shrubs) [?]. Figure 3 gives the details of root branching patterns of *R. soongorica*.

2.3 Data Processing and Analysis

The data analysis workflow for this study is illustrated in Figure 4 [Figure 4: see original paper]. Based on the node and link data, we calculated the topological parameters for each root system. Altitude (a) refers to the longest path (a path with the most links) from the root base to external links. The external path length (Pe) represents the sum of all path lengths from external links to the root base. Mean topological depth (b) is the average path length from external links to the root base and is calculated using the equation $b=Pe/v_0$. Mean external link length (le; mm) and mean interior link length (li; mm) refer to the average lengths of the external and interior links, respectively [?, ?, ?, ?].

The root topology of *R. soongorica* shrubs was estimated using the topological index (TI) and the modified topological index (TIM), and the formulas are as follows [?]:

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The TI values range from 0.53 to 1.00. When a TI value is closer to 1.00, it indicates a herringbone branching pattern, while a value closer to 0.53 suggests a dichotomous branching pattern [**?**]. TIM preserves the TI value when there is one lateral root per node and modifies it for cases with multiple branches per node. The range of TIM is the same as TI [**?**].

The proportionality factor (p) was defined as the ratio of CSA before and after branching and was used to describe the change in CSA at branching points in both taproot and lateral root nodes [**?**]. The allocation factor (q) was defined as the ratio of the maximum CSA after branching to the total CSA after branching, which can describe the distribution equity of CSA after branching [**?**, **?**]. The formulas are as follows:

The independence of p and q from shrub age and link diameter was tested by performing linear regressions between the branching parameters (p and q) and both shrub age and link diameter, and by testing the significance of the regression slopes. The self-similar branching pattern was confirmed when the branching parameters were not significantly different across age classes and did not depend on shrub age and link diameter [**?**].

We analyzed the CSA before and after branching using the following three methods. First, the average p value was analyzed by t-test with the null hypothesis that p=1.00 for each age class and the entire age sequence. Second, the diameter exponent (Δ; a generalization of area-preserving rule) for each root node was estimated using Newton’ s method, and the average Δ values for each age class and the entire age sequence were computed. Third, a linear regression through the origin (Δ=2.00) of CSA before branching against CSA after branching was performed using Equation 6, another generalization of the area-preserving rule [**?**]. The average Δ and regression slope (α) for each age class and the entire age sequence were tested by t-test, with the null hypothesis that Δ=2.00 and α=1.00. If the average p, Δ, or α values did not reject the null hypothesis, the area-preserving rule was confirmed. If p>1.00, Δ<2.00, or α>1.00, the CSA after branching was less than that before branching; if p<1.00, Δ>2.00, or α<1.00, the result was the opposite [**?**, **?**]. The formulas are as follows:

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Scaling relationships between RCD (mm) and total coarse root length (Lcr; mm), total coarse root biomass (Bcr; g), and topological parameters (v, v_0, a, b, and Pe), as well as between RD (mm) of a specific root segment and its total distal length (the length of all links behind this root segment) (Ld; mm) were analyzed using a logarithmically transformed univariate allometric function:

where y is the RSA parameter (e.g., Lcr, Bcr, v, v_0, a, b, Pe, and Ld); x is the RCD or RD; and f and c are the allometric coefficients. ln( )

This study conducted Analysis of Variance (ANOVA) and Least Significant Difference (LSD) tests to assess differences in root distribution, topological parameters, branching parameters, as well as the exponent Δ across age classes.

Pearson' s correlation matrix was used to analyze relationships between shrub age, root distribution, and topological parameters. All the statistical analyses were performed at the 0.05 significance level using Microsoft Excel Data Analysis Tools and SPSS 18.0 (SPSS Inc., Chicago, IL, USA).

3.1 Root Distribution and Topology of *R. soongorica*

The roots of *R. soongorica* were predominantly concentrated in the 10-50 cm soil layer, characterized by a prominent taproot with minimal branching (Figs. 2g and 3). At older age class, lateral roots extended more horizontally, while the taproot remained the primary and thickest root axis. Ntn, Nlr, and the proportion of taproot nodes with multiple lateral roots all increased significantly with age (Table 1 ; Fig. 5 [Figure 5: see original paper]). At all age classes, Bt accounted for more than half of the Bcr, and the proportion of Blcr relative to the Bcr also increased with age (Table 1; Fig. 5).

The v and v_0 increased significantly with age (Fig. 5; Table 2). The le showed no significant variation across age classes, while li decreased with age. At all age classes and throughout the entire sequence, li was consistently shorter than le. Maximal horizontal and vertical extensions, a, b, and Pe all increased with age. Both TI and TIM values decreased significantly with age. For TI, the null hypotheses equal to 1.00 or 0.53 were rejected across all age classes and the pooled data ($P<0.05$). For TIM, these hypotheses were rejected at the two older age classes and across the entire age sequence, but not at the younger age class 0-19 years ($P=0.06$).

3.2 Root Branching of *R. soongorica*

The average branching parameter p ranged from 1.09 to 1.20 across the three age classes, with an overall average of 1.13 (Table 3). Values for each age class and the entire age sequence differed significantly from the null hypothesis of $p=1.00$, with no significant differences among different age classes. The average q value per node showed an overall average of 0.75 across all age classes, showing no significant differences among different age classes.

Linear regressions of p with shrub age (Adjusted $R^2=0.006$ and $P=0.12$) and link diameter (Adjusted $R^2=0.005$ and $P=0.13$) were not significant (Table 3; Fig. 6 [Figure 6: see original paper]). The independence of q values from shrub age (Adjusted $R^2= -0.004$ and $P=0.91$) and link diameter (Adjusted $R^2= -0.004$ and $P=0.91$) was also confirmed for all root nodes (Adjusted $R^2= -0.002$ and $P=0.43$) (Table 3; Fig. 6).

The average Δ values across the three age classes ranged from 1.71 to 1.95, with an overall average of 1.85 (Table 3). For age classes 0-19 and 20-29 years, the null hypothesis of $\Delta=2.00$ was not rejected ($P>0.05$). However, for the age class \$ \$30 years and the entire age sequence, the average Δ values were significantly lower than 2.00 (Table 3).

A significant positive linear relationship was observed between CSA before and after branching across all age classes and the entire age sequence (Fig. 7 [Figure 7: see original paper]). The slope α differed significantly from 1.00 at all age classes, except for the age class \$ \$30 years (Fig. 7).

3.3 Root-Related Allometric Relationships of *R. soongorica*

The $\log_{10}$-transformed RCD exhibited a strong linear relationship with $\log_{10}$-transformed Lcr in the pooled data, with a slope of 1.77 ($P<0.05$; Fig. 8a [Figure 8: see original paper]). The scatter plot of $\log_{10}$-transformed RD and Ld showed a wider scattering (Adjusted $R^2=0.578$ and $P<0.05$) than that of $\log_{10}$-transformed RCD and Lcr (Fig. 8b). The $\log_{10}$-transformed RCD exhibited a consistent relationship with $\log_{10}$-transformed Bcr, with a regression slope of 2.31 (Adjusted $R^2=0.892$ and $P<0.05$) across all age classes (Fig. 8c).

The regression between $\log_{10}$-transformed RCD and v yielded a slope of 1.51, with an intercept of -0.88 and an Adjusted R^2 of 0.733. The regression between $\log_{10}$-transformed RCD and v_0 yielded a slope of 1.27, with an intercept of -0.80 and an Adjusted R^2 of 0.742. The regression between $\log_{10}$-transformed RCD and a had a slope of 1.01, an intercept of -0.58, and an adjusted R^2 of 0.668. The regression between $\log_{10}$-transformed RCD and b showed a slope of 0.78, with an intercept of 0.08 and an Adjusted R^2 of 0.662. The regression between $\log_{10}$-transformed RCD and Pe yielded a slope of 2.05, with an intercept of -1.21 and an Adjusted R^2 of 0.718 (Table 4).

4.1 Root Topology and Its Adaptive Strategy

In this study, the maximal vertical extension of coarse roots for *R. soongorica* increased with age, but averaged only 387.4 mm, which is shallower than previously reported for this species in the Hexi Corridor, Northwest China [**?**]. This relatively shallow root system is likely a response to the extreme drought conditions in the study area, where groundwater is deep, and soil moisture is primarily replenished through precipitation and condensation [**?**, **?**]. Furthermore, since nutrients are concentrated in the topsoil in this region [**?**], horizontal root growth may be more advantageous than deep vertical growth for accessing both water and nutrients. Indeed, we observed a significant positive correlation between shrub age and maximal horizontal extension of coarse roots. This finding aligns with previous studies [**?**, **?**, **?**], which suggested that drought conditions promote more economical root systems, encouraging root elongation toward areas with higher water availability.

The average Nlr, the proportion of nodes with multiple lateral roots, and the biomass ratio of lateral roots all increased with age, further supporting the idea that *R. soongorica* shrubs primarily develop lateral roots with age to enhance nutrient acquisition. This pattern aligns with the benefit-cost theory, which suggested that plants allocate more carbon to root components that improve nutrient uptake [?]. Similarly, studies by Dhief et al. [?] and He et al. [?] have shown that under water stress, plants increase lateral root length and biomass to expand their horizontal range and reduce root competition. The le values did not differ significantly across age classes, likely due to the increased branching of lateral roots, with many external links arising from lateral root branches rather than directly from the taproot (Fig. 3). Overall, the increased lateral root branching and biomass allocation, along with the expansion of the root foraging range, may represent an adaptive strategy for shrubs in arid environments.

The average TI and TIM values for *R. soongarica* were 0.89 and 0.96, respectively, indicating a branching pattern resembling a herringbone structure, consistent with the findings on desert plants by Yang et al. [?] and Li et al. [?]. According to Fitter [?], herringbone root systems, characterized by fewer branches and longer root extension, are advantageous in environments with limited water or nutrients. This trait aligns with the root characteristics of *R. soongorica* [?, ?] and may be an adaptation to the resource scarcity in this region [?]. In this study, the topological indices TI and TIM of *R. soongorica* decreased with age, suggesting that the species adjusts its root topology as it matures. These findings are in agreement with the study results of Oppelt et al. [?], who observed a similar decrease in four plant species in Botswana. Overall, root topology may be influenced by both environmental conditions and self-regulation, particularly in arid areas, making *R. soongorica* a useful indicator of shrub adaptive strategies.

4.2 Root Branching Characteristics

The average p and q did not differ significantly across age classes and the entire age sequence, confirming their independence from both shrub age and link diameter (Table 3). This suggested a self-similar branching pattern in the root systems. The constant CSA rule likely contributes to a uniform hydraulic architecture across the root systems, enhancing water transport efficiency, reducing hydraulic resistance, and ensuring consistent distribution of water and nutrients throughout the root systems [?]. Similar patterns have been observed in other common shrub species in the steppe desert of North China, including *N. tangutorum*, *Tamarix chinensis*, *Periploca sepium*, and *Calligonum roborovskii* [?, ?, ?].

The area-preserving rule did not apply to the root systems of *R. soongarica*, as all three methods consistently showed a reduction in CSA after branching compared to that before branching. This reduction in CSA may be attributed to lateral root embolism [?, ?]. Under drought conditions, terminal roots often experience embolism and die off, reducing CSA towards the root tips. This could help isolate parts of the plant from the effects of the arid soil layer [?]. Another possible explanation for the decrease is the higher proportion of inactive heartwood in thicker roots, which reduces the CSA available for water and nutrient transport, thus increasing the CSA ratio before and after branching [?, ?]. Similar findings were reported in the study of *N. tangutorum* in the central Hexi Corridor [?].

4.3 Allometric Relationships of the Root Systems

The $\log_{10}$-transformed Lcr, Bcr, and topological parameters of *R. soongorica* showed strong correlations with $\log_{10}$-transformed RCD, consistent with previous studies [?, ?]. An allometric relationship between $\log_{10}$-transformed Bcr and RCD was reported by van Noordwijk et al. [?] and Oppelt et al. [?]. Similarly, Yang et al. [?] demonstrated that root configuration parameters in species such as *Tamarix taklamakanensis*, *C. roborovskii*, and *Apocynum venetum* could be predicted by RCD. This correlation likely results from the self-similar branching pattern of the root systems [?]. Our results confirmed that both the CSA ratio before and after branching and the ratio of maximum to total CSA after branching remained consistent across age classes and the entire age sequence. Thus, the constant CSA rule may enable accurate estimations of coarse root parameters. Based on these scaling relationships, RCD could serve as a predictor for the RSA of *R. soongorica*, offering an effective means of indirectly assessing the spatial distribution of roots in the soil and their nutrient absorption efficiency.

5 Conclusions

This study revealed key characteristics of the RSA of *R. soongorica* shrubs in the Alxa steppe desert. The results showed that *R. soongorica* primarily developed lateral roots in shallow soil layers as the shrub ages, an adaptive trait that enhances its ability to expand nutrient acquisition and efficiently capture rainwater, condensation, and nutrients from the upper soil layers. The root topology followed a herringbone-like structure, which minimizes overlap and reduces nutrient competition. A consistent reduction in root CSA after branching was observed across various age classes and root segment diameters. This stable branching pattern enables accurate estimates of Lcr, Bcr, and topological parameters through allometric equations. Our findings enhance the understanding of the RSA of *R. soongorica* and offer practical insights for estimating root parameters, with implications for vegetation restoration and management in arid areas.

Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author Contributions

Conceptualization: WANG Xinping, MA Xiongzhong; Methodology: MA Xiongzhong, XIONG Weihong; Formal analysis: MA Xiongzhong, XIONG Weihong; Writing - original draft preparation: MA Xiongzhong; Writing - review and editing: MA Xiongzhong, WANG Xinping, XIONG Weihong; Funding acquisition: MA Xiongzhong; Supervision: WANG Xinping. All authors approved the manuscript.

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Note: Figure translations are in progress. See original paper for figures.