Shifting patterns in fine root distribution of four xerophytic species across soil structural gradients and years of growth

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Abstract

1. Fine root distribution influences the potential for resource acquisition in soil profiles, which defines how plants interact with local soil environments; however, a deep understanding of how fine root vertical distribution varies with soil structural variations and across plant ages is lacking. 2. We subjected four xerophytic species native to an arid valley of China, Artemisia vestita, Bauhinia brachycarpa, Sophora davidii, and Cotinus szechuanensis, to increasing rock fragment content (RFC) treatments (0%, 25%, 50%, and 75%, v v-1) in an arid environment and measured fine root vertical profiles over four years of growth. 3. Fine root depth and biomass of woody species increased with increasing RFC, but the extent of increase declined with plant age. Increasing RFC also increased the degree of interannual decreases in fine root diameter. The limited supply of soil resources in coarse soils explained the increases in rooting depth and variations in the pattern of fine root profiles across RFC. Fine root depth and biomass of the subshrub species (A. vestita) in soil profiles decreased with the increase in RFC and plant age, showing an opposite pattern from the other three woody species. 4. Within species, the annual increase in fine root biomass varied with RFC, which led to large interannual differences in the patterns of fine root profiles. Capacity of younger or subshrub plants to cope with soil environmental changes were greater than the older or shrub plants. These results provide insights into the limitations of soil resources in dry and rocky environments, and have management implications for degraded agroforest ecosystem.

1 Introduction

The dimensions of rooting systems, indicated by root depth and lateral extent, represent the amount of soil space occupied, which determines the uptake of resources by fine roots (Schenk and Jackson, 2002; Zhou et al., 2020; Freschet et al., 2021). Adjustment of root distribution in soil profiles is crucial for plant resource acquisition and can thus affect plant resilience to environmental stress (Fan et al., 2017; Zhou et al., 2020). For example, deep roots are a key strategy for xerophytes to survive in arid ecosystems (Schenk and Jackson, 2002; Zhou et al., 2020; Fan et al., 2017). Numerous studies have found that fine roots of woody plants are concentrated in shallow soil (Huang et al., 2008; Zewdie et al., 2008; Gwenzi et al., 2011; Gao et al., 2020; Li et al., 2020; Yang et al., 2021), whereas deep roots occur in seasonally dry areas (Schenk and Jackson, 2005). The fine root vertical pattern of many plants exhibits high plasticity under soil heterogeneity (Padilla and Pugnaire, 2007; Li et al., 2020; Luo et al., 2021). Therefore, understanding the pattern of root distribution across environmental gradients and plant ages may provide insight into the adaptive processes of plant under environmental stress.

Soil heterogeneity is caused by the patchy distribution of coarse particles and nutrients in soil profiles (Huang et al., 2023a, 2023b). Coarse parts of soil (particle size $>$ 2 mm), usually called rock fragments, are widespread in terrestrial ecosystems and their content plays an important role in soil hydrological conditions such as infiltration (Poesen and Lavee, 1994; van Wesemael et al., 2000; Zhou et al., 2009; Zhang et al., 2011; Zhang et al., 2016). Many soils contain rock fragments as a result of processes of soil genesis and human activities such as tillage and resource extraction (Hu et al., 2021). Rock fragment content (RFC) is critical for other soil properties, such as soil physical structure (Xu et al., 2012; Gargiulo et al., 2015, 2016), water and nutrient availability (Rytter, 2012; Qin et al., 2015; Zhang et al., 2016; Ceacero et al., 2020), and microbial composition (Certini et al., 2004; Hong et al., 2021; Huang et al., 2023a). In soils with high RFC (Rytter, 2012; Ceacero et al., 2020; Huang et al., 2023b), growth and biomass accumulation decreases in plants (Mi et al., 2016; Hu et al., 2021), but the allocation ratio of the below-ground parts increases (Hu et al., 2021). The rocky soil, water stress, and infertile environment limits agroforest development of the arid area. However, little is known about the vertical distribution pattern of fine root profiles in response to changes in RFC.

Plants adjust the soil space colonized by roots to obtain sufficient resources to cope with variations in the soil particle composition (Schenk and Jackson, 2002, 2005; Bengough, 2003). A strong sensitivity of rooting depth to local soil hydrological conditions has been identified (Schenk and Jackson, 2005; Fan et al., 2017; Zhou et al., 2020), whereby roots remain shallow in waterlogged land, but usually deepen in arid regions (Schenk and Jackson, 2002; Fan et al., 2017). Soil hydrology is determined by soil texture (Sperry and Hacke, 2002; Fan et al., 2017); coarse-grained (sandy or gravel) soils with low water-holding capacity allow deep infiltration profiles that encourage deep roots (Schenk and Jackson, 2005; Fan et al., 2017; Zhou et al., 2020). The coarse particles present in the soil also increase macropores and reduce mechanical resistance (Xu et al., 2012; Gargiulo et al., 2015, 2016), which is conducive to the penetration of the root system into the deep layer (Clark et al., 2002; Bengough, 2003). However, whether the rooting depth increases when the content of coarse soil particles increases and water and nutrient levels decrease remains to be explored.

The vertical profile of fine roots is also regulated by genotype, presenting as an inherent characteristic of species with wide interspecific variation (Peek et al., 2005; Gao et al., 2020; Li et al., 2020; Zhou et al., 2020; Luo et al., 2021). Simultaneously, stand age determines the spatial distribution of roots (Peek et al., 2005; Zhang et al., 2018). Previous studies have focused on the seasonal dynamics of fine root distribution in the short term, mainly explaining the rooting strategies of plants in response to the dry-wet season (Cheng et al., 2002; O'Grady et al., 2005; Wang et al., 2016). These observations have not yet provided a deep understanding of the dynamic patterns in fine root distribution and resource acquisition of woody plants across different ages and their time cumulative responses to soil heterogeneity.

In the present study, we observed the fine root vertical profiles of four xerophytic species along an RFC gradient (0%, 25%, 50%, and 75%, v v^{-1}) and during three years of growth (the second, third, and fourth years) in the arid valley environment of western China (Hu et al., 2021). These four species are important native species in the arid valleys of the Hengduan Mountain region, with irreplaceable ecological value in vegetation restoration and soil and water conservation (Li et al., 2008, 2009; Wu et al., 2008; Bao et al., 2012). We examined fine root biomass and morphology across the soil layers along the RFC gradient for three years of growth. Our objectives were to investigate: 1) how the vertical pattern of fine root depth and traits varied with the RFC gradient, 2) the temporal pattern of fine root depth and traits along soil profiles and RFC, and 3) interspecific differences in the dynamic response of fine root depth and vertical distribution to the RFC gradient. We hypothesized that: 1) root distribution deepened with the increase in RFC, based on the characteristics of poor water-holding capacity and low strength of coarse soils (Bengough, 2003; Schenk and Jackson, 2002, 2005; Fan et al., 2017); 2) with the increase in age, the response of root distribution to changes in RFC showed a cumulative decreasing effect of time, because younger plants (seedlings) are more sensitive to soil heterogeneity than older ones (Padilla and Pugnaire, 2007).

2 Materials and methods

2.1 Study site

The study site is located at Jingzhou Hill, Maoxian County, in the arid valley of the Minjiang River, Sichuan, China (31°70'N, 103deg87'E, altitude 1637 m). The RFC ranges from 1% to 65% (g g^{-1}), and most rock fragments have a particle size larger than 10 mm (Bao et al., 2012). These characteristics served as the basis for the design of the RFC gradient and selection of particle size. The mean annual precipitation at the nearest climate station (Maoxian County Meteorological Station, 2 km from the study site) was 495 mm, with 83% of the precipitation occurring during the growing season from May to October. The mean annual potential evaporation is 1332 mm, and the annual air temperature is 15.6 . The site has historically been cultivated for agricultural crops, with potatoes and celery planted 2 years before the start of the present study. Typically, cinnamon soil has a clay loam with coarse texture and low fertility (Bao et al., 2012). The soil depth is typically 50–70 cm.

2.2 Experimental design

Our study was conducted under semi-controlled field conditions over 4 years in the arid valley of the Minjiang River. The experiment used a randomized block design with eight treatments as combinations of four plant species and four RFC (0%, 25%, 50%, and 75% volumetric content, v v^{-1}). Each treatment had three replicates (plots), making a total of 48 plots (4 RFC x 4 species x 3 replicates) in the study. The four xerophytic species evaluated were*Artemisia vestita* , *Bauhinia brachycarpa* , *Sophora davidii* , and *Cotinus szechuanensis* , which are native to the arid valley. They were chosen because of their ecological importance and divergent root performance: *A. vestita* , a fast-growing subshrub with shallow root distribution; *B. brachycarpa* , a non-nitrogen-fixing legume shrub with a thin and high branching root system (root branching density = 1.47); *S. davidii* , a nitrogen-fixing legume shrub with thick and low branching root system (root branching density = 1.07); and *C. szechuanensis* , a tall shrub with developed root hairs and mycorrhiza. For microhabitat heterogeneity, differences in plant adaptations are recognized based on aboveground measurements (Li et al., 2008; Wu et al., 2008; Hu et al., 2021), whereas the variation in rooting profile and its ecological indicator is not well known.

Each plot was represented by a pit, with dimensions of 1 m x 1 m x 0.5 m (length x width x depth) and 50 cm spacing between plots. The soil at a depth of 0–50 cm was excavated from each pit. Subsequently, the walls of each pit were lined with polyethylene film to prevent interference from external conditions, and the bottom of the plot was left unlined to allow natural drainage. Fine soil particles (< 2 mm in diameter) and rock fragments (10–20 mm in diameter) were collected, mixed uniformly, and filled back into each pit to obtain the desired RFC.

Soil from all pits was then air dried for a week, and fine soil particles were collected by passing the dried soil through a 2 mm sieve and all the soil was then mixed uniformly. Initial soil properties in the samples (n = 6) were as follows: total carbon, 15.3 +- 0.09 g kg^{-1}; total nitrogen, 2.31 +- 0.02 g kg^{-1}; and total phosphorus, 0.61 +- 0.01 g kg^{-1}. Thin-bedded limestone (dominated by phyllite), which is commonly found in regional soil, was used for the rock fragments in this study. A sufficient amount of rock fragments was collected from the coarse soil part ([?] 2 mm) that had not passed through the sieve and from nearby land. The crushed rock materials were first passed through a 10 mm sieve and then a 20 mm sieve, leaving rock fragments with a particle size of 10–20 mm for use. The density of thin-bedded limestone was 2.56 +- 0.03 g cm^{-3} (n = 12), as measured by the water displacement method (Wang et al., 2017). After uniform mixing, fine soil particles and rock fragments were filled back into each pit at the desired RFC in April 2018. Each plot was irrigated with 100 L of water and left for soil to stabilize.

Sowing in each pit was performed at a depth of 0.5–1 cm with an equidistant interval pattern of nine points (25 cm equidistance between two points) in April 2018 (Hu et al., 2021). Seeds of the four species were collected from their natural habitats in the arid valley of the Minjiang River (31deg42'N, 103deg53'E, altitude range of 1600–1920 m) in August to October 2017, air-dried for 4–8 days, and stored at room temperature (10–25 degC). All the seeds were disinfected by immersion in 2.5% NaClO for 1 h and then sown in each plot. Seedlings were watered weekly after sprouting to prevent early losses. They were thinned 2 months after sprouting (Hu et al., 2021), leaving four average-sized seedlings per plot and an interval of approximately 50 cm between seedlings. The plots were weeded twice a week to ensure normal plant growth.

2.3 Measurements

2.3.1 Root and soil sampling

One average individual plant was selected in each plot for sampling roots in late September 2019, 2020, and 2021, representing plant growth for the second, third, and fourth years, respectively. Soil cores (7 cm inner diameter) were used to sample root segments and soil from vertical soil profiles. In each plot, two cores were extracted at 10 cm from the plant base in different directions. Each soil core was sampled to a depth of 50 cm and divided into five layers (0–10, 10–20, 20–30, 30–40, and 40–50 cm) in the second and third years. Sampling of the 50–70 cm soil layer was performed in the fourth year. The root segments and soil of each soil layer from the two cores were mixed into one sample in each plot to estimate the root morphology and dry weight.

2.3.2 Vertical distribution

After separating root segments from the soil, root samples were separated into coarse and fine roots (< 2 mm in diameter). Fine root samples were carefully washed with deionized water and scanned using a root image scanner (Epson V800; Seiko Epson Corp., Japan). The average diameter, total length, and total volume of fine roots in each plot were determined using the software Win-RHIZO 2020 (Regent Instruments, Canada). The scanned fine roots were oven-dried at 65 degC for 48 h and then weighed. Finally, the biomass, length density, specific length, and tissue density of fine roots were calculated using the following formulas:

Fine root biomass (g m^{-2}) = Fine root dry mass (g) / Soil core sectional area (m^{2})

Fine root length density (cm cm^{-3}) = Fine root length (cm) / Soil core volume (cm^{3})

Specific fine root length (m g^{-1}) = Fine root length (m) / Fine root dry mass (g)

Tissue density (g cm^{-3}) = Fine root dry mass (g) / Fine root volume (cm^{3})

The rooting depth is indicated by β value. Low β values correspond to shallow root allocation, whereas high β values correspond to an increased proportion of roots with depth.β is a simple numerical index of the rooting distribution based on the asymptotic equation:

$$Y = 1 - \beta^{\delta}$$

where d is the soil depth (cm), Y is the cumulative root biomass fraction from the surface to a soil depth of d , andβ is the fitted coefficient.

2.3.3 Soil properties

Soil was also sampled from soil cores along the vertical soil profile (see section 2.3.1). Soil samples from each layer were divided into two subsamples. Fresh subsamples were immediately weighed and oven-dried at 105 °C to determine the soil water content (SWC, g g^{-1}). The remaining soil subsamples were air-dried and passed through a 100-mesh (0.15 mm) sieve to determine soil physicochemical properties. Soil total carbon (TC) and total nitrogen (TN) levels were determined by combustion in an elemental analyzer (Vario MAX; Elementar, Germany), and total phosphorus (TP) was measured using the sulfuric acid-soluble perchlorate acid-molybdenum antimony colorimetric method (Hu et al., 2016). Dissolved organic carbon was extracted with deionized water (1:5 w/v soil to water) and determined using an elemental analyzer (Vario Macro Analyzer; Elementar, Germany). Ammonium nitrogen ($NH_4{}^{+}$-N) and nitrate nitrogen ($NO_3{}^{-}$-N) were extracted in the 2 mol L^{-1} KCl solution, and the supernatant was measured using a flow analyzer (SEAL Analytical, Germany). Available phosphorus (aP) was extracted with 0.5 mol L^{-1}$NaHCO_3$ at pH 8.5, and then determined by molybdenum antimony anti-colorimetry. Soil pH was determined in a 1:2.5 (w/v) soil-water suspension (SevenEasyS20; Mettler Toledo, USA) (Huang et al., 2023b).

2.4 Statistical analyses

Three-way analysis of variance (ANOVA) was used to examine the effects of RFC, year of growth, plant species, and their interactions on fine root traits. Average root traits of entire soil profiles were used to calculate the percentage variation between rock-free soil and RFC treatments, as well as between the second year and other years. Thus, the variation range between RFC treatments and years of growth could be clearly indicated by points and lines. One-way ANOVA was used to determine significant differences inβ , biomass, length density, specific length, diameter, and tissue density of fine roots between RFC treatments. Data meeting the assumption of homogeneity of variance were tested by least significant difference (LSD); otherwise, data were analyzed using a non-parametric test (Kruskal-Wallis). The relationships between fine root traits and soil properties in the soil profile were tested using linear fitting. Principal component analysis was performed using the mean values of fine root traits on the entire soil profile and β to obtain an overview of the multidimensional root functions of different years of growth and species. We also performed redundancy analysis using fine root traits and soil properties in each soil layer of the second and third years along the RFC gradient. Data were analyzed using SPSS 25.0 (IBM, USA) for means and ANOVA. Theβ coefficient, line graph, and histogram were generated using the software Origin 2018 (OriginLab Corporation, USA). Principal component and redundancy analyses were implemented using the package "vegan" in R software (version 4.0.4; R Core Team, Austria).

3 Results

3.1 Rooting depthwith different RFC treatments

The fine root depth of the three woody species increased with the increase in RFC gradient, and these species exhibited the deepest distribution at 75% RFC over the 3 years (Fig. 1 and 2). However, the rooting pattern of fine roots in *A. vestita* was contrary to that of the other woody species along the RFC gradient ($P < 0.01$, Table S1). The fine root depth coefficient (β) of*A. vestita* decreased with increasing RFC and was the largest in rock-free soil over the 3 years (Fig. 1 and 2 a). With the increase in age, the variation range of fine root depth along the RFC gradient showed an increasing trend in *A. vestita* (Fig. 2 a–d), but showed a decreasing pattern for the three woody species (Fig. 2)

3.2 Vertical distribution of fine roots with different RFC treatments

Plants generally distributed a large proportion of fine roots in the soil layer above 30 cm (more than 60%, Fig. 3 and S1). The vertical distribution of fine root biomass varied significantly between the different RFC treatments and species ($P < 0.01$, Table S1). Fine root biomass of woody species increased in most soil layers at 50–75% of RFC, and in particular, biomass increased in soil depth below 30 cm (Fig. 3 and S1). Along the RFC gradient, the increasing range of average fine root biomass in woody species was the greatest in the first year (Fig. 2). In 50–75% of RFC, the fine roots of *A. vestita* were concentrated in the surface layer, whereas those of the other three species were distributed in deep soils (Fig. 3 and S1).

Vertical patterns of fine root length density among RFC treatments, years, and species were similar to those of fine root biomass (Fig. 2, 3, and S2). The fine root specific length, diameter, and tissue density of the four species did not show distinct changes with varying soil profiles (Fig. S3–S5). With the increase in RFC, the average fine root specific length and tissue density increased in all species; however, the average diameter decreased (Fig. 2).

3.3 Temporal dynamics of fine root distribution with growth

The fine root distribution patterns in the soil profiles did not change with years of growth (Fig. 3 and S2–S5); however, the depth and mean values of fine root traits in the entire soil profile changed considerably (Fig. 4 and 5). Rooting depth, biomass, and length density of fine roots in the three woody species increased with increasing years, and the range of increase declined with increasing RFC (Fig. 4). However, these parameters in *A. vestita* decreased with increasing years (Fig. 3, 4, and S1). For all species, fine root specific length increased and its diameter decreased with increase in years for all RFC levels (Fig. 4 and 5), and the interannual variations were maximum under 75% RFC (Fig. 4).

3.4 Relationship between root traits and soil properties

The rooting depth of the four species was negatively correlated with SWC and nutrient content along the RFC gradient ($P < 0.05$, Fig. 6). Reductions in soil water, TC, TN and TP were the main factors influencing the depth of the fine root profiles under high RFC conditions (Fig. 6). Variations in SWC along the RFC gradient was the main explanatory factor for changes in fine root traits across soil profiles (Fig. 7 and Table

S2). Fine root biomass, length density, and specific root length all showed an increasing trend with the increase in RFC and were significantly correlated with the decrease in both SWC and available phosphorus (Fig. 7).

4 Discussion

Our findings support the first hypothesis that the vertical depth of fine roots in woody species increases with increasing RFC. Plants distributed more than 60% of fine root biomass in a soil depth above 30 cm and their presence reduced exponentially with soil depth. With an increase in RFC, fine root biomass and length density in most soil layers showed increasing trends, and this increase was highly noticeable in soil layers below 30 cm. The increase in fine root depth, average biomass, and length density range of woody species with increasing RFC were maximum in the second year, but minimum in the fourth year, which is consistent with our second hypothesis. Fine root diameter in all species decreased with increasing plant age, and the thinnest roots were found in soil profiles with 75% RFC. We also found that fine root depth, biomass, and length density of*A. vestita* decreased with increasing RFC and age, whereas the other three woody species presented maximum values under 75% RFC and in the last year.

4.1 Fine root depth increased with RFC

The potential fine root depth (β) in woody species increased with increasing RFC gradient over 3 years (Fig. 1 and 2). Fine root biomass below a soil depth of 30 cm increased noticeably at high RFC (Fig. 3); these adjustments of below-ground biomass in vertical profiles caused the β to increase along the RFC gradient. A deep root distribution implies that plants occupy increased vertical space in the soil and have a better chance of accessing adequate resources in soils with high RFC (Jackson et al., 2000; Padilla and Pugnaire, 2007; Zhou et al., 2020; Freschet et al., 2021). The coarse texture of the rocky soil resulted in rapid infiltration, which led to deep water infiltration in the soil profile (Schenk and Jackson, 2002, 2005; Fan et al., 2017). Plants typically extend the vertical distribution of roots to follow deep infiltration in coarse soils (Schenk and Jackson, 2002, 2005; Laio et al., 2016; Fan et al., 2017). In addition, the increase in RFC also led to a decrease in water and nutrient levels (Fig. 3 and S6), which encouraged plants to increase root depth and biomass in the soil profiles to ensure resource access (Fig. 6; Jackson et al., 2000; Padilla and Pugnaire, 2007; Li et al., 2020; Zhou et al., 2020).

Across the soil profiles, both the length density and specific length of fine roots increased in all observed species with increasing RFC (Fig. 2 and 7). Increases in length density and specific length of fine roots in soil profiles can promote the exploration range of roots in soil and facilitate root access to limited soil water and nutrients in high RFC environments (Crain and Dybzinski, 2013; Comas and Eissenstat, 2009; Freschet et al., 2018, 2021). Soils with high RFC also showed an overall decrease in fine root diameter (Fig. 2, 7, and S4). This was because soil macroporosity increases with increasing RFC (Huang et al., 2023b), which reduces the soil mechanical resistance (Xu et al., 2012; Gargiulo et al., 2016) and results in finer root systems (Bengough, 2003; Clark et al., 2003). Finer roots are beneficial for root-soil contact and resource acquisition in barren soil with high gravel content (Bengough, 2003; Ma et al., 2018; Freschet et al., 2020).

4.2 Fine root vertical profile varied with growth

An important finding of this study is that with increasing growth, the changes in soil structures have a cumulative decreasing effect on the fine root vertical distribution. Over the years, the variation ranges in fine root depth, biomass, and length density along the RFC gradient showed a decreasing trend in three woody species (Fig. 2), which was consistent with our second hypothesis. In these three woody species, fine root depth and biomass increased with age (Fig. 1 and 2). These results suggest that seedlings are more sensitive to soil heterogeneity than adults, which is consistent with the results of a previous study (Padilla and Pugnaire, 2007). Deepening of the fine roots suggested that older plants were able to access multiple resources and thus adapt to resource constraints with increasing RFC (Schenk and Jackson, 2005; Padilla and Pugnaire, 2007; Li et al., 2020; Zhou et al., 2020).

In addition, soil with 75% RFC aggravated the degree of thinning of fine roots with increasing plant age in all species (Fig. 4). The increase in macropores in soil with 75% RFC reduced mechanical resistance, resulting in finer roots with each passing year (Clark et al., 2002; Bengough, 2003; Gargiulo et al., 2015, 2016). Specific fine root length in the soil profile increased with increasing years of growth, and the largest increase was found under 75% RFC (Fig. 4). In soils with high RFC, poor resources may be an important reason for long roots (Freschet et al., 2015, 2018). Finer and longer roots facilitate older plants to be in contact with the soil and explore larger soil spaces, which is beneficial for obtaining more resources (Crain and Dybzinski, 2013; Chen et al., 2018; Freschet et al., 2020; Lu et al., 2022).

4.3 Fine root vertical profile varied between species

The vertical distribution of fine roots differed significantly between the four species (Fig. 1–3 and 5). Significantly different from the three woody species, in *A. vestita* , the fine root biomass and length density were highly concentrated in the surface soil, especially under 50–75% of RFC (Fig. 3, S1, and S2). This result suggests that*A. vestita* tends to rapidly acquire transient resources in shallow soils (Jobbágy and Jackson, 2001; Valverdes et al., 2007; Li et al., 2020), such as during occasional rainfall events but might be poor at adapting to long-term resource limitations. The other three woody species had more roots in deep soils (Fig. 1); therefore, they were more resistant to environmental pressure (Schenk and Jackson, 2005; Zhou et al., 2020).

We also found interspecific differences in the degree of variation and vertical profiles of fine roots across RFC gradient and age (Fig. 1–4 and S2–S5). The fine root depth of the three woody species showed an increasing trend with an increase in RFC and age (Fig. 2 and 4). Woody plants deepen root distribution to obtain resources in resource-constrained, highly rocky soil, but this trend became weaker with increasing age (Fig. 2). In contrast, *A. vestita* showed shallow fine root profiles in soils with high RFC and in older plants (Fig. 1 and 2). The results further confirmed that *A. vestita*differs significantly from woody species; it exhibits an opportunistic resource acquisition strategy but has poor resistance to environmental pressure (Jobbágy and Jackson, 2001; Valverdes et al., 2007; Schenk and Jackson, 2005; Zhou et al., 2020). Thus, the fine root biomass of*A. vestita* decreased with age, whereas that of woody species increased with each passing year (Fig. 4).

5 Conclusion

The results of this study suggest that increases in RFC promote deep distribution of fine roots in the three woody species, mainly owing to the low water and nutrient levels of the coarse soil and penetration into the deep soil layer. High RFC also increased the biomass and length density of fine roots in the soil profile, particularly in the soil layer below 30 cm, which prompted plants to occupy deep soil spaces. With increasing age, the changes in soil structure had a cumulative decreasing effect on fine root vertical distribution; that is, the increasing years of growth reduced the variation ranges in fine root depth and biomass of the three woody species along the RFC gradient. The RFC also influenced the decrease in range of fine root diameter over years, with the greatest range observed under 75% RFC. We also found that interspecific differences in root distribution and the dynamic response to RFC gradient, fine root depth, and biomass of *A. vestita* decreased with the increase in soil RFC and age, which was inconsistent with the increasing trend in woody species. These results provide insight into the adaptive processes of plant under rocky soils and have profound management implications for tillage in degraded ecosystems.

Author contributions statement

Hui Hu, Fanglan Li and Weikai Bbao conceived the ideas and designed methodology; Hui Hu and Long Huang collected and analyzed data; Hui Hu and Fanglan Li wrote the manuscript. All authors contributed critically to the draft and gave final approval for publication.

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Conflict of interest statement

The authors have no conflict of interest to declare.

Data availability statement

Data are publicly available through the Dryad repository (https: //doi.org/10.5521/dryad.12311).

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