

Phylogenetic signals, biomass allocation, and variation patterns collectively reflect the adaptive strategies of root system architecture of annual ephemerals

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Abstract

Root system architecture is limited by phylogenetic relationships and ultimately affect the biomass allocation of resource acquisition organs. However, many studies have only focused on the impact of environmental driven trait variation and biomass allocation on root system architecture, neglecting the impact of phylogenetic relationships. Therefore, biomass allocation and phylogenetic relationship affect the root system architecture and its variation patterns were investigated in annual ephemerals. We found that the interspecific variation of root tissue density (RTD) was the highest (51.63%), and the topological index (TI) was the lowest (5.92%). Moreover, the range of intraspecific variation for specific root length (SRL) and specific surface area (SRA) is high, and the TI is low. This convergence and divergence of root traits reflect the Phenotypic plasticity of roots and their adaptation to environmental filtering and interspecific competition. Maximum root depth (MRD) was detected significantly and weakly phylogenetic signal (0

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Abstract: Root system architecture is limited by phylogenetic relationships and ultimately affect the biomass allocation of resource acquisition organs. However, many studies have only focused on the impact of environmental driven trait variation and biomass allocation on root system architecture, neglecting the impact of phylogenetic relationships. Therefore, biomass allocation and phylogenetic relationship affect the root system architecture and its variation patterns were investigated in annual ephemerals. We found that the interspecific variation of root tissue density (RTD) was the highest (51.63%), and the topological index (TI) was the lowest (5.92%). Moreover, the range of intraspecific variation for specific root length

(SRL) and specific surface area (SRA) is high, and the TI is low. This convergence and divergence of root traits reflect the Phenotypic plasticity of roots and their adaptation to environmental filtering and interspecific competition. Maximum root depth (MRD) was detected significantly and weakly phylogenetic signal ($0 < K < 1$, $P < 0.05$). The leaf mass fraction (LMF), which is significantly positively correlated with MRD, SRA, and SRL, reflects the water demand of plants. Meanwhile, the root mass fraction (RMF), which is significantly positively correlated with MRD, is the foundation for exploring soil spatial roots. These correlations are influenced by phylogenetic relationships. Although biomass allocation indicators and trait variation indicators can reflect the adaptive strategies of annual ephemerals, the impact of phylogenetic relationships is equally important.

Key word: Interspecific variation; Intraspecific variation; Root mass fraction; Leaf mass fraction;

1. Introduction

Root system architecture refers to the morphological traits and branching patterns of root system in soil matrix, which play a prominent role in exploring soil space and acquiring resources (Lynch, 1995; Laboski et al., 1998; Tracy et al., 2015). The root morphological traits are closely related to their efficiency in obtaining water and nutrients from the soil, exploring soil space, and ability to resist environmental stress (Markesteyn and Poorter, 2009; Freschet et al., 2017; Weemstra et al., 2021b). Branching patterns are often described by topological index (TI), and different branching patterns generally represent the internal competition patterns of root system and their adaptability to different soil habitats (Oppelt et al., 2001; Spanos et al., 2008). As a consequence, root system architecture has a profound impact on the growth and development of plant individuals, which is the basis for them to adapt to constantly changing environmental conditions (Alvarez-Flores et al., 2014; Hogan et al., 2020).

Interspecific and intraspecific variation of traits is the cornerstone for coexistence of different plant species and construction of stable plant community (Violle et al., 2012; Weemstra et al., 2021a). Research on variations of plant functional traits at different ecological scales has found that interspecific and intraspecific variations are important indicators of plant response and adaptation to environmental changes, as well as resource competition strategies (Wright et al., 2004; Bu et al., 2017). Although interspecific variation has gained more attention in ecological research based on functional traits, increasing empirically published evidence demonstrated that intraspecific variation is an ecological indicator that cannot be ignored because of representation of plant response to environmental changes and phenotypic plasticity (Albert et al., 2010a; Siefert et al., 2015; Defrenne et al., 2019). However, the published studies have focused more on the interspecific variation of root morphological traits (Weemstra et al., 2016; Erktan et al., 2018; Carmona et al., 2021), neglecting the important indicative role of intraspecific variation in traits based underground ecology research.

The phylogenetic relationship of species is an important genetic factor that affects the variation of root system architecture traits (Hogan et al., 2020), and this impact may be stronger than environmental factors including climate change and mycorrhizal status, although they have been considered important factors affecting root system architecture variation (Maherali, 2017; Valverde-Barrantes et al., 2017; Lozano et al., 2020). The root trait phylogenetic conservatism (RTPC) hypothesis suggests that differences between root traits in related species may be smaller compared to phylogenetic structures with weak leaf traits, thereby exhibiting strong phylogenetic conservatism (Valverde-Barrantes et al., 2014; Liu et al., 2019). Research on morphological traits of fine root on a global scale suggested that specific root length (SRL), root diameter (RD), and other root system architecture traits of woody plants are limited by species evolutionary history, so that demonstrate similarity in root traits among related species (Kong et al. 2014; Valverde-Barrantes et al. 2017; Ma et al. 2018; Zhou et al. 2018). However, the diversity of root system functions and the complexity of soil environment may lead to the impact of species evolutionary history on root system architecture traits that is not consistent with the expectations of the RTPC hypothesis (Kramer-Walter et al., 2016; Wang et al., 2018). Consequently, it is necessary to conduct more empirical research to verify whether phylogenetic relationships have a significant impact on the formation and development of root system architecture.

Plants can respond to potential environmental stress by changing organ morphological traits and the proportion of biomass in each organ (Bouma et al., 2001; Poorter et al., 2012; Freschet et al., 2018; Zhou et al., 2019). By balancing the biomass and morphology of the organs responsible for resource acquisition, coexisting species can achieve a balance between aboveground and underground resource acquisition (Freschet et al., 2015a). Specifically, the adaptive changes in root system architecture determine the foraging characteristics and the ways in which underground resources are acquired and conserved (Guo et al., 2008; Alvarez-Flores et al., 2014; Hogan et al., 2020), which directly affect the material accumulation and morphogenesis of the aboveground parts of plant (Dannowski and Block, 2005). Conversely, the development and expansion of roots in soil depend on the carbon fixed by photosynthesis in plant leaves (Willaume and Pagès, 2011). Therefore, plant functional traits are potential covariates that explain biomass allocation, and there may be synergies or trade-offs between them (Yin et al., 2019). It is worth noting that this relationship may depend on phylogenetic relationships, which can be demonstrated through correlation analysis of Phylogenetic Independent Contrast (PIC) values (Felsenstein, 1985; Paradis and Schliep, 2019).

Annual ephemeral plants are an important component of desert early spring vegetation in northern Xinjiang, China (Mao and Zhang, 1994). They are unique plant group with a distinctive life history, which utilize winter snow melt water and relatively sufficient precipitation in spring to quickly germinate and grow in early spring (Zhang et al., 2020). As a consequence, they can quickly complete their life cycle before the onset of a dry and hot summer climate (Mao and Zhang, 1994; Wang et al., 2021). Through long-term adaptive evolution, this plant group has formed an ecological strategy suitable for harsh desert environments (Lan and Zhang, 2008; Shi et al., 2006). The most published researches have focused on the adaptive characteristics of the aboveground parts of annual ephemerals (Cheng and Tan, 2009; Xiao et al., 2014; Lu et al., 2015; Mamut et al., 2018), with relatively few studies on root systems. In addition, published empirical experiments mainly focus on the impact of environmental factors on the growth and biomass allocation patterns of annual ephemerals (Cheng et al., 2006; Mamut et al., 2019; Qiu et al., 2007; Zhang et al., 2020), with little attention paid to the ecological adaptation of root system architecture of annual ephemerals to the desert environment in the genetic context.

Therefore, this study attempts to solve the following scientific problems by studying the root system architecture traits of 47 annual ephemerals. i) What are the variation patterns of root architecture traits in annual ephemeral species? and ii) are they influenced by the phylogenetic relationship of the species? iii) How do annual ephemerals adapt to desert environments through coordination or trade-offs between root system architecture traits and biomass allocation?

2. Materials and methods

2.1. Geography of the study area

The study site is located in the desert (34 ° 09 ' - 49 deg 08 ' N and 73 deg 25 ' - 96 deg 24 ' E) of the Junggar Basin in northern Xinjiang Uygur Autonomous Region (hereafter Xinjiang), China.. It is characterized by drought and little rain in desert habitat, strong environmental heterogeneity and high seasonal precipitation. The annual average precipitation does not exceed 200mm, and the annual average temperature is -4 to 9 , which is a typical continental arid desert climate. Natural vegetation mainly consists of shrubs, perennial herbs, and ephemerals (Ma et al., 2021). Precipitation is mainly concentrated in spring and early summer, and there is relatively stable snow cover in winter, which provides favorable environmental conditions for the successful completion of the life cycle of ephemerals in the region (Shi et al., 2006; Zhang et al., 2020). During the peak growing season of ephemeral plants, their vegetation coverage can reach 40%.

2.2. Field investigation and sample collection

Complete plant individuals with vigorous growth were collected from April to May 2022. In order to avoid the impact of developmental stages, we uniformly sampled at the peak flowering period of each species. The seven sampling sites were set up in the study area (Fig. 1). For eliminating the influence of terrain factors, we have ensured the similarity of the terrain of the seven sampling sites when setting up the quadrat. At each sampling site, 10m x 10m quadrat was set, and the plant height and root collar diameter of each plant

in the quadrat were investigated. The average value was taken as the standard sample for sampling.

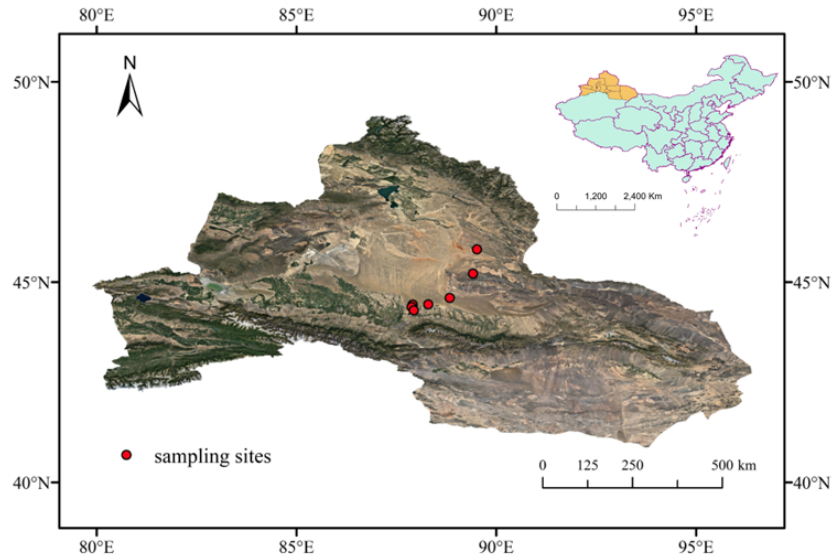


Figure 1. Distribution of sampling sites of annual ephemerals in the desert of northern Xinjiang, China

In the quadrat, we selected 10 plants whose plant height and root collar diameter are similar to the standard plants, and used big shovel, small shovel, 30cm steel ruler, brush and other tools to dig all plant roots in situ with "trench method" (Shan et al., 2012). That is, a volume of 10cm × 5cm × 40cm trench at a distance of 3-4 cm from the individual plant was dug with big shovel. Then, the soil around the root was cleared into the trench with small shovel. When the larger diameter taproot was exposed, in order to avoid root system damage, we used a steel ruler to continue to clean the soil around the finer root branches. After the root system of plant was completely exposed, the maximum root depth (MRD) of them were measured in situ with a tape measure and recorded it. After that, carefully placed the plant individuals in a plastic bag, and then transported them to store in an ice box back to the laboratory.

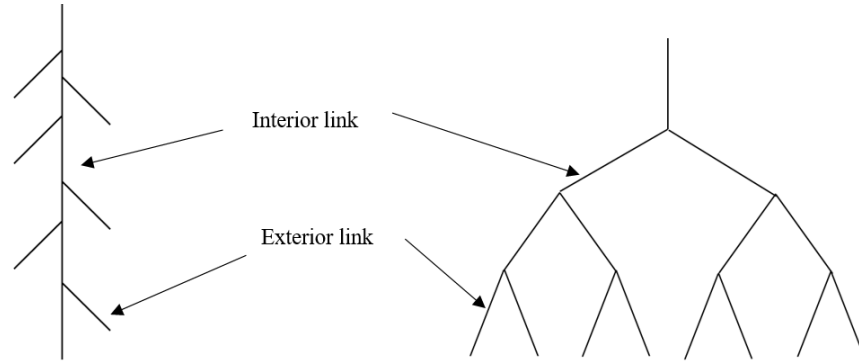
2.3. Trait measurements and calculations

After washing the impurities on the surface of the collected root systems with distilled water, the relevant parameters were measured. The roots of each plant were scanned using the Epson Perfection V850 Pro Scanner (Epson, Los Alamitos, CA USA), then the scanned root images were numbered and stored in a computer. Each image was analyzed using the root analysis system software Win-RHIZO Pro 2013 (Regent Instruments Inc., Canada) to measure total root length (TRL), root surface area (RSA), root diameter (RD), and root volume (RV). After scanning, the root system and the aboveground part were put into different empty envelopes respectively, and dried them to constant weight in an 80 oven. The dry weight of each part was weighed with the electronic balance (0.1mg). The specific root length (SRL) was calculated as the ratio of total root length to biomass, the root mass fraction (RMF) was root biomass to individual plant biomass, the specific root area (SRA) was surface area to biomass, and the root tissue density (RTD) was biomass to root volume.

2.4. Calculation of root topology

According to the root branching theory proposed by Fitter and Stickland (1991), there are two extreme types of root branching pattern: i) herringbone branching with relatively simple branches and ii) dichotomous branching with relatively complex branches. This theory applies river branching theory to the study of root branching patterns, using topological index (TI) to describe the branching patterns of different root

systems. The TI was calculated as the ratio of lgA to lgM (Fig. 2). If TI is 1, the root system is a herringbone branching, and TI is 0.5 that it is a dichotomous branching.



herringbone branching dichotomous branching

$$M=7(A=7) \quad M=8(A=4)$$

Figure 2. The schematic diagram of topological structure of root system. Altitude (A) is the number of connections from the root collar to one of the longest channels at the root tip. Magnitude(M) is the total number of all exterior connections.

2.5. Constructing the phylogenetic tree

We have collected 47 species of annual ephemerals from 13 families, 41 genera, and deserts in northern Xinjiang, China. With the help of the *Flora of China* section of the *iplant* website (<http://www.iplant.cn/>) is provided to retrieve the latest revised Latin scientific names of various species based on their Chinese scientific names. Using the **plantlist** package and **V. PhyloMaker** package to construct an evolutionary tree based on the APG IV system in R 4.2.1 (Zhang, 2018; Jin & Qian, 2019). Visualization of phylogenetic tree was help of online software iTOL (<https://itol.embl.de/tree/>).

2.6. Data analysis

This study calculated the average value of root system architecture traits for each species, and the trait values for each species were derived from 10 plant individuals. We calculated the variation coefficient (CV , Standard error divided by average and multiplied by 100%) of each root system architecture trait. Blomberg's K value is used to test phylogenetic signals of various root system architecture traits (Blomberg et al., 2003). The `ReorderData()` function in the **evobiR** package was used to rearrange the root system architecture trait data in the order of the evolutionary tree, and then the `phylosig()` function in the **phytools** package in R 4.2.1 was used to calculate the Blomberg's K value, which was set to 999 times repeatedly (Kraft et al., 2010; Revell, 2012). The `pic()` function in the **ape** package was used to calculate the Phylogenetic Independent Contrast (PIC) value of each trait (Felsenstein, 1985; Paradis and Schliep, 2019). The `sma()` function of the **smatr** package was used to achieve standardized principal axis (SMA) regression analysis that is used to analyze the correlation between traits. Origin 2021 (Origin Lab Corporation, Northampton, MA, USA) was used to exert data visualization.

3. Result

3.1. the CV_{inter} and CV_{intra} of root system architecture traits

Interspecific variation (CV_{inter}) can reflect the long-term adaptation of root system to the environment, while intraspecific variation (CV_{intra}) is an important indicator of trait plasticity. The CV_{inter} and CV_{intra} are important ecological indicators. The CV_{inter} of RTD is the highest at 51.63%, while TI is the lowest at 5.92% (Table1). The CV_{intra} ranges of SRA, SRL, and RTD are relatively large, ranging from 11.77 to

75.76%, 14.02 to 86.51%, and 4.17 to 78.45%, respectively. However, the CV_{intra} range of TI is the smallest, ranging from 0.30 to 10.62% (Fig. 3).

Table 1. Characteristics and interspecific variation coefficients of root system architecture of 47 annual ephemerals in desert of northern Xinjiang, China

Trait	Abbreviation	Mean (\pm SE)	Max	Min	$CV\%$
Maximum root depth(cm)	MRD	14.27 \pm 6.06	29.69	3.71	42.46%
Root diameter (mm)	RD	0.36 \pm 0.12	0.74	0.17	32.45%
Specific root length ($cm \cdot g^{-1}$)	SRL	1209.19 \pm 600.42	3262.09	294.54	49.65%
Specific root area ($cm^2 \cdot g^{-1}$)	SRA	123.17 \pm 46.92	286.09	24.44	38.10%
Root tissue density ($g \cdot cm^{-3}$)	RTD	1.41 \pm 0.73	3.59	0.55	51.63%
Topological index	TI	0.95 \pm 0.06	1.00	0.77	5.92%

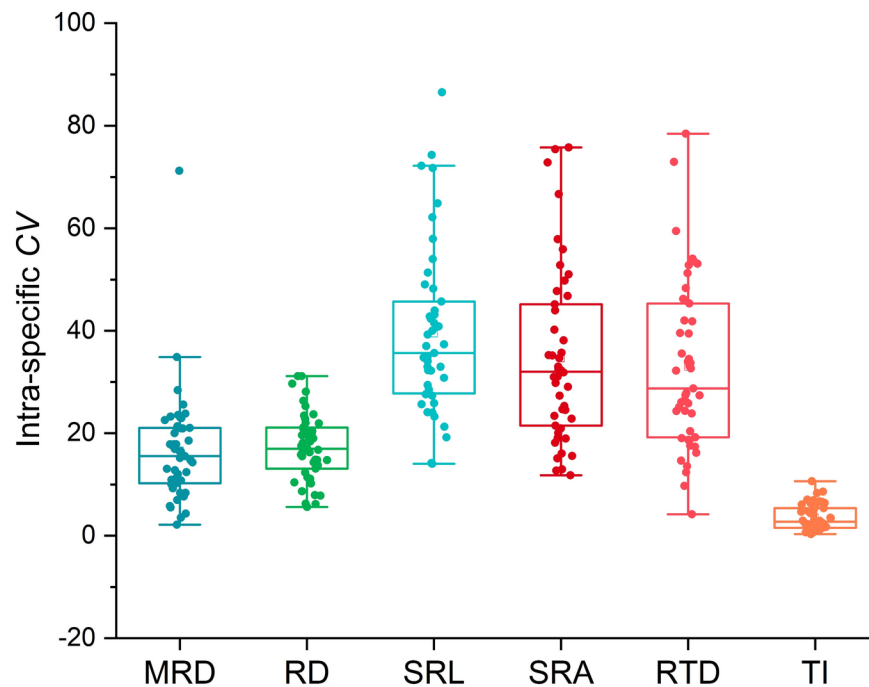


Figure 3 Intraspecific variation coefficients in root system architecture traits of 47 annual ephemerals in the desert of northern Xinjiang, China.

3.2. Phylogenetic signal of root system architecture traits

Phylogenetic signal is also important ecological indicator for detecting the impact of phylogenetic relationship between species on traits. We constructed a phylogenetic tree of annual ephemerals in this study based on the APG IV (Angiosperm Phylogeny Group) plant classification system (Fig. 4). Blomberg's K values for six root system architecture traits were immediately detected (Table 2). The results showed that the K value of MRD was 0.409, showing a significantly and weakly phylogenetic signal ($0 < K < 1$, $P < 0.05$). However, no significantly phylogenetic signals were detected for the other five root system architecture traits ($K < 1$; $P > 0.05$).

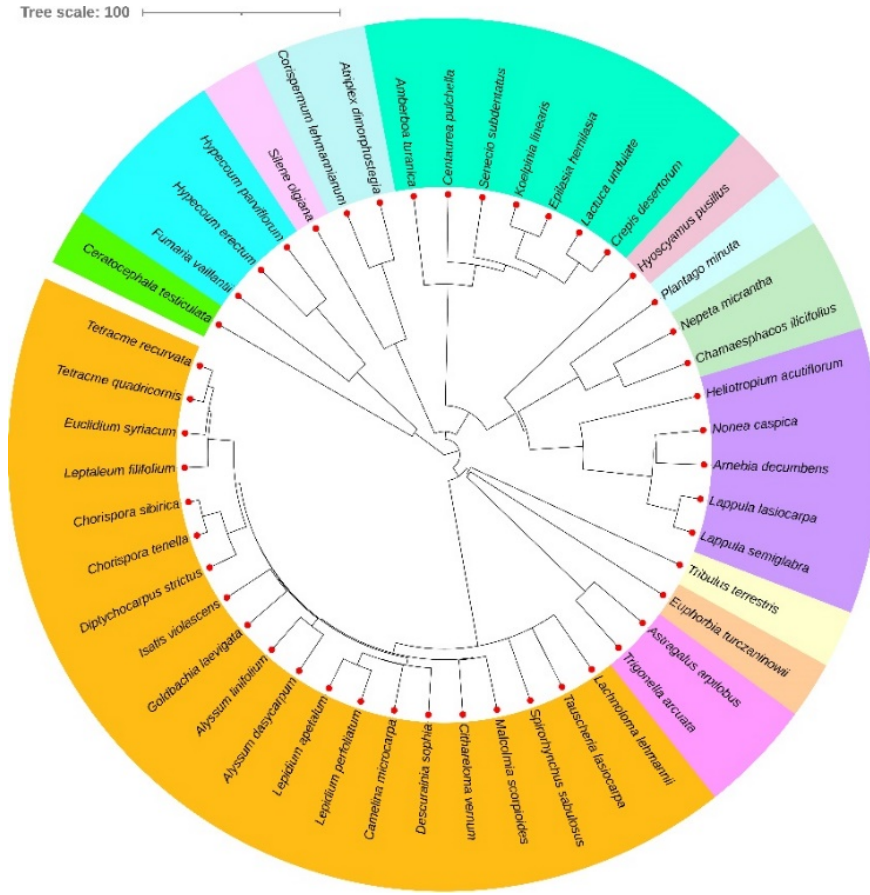


Figure 4 Phylogeny of 47 annual ephemerals based on APG IV in the desert of northern Xinjiang, China. Species from same family are indicated by same color.

Table 2. Phylogenetic signals of root system architecture traits of 47 annual ephemerals in the desert of northern Xinjiang, China.

Trait	Abbreviation	<i>K-value</i>	<i>P-Value</i>
Maximum root depth(cm)	MRD	0.409	0.008
Root diameter (mm)	RD	0.211	0.789
Specific root length (cm·g ⁻¹)	SRL	0.301	0.199
specific root area (cm ² ·g ⁻¹)	SRA	0.206	0.794
Root tissue density (g·cm ⁻³)	RTD	0.278	0.309
Topological index	TI	0.166	0.936

3.3. Relationship of root system architecture traits with LMF and RMF

The LMF and RMF are two important ecological indicators that can reflect the biomass allocation of plants to leaves and roots. In the present study, significantly positive correlation observed between LMF and MRD (Fig. 5a; $R^2 = 0.110$, $P = 0.022$). LMF had highly significant and positive correlation with SRL (Fig. 5c; $R^2 = 0.268$, $P = 0.000$) and SRA (Fig. 5d; $R^2 = 0.271$, $P = 0.000$). Significantly negative correlation was found between LMF and RTD (Fig. 5e; $R^2 = 0.102$, $P = 0.022$). R RMF had a highly significant and positive correlation with MRD (Fig. 6a; $R^2 = 0.173$, $P = 0.004$), but had a highly significant and negative correlation

with RD (Fig. 6b; $R^2 = 0.183$, $P = 0.002$). Except for the correlation between RMF and MRD, as well as between LMF and RTD, the correlation between other traits disappeared after removing the phylogenetic relationship (Fig. 5-6; Table 3).

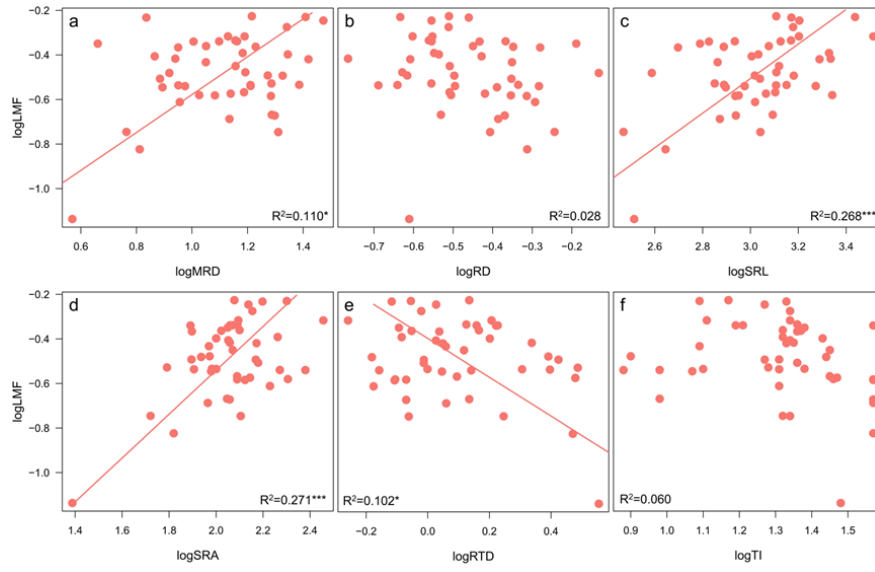


Figure 5 Relationships of leaf mass fraction (LMF) with maximum root depth (MRD), Root diameter (RD), Specific root length (SRL), specific root area (SRA), Root tissue density (RTD) and Topological index(TI). * indicates $P < 0.05$, ** indicates $P < 0.01$, and *** indicates $P < 0.001$. Standardised Major Axis (SMA) regressions were fitted to the data.

Table 3 The correlation between Physiological Independent Contrast (PIC) values of various traits.

	Leaf mass fraction (LMF)	Leaf mass fraction (LMF)	Leaf mass fraction (LMF)	Leaf mass fraction (LMF)
	slope	slope	R^2	P
Maximum root depth (MRD)	Maximum root depth (MRD)	0.023	0.033	0.9
Root diameter (RD)	Root diameter (RD)	0.831	0.000	0.9
Specific root length (SRL)	Specific root length (SRL)	0.000	0.015	0.4
Specific root area (SRA)	Specific root area (SRA)	-0.002	0.002	0.9
Root tissue density (RTD)	Root tissue density (RTD)	-0.167	0.089	0.0
Topological index (TI)	Topological index (TI)	1.619	0.008	0.9

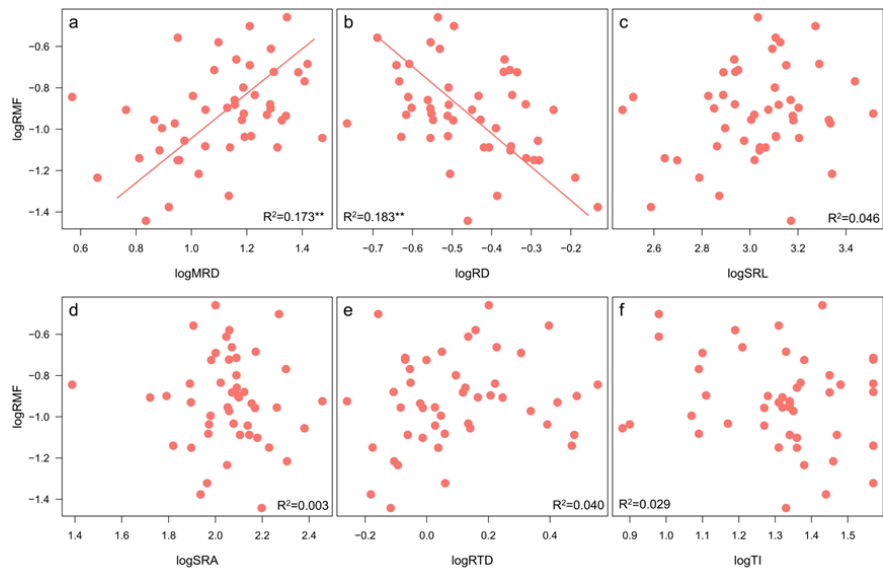


Figure 6. Relationships of root mass fraction (RMF) with maximum root depth (MRD), Root diameter (RD), Specific root length (SRL), specific root area (SRA), Root tissue density (RTD) and Topological index(TI). * indicates $P < 0.05$, ** indicates $P < 0.01$, and *** indicates $P < 0.001$. Standardised major axis (SMA) regressions were fitted to the data.

4. Discussion

4.1. The differences in variation patterns of different root traits enhance the adaptability of the root system

Interspecific variation in plant traits is the basis for coexistence of different species in similar habitats (Diaz et al., 2004). Analogy to leaf trait variation, interspecific variation in root system architecture trait can partly explain the impact of habitat filtering and interspecific competition on plant root strategies at a local scale (Bu et al., 2017; Hajek et al., 2013; Hogan et al., 2020). In the present study, the degree of CV_{inter} of the six root system architecture traits is distinct (Table 1). Among them, the RTD is the highest, and the TI is the lowest (Table 1). The results manifested that the RTD of annual ephemerals showed a divergent adaptation, while the branching pattern (TI) showed a convergent adaptation due to the combined effects of environmental filtering and similarity constraints (Grime, 2006). The divergence adaptation of RTD is conducive to these plants to reduce biological competition by adopting different root resource defense strategies when dealing with highly heterogeneous desert environments (Tjoelker et al., 2005; Lan and Zhang, 2008; Xu et al., 2021). Meanwhile, the convergence of root branching patterns caused by environmental filtering towards more simple herringbone branching patterns can effectively reduce the carbon investment cost of underground root construction, allowing annual ephemerals to allocate more resources to the growth of the aboveground parts (Qiu et al., 2007; Spanos et al., 2008; Tsakalidimi et al., 2009).

Intraspecific variation refers to the differences in genetic material and phenotypic characteristics between different botany individuals from the same species (Albert et al., 2010b). The variation of genetic material between different individuals of the same species and the phenotypic plasticity in response to environmental changes may cause intraspecific variation of plant functional traits (Jung et al., 2014). In the present study, the variation range of CV_{intra} in root architecture traits related to acquisition of resources (e.g., SRL, SRA) and resistance to environmental (e.g., RTD) interference is relatively large, showing a certain degree of divergence (Fig. 3). This may be because the annual ephemeral species collected in this study are all distributed in heterogeneous desert habitats with low species richness and relatively scarce resources, which causes some species to exhibit high plasticity in root resource acquisition or defense traits (Siefert et al.,

2015). This may be crucial for them to adapt to desert environment, because when resource availability changes rapidly in time and space, high phenotypic plasticity represents that plants have certain adaptive advantages (Hajek et al., 2013). Additionally, this divergence in the plasticity of resource acquisition traits and defense traits of different species may help plant individuals (even different individuals from the same species) occupy different ecological niche, thus promoting the coexistence of annual ephemeral plants in limited resource habitats (Bu et al., 2017).

4.2. The phylogenetic relationship is an underlying factor affecting root system architecture traits

Some functional traits of plants may be influenced by phylogenetic relationships among species, and exhibit a conservatism of phylogeny (Felsenstein, 1985). The closer the genetic relationship, the more similar the traits are (Ackerly and Reich, 1999; Kraft et al., 2010). Root system architecture, as an important functional trait that reflects the resource strategy of underground parts of plants, may also be significantly influenced by phylogenetic relationships among species during their formation and development (Kong et al. 2014; Ma et al. 2018; Zhou et al. 2018). This study examined the K values of phylogenetic signals for six root system architecture traits and found that different root system architecture traits were affected differently by the phylogenetic relationship (Table 2). Among them, significant and weak phylogenetic signals were detected for MRD, indicating that the root diameter of 47 annual ephemerals was affected to the same extent by phylogenetic relationship and environmental factors during their development (Table 2). In addition, in the present study, no significant phylogenetic signals were detected for the other root system architecture traits, which suggests that RD, SRL, SRA, RTD, and TI were not significantly affected by phylogenetic relationship among species (Kramer-Walter et al., 2016).

The results of this study indicate that RD does not exhibit a significant phylogenetic structure, which is consistent with some studies on woody plants (Kramer-Walter et al., 2016; Wang et al., 2019). However, the present result is not similar to the research results of Kong et al. (2014) and Ma et al. (2018) on the root system architecture traits of woody plants, whose research found that phylogenetic relationships have a significant impact on RD. The reasons for these differences may be related to differences in spatial scale, life types of plant, soil conditions, sampling time and methods, and sample size. On the one hand, compared to herbaceous plants, the growth and development of the root systems of woody plants may be subject to stronger directional selection and exhibit strong phylogenetic signals (Valverde-Barrantes et al., 2017). On the other hand, convergent evolution caused by habitat filtering may cause species with distant genetic relationships to exhibit similar functional traits (Wake, 1991), while divergent evolution caused by biological competition may cause species with closer genetic relationships to exhibit completely opposite functional traits (Blomberg et al., 2003).

4.3. The coordinated changes between root system architecture traits and RMF and LMF optimizes adaptive strategy

Plants can achieve a balance between resource acquisition and allocation through coordinated changes in biomass allocation and morphological characteristics (Chapin, 1991; Nicotra et al., 2010; Freschet et al., 2018). The LMF and RMF determines their future morphological changes and ultimately affects the way they obtain resources (Freschet et al., 2015b; Yin et al., 2019). The LMF is closely related to the water consumption capacity of plants, and the higher the LMF, the greater the water consumption and demand of its leaves (Yin et al., 2019). In the present study, LMF is significantly positively correlated with SRA and SRL (Fig. 5cd). This indicates that plants can mitigate water and water loss caused by high LMF by improving the absorption efficiency of root water and nutrient (Isaac et al., 2017; Wang et al., 2018). In addition, LMF and MRD also showed a significantly positive correlation (Fig. 5a). This may be another ecological strategy for plants to cope with the water consumption caused by high LMF, that is, by increasing the ability of root systems to explore the vertical space of the soil, greatly increasing the probability of encountering water rich areas (Martínez-Sánchez et al., 2003; Tsakalidimi et al., 2009). Moreover, the results of this study indicate a significant negative correlation between LMF and RTD (Fig. 5e). This may be because RTD is closely related to the resource conservation ability of the root system (Bergmann et al., 2020; Carmona et al., 2021),

so plants must achieve a balance between resource conservation and consumption among organs through the trade-off between LMF and RTD.

There may have a significant positive correlation between morphological characteristics and biomass proportion of ephemerals (Cheng et al., 2006; Zhang et al., 2020). In the present study, the positive correlation between RMF and MRD is significant (Fig. 6a), which further indicates that the exploration of soil vertical space by roots depends on the biomass investment of plants in the roots. Furthermore, the negative correlation between RMF and RD is significant (Fig. 6b). Roots with high root diameters have been proven to be resource conserving roots with slow metabolism and effective resistance to mechanical damage, herbivores, and drought stress (Withington et al., 2006; Kong et al., 2014; Weemstra et al., 2016). According to the functional equilibrium hypothesis, the increase in root biomass is due to resource constraints on root growth (Poorter et al., 2012; Freschet et al., 2018). Therefore, when the scarcity of underground resources leads to an increase in root biomass investment, what the root system most needs is to increase the ability to explore resources or the efficiency of acquiring resources, rather than conservating resource. The trade-off between RMF and RD enables the root system to achieve the optimal balance between resource investment and return. In addition, the phylogenetic relationship significantly affects the relationship between root architecture traits and the proportion of root and leaf biomass. This indicates that the coordinated changes between root architecture traits and the proportion of organ biomass may partly depend on the phylogenetic relationships between species.

Conclusion

The results of this study suggested that the annual ephemeral species adapt to the common effects of environmental filtration and interspecific competition through convergence or divergence of root system architecture traits. Additionally, the divergence of plasticity of traits related to resource acquisition (e.g. SRL, SRA) and the convergence of soil space exploration methods (e.g. TI) play an important role in the process of adapting to highly heterogeneous desert habitats. The evolutionary history of species significantly affects the development of MRD in annual ephemerals. The LMF reflects the water demand of plants, while the RMF is the foundation for root exploration of soil space. Although root trait variation patterns and biomass allocation are important ecological indicators reflecting root adaptation to the environment, the impact of phylogenetic relationships is equally important.

Author contributions

Dunyan Tan: Conceptualization(lead); Supervision(equal); Writing – review and editing(equal). **Mao Wang:** Funding acquisition(lead); Resources(equal); Supervision(equal); Writing – review and editing(equal). **Taotao Wang:** Data curation(lead); Formal analysis(lead); Investigation(lead); Methodology(equal); Writing – original draft(lead); Writing – review and editing(Supporting). **Bangyan Liu :** Data curation(equal); Investigation(equal). **Xuan Zhang:** Data curation(equal); Investigation(equal).

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Conflict of interest

The authors declared no potential conflicts of interest with respect to the research, author-ship, and publication of this article.

Data availability statement

The data that support the findings in the present study are available at: <https://osf.io/4gy6u/?view-only=aaafdf80ca304082ad64522d0d5629ce>

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