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ADAPTATION MECHANISM OF ROOT MORPHOLOGY AND CHEMICAL TRAITS IN HERBACEOUS PLANTS ON THE JINGPO LAKE LAVA PLATFORM, CHINA

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Abstract

Present study was conducted explore the functional traits of herbaceous root systems with varying life-histories adaptive strategies on Jingpo Lake lava platform. Seventeen dominant herbaceous species from the lava platform of Jingpo Lake was selected to determine the morphological and chemical traits of roots at different branching orders, and explored their resource acquisition strategies. Values varied between 0.11-75.47% for annuals and 13.57-94.81% for perennials with different life-histories plants. The smallest variation occurred in RCC, while the largest variation was observed in SRL. The SRL, RD, and RTD between two life-histories showed significant differences ($P < 0.05$). Correlations between root traits differed across plant life-histories and root sequences. Annual plants tend to favor an "acquisition" strategy, characterized by rapid "foraging", whereas perennial plants adopt a more "conservative" strategy with slower "foraging". Redundancy analysis indicated that soil pH accounted for the largest contribution (54.7%), followed by SANC (23.4%).

Introduction

Fine roots are traditionally defined as those with a diameter ≤ 2 mm, and they consist of 1-5 orders, with the 1-3 orders having the highest capacity for resource absorption and metabolism. Research has shown that the morphological traits and nutrient content of fine roots affect their physiological properties and reflect the nutrient availability of their habitat. These characteristics provide great significance to understand the adaptability of plants to their environment, as revealed by studies on climate, plant community composition, soil water and nutrients, and root systems (Du *et al.* 2022).

Herbaceous plants play a key role in heterogeneous ecosystems due to their strong ecological adaptability. They are distributed across a variety of soil types, including fluvial sand, saline soils, and alkaline soils. They are commonly used as pioneer species or group-forming plants, playing vital roles in various stages of community vegetation succession (Hou *et al.* 2024). Previous studies have shown that annual herbs, with short life-histories, high reproductive capacity, and rapid resource turnover, differ from perennials, which have higher nutrient storage rates and more efficient nutrient utilization in low-resource environments. These differences suggest varying resource allocation strategies and adaptive mechanisms between the two life-histories (Su *et al.* 2020). Differences in root traits among herbs can reveal their responses to environmental changes and their resource utilization strategies. The plant root economic spectrum (RES) refers to the interconnections among fine roots in terms of their morphology, nutrient content, and physiological characteristics (Li *et al*. 2024). Freschet *et al.*.(2018) identified global patterns of root trait variation, showing that climate, soil, and plant functional types are the primary drivers of spatial variation in root traits.

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Lava platforms are unique habitats created by volcanic eruptions, consisting of flat upland areas formed by lava flows (Cong *et al.* 2023). Most studies on the Jingpo Lake lava platform have concentrated on the ecological stoichiometric characteristics of vegetation communities and the soil microbial communities of different vegetation types (Peng 2017, Cong *et al.* 2020). However, research on the adaptation mechanisms of herbaceous plants in this habitat remains scarce. Moreover, research on root functional traits has lagged due to the considerable effort required to study plant underground parts and the limited availability of effective techniques, methods, and tools. This study aimed to determine specific root length, diameter, tissue density, specific surface area, carbon and nitrogen content in the 1-3 order roots of 17 herbaceous plants on the Jingpo Lake lava platform. The present study focuses on two main objectives: 1) To examine the relationships and differences in root functional traits among herbaceous plants with distinct life histories on the lava plateau; 2) To elucidate the resource acquisition strategies of these plants by analyzing the linkages between their root functional traits and soil physicochemical properties. Our findings are expected to reveal the adaptive mechanisms of herbaceous plants and offer a scientific basis for the sustainable management and conservation of these plants in the study area.

Materials and Methods

Jingpo Lake Geopark (120°30′-129°30′E, 43°46′-44°18′N) is situated in the Zhangguang-cailing and Laoyeling regions of Changbai Mountain, characterized by low mountains and hilly terrain. The lava platform is located in Jingpo Lake, Heilongjiang Province. Three 20 m x 50 m sample plots were subdivided into ten 10 m x 10 m squares. Each square was randomly selected from a set of ten 2.5 m x 2.5 m subplots. Between 10 and 20 healthy, mature plants were randomly selected to dig root samples within the soil layer of 0-20 cm. The roots were carefully collected by hand, washed with distilled water to remove adhering soil debris and roots from surrounding plants, and placed in a ziploc bag for subsequent morphological and chemical analysis. Additionally, three soil samples were collected from each plot at depths of 0-60 cm. Samples were taken at 5 cm intervals within the 0-20 cm depth and at 10 cm intervals within the 20-60 cm depth. Each soil sample was sieved through a 2 mm aperture sieve to remove plant roots, then mixed. The combined sample was transported to the laboratory, air-dried, ground, sieved through a 0.15 mm sieve, and placed in a Ziploc bag for chemical analysis.

The root subsamples were classified based on branch order using forceps, following the method described by Pregitzer *et al.* (2002). Distal roots (root tips) were classified as first-order roots, the parent root where two first-order roots connect as second-order roots, and the parent root connecting two second-order roots as third-order roots. Each root subsample was scanned using an Epson digital scanner (Expression 10000), and root diameter (RD, mm), total length, and volume were determined using the WinRHIZO root analyzer software (Pro2004b). The samples were then oven-dried at 65°C for 72 h to reach a constant weight (0.0001 g). Specific root length (SRL, m/g), specific root surface area (SSA, cm^2/g), and root tissue density (RTD, g/cm^3) were calculated. All dry root samples were analyzed using an elemental analyzer (ECS4010, Costech, Milan, Italy) to determine root concentration content (RCC, mg/g) and root nitrogen concentration (RNC, mg/g).

To explore trait variations in herbs with different life-histories (annuals and perennials), the coefficient of variation (CV) values for each trait were calculated separately for annual plants ($n = 11$) and perennial plants ($n = 6$). The mean and standard error for 1-3 order roots of annual herbs ($n = 11$) and perennial herbs ($n = 6$) were analyzed using one-way ANOVA. Before analysis, all data were tested for normality using the chi-square test. Differences between treatments were tested using Duncan's multiple range test (D) if the assumption of homogeneity was met; otherwise, Dunnett's T3 test (LSD, $\alpha = 0.05$) was used. Pearson correlation analysis and principal component analysis (PCA) were used to examine the interrelationships between root functional traits of orders 1-3. Redundancy analysis (RDA) was used to examine the relationship between plant root traits and soil physicochemical factors. Data were processed and visualized using Microsoft Excel 2024, SPSS software (2019, V. 27.0; SPSS Inc., Chicago, IL, USA), and ORIGIN. Principal component analysis was performed using ORIGIN, and redundancy analysis (RDA) was conducted using Canoco 5.

Results and Discussion

The variation in morphological and chemical traits of annual plants across all root orders was broad (Table 1). SRL variation was the greatest in first-order roots, while RTD and SSA showed substantial variation in second-order roots. The intensity of variation for SRL increased in third-order roots. Among the chemical traits of annual plants, RNC exhibited the greatest variation, while RCC showed the least variation. In perennial plants, RTD variation was greatest in first- and second-order roots, and the intensity of variation for all root traits increased in third-order roots. The variation in chemical traits of perennial roots was similar to that of annual plants. Overall, the mean coefficient of variation for root traits was 44.46% in annual plants and 50.02% in perennial plants, with variation higher in perennials than in annuals.

It was found that the morphological traits of roots across orders 1-3 differed between the two life-history groups of herbaceous plants (Table 2). SRL and SSA were higher in annual plants across all root orders, whereas RD and RTD were higher in perennial plants. The average SRL, RD, RTD and SSA of first-order roots in annual and perennial plants differed by 1.82, 0.75, 0.46, and 2.05 times, respectively. For second-order roots, differences were 1.89, 0.71, 0.53, and 2.05 times, respectively. For third-order roots, the differences were 1.11, 0.79, 0.69, and 1.37 times, respectively. However, none of these differences were significant ($P > 0.05$). Only the SRL of first- and second-order roots, the RD of first-order roots, and the RTD of second- and third-order roots differed significantly ($P < 0.05$) between the two life-history groups.

Among the chemical traits, RCC was lower in annual plants compared to perennial plants, while RNC and RC/N were higher in annual plants. However, none of these differences were significant ($P > 0.05$) (Table 2).

There are 3 positive and 5 negative correlations in the first-level roots of annual plants, 3 positive and 7 negative correlations in the second-level roots, and 3 positive and 5 negative correlations in the third-level roots (Table 3). SRL was negatively correlated with RD, and significantly negatively correlated with RNC and RCC. RD, on the other hand, was highly significantly positively correlated with RTD and SSA. SSA was highly significantly positively correlated with RD and SRL, while RTD was highly significantly negatively correlated with SRL. SSA was highly significantly positively correlated with RD, SRL and RC/N, while RTD was highly significantly negatively correlated with SRL. Additionally, SSA was negatively correlated with RNC.

The relationships between root morphological and chemical traits of perennials were similar to those of annuals, but more pronounced in perennials (Table 3). SRL was positively correlated with RNC and RCC, and highly significantly positively correlated with RC/N. There was a highly significant negative correlation between RCC and RTD, and a positive correlation between SSA and RC/N. SRL was significantly positively correlated with RC/N, while RTD showed a highly significant negative correlation with RNC and RC/N. The relationships between RNC, RC/N, RD and SRL were more pronounced, while the negative correlations between RTD and SSA, RNC and RCC were more significant. RNC and RCC were positively correlated across all root orders in both, but only RC/N showed a highly significant negative correlation with RCC and RNC in annual plants.

Table 1. Variation in root functional traits of herbaceous plants.

Type of plant	Root order	Root trait	Mean±SD	Max	Min	CV
Annual	1st-order root	RD	0.09±0.01	0.14	0.05	27.00%
		SRL	179.74±12.02	319.78	97.38	75.47%
		RTD	1.32±0.11	2.67	0.12	47.69%
		SSA	513.07±46.09	968.47	109.95	51.6%
	2nd-order root	RD	0.12±0.004	0.16	0.09	20.18%
		SRL	75.47±6.35	140.55	18.26	48.35%
		RTD	2.02±0.20	5.19	0.85	56.78%
		SSA	321.96±32.69	683.30	53.78	58.32%
	3rd-order root	RD	0.26±0.02	0.49	0.14	38.81%
		SRL	18.89±2.09	45.90	5.56	63.58%
		RTD	3.01±0.39	9.28	1.30	75.09%
		SSA	124.90±12.81	317.36	51.48	58.89%
		RNC	1.95±0.09	2.92	1.27	27.49%
		RCC	37.06±0.72	42.12	29.02	0.11%
		RC/N	20.03±0.61	25.06	13.88	17.53%
Perennial	1st-order root	RD	0.12±0.01	0.19	0.08	32.26%
		SRL	98.82±9.86	171.42	44.99	42.32%
		RTD	2.06±0.30	3.97	0.90	62.00%
		SSA	513.07±46.09	968.47	109.95	51.60%
	2nd-order root	RD	0.17±0.01	0.28	0.12	33.33%
		SRL	39.82±4.19	62.57	14.76	44.74%
		RTD	3.81±0.64	9.11	1.30	71.27%
		SSA	321.96±32.69	683.30	53.78	58.32%
	3rd -order root	RD	0.33±0.05	0.73	0.17	61.02%
		SRL	17.07±3.82	47.80	2.03	94.81%
		RTD	4.50±0.73	10.34	1.48	68.63%
		SSA	91.00±8.37	200.32	39.91	59.96%
		RNC	2.41±0.18	3.91	1.71	31.58%
		RCC	36.56±1.17	28.83	42.72	13.57%
		RC/N	16.24±0.95	23.31	10.52	24.88%

Mean ± SD. Different letters (a, b) within the same root order indicate significant differences between annual and perennial plants ($P < 0.05$). Abbreviations: SRL, specific root length (m/g); RD, root diameter (mm); RTD, root tissue density (g/cm^3); SSA, specific surface area (cm^2/g); RCC, root carbon concentration (mg/g); RNC, root nitrogen concentration (mg/g); RC/N, root carbon-to-nitrogen ratio.

Table 2. Morphological and chemical traits of plants.

Morphologica traits	Root order					
	1st-order root		2nd-order root		3rd-order root	
	Annual	Perennial	Annual	Perennial	Annual	Perennial
SRL	179.73±21.50a	98.82±18.18b	75.41±11.36a	39.81±7.74b	18.88±3.74a	17.07±7.04a
RD	0.09±0.01a	0.12±0.02b	0.12±0.01a	0.17±0.03a	0.26±0.03a	0.33±0.09a
RTD	1.32±0.02a	2.06±0.05a	2.02±0.36a	3.81±1.18b	3.01±0.70a	4.39±1.34b
SSA	590.07±140.34a	288.31±75.60a	321.95±58.48a	156.79±41.88b	124.90±22.92a	91.00±25.21a
Chemical traits	Annual			Perennial		
RCC	1.94±0.17a			2.39±0.33a		
RNC	37.03±1.29a			36.55±2.16a		
RC/N	20.01±1.09a			16.24±1.75a		

Different letters indicate significant differences ($P < 0.05$).

Principal component analysis (PCA) showed that PC1 and PC2 cumulatively explained 72.30, 71.10 and 69.70% of the total variation in root traits across orders 1-3, respectively (Fig. 1). In first-order roots, annuals were primarily distributed on the right half of the PC1 axis, which was highly correlated with SSA and SRL, while perennials were mostly located on the left half, which was highly correlated with RNC (Fig. 1). Both second- and third-order roots of annual plants were primarily distributed on the right half of the PC1 axis, and RD and RTD of some annual plants increased with root order (Fig. 1). Along the first principal component from left to right, the gradient of RTD and RD gradually decreased, while that of SRL and SSA gradually increased. Annual plants were mainly distributed in the positive region of the first principal component axis, characterized by high SSA and SRL. Some moved to the negative region as root order increased. In contrast, perennial plants were primarily distributed in the negative region of the first principal component axis, with higher RD and RTD. Redundancy analysis (RDA) of root traits from 17 herbaceous plants and soil factors revealed that axes 1 and 2 explained 36.91% of the relationship between root traits and environmental factors. Regarding the individual contribution of environmental variables, soil pH had the highest contribution (54.7%), followed by SANC (23.4%), with the remaining variables contributing less. The correlation strength between root functional traits and soil nutrients was as follows: pH > SANC > SNNC > STNC > SAPC > STCC > STPC > STKC > SWC. STPC was positively correlated with RC/N and RCC, STKC with RD of third-order roots, and SANC and SNNC with RNC. pH and SWC were positively correlated with RD of second-order roots and RTD of first-order roots. STNC and SAPC were positively correlated with RTD of second- and third-order roots (Fig. 2).

In this study, root traits across all orders of the two herbaceous plants on the lava platform exhibited varying degrees of variability. Both annuals and perennials showed the largest coefficient of variation for SRL and the smallest for RCC, suggesting that RCC is the most stable variable along the “investment-revenue” strategy axis. Among the different root orders, the variation in SRL was greatest in third-order roots across different life-history species, suggesting that root construction costs were more variable for third-order roots. Compared with the study by Ma *et al.* (2019) on the variation patterns of plant root attributes across 16 grassland sites in Inner Mongolia, observed a smaller coefficient of variation absorbing root root diameter (RD) and specific root length (SRL) in herbaceous plants from Jingpo Lake. This suggests that roots of herbaceous plants in Jingpo Lake are more focused on constructing defenses to adapt to the environment, compared to those in the grasslands of Inner Mongolia.

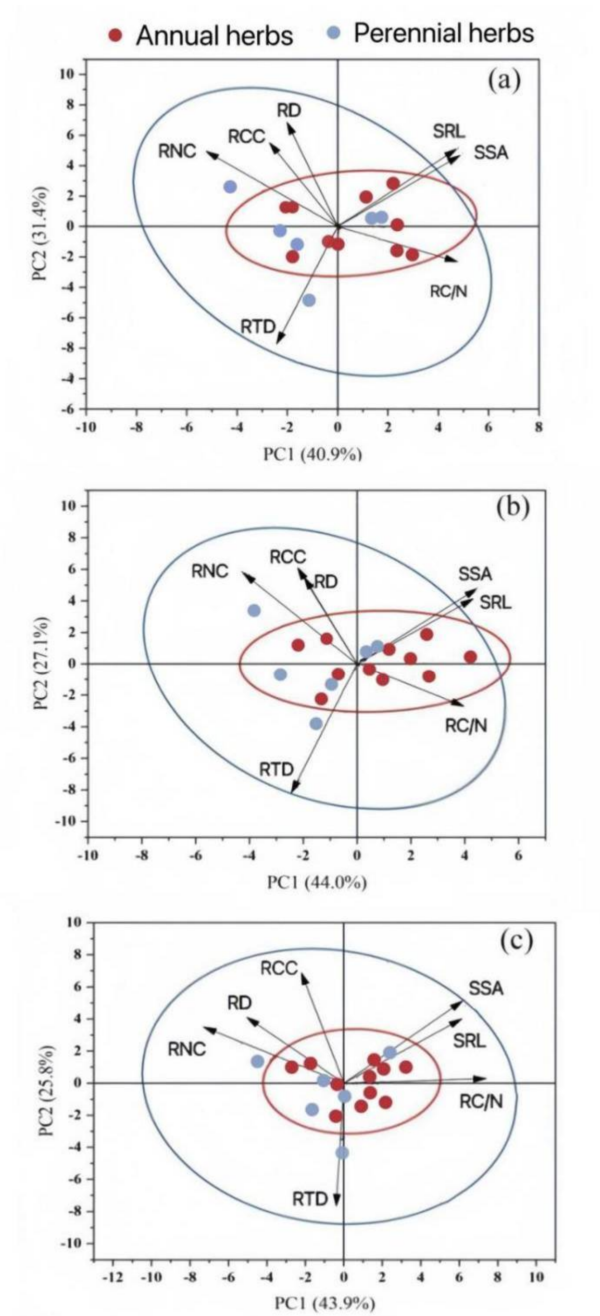

Fig. 1. Principal component analysis (PCA) of root morphological and chemical traits in seventeen herbaceous plants. a: first-order root, b: second-order root and c: third-order root.

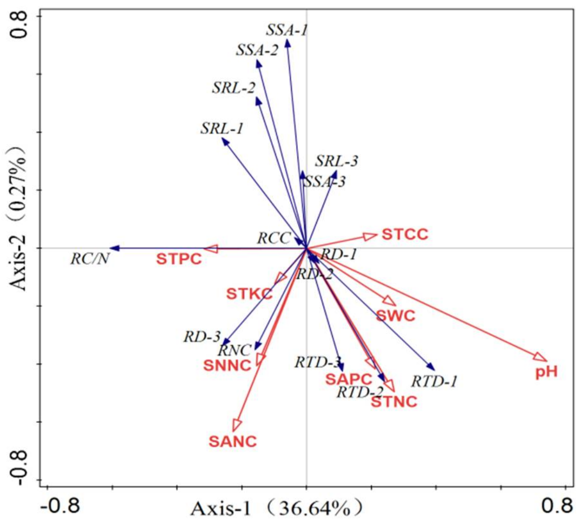

Fig. 2. Redundancy analysis of plant root traits and soil physicochemical factors in seventeen herbaceous plants.

Red arrows represent the soil factor and blue arrows represent traits of plant root. SWC: Soil water content, pH: Soil pH, STCC: Soil total carbon content, STNC: Soil total nitrogen content, STKC: Soil total potassium content, STPC: Soil total phosphorus content, SANC: Soil ammonium nitrogen content, SNNC: Soil nitrate nitrogen content, SAPC: Soil available phosphorus content. SSA-1, 2, 3: Represent the specific surface area of the first, second and third order root,respectively. RD-1, 2, 3: Represent the root diameter of the first, second and third order root, respectively. RTD -1, 2, 3: Represent the root diameter of the first, second and third order root, respectively. SRL-1, 2, 3: Represent the specific root length of the first, second and third order root, respectively.

Compared to different herbaceous plants, annuals had significantly larger SRL in first- and second-order roots than perennials, indicating stronger water and nutrient uptake capacity. Additionally, RD in first-order roots and RTD in second- and third-order roots were significantly lower in annuals, resulting in lower root construction costs and a theoretically shorter lifespan, but stronger reproductive ability (Comas *et al*. 2014). The wide dispersal of seeds allows offspring to occupy more environmental resources. Perennial plants have higher root construction costs and greater resistance to external stress compared to annuals, but are less efficient at absorbing and utilizing water and nutrients, with slower turnover rates. This finding is consistent with the study by Gao *et al.* (2017) on herbaceous plants in the water-level fluctuation zone of the Three Gorges Reservoir area. In first-order roots, perennial species exhibited greater root diameter (RD) than annuals, suggesting that perennial roots possess a stronger capacity to penetrate deeper soil layers and express higher growth potential (Tjoelker *et al*. 2005). Additionally, synergistic variation in key traits reduces competition for soil water and nutrients and fosters diverse resource acquisition strategies within communities (Mao *et al*. 2024).

In this study, SRL showed a significant negative correlation with RTD in second- and third-order roots, suggesting that most plants adopt a growth strategy where RTD increases as SRL decreases. The greater the RTD, the stronger the root’s resistance to physical injuries and mechanical stress. SSA typically shows a negative correlation with RTD in natural environments, reflecting the plant's strategy of resource allocation across different environments (Zhang 2014, Xu 2021). Roots balance the trade-off between resistance and search flexibility by adjusting RTD and SRL, consistent with studies by Zan *et al.* (2022) and Li *et al*. (2024), reflecting the plant’s nutrient uptake strategy.

Table 3. Correlation analysis of root morphological and chemical traits in annual and perennial herbaceous plants.

Root order	Trait	RD	SRL	RTD	SSA	RNC	RCC	RC/N
1st-order root	RD	1	**-0.555***	**0.775****	0.213	0.018	-0.398	-0.209
	SRL	**-0.412***	1	-0.147	**0.471***	**0.506***	**0.472***	**0.835****
	RTD	**0.504****	-0.059	1	0.168	-0.465	**-0.599****	0.147
	SSA	**0.583****	0.121	-0.031	1	-0.199	0.462	**0.491***
	RNC	-0.140	**-0.372****	-0.059	-0.244	1	**0.471***	**-0.795****
	RCC	-0.260	**-0.504****	-0.282	-0.312	**0.766****	1	0.126
	RC/N	-0.050	0.244	-0.122	0.093	**-0.930****	**-0.527****	1
2nd-order root	RD	1	0.358	0.045	**0.589***	0.112	-0.195	-0.218
	SRL	0.197	1	-0.450	**0.848***	-0.359	0.245	**0.524***
	RTD	-0.261	**-0.407****	1	-0.457	**-0.542***	**-0.846****	0.056
	SSA	**0.494****	**0.826****	**-0.422****	1	-0.160	0.336	0.451
	RNC	-0.310	-0.157	-0.057	**-0.362****	1	**0.471***	**-0.795****
	RCC	**-0.533***	-0.282	-0.200	**-0.494****	**0.766****	1	0.126
	RC/N	0.18	0.008	-0.116	0.189	**-0.930****	**-0.527****	1
3rd-order root	RD	1	**-0.616****	-0.388	-0.401	**0.775****	0.255	**-0.628****
	SRL	**-0.351****	1	-0.355	**0.930****	**-0.494***	0.276	**0.755****
	RTD	**-0.459****	0.043	1	**-0.529***	**-0.524***	**-0.785****	0.061
	SSA	0.220	**0.749****	-0.180	1	-0.426	0.410	**0.763****
	RNC	0.156	-0.175	-0.038	**-0.379***	1	**0.471***	**-0.795****
	RCC	-0.181	0.157	-0.103	-0.198	**0.766****	1	0.126
	RC/N	-0.125	0.258	-0.09	**0.476****	**-0.930****	**-0.527****	1

Bottom left and upper right shows the correlation analysis of annual and perennial herbaceous plants morphology and chemical traits. *, ** means significant at 0.05 and 0.01 level. Abbreviations as in Table 2.

The present study found a significant relationship between RD and RTD only in first-order roots of both perennial and annual plants. However, RTD and RD of first- and second-order roots were negatively correlated with RCC, suggesting that species with high RTD and larger RD have slower turnover rates and use more carbon for self-maintenance and new root construction.

In PCA, species with lower RD, RTD, and RCC tended to have higher SRL and SSA. Annual plants were primarily distributed in PC1, characterized by relatively thin roots with a large contact area with the soil, high absorption capacity, and high RNC representing an acquisition strategy with fast foraging. Perennial plants were located in PC2, characterized by long lifespan, strong tissue construction ability, and resistance, representing a conservative strategy with slower foraging. However, most perennial herbaceous plants exhibited a more greedy feature, showing a synergistic trend between the RNC of the acquisition trait and RD of the conserved trait, supporting our conclusions.

In this study, SANC was another key factor influencing root traits in herbs. SANC and SNNC were positively correlated with RNC and negatively correlated with SRL. The higher RNC in herbs indicates greater nutrient utilization and metabolism rates, which cannot fully meet their nitrogen demands, requiring additional nitrogen extraction from the soil (Li *et al.* 2020). Lava plateaus have complex microtopography, low water retention capacity, and nutrient deficiencies, particularly nitrogen. In response, plant roots adopt a strategy of rapid resource acquisition, increasing SRL and SSA to absorb nutrients and water efficiently. They also grow adventitious roots to expand their living space and reduce RD to accelerate resource turnover (Zheng *et al*. 2018). This suggests that plants can adopt adaptive growth strategies to compensate for habitat deficiencies and support their growth and reproduction.

This study investigated the root morphological and chemical traits of 17 herbaceous plants with different on the lava plateau. Present findings are as follows: perennial plants had higher root construction costs and greater resistance to external stress compared to annual plants. However, their ability to absorb water and nutrients, as well as their rate of turnover, was lower than that of annual plants. Strong correlations among most root morphological traits. However, RTD and RNC did not strictly follow this ecological axis. In most perennial herbaceous plants, a greedy pattern emerged, where the acquired trait (RNC) was synergistically linked with the conserved trait (RD). This suggests that plants adopt different strategies at various stages to combine resource traits that best support their growth. Root morphology and chemical traits in this region were primarily influenced by pH and SANC.

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