VARIATION IN LEAF PHENOTYPIC TRAITS AND ADAPTATION STRATEGIES OF FIVE RHODODENDRON SPECIES IN THE SEJILA MOUNTAIN

HAN, J. H.[1] – LU, J.[2,3*] – GUO, W. W.[1,2]

[1]*School of Ecology and Environment, Xizang University, 850000 Lhasa, China*
(e-mail: hjh17865664171@163.com (Han, J. H.))

[2]*Research Institute of Xizang Plateau Ecology, Xizang Agriculture and Animal Husbandry University, 860000 Nyingchi, China*

[3]*Key Laboratory of Forest Ecology in Xizang Plateau, Xizang Agricultural and Animal Husbandry University / Ministry of Education, 860000 Nyingchi, China*

[*]*Corresponding author*
e-mail: tibetlj@163.com

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Abstract. Leaf phenotypic traits reflect a plant's adaptability to the environment and its resource acquisition strategies. This study hypothesizes that there are significant differences in leaf traits among different Rhododendron species, with varying adaptive strategies. Using five Rhododendron species from the Sejila Mountain as study subjects, nine leaf phenotypic traits were measured and analyzed through correlation and principal component analyses. The results show significant differences in leaf traits among the five species, with the RWW species exhibiting larger trait variation coefficients, and the PGL trait having a significantly higher variation coefficient than other traits. RNH, RNR, and RBH lean toward the "slow investment-benefit" strategy, while RAB and RWW are closer to the "fast investment-return" strategy. These findings reveal differences in resource acquisition strategies among high-altitude Rhododendron species, providing valuable insights into plant adaptation to complex environments.
Keywords: *leaf traits, leaf economics spectrum, environmental response, high-altitude species, adaptability*

Introduction

The leaf is a crucial organ for energy and material conversion between plants and their environment. Leaf phenotypic traits are a significant aspect of plant functional traits. Since the leaf has the largest contact area with the environment, it is the most sensitive to environmental changes and an essential carrier for material exchange between plants, soil, and the atmosphere (Vendramini et al., 2002). Plant leaves are important for nutrient cycling and productivity intensity (Garnier et al., 2004), and maintaining terrestrial ecosystem functions (Wright et al., 2004). They also serve as a key entry point for studying plant responses to the environment. Leaf phenotypic traits are closely linked to plant growth rate and resource use efficiency (Zirbel et al., 2017). Typically, there is a tight correlation among various leaf phenotypic traits, and this correlation reflects the convergence of the plant's adaptive strategies to the habitat (Wright et al., 2004). Leaf phenotypic traits exhibit distinct variations under different topographic and microclimatic conditions. Even within the same environment, considerable differences in leaf phenotypic traits may arise among various species, representing a strategic approach for plant adaptation to their surroundings.

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Phenotypic traits play a crucial role in ecosystem functionality and serve as key botanical indicators of vegetation responses to environmental changes (Liu et al., 2015; Fu et al., 2020). They reflect to some extent the functional effects of vegetation on ecosystems and are an important link in the communication between vegetation and ecosystems (Lavorel et al., 2002). Plant phenotypic traits are influenced by both the plant itself and environmental factors. The plasticity of different plant tissues and organs plays a crucial role in adapting to environmental changes (Zirbel et al., 2017). Numerous studies have demonstrated that plants adapt more efficiently to environmental changes by coordinating and balancing changes in various phenotypic traits to form optimal functional combinations (Osnas et al., 2013; Li et al., 2022). Phenotypic traits, such as Leaf Dry Matter Content (LDMC), Specific Leaf Area (SLA), Specific Leaf Weight (SLW), and Leaf Tissue Density (LTD), reflect the survival adaptations of plants and represent the main dimensions of plant trait variation (Shen et al., 2022). The leaf economics spectrum employs the 'investment and return' paradigm to scrutinize plant phenotypic traits. Its objective is to gain a deep understanding of the functionality and significance of leaf traits, elucidating the strategies plants employ for resource acquisition. By studying the variation of phenotypic traits in Rhododendron species, we were able to effectively understand the mechanism of plant response to environmental changes at high altitudes (Wright et al., 2004; Onoda et al., 2017).

Rhododendron is one of the most species-rich genera in the Rhododendron family, with more than 1,000 species, and rhododendrons inhabit a wide range of environments and exhibit a wide range of forms (Sosnovsky et al., 2017). The genus is an important woody plant on the Xizangan Plateau and is also an established species in alpine and subalpine vegetation landscapes. At the same time, the genus is an important component of forest vegetation and plays an important role in the composition of plant communities, the coexistence of species and the maintenance of biodiversity (Yang et al., 2021). In the field of functional ecology, research on leaf phenotypic traits and adaptive strategies of Rhododendron species will help to understand the response mechanisms of Rhododendron species in the face of sensitive areas at high altitudes, and will provide an important reference for ecosystem stability in high altitude regions.

Sejila Mountain, as one of the ecological barriers of the Tibetan Plateau, boasts rich biodiversity and plays a crucial role in maintaining the stability of water resources in the surrounding areas. The Sejila Mountain is situated in the southeast of the Xizangan Plateau and the western part of the Hengduan Mountains. Due to the northward movement of the warm and humid currents from the Indian Ocean, the area receives a significant amount of rainfall annually, resulting in the formation of various forest vegetation types. The region encompasses tropical, subtropical, temperate, and frigid climatic zones, which are influenced by the warm and humid monsoon of the Indian Ocean. The winters are cold and dry, while the summers are cold and rainy, with distinct dry and wet seasons (Han et al., 2023). The area contains various types of primary forests, which are dominated by dark coniferous forests (Wang et al., 2019; Sun et al., 2022). The understorey vegetation is rich, and Rhododendron species are even more dominant. The response strategies of leaf phenotypic traits to the environment in Rhododendron species in the plateau region are unknown, so we hypothesised that under similar macrohabitat and resource conditions, different Rhododendron species would have different adaptive strategies through leaf phenotypic trait variation and be more adapted to the environment. To test this hypothesis, This study focuses on five typical Rhododendron species in the Sejila Mountain, *Rhododendron bulu*(RBH), *Rhododendron aganniphum* (RAB),

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Rhododendron nyingchiense (RNR), *Rhododendron nivale* (RNH), *Rhododendron wardii* (RWW). This study hypothesizes that there are significant differences in leaf traits among different rhododendron varieties, and their adaptive strategies vary accordingly. By measuring their phenotypic traits, the study compares the phenotypic trait variation of different rhododendron species and analyzes their leaf economic spectrum. This will help to better understand how rhododendron plants in the understory of Sejila Mountain respond to environmental changes and their ecological adaptation strategies, providing a theoretical basis for the sustainable development and stability of the Sejila Mountain ecosystem.

Materials and methods

Study area

Sejila Mountain is located in Bayi District, Linzhi City, at the junction of Nianqing Tanggula Mountain and Himalayas in the southeast of Xizang. The geographical location is 94°28'~94°51'E, 29°21'~29°51'N. It is located in the transition zone between semi humid and humid areas in southeast Xizang, with unique plateau ecological characteristics. The area is warm in winter and cool in summer, with distinct dry and wet seasons. The average annual temperature is 6–12℃, the average temperature of the warmest month is 10–18°C, the number of days ≥ 0°C is 210–350 days. The annual precipitation is 1,000–1,200 mm (Li et al., 2023). The soil is mainly mountainous brown soil (Zou et al., 2022). The arbor layer is mainly composed of moist coniferous and broad-leaved mixed forest zone in the warm temperate zone of mountains and cool moist dark coniferous forest zone in the temperate zone of mountains. The main dominant species are *Alnus nepalensis*, *Populous szechuanica var. Xizangica* and *Pinus densata*. The dominant species in shrub layer are *Viburnum kansuense*, *Rosa sericea*, *Elsholtzia fruticosa* and *Rhododendron nyingchiense*. The herb layer mainly including *Pilea insolens*, *Duchesnea indica*, *Fragaria moupinensis*, and *Eragrostis pilosa* (Han et al., 2023).

Methods

Sample plot setting and data collection

In July 2023, a survey of Rhododendron species was conducted in Sejila Mountain, Xizang. Leaves from RBH, RAB, RNR, RNH, and RWW plants were collected. A sample plot measuring 20 m ×20 m was established for each species (*Fig. 1*). We measured the longitude and latitude, elevation, slope, aspect and other factors of the quadrat with the real-time dynamic measuring instrument (RTK) (*Table 1*). Three adult single plants of each rhododendron in the sample plot were selected. From the sunny side of each plant, five disease-free and intact leaves were collected, trimmed with scissors, and immediately placed in a pre-prepared FAA fixative (5 ml 38% formaldehyde +5 ml acetic acid +5 ml glycerin+90 ml 90% alcohol) (Sobrado, 2007). The samples were then brought back to the laboratory for further use.

Leaf phenotypic traits determination

After bringing the collected leaves back to the laboratory, leaf thickness (LT, mm) and petiole length (PGL, mm) were measured using vernier calipers with 0.01 mm accuracy, The American LI-3000 C Leaf Area Meter was used to measure leaf length (LL, mm) and

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leaf area (LA, mm^2), The leaf blades' saturated fresh weight (DW, g) was measured using an electronic balance with an accuracy of 0.001 g. The blades were then dried in an oven at 80°C until they reached a constant weight, and the dry weight was measured, Calculation of specific leaf area (SLA, cm^2/g), specific leaf weight (SLW, mg/cm^2), leaf dry matter content (LDMC, g/g), and leaf tissue density (LTD, g/cm^3).

SLA= Leaf area/Leaf dry weight,

SLW= Leaf dry weight/Leaf area,

LDMC= Leaf dry weight/Leaf fresh weight,

LTD= Dry weight/(Leaf area × Leaf thickness).

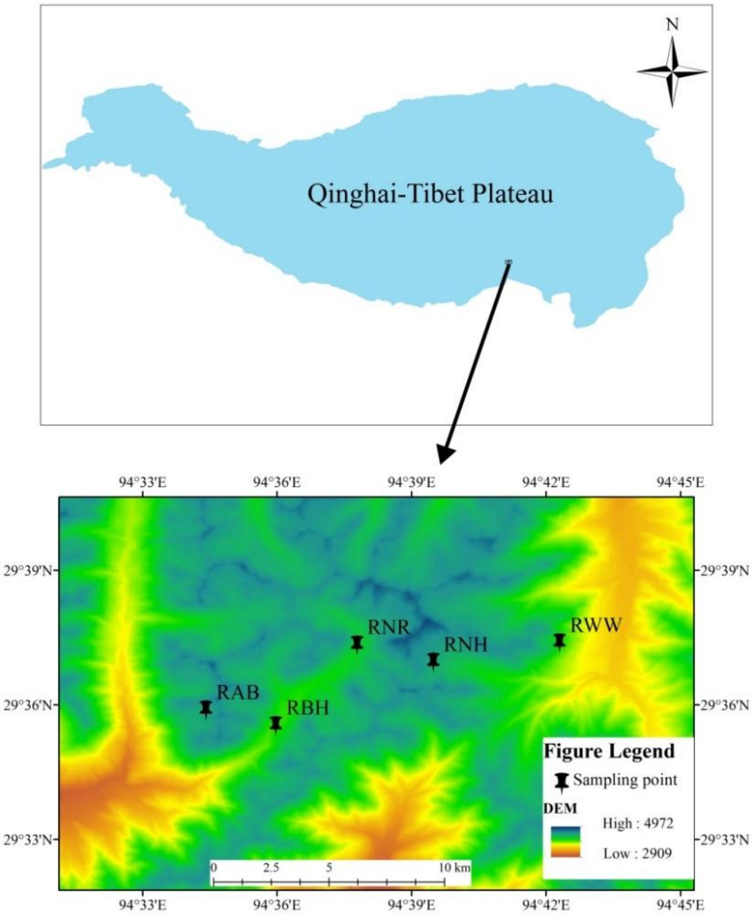

Figure 1. *Sampling diagram of study area. Note: RBH: Rhododendron bulu; RAB: Rhododendron aganniphum; RNR: Rhododendron nyingchiense; RNH: Rhododendron nivale; RWW: Rhododendron wardii*

Table 1. *Basic information of the research sites*

Species	Longitude	Latitude	Altitude/ m	Vegetation coverage/ %	Slope
RBH	94.60°E	29.59°N	4094.20	65	25°
RAB	94.57°E	29.60°N	4129.62	50	23°
RNR	94.63°E	29.62°N	4253.95	55	31°
RNH	94.66°E	29.62°N	4469.79	60	27°
RWW	94.71°E	29.63°N	4186.42	60	29°

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Data processing

The leaf phenotypic traits of five Rhododendron species were initially organized in Excel. For each phenotypic trait, the arithmetic mean and standard deviation were calculated, and the coefficient of variation CV= (standard deviation (SD) / mean (M)) × 100% was used to determine the degree of variation (Fan et al., 2022). SPSS 23 software was used to perform one-way ANOVA to test the significance of differences in leaf phenotypic traits among different species. Origin 2021 was used to generate the coefficient of variation radar chart, correlation analysis chart, and principal component analysis (PCA) chart. The coefficient of variation radar chart was used to quantitatively display the variation degree of each leaf phenotypic trait, helping to compare the relative variability between different traits. Correlation analysis revealed the relationships between different traits, aiding the understanding of their coordination in plant adaptation strategies. PCA, through dimensionality reduction, extracted the main variation patterns, revealing the key distinguishing features of leaf phenotypic traits among species and supporting functional strategy analysis.

Results

Characterisation of leaf phenotypic traits in five Rhododendron species

Leaf phenotypic traits were measured for five Rhododendron species to reveal differences between them. These traits provide an important basis for ecological adaptations and growth strategies. Significant differences were found in nine leaf phenotypic traits of the five Rhododendron species. *Table 2* shows that the LL of the five Rhododendron species ranged from 10.01 mm to 98.64 mm. RAB had the longest LL, which was significantly higher (P<0.05) than that of the other four species. The LL of RBH, RNR, and RNH were not significantly different (P>0.05). The LT of the five Rhododendron species ranged from 0.174 mm to 0.523 mm. RAB had the largest LT, while RNH had the smallest. There was no significant difference in LT between RBH, RNR, and RWW (P>0.05). In the analysis, it was found that LA of RAB and RWW were significantly greater (P<0.05) than RBH, RNR and RNH, with values of 2229.60 mm^2 and 2075.50 mm^2. The PGL of the five Rhododendron species were measured as follows: 21.74 mm for RWW, 9.72 mm for RAB, 2.72 mm for RNR, 2.64 mm for RNH, and 2.48 mm for RBH. The PGL of RWW differed significantly from that of the other four Rhododendron species (P<0.05). Of the five Rhododendron species, RAB had a significantly greater DW (P<0.05) than the other four species. However, there was no significant difference in the DW of RBH, RNR and RNH (P>0.05). The SLA values ranged from 38.90 cm^2/g to 156.49 cm^2/g. The SLA of RWW was significantly higher (P<0.05) than that of the other Rhododendron species. The SLA of RBH, RNR, and RNH were not significantly different (P>0.05) but were significantly greater (P<0.05) than that of RAB. The SLW of the five Rhododendron species ranged from 6.97 mg/cm^2 to 26.10 mg/cm^2. Notably, the SLW of RAB was significantly greater (P<0.05) than that of the other four Rhododendron species. There was no significant difference in SLW between RNR and RNH (P>0.05). Similarly, there was no significant difference in SLW between RNH and RBH (P>0.05). However, RWW was significantly different (P<0.05) from the other four Rhododendron species. The LDMC values ranged from 0.220 g/g to 0.262 g/g, while RAB and RNH showed no significant difference (P>0.05). However, they were significantly greater (P<0.05) than the other Rhododendron species. The

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LDMC of RBH and RWW did not show a significant difference (P>0.05). The five Rhododendron species had LTD values of 0.827 g/cm^3 for RNH, 0.656 g/cm^3 for RNR, 0.574 g/cm^3 for RBH, 0.500 g/cm^3 for RAB, and 0.321 g/cm^3 for RWW. Significant differences in nine phenotypic leaf traits were observed between five Rhododendron species. In terms of the measured phenotypic traits, RAB exhibited significantly higher values than the other four Rhododendron species for LL, LT, LA, DW, and SLW. Additionally, RWW showed significantly higher values than the other species for PGL and SLA, while RNH was significantly higher than the other species for LTD.

Table 2. *Comparison of leaf phenotypic traits in five Rhododendron species*

indicrs / specice	**LL/ mm**	**LT/ mm**	**LA/ mm^2**	**PGL/ mm**	**DW/ g**	**SLA/ (cm^2/g)**	**SLW/ (mg/cm^2)**	**LDMC/ (g/g)**	**LTD/ (g/cm^3)**
RBH	11.28± 0.453c	0.235± 0.009b	36.60± 1.733b	2.48± 0.206c	0.018± 0.001c	75.14± 1.305b	13.35± 0.228c	0.262± 0.009c	0.574± 0.022bc
RAB	98.64± 2.632a	0.523± 0.013a	2229.60± 71.863a	9.72± 0.755b	1.417± 0.059a	38.90± 1.784c	26.10± 0.969a	0.456± 0.020a	0.500± 0.171c
RNR	11.96± 0.558c	0.238± 0.011b	45.40± 4.028b	2.72± 0.165c	0.020± 0.002c	65.48± 2.689b	15.51± 0.638b	0.347± 0.009b	0.656± 0.024b
RNH	10.01± 0.314c	0.174± 0.009c	37.20± 3.003b	2.64± 0.282c	0.014± 0.001c	73.11± 2.887b	13.87± 0.553bc	0.448± 0.018a	0.827± 0.066a
RWW	76.35± 4.549b	0.216± 0.009b	2075.50± 148.145a	21.74± 1.157a	0.676± 0.048b	156.49± 14.075a	6.97± 0.738d	0.220± 0.026c	0.321± 0.029d

Note: The table presents mean±standard error data. Lowercase letters are used to indicate significant differences at P<0.05 for data in the same column. RBH: Rhododendron bulu; RAB: Rhododendron aganniphum; RNR: Rhododendron nyingchiense; RNH: Rhododendron nivale; RWW: Rhododendron wardii. Leaf length (LL, mm), Leaf thickness (LT, mm), Leaf area (LA, mm2), Petiole length (PGL, mm), Leaf blades' saturated fresh weight (DW, g), Specific leaf area (SLA, cm2/g), Specific leaf weight (SLW, mg/cm2), Leaf dry matter content (LDMC, g/g), Leaf tissue density (LTD, g/cm3)

Individual leaf phenotypic traits of plants show correlations under long-term environmental adaptation, leading to combinations of optimal functional traits adapted to specific environments (Yu et al., 2023). Pearson correlation analyses were conducted on plant leaf phenotypic traits, as shown in *Fig. 2*. LL showed a strong positive correlation with both LA and DW, with correlation coefficients of 0.99 and 0.97, respectively. LA and DW showed a significant positive correlation, with correlation coefficients of 0.93. There was no significant correlation between other leaf phenotypic traits.

Variation characteristics of leaf phenotypic traits in five Rhododendron species

The five Rhododendron species showed varying degrees of variation in leaf phenotypic traits. Plant traits converged and diverged in the same habitat, and the response and adaptive strategies of different species and traits to the same environmental stresses varied considerably (Tomlinson et al., 2014). *Fig. 3* shows the coefficients of variation for nine phenotypic leaf traits of five Rhododendron species. The coefficients of variation for individual leaf phenotypic traits of RWW were relatively larger than those of the other Rhododendron species. Similarly, the coefficients of variation for PGL were relatively larger than the other leaf phenotypic traits.

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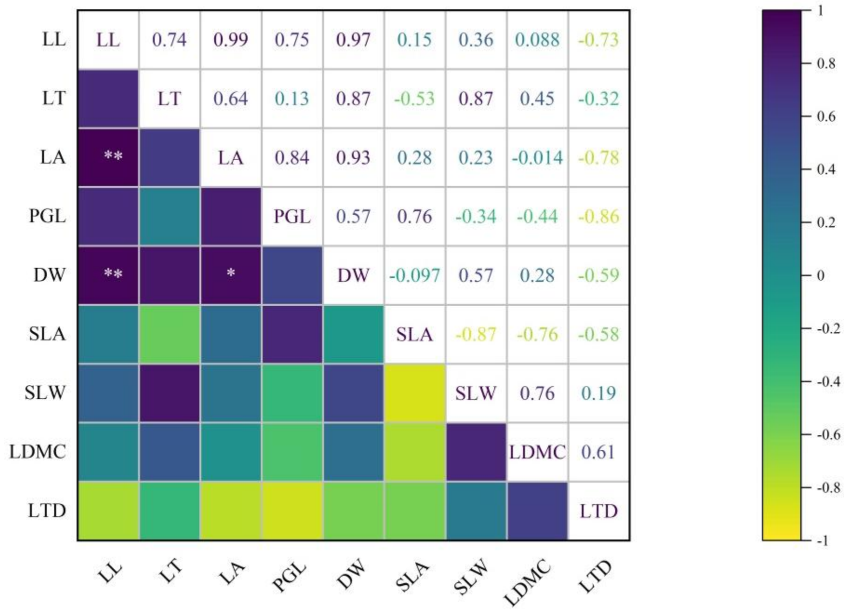

Figure 2. *Correlation analysis of leaf phenotypic traits in five Rhododendron species. Note: Correlation is significant at 0.01 and 0.05 level*

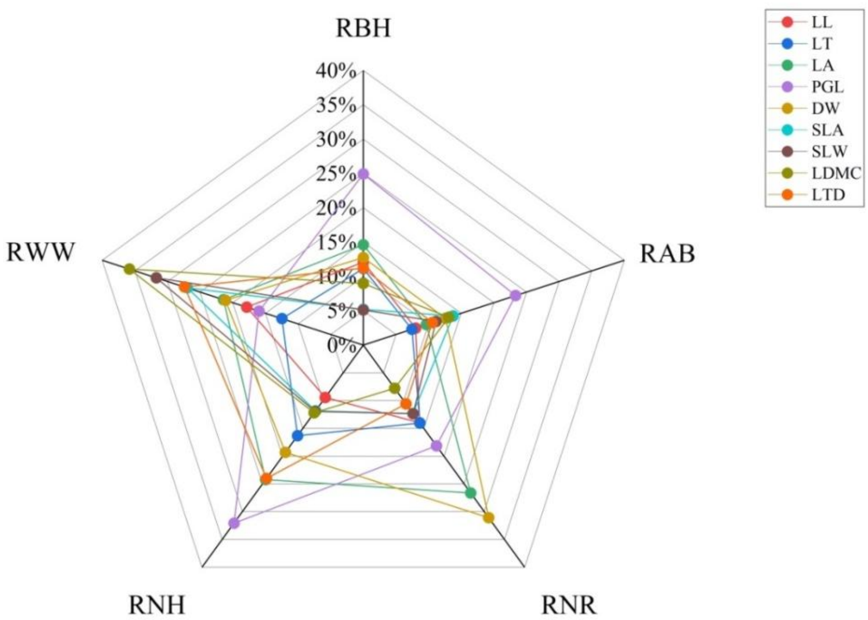

Figure 3. *Radar plots of coefficients of variation for leaf phenotypic traits in five Rhododendron species*

The variation of the nine leaf phenotypic traits in RBH ranged from 5.12% to 24.91%. The highest coefficient of variation, at 24.91%, was observed for PGL, followed by 14.61% for LA. SLW exhibited the smallest coefficient of variation at 5.12%. The maximum coefficient of variation for PGL was 23.32% for RAB, 13.76% and 13.10% for SLA and LDMC respectively, and the minimum coefficient of variation was 7.46% for LT. The variability of leaf phenotypic traits in RNR ranged from 7.76% to 31.06%, with

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DW having the highest coefficient of variation, followed by LTD. The maximum coefficient of variation of PGL was 32.05% for RNH and the minimum coefficient of variation was 32.05% for LL. The coefficient of variation for leaf phenotypic traits ranged from 12.46% to 35.84% for RWW. LDMC had the highest coefficient of variation, followed by SLW at 31.72%. Among the indicators of the nine leaf phenotypic traits, the coefficient of variation for LL is highest in RWW at 17.87%, followed by RNR at 13.99%. The coefficient of variation for LT is highest in RNH at 16.30%, and the lowest is observed in RAB at 7.46%. The coefficient of variation for LA and PGL is highest in RNH within their respective phenotypic traits. The coefficients of variation for SLA, SLW, LDWC and LTD were all greatest for RWW. The pronounced variability in PGL among the five Rhododendron species underscores a notable adaptability to diverse environmental conditions. Inhabitants of distinct microenvironments, these species exhibit heightened variability in PGL, reflecting their adaptive prowess. Within the realm of leaf phenotypic traits in RWW, the conspicuous largeness of coefficients of variation implies a considerable degree of diversity and plasticity. This diversity and plasticity within RWW's leaf phenotypic traits represent dynamic responses to environmental fluctuations, highlighting the species' robust adaptability.

Environmental adaptation strategies of five Rhododendron species

In the course of plant growth and prolonged adaptation to their environment, an intricate interplay of physiological, developmental, and environmental factors results in a myriad of trait combinations. Species sharing similar traits are selectively placed into comparable ecological niches through the process of environmental filtering. Under identical climatic conditions, these species showcase diverse environmental adaptation strategies (Thakur et al., 2023). As the results of the principal component analysis in *Fig. 4* show, the eigenvalues associated with the principal components along axis 1 contributed to 53.1% of the overall variance, while those along axis 2 contributed to 41.3% of the total variance. The cumulative sum of the eigenvalues on axes 1 and 2 accounted for a substantial 94.4% of the total variance. Various leaf phenotypic traits display diverse magnitudes of loading on distinct principal components. SLW, LT, DW, LL, LA, PGL, SLA leaf phenotypic traits were positively correlated with the first principal component. LTD, LDMC, SLW, LT, DW, LL were positively correlated with the second principal component. LTD exerted the most pronounced influence on both RNH and RNR, with LDMC following closely behind. For RBH, LTD emerged as the pivotal phenotypic trait exerting a substantial impact. In the case of RWW, PGL and SLA stood out as the key contributors, while LL, LA, DW, PGL, and LT collectively had a significant effect on RAB.

One side of Axis 1 exhibits prominent values for phenotypic trait indicators including SLW, LT, DW, LL, LA, PGL, and SLA, coupled with lower values for LDMC and LTD. The discernible divergence in the ordination of species-trait relationships among the nine leaf phenotypic traits distinctly classifies the five Rhododendron species into two functional groups. RNH, RNR, and RBH are positioned in the negative domain of the first principal component axis, showcasing elevated levels of LDMC and LTD. This pattern suggests that these three Rhododendron species align more closely with the leaf economics spectrum of 'slow investment–benefit' type species. In contrast, RAB and RWW exhibit a converse trend, placing them in proximity to the 'fast investment–return' type species on the leaf economics spectrum. Higher LL, LT, LA and PGL metrics reflect a better capture of sunlight for photosynthesis and a higher level of energy capture. Higher

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DW metrics reflect rapid plant growth in an environment with sufficient resources to accumulate more biomass. Larger SLAs and SLWs may be an indication that plants are investing more biomass in leaf construction for greater growth. A higher LDMC indicates that plants have a tendency to accumulate and store carbon in their leaves. A higher LTD reflects the plant's greater focus on the stable accumulation of resources and the firmness of the leaf structure. In principal component analysis, the first principal component axis is akin to the 'investment–return' strategy axis as postulated in the Resource-Use Efficiency Spectrum (RES) theory.

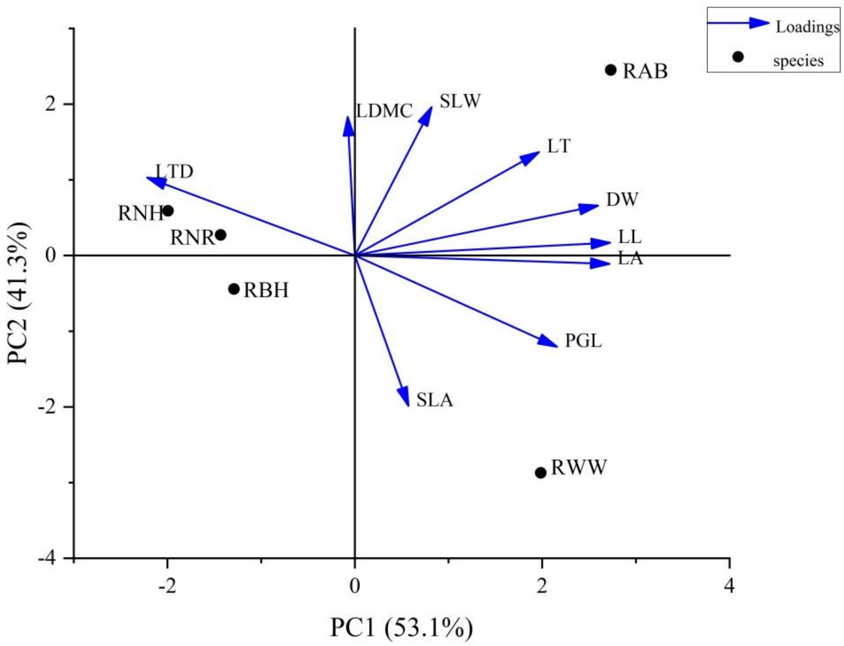

Figure 4. *Principal component analysis of leaf phenotypic traits in five Rhododendron species*

Discussion

Characterisation of leaf phenotypic traits and adaptation strategies

The direct and indirect associations of leaf phenotypic traits, comprehensively integrated and balanced along the leaf economics spectrum, elucidate the diverse positions occupied by different species within this spectrum. These positions serve to reflect the adaptive strategies employed by various species in response to changes in their respective habitats (Pan et al., 2020). The study of the plant leaf economics spectrum offers a fresh perspective on the influence of global climate change on plants and their adaptation mechanisms, which is a popular topic in ecological research (Li et al., 2022). The findings from a phenotypic trait investigation on five Rhododendron species in the Sejila Mountain reveal notable distinctions across nine leaf phenotypic traits among these botanical entities (Yang et al., 2021). In terms of these phenotypic traits, RAB exhibited significantly higher values than the other four Rhododendron species in LL, LT, LA, DW, and SLW, while RWW showed significantly higher values than the other four Rhododendron species in PGL and SLA. RNH levels were significantly higher in LTD compared to other four Rhododendron species. RAB may have greater potential for leaf photosynthesis and biomass accumulation. This is due to RAB's access to sunlight for

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photosynthesis and its ability to adapt to the environment through nutrient use. The prominence of species in leaf phenotypic traits signifies the manifestation of adaptive strategies and growth dynamics within their respective ecological niches (Salmela et al., 2020). The SLA of the five Rhododendron species exhibits a range from 38.90 cm^2/g to 156.49 cm^2/g, while the LDMC varies from 0.220 g/g to 0.456 g/g. Within the context of a high-altitude, low-temperature environment and relatively nutrient-deficient soil in the study area, this phenotypic trait combination underscores a specialized adaptation to the unique climatic conditions. It reflects a strategic equilibrium in plant resource utilization, highlighting a nuanced response to the challenging environmental factors (Yang et al., 2023).

Via synergistic variations in phenotypic traits, plants orchestrate optimal functional combinations among these traits, strategically aiming to attain proficient adaptation to the dynamically shifting external environment (Mello et al., 2020). In correlation analyses, highly significant positive correlations were found between LL and LA and DW, as well as significant positive correlations between LA and DW. Same results as study by Chang et al. (2021), suggesting coordination between an important leaf phenotypic trait (Benavides et al., 2020; Yang et al., 2022). This positive correlation likely signifies a consistent response in plant growth and development. Plants with larger LL appear inclined towards exhibiting greater LA and DW. These coordinated variations may be influenced by environmental factors and further suggest an association of these leaf phenotypic traits with an efficient photosynthetic and resource acquisition strategy. This association facilitates rapid growth and high productivity, embodying a strategic resource 'investment' (Li et al., 2022). And plant leaves in turn provided an income stream of photosynthates. This kind of investment in plants through photosynthesis is sustained throughout the whole life period, namely, the photosynthesis of plants can maintain leaf growth and reinvest in it, and provide a source of energy for stems and other parts of plants (Pastore, 2022). This investment pays off throughout the life of the plant through photosynthesis, which allows the plant to sustain and reinvest in its leaves and provide energy for the stem and other parts of the plant (Weraduwage et al., 2016). Nevertheless, the lack of significant correlations among other leaf phenotypic traits suggests potential regulation by more complex factors.

Plants adapt to environmental changes through differences in leaf phenotypic traits and their coordinated variations, showing how they optimize photosynthesis and resource acquisition strategies to enhance survival competitiveness. The differences in leaf phenotypic traits of the five Rhododendron species in the Sejila Mountain region reflect their adaptability to specific environments, while the significant correlations between traits suggest that plants achieve efficient resource utilization through coordinated responses during growth. Additionally, the lack of significant correlations between certain traits may be regulated by various complex factors, further supporting the evolutionary theory that species may adopt different evolutionary paths when facing different environments. This provides new empirical support for ecological and evolutionary theories, emphasizing the diversity and complexity of plant adaptive strategies.

Characterisation of leaf phenotypic trait variation and adaptation strategies

During community construction, the distribution of plant trait values is influenced by habitat filtering mechanisms and biotic competition. This study unveils varying degrees of variability in leaf phenotypic traits among five Rhododendron species in the Sejila

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Mountain. The amplitude of variation for the nine studied leaf phenotypic traits ranges from 5.12% to 35.84%. This variability is likely attributed to the Rhododendron species being understory plants, experiencing the dynamic conditions of the understory environment. The considerable differences in adaptation to microenvironmental conditions among distinct Rhododendron species may contribute significantly to the observed trait variation (Qiu et al., 2022). The mean coefficient of variation for LL is the lowest among the nine leaf phenotypic traits, suggesting a relative stability in this trait across the five Rhododendron species. In contrast, the mean coefficient of variation for PGL is the highest, pointing to its likely susceptibility to a broader array of environmental factors. Furthermore, the trait PGL demonstrates higher plasticity. Plants exhibit prolonged adaptation to their surrounding environment, with the extent of trait variation differing according to the habitat (Westoby et al., 2006). This phenomenon is particularly pronounced in the intricate and diverse environments of the Qinghai-Xizangan Plateau, where leaf phenotypic traits manifest heightened levels of variability and uncertainty (Wang et al., 2020; Fan et al., 2022).

Habitat filtering mechanisms and biological competition jointly influence the distribution of plant trait values during community assembly. The variation in leaf phenotypic traits of five Rhododendron species in Sejila Mountain reveals differences in plant adaptation to the variable understory habitat, especially the larger variation and plasticity observed in the PGL trait, indicating a higher sensitivity of this trait to environmental factors. These results support the idea that plant trait variation is influenced by habitat, especially in complex environments such as the Tibetan Plateau, where leaf phenotypic traits exhibit greater variability and uncertainty. This provides new empirical support for ecological and evolutionary theories, emphasizing how plants optimize resource acquisition and survival competitiveness through trait variation and adaptation strategies in different environments, thus driving species evolution and adaptation in complex ecosystems.

Environmental adaptation strategies

The leaf economics spectrum is a combination of traits that mutually balance or co-vary, providing a quantitative description of the relationships among plant leaf traits (Wright et al., 2004). Alterations in leaf phenotypic traits serve as pivotal strategies for plants to adapt to changing environments. Correlated traits related to rapid investment and returns may enhance plant growth in nutrient-rich environments. Conversely, traits associated with slow investment and returns could extend the residence time of resources within the plant. Limitations imposed by lower temperatures, shorter growing seasons, and limited resources at higher altitudes constrain plant growth. Consequently, plants employ varied strategies to adeptly navigate such challenging environments (Hikosaka et al., 2021). This study focuses on five Rhododendron species from the same location, which share a similar broad habitat and resources. However, the high altitude, short growing season, and significant diurnal temperature variation impose considerable survival pressures on the plants, particularly due to fluctuations in water availability and temperature. As a result, plants must adjust their leaf physiological structure and function to optimize water use efficiency and growth rate, thereby enhancing their ability to grow under extreme conditions of low temperature, high light intensity, and low oxygen availability. The findings indicate a conspicuous divergence in the species-trait hierarchy for these nine leaf phenotypic traits, ultimately resulting in the clear delineation of the five Rhododendron species into two distinct functional groups. RNH, RNR, and RBH are

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located in the negative region of the first principal component axis, with higher LDMC and LTD values, indicating that these three Rhododendron species exhibit characteristics of the "slow investment–benefit" strategy in the leaf economic spectrum. This suggests that these plants may cope with limited water and nutrients by extending the retention time of resources within their tissues. This strategy helps them maximize resource use during the short growing season and mitigate physiological stress caused by cold and drought. In contrast, RAB and RWW are positioned closer to the "fast investment–return" strategy in the leaf economic spectrum, which may be related to their growth in warmer or relatively moisture-rich areas. This allows these species to capture and utilize available resources more quickly through higher resource investment and faster growth rates.This underscores the varied adaptive strategies of different species to microenvironments and reveals functional strategy divergence among coexisting species resulting from competition exclusion (Zhang et al., 2010). The position of plants in the leaf economics spectrum also indicates that plants can adjust their structure and physiological traits to adapt to different environmental (Nolting et al., 2021), and the emergence of leaf economics spectrum also provides a new perspective to explore the adaptability of plants.

Through the analysis of the leaf economic spectrum, plants demonstrate different habitat adaptation strategies, especially in high-altitude areas with limited resources and short growing seasons. Species adopting the " slow investment–benefit" strategy rely on longer resource accumulation to cope with cold and drought, enhancing their survival ability in harsh environments. In contrast, species following the "fast investment-return" strategy can grow rapidly and efficiently utilize resources in resource-rich environments. These different survival strategies highlight how plants optimize resource use by adjusting leaf traits in extreme environments, thereby increasing their survival competitiveness, and reveal functional strategy divergence among coexisting species.

Conclusion

This study aims to explore the variation in leaf phenotypic traits and adaptation strategies among five Rhododendron species in the Sejila Mountain. By thoroughly analyzing the characteristics and variability of leaf phenotypic traits, the research seeks to provide a comprehensive understanding of the environmental adaptation strategies employed by plants. The findings reveal that the leaf phenotypic traits of the five Rhododendron species in the Sejila Mountain are intricately linked yet exhibit substantial differences. In order to endure and reproduce effectively in high-altitude environments, plants have employed distinct adaptive strategies through the nuanced balance of traits. Specifically, RNH, RNR, and RBH closely align with the 'slow investment—benefit' paradigm of the leaf economics spectrum, while RAB and RWW gravitate towards the 'fast investment—return'. The 'slow investment—benefit' species are generally suited to resource-poor, stable environments such as high altitudes, arid areas or poorly lit forest floors, where they have low growth rates but are highly adaptable in the long term, while the 'fast investment—return' species are better suited to resource-rich, competitive environments, where they have faster growth rates and higher reproductive rates. Selection of appropriate species is essential for effective ecological restoration and conservation efforts to maintain ecosystem stability.

Based on the findings of this study, several conservation and restoration strategies are proposed to enhance the adaptability of Rhododendron species in the Sejila Mountain region. Maintaining environmental conditions that support the diverse phenotypic traits

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of these plants in high-altitude areas is crucial, along with minimizing human disturbance and protecting natural habitats to prevent disruption of their adaptive strategies. For species exhibiting a "slow investment–benefit" strategy, such as RNH, RNR, and RBH, habitat conservation should be prioritized. For species with a "fast investment–return" strategy, such as RAB and RWW, targeted restoration efforts, including controlled planting and resource management, can support their growth. Continuous environmental monitoring will help track changes in plant adaptation and allow for adjustments to conservation strategies. Additionally, promoting eco-tourism and public education can raise awareness of the importance of plant adaptability in high-altitude ecosystems, ensuring local support for conservation efforts and promoting sustainable development.

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REFERENCES

[1] Benavides, R., Carvalho, B., Bastias, C. C., Escudero, A., Valladares, F. (2020): Intraspecific perspective of phenotypic coordination of functional traits in Scots pine. – PLoS ONE 15(2): 1-15. https://doi.org/10.1371/journal.pone.0228539.

[2] Chang, Y., Xu, C., Yang, H., Zhou, J., Hua, W., Zhang, S., Zhong, Q., Li, B. (2021): Leaf Structural Traits Vary with Plant Size in Even-Aged Stands of *Sapindus mukorossi*. – Frontiers in Plant Science 12. https://doi.org/10.3389/fpls.2021.692484.

[3] Fan, B., Ma, Z., Gao, P., Lu, J., Ding, N., Sun, K. (2022): Functional Traits of Male and Female Leaves of *Hippophae tibetana* on the Eastern Edge of the Tibetan Plateau and Their Altitudinal Variability. – Plants 11(19). https://doi.org/10.3390/plants11192484.

[4] Fu, R., Zhang, Z., Hu, C., Peng, X., Lu, S., Hu, G. (2020): Bibliometric analysis of research trends and focuses of plant functional traits. – IOP Conference Series: Earth and Environmental Science 615(1). https://doi.org/10.1088/1755-1315/615/1/012102.

[5] Garnier, E., Cortez, J., Billès, G., Navas, M. L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J. P. (2004): Plant functional markers capture ecosystem properties during secondary succession. – Ecology 85(9): 2630-2637. https://doi.org/10.1890/03-0799.

[6] Han, J., Yin, H., Xue, J., Zhang, Z., Xing, Z., Wang, S., Chang, J., Chen, X., Yu, B. (2023): Vertical distribution differences of the understory herbs and their driving factors on shady and sunny slopes in high altitude mountainous areas. – Frontiers in Forests and Global Change 6. https://doi.org/10.3389/ffgc.2023.1138317.

[7] Hikosaka, K., Kurokawa, H., Arai, T., Takayanagi, S., Tanaka, H. O., Nagano, S., Nakashizuka, T. (2021): Intraspecific variations in leaf traits, productivity and resource use efficiencies in the dominant species of subalpine evergreen coniferous and deciduous broad-leaved forests along the altitudinal gradient. – Journal of Ecology 109(4): 1804-1818. https://doi.org/10.1111/1365-2745.13603.

[8] Lavorel, S., Garnier, E. (2002): Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. – Functional Ecology 16(10): 545-556.

[9] Li, J., Chen, X., Niklas, K. J., Sun, J., Wang, Z., Zhong, Q., Hu, D., Cheng, D. (2022): A whole-plant economics spectrum including bark functional traits for 59 subtropical woody plant species. – Journal of Ecology 110(1): 248-261. https://doi.org/10.1111/1365-2745.13800.

[10] Li, X., He, D., Chen, G., Yang, J., Yang, Z., Guo, X. J., Wang, C., Zhu, S., Huang, Y., Chen, H., Huang, G., Zhang, D., Ye, C. (2022): Responses of leaf functional traits to

different hydrological regimes and leaf economics spectrum in the water level fluctuation zone of Three Gorges Reservoir, China. – Frontiers in Plant Science 13. https://doi.org/10.3389/fpls.2022.939452.

[11] Li, Y., Fu, F., Li, J., Chen, W., Ding, H., Xiao, S. (2023): Stoichiometric Characteristics of *Abies georgei* var. smithii Plants in Southeast Tibet. – Sustainability (Switzerland) 15(11). https://doi.org/10.3390/su15118458.

[12] Liu, X., Ma, K. (2015): Plant Functional Traits - Concepts, Applications and Future Directions. – Scientia Sinica Vitae 45(4): 325-339. https://doi.org/10.1360/n052014-00244.

[13] Mello, F. N. A., Estrada-Villegas, S., Defilippis, D. M., Schnitzer, S. A. (2020): Can functional traits explain plant coexistence? A case study with tropical lianas and trees. – Diversity 12(10): 1-15. https://doi.org/10.3390/d12100397.

[14] Nolting, K. M., Prunier, R., Midgley, G. F., Holsinger, K. E. (2021): Intraspecific trait variation influences physiological performance and fitness in the South Africa shrub genus Protea (Proteaceae). – Annals of Botany 127(4): 519-531. https://doi.org/10.1093/aob/mcaa060.

[15] Onoda, Y., Wright, I. J., Evans, J. R., Hikosaka, K., Kitajima, K., Niinemets, Ü., Poorter, H., Tosens, T., Westoby, M. (2017): Physiological and structural tradeoffs underlying the leaf economics spectrum. – New Phytologist 214(4): 1447-1463. https://doi.org/10.1111/nph.14496.

[16] Osnas, J. L. D., Lichstein, J. W., Reich, P. B., Pacala, S. W. (2013): Global leaf trait relationships: Mass, area, and the leaf economics spectrum. – Science 340(6133): 741-744. https://doi.org/10.1126/science.1231574.

[17] Pan, Y., Cieraad, E., Armstrong, J., Armstrong, W., Clarkson, B. R., Colmer, T. D., Pedersen, O., Visser, E. J. W., Voesenek, L. A. C. J., van Bodegom, P. M. (2020): Global patterns of the leaf economics spectrum in wetlands. – Nature Communications 11: 4519. https://doi.org/10.1038/s41467-020-18354-3.

[18] Pastore, M. A. (2022): Bringing the underground to the surface: Climate change stressors negatively affect plant growth, with contrasting above and belowground physiological responses. – Plant Cell and Environment 45(8): 2267-2270. https://doi.org/10.1111/pce.14379.

[19] Qiu, J., Han, A., He, C., Dai, X., Jia, S., Luo, Y., Hao, Z., Yin, Q. (2022): Functional Traits of Quercus aliena var. acuteserrata in Qinling Huangguan Forest Dynamics Plot: The Relative Importance of Plant Size and Habitat. – Forests 13(6). https://doi.org/10.3390/f13060899.

[20] Salmela, M. J., Velmala, S. M., Pennanen, T. (2020): Seedling traits from root to shoot exhibit genetic diversity and distinct responses to environmental heterogeneity within a tree population. – Oikos 129(4): 544-558. https://doi.org/10.1111/oik.06797.

[21] Sobrado, M. A. (2007): Relationship of water transport to anatomical features in the mangrove Laguncularia racemosa grown under contrasting salinities. – New Phytologist 173(3): 584-591. https://doi.org/10.1111/j.1469-8137.2006.01927.x.

[22] Sosnovsky, Y., Nachychko, V., Prokopiv, A., Honcharenko, V. (2017): Leaf architecture in Rhododendron subsection Rhododendron (Ericaceae) from the Alps and Carpathian Mountains: Taxonomic and evolutionary implications. – Flora: Morphology, Distribution, Functional Ecology of Plants 230: 26-38. https://doi.org/10.1016/j.flora.2017.03.003.

[23] Sun, X., Wang, G., Sun, J., Sun, S., Hu, Z., Song, C., Lin, S. (2022): Contrasting water sources used by a coniferous forest in the high-altitude, southeastern Tibetan Plateau. – Science of the Total Environment 849: 157913. https://doi.org/10.1016/j.scitotenv.2022.157913.

[24] Thakur, D., Hadincová, V., Schnablová, R., Synková, H., Haisel, D., Wilhelmová, N., Dostálek, T., Münzbergová, Z. (2023): Differential effect of climate of origin and cultivation climate on structural and biochemical plant traits. – Functional Ecology 37(5): 1436-1448. https://doi.org/10.1111/1365-2435.14291.

[25] Tomlinson, K. W., Poorter, L., Bongers, F., Borghetti, F., Jacobs, L., Van Langevelde, F. (2014): Relative growth rate variation of evergreen and deciduous savanna tree species is driven by different traits. – Annals of Botany 114(2): 315-324. https://doi.org/10.1093/aob/mcu107.
[26] Vendramini, F., Díaz, S., Gurvich, D. E., Wilson, P. J., Thompson, K., Hodgson, J. G. (2002): Leaf traits as indicators of resource-use strategy in floras with succulent species. – New Phytologist 154(1): 147-157. https://doi.org/10.1046/j.1469-8137.2002.00357.x.
[27] Wang, J., Wang, G., Fu, Y., Chen, X., Song, X. (2019): Short-term effects of nitrogen deposition on soil respiration components in two alpine coniferous forests, southeastern Tibetan Plateau. – Journal of Forestry Research 30(3): 1029-1041. https://doi.org/10.1007/s11676-018-0678-6.
[28] Wang, C. S., Lyu, W. W., Jiang, L. L., Wang, S. P., Wang, Q., Meng, F. D., Zhang, L. R. (2020): Changes in leaf vein traits among vein types of alpine grassland plants on the Tibetan Plateau. – Journal of Mountain Science 17(9): 2161-2169. https://doi.org/10.1007/s11629-020-6069-4.
[29] Weraduwage, S. M., Kim, S. J., Renna, L., Anozie, F. C., Sharkey, T. D., Brandizzi, F. (2016): Pectin methylesterification impacts the relationship between photosynthesis and plant growth. – Plant Physiology 171(2): 833-848. https://doi.org/10.1104/pp.16.00173.
[30] Westoby, M., Wright, I. J. (2006): Land-plant ecology on the basis of functional traits. – Trends in Ecology and Evolution 21(5): 261-268. https://doi.org/10.1016/j.tree.2006.02.004.
[31] Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornellssen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Villar, R. (2004): The worldwide leaf economics spectrum. – Nature 428(6985): 821-827. https://doi.org/10.1038/nature02403.
[32] Yang, K., Chen, G., Xian, J., Yu, X., Wang, L. (2021): Scaling relationship between leaf mass and leaf area: A case study using six alpine Rhododendron species in the Eastern Tibetan Plateau. – Global Ecology and Conservation 30(May): e01754. https://doi.org/10.1016/j.gecco.2021.e01754.
[33] Yang, K., Chen, G., Xian, J., Chen, W. (2022): Varying Relationship Between Vascular Plant Leaf Area and Leaf Biomass Along an Elevational Gradient on the Eastern Qinghai-Tibet Plateau. – Frontiers in Plant Science 13(April): 1-12. https://doi.org/10.3389/fpls.2022.824461.
[34] Yang, J., Gao, Y., Zhao, C., Chen, H. (2023): Leaf phenotypic plasticity and integration balance plant adaptation to water table decline: a mesocosm experiment. – Plant and Soil 497: 611-627. https://doi.org/10.1007/s11104-023-06418-4.
[35] Yu, J., Li, Q., Wu, X., Zhu, C., Huang, S., Yang, F., Hou, X. (2023): Adaptational responses of leaf functional traits of Dicranopteris dichotoma to environmental factors in different vegetational restoration stages. – Global Ecology and Conservation 44: e02484. https://doi.org/10.1016/j.gecco.2023.e02484.
[36] Zhang, Z. H., Hu, G., Zhu, J. D., Luo, D. H., Ni, J. (2010): Spatial patterns and interspecific associations of dominant tree species in two old-growth karst forests, SW China. – Ecological Research 25(6): 1151-1160. https://doi.org/10.1007/s11284-010-0740-0.
[37] Zirbel, C. R., Bassett, T., Grman, E., Brudvig, L. A. (2017): Plant functional traits and environmental conditions shape community assembly and ecosystem functioning during restoration. – Journal of Applied Ecology 54(4): 1070-1079. https://doi.org/10.1111/1365-2664.12885.
[38] Zou, Z., Yuan, K., Ming, L., Li, Z., Yang, Y., Yang, R., Cheng, W., Liu, H., Jiang, J., Luan, T., Chen, B. (2022): Changes in Alpine Soil Bacterial Communities with Altitude and Slopes at Mount Shergyla, Tibetan Plateau: Diversity, Structure, and Influencing Factors. – Frontiers in Microbiology 13(May): 1-11. https://doi.org/10.3389/fmicb.2022.839499.

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