Leaf Functional Trait Variation and Trade-offs Among Dominant Desert Plant Species in the Hexi Corridor (Postprint)

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Abstract

The variation characteristics and trade-off relationships of leaf functional traits among different life-form plants in the Hexi Corridor are of significant importance for maintaining ecosystem stability in this region. To understand the adaptation mechanisms and ecological strategies of different life-form plants to arid environments, survey plots were established along a natural precipitation decreasing gradient from southeast to northwest in the Hexi Corridor, covering eastern, middle, and western sections, with 26 dominant desert plant species selected (14 shrubs and 12 herbs) to analyze the variation characteristics and regional patterns of 14 key leaf functional traits and explore trade-off relationships among leaf functional traits and adaptation strategies. The results showed that: (1) The coefficients of variation for leaf bound water content (BW), carbon to phosphorus ratio (C:P), plant height (H), and leaf free water content (FW) in dominant desert plant species of the Hexi Corridor exceeded 100%. (2) Plants in different regions of the Hexi Corridor (eastern, middle, and western sections) exhibited diverse survival strategies. In the eastern section, both shrubs and herbs were positioned closer to the 'slow investment-return' end of the Leaf Economics Spectrum (LES). In the middle section, shrubs were located at the 'slow investment-return' end of the LES, whereas herbs were positioned closer to the 'fast investment-return' end. In the western section, shrubs adopted a 'fast investment-return' strategy under resource-rich conditions, while herbs employed a 'slow investment-return' strategy under adverse soil conditions. In summary, plant survival strategies are influenced by multiple ecological factors and achieve adaptation to arid environments through optimized combinations of traits and trade-off allocation of resources.

Full Text

Variation and Trade-offs in Leaf Functional Traits of Dominant Desert Plant Species in Hexi Corridor

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Abstract

The characteristics of variation in leaf functional traits among different plant life forms and their trade-off relationships in the Hexi Corridor are crucial for maintaining ecosystem stability in this region. To understand the adaptive mechanisms and ecological strategies of different life forms in arid environments, we established survey plots in the eastern, central, and western sections along a natural precipitation gradient from southeast to northwest across the Hexi Corridor. We selected 26 dominant desert plant species (14 shrubs and 12 herbaceous plants) and analyzed the variability and regional patterns of 14 key leaf functional traits, while examining trade-off relationships and adaptive strategies among these traits. The results showed that: (1) The coefficient of variation for leaf bound water content (BW), carbon-to-phosphorus ratio (C:P), plant height (H), and leaf free water content (FW) exceeded 100%. (2) Plants exhibited diverse survival strategies across different regions: species in the eastern section adopted a "slow-return" strategy; shrubs and herbs in the central section displayed "slow-return" and "fast-return" strategies, respectively; while shrubs in the western section adopted a "rapid resource acquisition" strategy under resource-rich conditions, and herbaceous plants adopted a "slow-return" strategy under unfavorable soil conditions. In conclusion, plant survival strategies are influenced by multiple ecological factors, and adaptation to arid environments is achieved through optimized trait combinations and resource allocation trade-offs.

Keywords: desert plants; functional traits; leaf economics spectrum; Hexi Corridor

Introduction

Plant functional traits represent key attributes that enable plants to perform important roles in ecosystems, directly affecting their establishment, growth, and survival. These traits reflect plant adaptive strategies under various environmental pressures, either individually or in combination. They influence not only individual plant performance but also community structure and function, thereby affecting ecosystem processes such as nutrient cycling, water utilization, and energy flow, ultimately altering entire ecosystem dynamics. Phenotypic plasticity of leaf functional traits—morphological and physiological changes in response to environmental variation—provides an objective reflection of individual plant response strategies. Through long-term adaptation, plants adjust their functional traits to cope with changes in environmental factors such as climate, topography, and soil. Trait interactions (trait combinations) are more effective than single traits in matching plant responses to drought stress, indicating that plants rely not on isolated characteristics but on integrated performance of interconnected functional traits to adapt to environmental changes.

Previous research on desert plant functional traits has focused primarily on small-scale comparisons and correlation analyses among different life forms, as well as responses of ecological stoichiometric traits to water and salinity changes. However, studies addressing patterns and trade-off relationships of leaf functional traits across life forms in desert plants remain relatively scarce. While trade-off relationships among plant functional traits are typically examined through large-scale interspecific trait data, some studies suggest that correlations among leaf traits are stronger at smaller spatial scales. This implies that conclusions from large-scale studies may not directly apply to small-scale investigations, as high correlations at local scales likely reflect strong influences of local environmental factors that drive consistent trait combinations within relatively narrow ecological niches. Therefore, in-depth investigation of trade-off relationships among leaf functional traits of desert plants at local scales can complement and refine large-scale research findings, revealing plant adaptation mechanisms in specific environments and making them more broadly applicable across different ecosystems.

Desert plants have adapted to arid climates and special natural conditions, possessing unique physiological and morphological characteristics. Consequently, studying variation in leaf functional traits and trade-off strategies of dominant desert species can help reveal how these plants respond to environmental changes and provide deeper understanding of their growth, development, and ecological response mechanisms. The Hexi Corridor desert region, located at the northern foothills of the Qilian Mountains, presents a natural aridity gradient intensifying from east to west, creating an ideal natural laboratory for studying these distinctive desert plants. This research established plots in three regions from southeast to northwest across the Hexi Corridor, selecting 26 dominant desert species to measure 14 leaf functional traits, aiming to reveal adaptive strategies of different regional plants under drought stress through analysis of trait variation patterns and trade-off relationships.

1 Materials and Methods

1.1 Study Area Overview

The Hexi Corridor (37°10 ~42°50 N, 93°20 ~104°00 E) is located in northwestern Gansu Province, extending approximately 1000 km with a total area of 27.11$×10^{4}$ km^2, accounting for about 60% of Gansu' s total area. The region features diverse landforms and numerous rivers, including three major inland river systems: the Shiyang River, Heihe River, and Shule River. Water resource utilization in these rivers far exceeds international warning thresholds, leading to ecological and environmental problems including vegetation degradation and desertification at various temporal and spatial scales. The distribution of study plots and surveyed dominant desert plant species is shown in [Figure 1: see original paper].

1.2 Experimental Design

Along the natural precipitation gradient in the Hexi Corridor, we established 16 fixed sample belts (designated HX1-HX16), with each belt containing survey plots. Within each plot, we randomly established 20 m × 20 m shrub quadrats, and at each corner of these quadrats, we set up 1 m × 1 m herbaceous quadrats. Community surveys and leaf functional trait sampling were conducted in each quadrat.

1.3 Leaf Functional Trait Measurement

We measured 14 leaf functional traits: leaf total water content (TWC), relative water content (RWC), bound water content (BW), free water content (FW), bound-to-free water ratio (BW:FW), leaf carbon content (C), leaf nitrogen content (N), carbon-to-nitrogen ratio (C:N), leaf phosphorus content (P), carbon-to-phosphorus ratio (C:P), leaf dry matter content (LDMC), specific leaf volume (SLV), specific leaf area (SLA), leaf thickness (LT), plant height (H), and leaf succulence (Suc).

Fresh leaf mass was weighed using an analytical balance (precision 0.0001 g). Leaf thickness was measured at the middle portion of leaves using a vernier caliper. Leaf area (LA) was scanned using a leaf area meter. Fresh leaves were soaked in deionized water in darkness for 24 hours, then saturated fresh mass was weighed. Leaves were oven-dried at 105°C for 30 minutes, then at 80°C to constant weight for dry mass measurement. Leaf carbon content was determined using the potassium dichromate method, nitrogen content by the Kjeldahl method, and phosphorus content by molybdenum-antimony colorimetry after H_2SO_4-H_2O_2 digestion. Relevant indices were calculated as follows:

$$\mathrm{TWC} = \frac{\mathrm{LFW} - \mathrm{LDW}}{\mathrm{LDW}} \times 100$$

$$\mathrm{RWC} = \frac{\mathrm{LFW} - \mathrm{LDW}}{\mathrm{LSFW} - \mathrm{LDW}} \times 100$$

$$\mathrm{LDMC} = \frac{\mathrm{LDW}}{\mathrm{LFW}} \times 1000$$

$$\mathrm{SLA} = \frac{\mathrm{LA}}{\mathrm{LDW}}$$

$$\mathrm{SLV} = \frac{\mathrm{LV}}{\mathrm{LA}}$$

$$\mathrm{Suc} = \frac{\mathrm{LFW} - \mathrm{LDW}}{\mathrm{LA}}$$

where LFW is leaf fresh weight, LDW is leaf dry weight, LSFW is leaf saturated fresh weight, LA is leaf area, and LV is leaf volume.

1.4 Statistical Analysis

We used one-way ANOVA to analyze variation and significance of leaf traits among different regions, and independent sample t-tests to analyze variation and significance of each trait. Principal Component Analysis (PCA) was employed to examine distribution patterns of leaf functional traits.

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2 Results

2.1 Variation in Leaf Functional Traits of Dominant Shrubs and Herbs in Hexi Corridor

Interspecific differences in leaf functional traits are shown in . For shrubs, the coefficient of variation was highest for leaf nitrogen-to-phosphorus ratio (172.57%), followed by leaf carbon-to-phosphorus ratio (127.13%), leaf phosphorus content, and bound-to-free water ratio (122.20% and 104.67%, respectively), while leaf relative water content showed the lowest variation (14.76%). For herbs, the bound-to-free water ratio exhibited the highest coefficient of variation (132.54%), followed by bound water content (103.22%), while leaf relative water content again showed the lowest variation (19.23%). Substantial differences existed between maximum and minimum values for each trait. These results indicate that shrub leaf nitrogen-to-phosphorus ratio, carbon-to-phosphorus ratio, phosphorus content, and bound-to-free water ratio, as well as herb bound-to-free water ratio and bound water content, are highly sensitive to the aridity gradient, whereas leaf relative water content remains relatively stable.

2.2 Principal Component Analysis of Leaf Functional Traits in Eastern, Central, and Western Hexi Corridor

PCA of shrub traits revealed that the first and second principal components explained 28.74% and 16.57% of variance, respectively, with a cumulative explanation of 45.31%. The first principal component was positively correlated with leaf bound water content, total water content, and specific leaf volume, and negatively correlated with leaf dry matter content. The second principal component was positively correlated with leaf thickness and free water content, and negatively correlated with specific leaf area (). Combined with [Figure 2: see original paper], shrub traits varied significantly along the first axis: eastern section shrubs showed high leaf total water content and bound water content but low leaf dry matter content, plant height, leaf carbon content, and carbon-to-nitrogen ratio; central section shrubs displayed higher water physiological traits and lower leaf dry matter content; while western section shrubs exhibited high leaf total water content, bound water content, specific leaf volume, and leaf succulence.

For herbaceous plants, the first and second principal components explained 36.67% and 20.80% of variance, respectively, totaling 57.47%. The first principal component was positively correlated with leaf total water content, bound water content, and succulence, and negatively correlated with leaf dry matter content. The second principal component was positively correlated with leaf relative water content and negatively correlated with leaf nitrogen content and nitrogen-to-phosphorus ratio (). Eastern section herbs showed high leaf total water content, bound water content, and succulence with low leaf dry matter content. Central section herbs exhibited higher leaf total water content, bound water content, succulence, and nitrogen-to-phosphorus ratio with low leaf dry matter content. Western section herbs displayed high leaf total water content, bound water content, relative water content, and succulence, also with low leaf dry matter content ([Figure 2: see original paper]).

2.3 Differences in Leaf Functional Traits Among Eastern, Central, and Western Sections of Hexi Corridor

Comparisons among the three sections revealed that eastern section shrubs had significantly higher leaf total water content, bound water content, bound-to-free water ratio, specific leaf volume, and succulence than western section shrubs ($P < 0.05$), with central section shrubs showing intermediate values. Eastern section shrubs also had significantly higher leaf dry matter content and plant height than central and western shrubs. All regions showed leaf nitrogen-to-phosphorus ratios > 20, indicating widespread phosphorus limitation, most severe in the central section (highest ratio).

For herbaceous plants, eastern and western sections showed higher leaf relative water content, leaf dry matter content, and carbon-to-nitrogen ratio, but lower bound water content, nitrogen content, and nitrogen-to-phosphorus ratio, all significantly different from the central section ($P < 0.05$). The eastern section herb community nitrogen-to-phosphorus ratio was 16.7, suggesting co-limitation by nitrogen and phosphorus, while central and western sections had ratios > 20, indicating phosphorus limitation, most severe in the central section ().

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3 Discussion

3.1 Analysis of Leaf Functional Trait Differences

Plants can balance negative effects of resource competition through phenotypic plasticity, with the magnitude of trait variation reflecting their ecological adaptive range. Bound water, free water, and their ratio are closely related to plant growth and stress resistance. When the bound-to-free water ratio is high, protoplasm exists in a gel state, metabolic activity weakens, and growth slows, but resistance increases. This study found high variability in shrub bound-to-free water ratio and herb bound water content and bound-to-free water ratio (>100%), indicating high sensitivity to the aridity gradient. Shrub bound water content and bound-to-free water ratio, and herb bound water content, were significantly lower in the eastern section than in other sections. Under drought stress, some free water converts to bound water in desert plant tissues, which helps slow metabolism. Increased bound water content and bound-to-free water ratio enhance leaf tissue osmotic potential, improving water retention capacity of protoplasm colloids and effectively reducing damage from drought stress, allowing plants to maintain minimal physiological requirements under extreme resource limitation.

Carbon serves as substrate and energy for physiological and biochemical processes. Nitrogen is a key component of many photosynthetic enzymes and proteins, participating in chlorophyll synthesis and determining photosynthetic capacity. Phosphorus is crucial for photosynthetic pigment synthesis and participates in energy transfer as ATP. This study found high variation in leaf phosphorus content (>100%) but low variation in leaf carbon and nitrogen content, possibly reflecting plant self-regulation mechanisms that adjust nutrient content to cope with drought while maintaining balance within limits, or reflecting soil nutrient availability. Leaf nitrogen-to-phosphorus ratio typically assesses whether plant growth is limited by nitrogen or phosphorus. In the Hexi Corridor, all nitrogen-to-phosphorus ratios exceeded 20, indicating widespread phosphorus limitation, most severe in the central section. Since leaf phosphorus content is partially influenced by soil phosphorus availability, this may explain significant variation in shrub leaf phosphorus content. High leaf carbon-to-phosphorus ratio reflects plant growth efficiency and nutrient uptake efficiency, with higher ratios indicating greater phosphorus use efficiency.

3.2 Patterns of Leaf Functional Traits

Plants adjust trait plasticity to adapt to environmental changes, with this capacity determining survival and reproductive success, especially in extreme environments. Shrubs, as primary species for windbreak and sand fixation, are crucial for understanding adaptation mechanisms to harsh conditions. Eastern section shrubs showed high leaf dry matter content, plant height, carbon content, and carbon-to-nitrogen ratio but low water traits. Central section shrubs adopted strategies of high leaf dry matter content and high water physiological traits. Western section shrubs exhibited high leaf total water content, bound water content, leaf thickness, specific leaf volume, and succulence, closely related to halophyte community adaptation to saline stress.

Herbaceous plants, such as alfalfa, have drought-resistant and soil-fixing capabilities, and studying their functional traits can provide scientific basis for desert ecosystem restoration and sustainable management. Eastern section herbs were concentrated along the first PCA axis, with high leaf total water content, bound water content, succulence, nitrogen content, and nitrogen-to-phosphorus ratio but low leaf dry matter content. Central section herbs showed high leaf total water content, bound water content, succulence, and nitrogen-to-phosphorus ratio with low leaf dry matter content. Western section herbs displayed high leaf total water content, bound water content, relative water content, succulence, and leaf dry matter content.

Both shrubs and herbs adapt to environmental gradients by increasing leaf total water content, bound water content, and leaf dry matter content. Increased total water content enhances drought tolerance, while bound water helps maintain cell wall integrity, crucial for abiotic stress tolerance. Increased free water content promotes solute accumulation, enhancing osmotic regulation and water stress resistance. Leaf dry matter content, related to leaf tissue density, affects growth rate, leaf lifespan, and resource storage. Morphologically, shrubs optimize resource use by increasing leaf thickness and adjusting specific leaf volume to build more effective protective structures. Increased leaf nitrogen content enhances leaf water retention, further improving drought adaptation. Herbaceous plants regulate leaf nitrogen content and nitrogen-to-phosphorus ratio to promote photosynthesis and improve drought adaptation. These mechanisms enable different life forms to optimize resource use and enhance survival under drought, poor soil, and saline-alkali stresses.

3.3 Trade-off Strategies of Leaf Functional Traits

Studying variation and trade-off strategies of leaf functional traits is essential for understanding plant ecological adaptation under different environmental conditions. Functional traits reflect trade-offs between resource acquisition and conservation, revealing complex ecological adaptation strategies under environmental pressure. Wright et al. proposed the "leaf economics spectrum" concept, revealing two investment strategies: a "fast-return" strategy characterized by low-cost leaves (low leaf mass per area), common in herbs and grasses, and a "slow-return" strategy characterized by high-cost leaves (high leaf mass per area). Although the leaf economics spectrum is universal at global scales, at regional scales, trade-offs between functional traits and adaptive strategies are also influenced by community composition, life form, and special topography.

Among functional trait parameters, leaf dry matter content, nitrogen content, phosphorus content, leaf thickness, and water physiological traits are optimal variables along the resource-use axis, showing good predictability. Eastern section shrubs showed high leaf dry matter content and low water physiological traits, indicating that with low leaf water content, shrubs increase dry matter content to improve tolerance and resistance against drought, consistent with previous research. In the high-elevation central section with nutrient-rich environments, shrubs also tended toward high leaf dry matter content and low leaf thickness, adopting a "slow-return" strategy, suggesting elevation may be an important factor mediating plant survival strategy selection. Herbaceous plants showed high leaf nitrogen content and nitrogen-to-phosphorus ratio, adopting a "fast-return" strategy with rapid photosynthesis and growth rates, consistent with previous studies.

In the resource-rich western section, shrubs had low leaf dry matter content, short stature, and high water physiological traits, positioning them on the "fast-return" side of the leaf economics spectrum. However, under conditions where soil texture limits available phosphorus, herbaceous communities increased leaf dry matter content, decreased leaf nitrogen content, reduced leaf water content, and showed low photosynthetic rates, presenting a "slow-return" strategy on the leaf economics spectrum. Thus, different life forms of desert plants employ different environmental adaptation strategies through trade-offs among leaf functional trait combinations.

4 Conclusion

This study investigated 26 dominant desert plant species in the Hexi Corridor, analyzing 14 morphological, water physiological, and ecological stoichiometric traits to reveal variation patterns and regional differences in functional traits among different life forms. The findings demonstrate that: (1) Desert plants exhibit significant variation in leaf functional traits, with shrubs showing high sensitivity in nitrogen-to-phosphorus ratio, carbon-to-phosphorus ratio, phosphorus content, and bound-to-free water ratio, while herbs show high sensitivity in bound water content and bound-to-free water ratio. (2) Different life forms in different regions adopt varying ecological strategies: eastern section plants show a "slow-return" strategy; central section shrubs and herbs display "slow-return" and "fast-return" strategies respectively; western section shrubs adopt a "fast-return" strategy under resource-rich conditions, while herbs adopt a "slow-return" strategy under poor soil conditions. (3) Plant survival strategies are influenced by multiple ecological factors, achieving adaptation to arid environments through optimized trait combinations and resource allocation trade-offs. These results provide a scientific basis for understanding desert plant adaptation mechanisms and offer guidance for vegetation restoration and management in arid regions.

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