Postprint: Study on the Relationship Between Soil Factors and Leaf Functional Traits in Nitraria Shrub Sand Dunes at Different Successional Stages

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Abstract

The relationship between plant functional traits and the environment constitutes a focal point of functional trait research; environmental factors drive changes in plant functional traits, thereby promoting community succession. This study investigated Nitraria tangutorum shrub sand dunes at different successional stages (development stage, stable stage, decline stage, severe decline stage) in Minqin, analyzing differences in leaf functional traits of N. tangutorum across these stages and their relationships with soil factors, aiming to reveal the adaptive strategies of N. tangutorum to soil environments in arid desert regions. The results indicate: (1) Leaf thickness, leaf dry matter content, and leaf total phosphorus content of N. tangutorum differ significantly among different successional stages ($P<0.05$), while other leaf functional traits show no significant differences ($P>0.05$). The coefficient of variation for leaf functional traits of N. tangutorum ranges from 0.39% to 11.99%, all exhibiting weak variation, with specific leaf area being the highest (11.99%) and leaf total carbon content being the lowest (0.39%). (2) Certain correlations exist among leaf functional traits of N. tangutorum; leaf thickness, leaf dry matter content, and leaf total nitrogen content can serve as primary indicators of changes in leaf functional traits of N. tangutorum. (3) Except for pH, soil factors of N. tangutorum shrub sand dunes exhibit a trend of first increasing and then decreasing with increasing degradation degree, with minimum values appearing at the development stage and maximum values at the decline stage. Soil available phosphorus content and total nitrogen content are the main soil factors influencing changes in leaf functional traits of N. tangutorum. These findings deepen our understanding of the succession of N. tangutorum shrub sand dunes and provide an important reference basis for the restoration and protection of desert ecosystems.

Full Text

Relationship between Soil Factors and Leaf Functional Traits of *Nitraria tangutorum* Shrub at Different Succession Stages

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Abstract

The relationship between plant functional traits and environmental factors represents a central focus in functional trait research. Environmental factors drive changes in plant functional traits, thereby promoting community succession. This study examined *Nitraria tangutorum* shrubs at different succession stages (development stage, stable stage, decline stage, and severe recession stage) in Minqin County, Gansu Province, analyzing differences in leaf functional traits and their relationships with soil factors to reveal the adaptation strategies of *N. tangutorum* to the soil environment in arid desert regions. The results showed that: (1) Significant differences existed in leaf thickness, leaf dry matter content, and leaf total phosphorus content among different succession stages ($P<0.05$), while other leaf functional traits showed no significant differences ($P>0.05$). The variation range of leaf functional traits in *N. tangutorum* was 0.39%~11.99%, all exhibiting weak variation, with specific leaf area showing the greatest variation (11.99%) and total carbon content the smallest (0.39%). (2) Certain correlations existed among leaf functional traits of *N. tangutorum*; leaf thickness, leaf dry matter content, and leaf total nitrogen content could serve as primary indicators of leaf functional trait variation. (3) Additionally, soil factors in *N. tangutorum* shrub nebkhas showed a trend of initially increasing then decreasing with increasing degradation, with minimum values appearing at the development stage and maximum values at the decline stage. Soil available phosphorus and total nitrogen content were the main soil factors influencing leaf functional trait variation in *N. tangutorum*. These findings deepen our understanding of *N. tangutorum* nebkha succession and provide an important reference for the restoration and protection of desert ecosystems.

Keywords: *Nitraria tangutorum*; leaf functional traits; soil factors; succession stages; Minqin County

Introduction

Plant functional traits represent the results of long-term plant adaptation to the external environment, with differences primarily manifested in nutrient element allocation and morphological structure among organs (leaves, stems, roots, and reproductive structures). Leaves are particularly sensitive to environmental change and highly plastic, carrying substantial information about environmental variation. Leaf functional traits are closely related to plant biomass and resource acquisition and utilization. The relationship between plant functional traits and environmental factors constitutes a hot topic in functional trait research, with soil considered the dominant factor influencing plant functional traits. Previous studies have demonstrated that soil can explain 33%~60% of trait variation such as specific leaf area. Research in subtropical evergreen broad-leaved forests found that soil water content and nitrogen content are the main soil factors causing spatial variation in plant functional traits. Studies in alpine meadows have shown that soil moisture and nutrient availability jointly influence plant functional traits. Investigations of island plant succession have identified soil organic matter and total nitrogen as key environmental factors affecting functional trait changes during succession. For temperate meadows, critical soil factors influencing community functional traits include soil carbon, total nitrogen, and bulk density, while for dry meadows it is soil bulk density, and for forest edge meadows it is the soil carbon-to-nitrogen ratio. Research on degraded succession stages has shown that community soil nutrients affect changes in plant functional traits. Therefore, studies on plant functional trait responses to soil factor changes at different succession stages can better reveal plant adaptation strategies to external environmental conditions.

Shrub nebkhas are a type of aeolian depositional landform developed under vegetation influence, representing a unique geomorphological type in China' s arid desert regions. They are widely distributed in the Minqin oasis-desert transition zone, predominantly composed of *Nitraria tangutorum* nebkhas. *Nitraria tangutorum* is a xerophytic or super-xerophytic shrub that is drought-resistant and barren-tolerant. After sand burial, its branches can produce new adventitious roots in moist sand, accumulating sand into mounds and forming fixed or semi-fixed shrub nebkhas. This species represents the largest surviving natural vegetation type in the Minqin arid desert region, playing a tremendous ecological role in windbreak, sand fixation, and maintaining oasis stability. Current research on *N. tangutorum* nebkhas in Minqin has primarily focused on soil respiration and community characteristics, with relatively few studies on leaf functional traits. Therefore, this study measured leaf functional traits of *N. tangutorum* in desert areas of Minqin at different succession stages (development stage, stable stage, decline stage, and severe recession stage), comparatively analyzed variation differences and interrelationships of leaf functional traits among stages, and revealed the influence of soil factors on leaf functional traits. This research deepens understanding of *N. tangutorum* nebkha succession and provides an important reference for desert ecosystem restoration and protection.

1 Study Area and Methods

1.1 Study Area Overview

The study area was located in the Minqin oasis-desert transition zone at the southeastern edge of the Badain Jaran Desert, with geographical coordinates of 38°34 ~39°38 N, 102°53 ~102°58 E and an elevation of 1376~1383 m. The region has a temperate continental arid climate with low precipitation, averaging 115.2 mm annually, and high evaporation, reaching 2419.6 mm—21 times the precipitation. The area has abundant heat resources and long sunshine duration, with annual average sunshine of 2832.1 h. The climate is characterized by strong winds and frequent sand, with an average wind speed of 2.5 m • s-1. The soil type is primarily aeolian sandy soil. Existing vegetation includes both natural and artificial types, with main shrub species including *Haloxylon ammodendron*, *Nitraria tangutorum*, and *Calligonum mongolicum*, and herbaceous species mainly including *Halogeton glomeratus*, *Salsola collina*, and *Agriophyllum squarrosum*.

1.2 Experimental Design and Methods

The experimental plots were established at the Minqin Comprehensive Desert Control Experimental Station (103°05 E, 38°35 N), near a dustfall observation tower in the concentrated distribution zone of *Nitraria tangutorum* nebkhas in the Minqin oasis-desert transition zone. Based on field surveys and existing classification standards, four different succession stages of *N. tangutorum* nebkhas were selected as study objects: development stage, stable stage, decline stage, and severe recession stage. The size, vegetation growth status, and aeolian accumulation conditions of nebkhas at each stage were relatively consistent to reduce experimental error, with three replicates per stage. Investigations were conducted on nebkha height, length, vegetation, and soil conditions. The basic characteristics of *N. tangutorum* nebkhas at different succession stages are shown in Table 1.

Sampling was conducted in July 2019 when plants were growing vigorously. Mature leaves from the upper-middle canopy were collected from five directions (east, west, south, north, and top) of nebkhas at each succession stage for leaf functional trait determination. Soil samples from the 0~60 cm layer were collected from the top of nebkhas using a soil auger, with three replicates per stage.

1.2.1 Leaf Functional Trait Measurement

- N. tangutorum* leaves and their attached twigs were cut and placed in a cooler for transport to the laboratory. Leaf fresh weight (mf) was measured immediately. Leaves were then completely immersed in deionized water until saturated (approximately 30 min), and leaf saturated weight (mt) was measured. Leaf length (L), width, and thickness were measured using a ruler and digital calipers. Leaf area (A) was determined using a leaf area meter (Yaxin-1241). Scanned leaves were placed in aluminum boxes, oven-dried at 105°C for 30 min, then dried at 70°C to constant weight to obtain leaf dry weight (md). Leaf water content (LWC) and leaf dry matter content (LDMC) were calculated as:

LWC (%) = (mf - md) / mf × 100
LDMC (mg・g-1) = md / mt × 1000

Specific leaf area (SLA) was calculated as SLA = A / md. Dried leaf samples were ground and passed through a 0.125 mm sieve for nutrient and carbon isotope analysis. Leaf stable carbon isotope (δ13C, ‰) was measured using a Picarro G2131-i CO2 isotope analyzer (USA). Leaf total carbon (C, mg・g-1) and total nitrogen (N, mg・g-1) were determined using a Costech ECS 4024 elemental analyzer (Italy). Leaf total phosphorus (P, mg・g-1) was measured using the molybdenum-antimony colorimetric method.

1.2.2 Soil Factor Measurement Six soil factors were measured: moisture content, organic matter, total nitrogen, available phosphorus, pH, and electrical conductivity. Soil moisture content was determined using the oven-drying method. Soil organic matter was measured using the potassium dichromate oxidation-external heating method. Total nitrogen was determined using the semi-micro Kjeldahl method. Available phosphorus was extracted with sodium bicarbonate and measured using the molybdenum-antimony colorimetric method. Soil pH was measured using the electrode method, and electrical conductivity was determined using a conductivity meter.

1.3 Data Statistics and Processing

Microsoft Excel 2003 and SPSS 19.0 were used for data statistics and analysis. The coefficient of variation (CV) was calculated to analyze the degree of variation. Generally, CV $\leq$ 20% indicates weak variation, 20% $<$ CV $\leq$ 50% indicates moderate variation, and CV $>$ 50% indicates strong variation. One-way ANOVA was used for variance analysis and multiple comparisons, Pearson correlation analysis was used to examine relationships among leaf functional traits, principal component analysis (PCA) was used to screen main indicators affecting leaf functional trait variation, and stepwise regression analysis was used to identify main soil factors influencing leaf functional traits.

2 Results

2.1 Differences in Leaf Functional Traits of *N. tangutorum* at Different Succession Stages

Leaf thickness showed an increasing trend with nebkha succession, with significant differences between the decline stage, severe recession stage and the stable stage, development stage ($P<0.05$). Leaf dry matter content showed a trend of first increasing then decreasing, reaching its maximum at the decline stage. Leaf total nitrogen content at the severe recession stage was significantly higher than at the development stage ($P<0.05$). Leaf total phosphorus content at the stable stage was significantly higher than at the development stage ($P<0.05$). Other leaf functional traits showed no significant differences among stages ($P>0.05$). Leaf length, leaf water content, and specific leaf area showed overall decreasing trends, while leaf stable carbon isotope showed an increasing trend. The coefficient of variation for all leaf traits at different succession stages indicated weak variation, with specific leaf area showing the greatest variation (11.99%) and total carbon content the smallest (0.39%) (Table 2).

2.2 Correlation and Principal Component Analysis of Leaf Functional Traits

2.2.1 Correlation Analysis of Leaf Functional Traits Pearson correlation analysis of leaf functional traits at different succession stages (Table 3) showed that leaf length was significantly negatively correlated with leaf total nitrogen content ($P<0.05$). Leaf thickness was significantly negatively correlated with leaf water content and significantly positively correlated with leaf dry matter content ($P<0.05$). Leaf water content was significantly negatively correlated with leaf dry matter content ($P<0.05$). Specific leaf area was extremely significantly positively correlated with leaf total carbon content ($P<0.01$). Other correlations among leaf functional traits were not significant ($P>0.05$).

2.2.2 Principal Component Analysis of Leaf Functional Traits Principal component analysis of leaf functional traits showed that the common factor variance of each indicator was relatively large, with leaf width having the smallest common factor variance at 30.009%. Using eigenvalues >1 as the criterion, three principal components were extracted with eigenvalues of 3.746, 1.277, and 1.136, respectively. The contribution rates of the three principal components were 20.776%, 15.954%, and 14.198%, respectively, with a cumulative contribution rate of 80.938%. These three principal components represented the main factors influencing leaf functional trait variation. Based on comprehensive score ranking, leaf thickness, leaf dry matter content, and leaf total nitrogen content could serve as primary indicators of leaf functional trait variation (Table 4).

2.3 Differences in Soil Factors of *N. tangutorum* Nebkhas at Different Succession Stages

With increasing succession of *N. tangutorum* nebkhas, soil factors (except pH) showed a trend of first increasing then decreasing, with minimum values at the development stage and maximum values at the decline stage. The decline stage showed significant differences from other stages ($P<0.05$). Soil pH showed the opposite trend, with minimum values at the decline stage and maximum values at the development stage. Overall, as nebkha succession progressed, soil water content, organic matter, total nitrogen, available phosphorus, and electrical conductivity initially increased then decreased, declining again at the severe recession stage (Table 5).

2.4 Relationship Between Leaf Functional Traits and Soil Factors

Leaf width, leaf thickness, leaf water content, leaf dry matter content, leaf total nitrogen content, and leaf stable carbon isotope were significantly correlated with soil factors ($P<0.05$), while leaf length, specific leaf area, leaf total carbon content, and leaf total phosphorus content showed no significant correlation with soil factors ($P>0.05$). Stepwise regression analysis showed that leaf width and leaf water content were significantly correlated with soil available phosphorus content ($P<0.05$); leaf thickness was extremely significantly correlated with soil total nitrogen content ($P<0.01$); leaf total nitrogen content was significantly correlated with soil electrical conductivity ($P<0.05$); and leaf stable carbon isotope was significantly correlated with soil water content ($P<0.05$). Thus, leaf functional traits of *N. tangutorum* were mainly affected by soil available phosphorus, total nitrogen, electrical conductivity, and water content, with available phosphorus and total nitrogen being the primary soil factors influencing leaf functional traits at different succession stages (Table 6).

3 Discussion

3.1 Changes in Leaf Functional Traits of *N. tangutorum* with Nebkha Succession

Indicators such as leaf length, leaf width, leaf thickness, specific leaf area, and leaf dry matter content reflect plant resource acquisition and utilization capabilities, which are closely related to plant growth and survival. In this study, leaf length gradually decreased with succession, leaf thickness gradually increased, and specific leaf area and leaf dry matter content showed trends of first increasing then decreasing. These patterns may be related to differences in survival strategies of *N. tangutorum* at different succession stages. As succession progressed, leaf traits shifted from an exploitative strategy (longer, thinner leaves with higher specific leaf area and dry matter content) to a conservative strategy (shorter, thicker leaves with lower specific leaf area and dry matter content). This indicates that in early succession stages, *N. tangutorum* had higher growth rates and resource acquisition capacity, while in middle and late stages, it adapted to the environment by reducing specific leaf area and increasing leaf thickness, decreasing heat exchange with the atmosphere and allocating more organic matter to protective tissues or mesophyll density to improve water use efficiency.

Leaf stable carbon isotope reflects plant water use efficiency. In this study, leaf stable carbon isotope showed a trend of first decreasing then increasing with nebkha succession. The reason may be that in early and middle succession stages, canopy closure and litter improved soil nutrients and moisture, making resources more abundant. At the severe recession stage, nebkha activation reduced soil nutrients and moisture. However, leaf stable carbon isotope did not reach significant difference levels among succession stages. Leaf total carbon, nitrogen, and phosphorus contents also showed certain differences among stages, possibly related to plant self-regulation mechanisms and nutrient element content in nebkha soils.

3.2 Correlation and Principal Component Analysis of Leaf Functional Traits

Plant leaf functional traits do not function in isolation but are correlated, achieving coordination and trade-offs through regulating resource allocation to improve adaptation to the external environment. In this study, leaf thickness was negatively correlated with specific leaf area and significantly positively correlated with leaf dry matter content ($P<0.05$), consistent with Ohashi et al.' s findings. As nebkha succession progressed, *N. tangutorum* improved water use efficiency by reducing specific leaf area and increasing leaf thickness. Specific leaf area was extremely significantly positively correlated with leaf total carbon content ($P<0.01$), because specific leaf area reflects plant resource acquisition capacity, which is closely related to carbon assimilation and resource utilization.

Principal component analysis should focus on indicators with high composite scores. In this study, leaf thickness, leaf dry matter content, and leaf total nitrogen content could serve as primary indicators of leaf functional trait variation. Leaf thickness and dry matter content comprehensively reflect plant resource utilization capacity, while nitrogen content affects physiological processes and carbon allocation. Together, they demonstrate that *N. tangutorum* adapts to the Minqin arid desert environment by adjusting its physiological characteristics.

3.3 Relationship Between Leaf Functional Traits and Soil Factors

Soil environment provides material and energy for plant growth and development, significantly influencing plant growth strategy selection. In this study, as *N. tangutorum* nebkhas succeeded, soil factors (except pH) showed a trend of first increasing then decreasing, consistent with previous research showing that mature nebkhas have higher soil water content and nutrients than early stages. Soil water content at the decline stage was higher than at other stages, differing from some previous studies, mainly due to differences in nebkha crust, vegetation coverage, fixation degree, and groundwater.

Plant-soil interactions involve strong material transformation. On one hand, plant litter releases nutrients back to soil through microbial decomposition while roots affect soil physicochemical properties; on the other hand, soil provides water and nutrients for plant growth, affecting functional trait changes. This study found that leaf width, leaf thickness, leaf water content, leaf dry matter content, leaf total nitrogen content, and leaf stable carbon isotope were significantly correlated with soil factors ($P<0.05$), indicating that *N. tangutorum* leaf functional traits respond significantly to soil factor changes.

Soil available phosphorus content was the main factor affecting these leaf functional traits. Phosphorus directly participates in oxidative phosphorylation and photophosphorylation during plant growth, limiting photosynthesis and chlorophyll fluorescence and affecting nitrogen absorption. Zhang et al.' s research on *Pinus tabuliformis* also found that leaf thickness, dry matter content, total nitrogen, and total phosphorus were related to soil phosphorus content. Soil electrical conductivity reflects soil salinity; this study found leaf total nitrogen content was significantly positively correlated with electrical conductivity ($P<0.05$), consistent with Cao et al.' s findings, possibly because high salinity inhibits protein synthesis, leading to increased amino acids and nitrogen content. Numerous studies have shown that plant carbon isotope values decrease with increasing water availability. This study found leaf stable carbon isotope was significantly negatively correlated with soil water content ($P<0.05$), indicating that soil water content significantly affects leaf water use efficiency in *N. tangutorum*.

In summary, *N. tangutorum* nebkha degradation manifests not only in nebkha activation and growth decline but also in significant changes in leaf functional traits driven by soil nutrient changes. The results reveal the role of soil factors in nebkha succession and their influence on community construction mechanisms, providing an important reference for desert ecosystem restoration and protection.

4 Conclusion

This study analyzed differences in leaf functional traits of *N. tangutorum* at different succession stages and their relationships with soil factors, reaching the following main conclusions:

(1) As *N. tangutorum* nebkhas succeeded, leaf traits shifted from an exploitative strategy (longer, thinner leaves with higher specific leaf area and dry matter content) to a conservative strategy (shorter, thicker leaves with lower specific leaf area and dry matter content). The variation range of leaf functional traits was 0.39%~11.99%, all showing weak variation, with specific leaf area showing the greatest variation (11.99%) and total carbon content the smallest (0.39%).

(2) Certain correlations existed among leaf functional traits of *N. tangutorum*, which adapted to the extremely arid environment through specific synergistic/trade-off functional combinations. Leaf thickness, leaf dry matter content, and leaf total nitrogen content could serve as primary indicators of leaf functional trait variation.

(3) Soil factors in *N. tangutorum* nebkhas showed a trend of first increasing then decreasing with degradation, with minimum values at the development stage and maximum values at the decline stage. Leaf functional traits were affected by multiple soil factors, with soil available phosphorus and total nitrogen content being the main soil factors influencing leaf

functional trait variation.

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