

## Postprint: Leaf Structural and Chemical Trait Responses of *Tamarix ramosissima* to Soil Moisture Variation

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### Abstract

Desert plants have developed unique leaf functional traits through their struggle with extreme environments, representing one of their ecological strategies to adapt to long-term drought stress. This study investigated *Tamarix ramosissima* under different soil moisture conditions on the northern edge of the Tarim Basin, examining its population characteristics, leaf structural and chemical traits, and main soil physicochemical properties. The results showed: (1) Soil moisture significantly affected traits including leaf total nitrogen, total phosphorus, C:P, C:N, average leaf thickness, and average leaf area in *Tamarix*. (2) With increasing soil water content, the leaf N:P ratio exhibited a decreasing trend, with growth gradually shifting from phosphorus limitation to nitrogen limitation. (3) Leaf total phosphorus content was extremely significantly negatively correlated with C:P and N:P ( $P < 0.01$ ), while C:N was significantly positively correlated with average leaf area ( $P < 0.05$ ). (4) Soil water content is a crucial factor influencing leaf functional traits in *Tamarix*, which adapts to arid environments through synergistic variations among certain leaf traits. These findings provide a scientific basis for evaluating plant ecological adaptability during ecological protection and restoration in arid desert regions.

### Full Text

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**Responses of Leaf Structural and Chemical Traits of *Tamarix ramosissima* to Soil Water Changes**

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## Abstract

Desert plants have developed unique leaf functional traits through long-term adaptation to extreme environments, representing one of their ecological strategies for coping with persistent drought stress. This study investigated *Tamarix ramosissima* populations under different soil water conditions at the northern edge of the Tarim Basin, analyzing their leaf structural and chemical traits alongside key soil physicochemical properties. The results revealed three main findings: (1) Soil water content significantly affected multiple leaf traits of *T. ramosissima*, including total nitrogen content, total phosphorus content, C:P ratio, C:N ratio, mean leaf thickness, and mean leaf area. (2) As soil water content increased, the N:P ratio of *T. ramosissima* leaves decreased, indicating a gradual shift from phosphorus-limited to nitrogen-limited growth. (3) Total phosphorus content showed a highly significant negative correlation with both C:P and N:P ratios ( $P < 0.01$ ), while C:N ratio exhibited a significant positive correlation with mean leaf area ( $P < 0.05$ ). These findings demonstrate that soil water content is a crucial factor influencing leaf functional traits in *T. ramosissima*, and that the species adapts to arid environments through coordinated changes among certain leaf traits. This study provides a scientific basis for evaluating plant ecological adaptation during ecological conservation and restoration efforts in arid desert regions.

**Keywords:** *Tamarix ramosissima*; soil water content; leaf traits; ecological strategy; Tarim Basin

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## 1 Introduction

Soil moisture constitutes a vital component of soil, influencing soil formation and development as well as physical, chemical, and biological processes. As a key indicator of drought and land conditions, soil water content affects water and energy exchange in desert ecosystems and constrains their stability. Soil moisture conditions vary across different environments due to differences in climate, vegetation, topography, and soil texture. In arid regions where water resources are scarce, soil moisture represents the primary limiting factor for

plant growth, affecting seed survival rates, individual morphological characteristics, physiological traits, nutrient utilization strategies, life history patterns, and community features. These characteristics directly or indirectly influence plant fitness, thereby affecting individual and population growth, reproduction, and survival. Such characteristics are termed plant functional traits, which can be used to predict plant performance and distribution, explain diversity-productivity relationships, assess plant community responses to disturbance, and study ecosystem functions.

Leaf traits have become a research hotspot in ecology in recent years. Leaves represent the plant organ with the largest contact area with the external environment and are most sensitive to environmental changes, making them easy to observe and measure. Among leaf traits, structural and chemical characteristics receive the most attention. Structural traits reflect leaf biochemical architecture, including leaf area, thickness, specific leaf area, leaf dry matter content, and leaf mass per area, while chemical traits reflect leaf metabolism, including elemental composition and their proportional relationships. Numerous studies have examined how soil water variation affects leaf structural and chemical traits. At the global scale, leaf dry mass content increases with intensifying water stress. Feng et al. found that severe water stress significantly reduced total leaf area of *Zygophyllum xanthoxylum* and *Caragana korshinskii*. Xiong et al. observed that drought stress significantly increased the carbon-to-nitrogen ratio in maize leaves, likely due to drought-induced leaf senescence. Ren et al. discovered that under simulated precipitation increase, *Nitraria tangutorum* could enhance carbon sequestration capacity by expanding stomata. Ogaya et al. found that drought reduced leaf thickness and leaf mass per area in *Quercus ilex* and *Phillyrea latifolia*. However, research on leaf trait variation and trade-offs in extremely arid regions remains relatively limited.

The northern edge of the Tarim Basin experiences scarce precipitation and intense evaporation, representing an extremely arid and ecologically highly sensitive region in China. *Tamarix ramosissima* (hereafter referred to as tamarisk), due to its drought, salt, and barren tolerance, serves as a keystone species in this region and plays a crucial role in maintaining desert ecosystem stability. Groundwater levels vary considerably in this area, resulting in substantial differences in soil moisture conditions. This study aims to analyze the variation trends and correlations of tamarisk leaf structural and chemical traits under different soil water conditions, explore the ecological adaptation strategies of this typical desert plant, and provide a scientific basis for evaluating plant ecological adaptation during ecological conservation and restoration in arid desert regions.

### 1.1 Study Area Overview

The study area is located around Alar City at the northern edge of the Tarim Basin, with an average elevation of 1013 m. The region features a warm temperate continental arid climate, with an annual average temperature of 10.8°C, daily temperature range of 14–16°C, mean annual precipitation of 48.5 mm,

mean annual evaporation of approximately 2000 mm, and an average frost-free period of 220 days. The main soil types include irrigation desert soil, brown desert soil, saline soil, and aeolian soil. Vegetation cover is low, approximately 15–20%, with sparse species. Representative species include *Tamarix ramosissima*, *Populus euphratica*, *Haloxylon ammodendron*, *Phragmites australis*, *Alhagi sparsifolia*, and *Karelinia caspica*. Among these, tamarisk is the most widely distributed dominant species. Due to its characteristics of drought resistance, salt tolerance, and deep root systems, tamarisk plays an important role in climate regulation, saline soil improvement, and desertification control.

## 1.2 Survey and Sampling

In May 2021, we established sample plots in three habitats—oasis, transition zone, and desert—representing high, medium, and low soil water conditions, with soil water contents of 30.50%–32.85%, 17.23%–24.87%, and 0.07%–1.16%, respectively. Within each plot, we set up 20 m × 20 m survey quadrats and recorded detailed quantitative characteristics (density, coverage) and morphological features (height, crown width) of tamarisk populations. After completing the surveys, we selected tamarisk individuals with similar morphology and good growth, collected mature healthy leaves, placed them in envelopes, and transported them in a cooler to the laboratory. Simultaneously, we collected soil samples using a soil auger at 0–20 cm depth, removing surface litter, plant roots, stones, and other impurities before mixing thoroughly. The samples were divided into three portions: one placed in an aluminum box for soil water content determination, one in a sealed bag for soil physicochemical property analysis, and one stored separately.

## 1.3 Leaf Trait Measurement

Leaf trait measurements were conducted in May 2021. The structural traits measured included leaf area (LA), leaf thickness (LT), specific leaf area (SLA), leaf tissue density (LTD), and leaf dry matter content (LDMC). Chemical traits included leaf organic carbon content (C), nitrogen content (N), and phosphorus content (P).

**Structural trait measurement methods:** We selected fully expanded, healthy, and intact leaves. A portable scanner (CanoScan LiDE300) was used to obtain leaf images, which were analyzed using Win-RHIZO Pro 2009b software to determine leaf area. Leaf thickness was measured using a vernier caliper with 0.01 mm precision. Scanned leaves were oven-dried at 105°C for 0.5 hours, then at 75°C to constant weight to obtain leaf dry mass (LDMC). Specific leaf area and leaf tissue density were calculated using the formulas:  $SLA = LA/LDMC$  and  $LTD = LDMC/(LT \times LA)$ .

**Chemical trait measurement methods:** Dried leaves were ground using a grinder (NM200, Retsch, Germany) and passed through a 0.15 mm sieve before storage in sealed bags. Organic carbon content was determined using the potas-

sium dichromate external heating method. Total nitrogen was measured using an automatic Kjeldahl nitrogen analyzer (Kjeltec, Sweden). Phosphorus content was determined using the molybdenum-antimony anti-colorimetric method.

#### 1.4 Soil Index Measurement

Soil indices measured included soil water content (SWC), pH, and electrical conductivity (EC). Soil water content was determined using the drying method. pH and electrical conductivity were measured using the electrode potential method (soil-water ratio 1:5).

#### 1.5 Data Statistical Analysis

Data were organized using Excel 2019 and plotted using OriginPro 2019. One-way ANOVA was performed using R language to compare differences in plant leaf traits and soil indices under different soil water conditions. Pearson correlation analysis was used to examine relationships among leaf traits under different soil water conditions. Principal component analysis (PCA) was employed to identify the main factors driving leaf trait variation. In the PCA biplot, arrows represented tamarisk leaf structural and chemical traits, with the angle between arrows indicating correlation strength (larger angles indicate weaker correlations) and arrow length indicating the contribution to the first two ordination axes.

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## 2 Results and Analysis

### 2.1 Tamarisk Population Characteristics and Soil Physicochemical Properties Under Different Soil Water Conditions

Tamarisk height, crown width, and coverage differed significantly among soil water conditions ( $P < 0.05$ ). Height, crown width, and coverage under low soil water conditions were significantly lower than under high soil water conditions ( $P < 0.05$ ). Soil water content and electrical conductivity also differed significantly among conditions ( $P < 0.05$ ), with electrical conductivity under low soil water conditions significantly higher than under high conditions ( $P < 0.05$ ). As soil water content increased from low to high, plant coverage showed an increasing trend, while soil electrical conductivity showed the opposite trend. Plant coverage under high soil water conditions increased by 1.77 times compared to low conditions, while soil electrical conductivity decreased by 81.7%.

### 2.2 Variation in Tamarisk Leaf Traits

**2.2.1 Chemical Trait Variation** Tamarisk leaf total phosphorus, total nitrogen, C:P, C:N, and other chemical traits differed significantly among soil water conditions ( $P < 0.05$ ). C:P and N:P ratios under low soil water conditions were significantly higher than under medium conditions ( $P < 0.05$ ), increasing by

47.4% and 45.2%, respectively. Total phosphorus and total nitrogen contents under low soil water conditions were significantly lower than under medium conditions ( $P < 0.05$ ), decreasing by 31.8% and 25.0%, respectively.

[Figure 1: see original paper]

**2.2.2 Structural Trait Variation** Tamarisk leaf mean thickness and mean area differed significantly among soil water conditions ( $P < 0.05$ ). As soil water conditions shifted from low to high, both mean thickness and mean area peaked under medium soil water conditions. Mean thickness under medium conditions was significantly higher than under high conditions ( $P < 0.05$ ), while mean area under medium conditions was significantly higher than under low conditions ( $P < 0.05$ ). No significant differences were observed between low and high conditions for either trait.

[Figure 2: see original paper]

### 2.3 Correlations Among Tamarisk Leaf Traits

As shown in , total phosphorus content showed a highly significant negative correlation with C:P and N:P ratios ( $P < 0.01$ ) and a significant negative correlation with mean leaf thickness ( $P < 0.05$ ). Total nitrogen content showed a highly significant negative correlation with C:N ratio ( $P < 0.01$ ) and significant negative correlations with mean leaf thickness ( $P < 0.05$ ). C:N ratio showed a significant positive correlation with mean leaf area ( $P < 0.05$ ). Mean leaf thickness showed a significant positive correlation with leaf tissue density ( $P < 0.05$ ).

### 2.4 Principal Component Analysis of Tamarisk Leaf Traits

The principal component loading matrix () showed that the first, second, and third principal components explained 51.3%, 24.7%, and 14.5% of total variance, respectively, collectively accounting for 90.5% of variance. The first principal component was most strongly influenced by C:P ratio, leaf tissue density, and organic carbon content. The second principal component was most strongly influenced by mean leaf area, mean leaf thickness, and organic carbon content. The third principal component was most strongly influenced by total phosphorus, total nitrogen, and specific leaf area.

In the PCA biplot ([Figure 3: see original paper]), C:P ratio, leaf tissue density, and specific leaf area were positively correlated with the first ordination axis, while organic carbon, total phosphorus, total nitrogen, and mean leaf thickness were negatively correlated with the first axis. Total phosphorus was negatively correlated with C:P and N:P ratios. Total nitrogen was negatively correlated with C:N ratio. Mean leaf thickness was positively correlated with mean leaf area. The long arrows for C:P ratio, total phosphorus, and specific leaf area indicated their strong contributions to the first two axes, making them the primary factors representing leaf trait variation. As soil water conditions shifted from

low to high, tamarisk leaf nitrogen and phosphorus contents changed markedly, with the highest values under high soil water conditions.

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### 3 Discussion

#### 3.1 Effects of Soil Water on Tamarisk Leaf Chemical Traits

Soil water content directly affects plant metabolic processes. This study showed that tamarisk leaf total nitrogen and phosphorus contents were higher under low soil water conditions ([Figure 1: see original paper]). Elevated nitrogen levels can promote protein accumulation and transformation and maintain normal nitrogen metabolism before water deficit occurs. Phosphorus can improve plant water relations and enhance drought adaptation capacity. Under severe water deficiency, roots allocate more absorbed nitrogen and phosphorus to leaves, increasing leaf N and P content to mitigate adverse effects of drought on photosynthesis and other metabolic activities. This explains why tamarisk leaf nitrogen and phosphorus contents were relatively high under low soil water conditions, consistent with findings by Li et al.

However, this study also found that leaf nitrogen and phosphorus contents were lowest under medium soil water conditions. This may be attributed to two factors. First, drought stress inhibits microbial respiration, reducing nitrogen and phosphorus mineralization rates and limiting root absorption of mineral elements due to increased xylem sap viscosity, resulting in less N and P transport from roots to leaves. Second, tamarisk density was higher in medium water conditions (), intensifying inter-plant competition for nutrients and reducing N and P acquisition per individual. Under high soil water conditions, increased soil microbial biomass enhances organic matter decomposition rates, and improved nutrient diffusion in soil solution increases nutrient availability, promoting plant absorption. Consequently, leaf total nitrogen and phosphorus under high water conditions exceeded those under medium conditions, while C:N and C:P ratios were lower.

The N:P ratio threshold is commonly used to identify soil nutrient limitations, with studies indicating that growth is primarily phosphorus-limited when  $N:P > 16$  and nitrogen-limited when  $N:P < 14$ . Our results show that tamarisk growth was phosphorus-limited under low and medium soil water conditions but shifted to nitrogen limitation under high soil water conditions.

#### 3.2 Effects of Soil Water on Tamarisk Leaf Structural Traits

This study demonstrated that tamarisk leaf mean thickness and mean area were significantly affected by water, peaking under medium soil water conditions and decreasing under both low and high conditions ([Figure 2: see original paper]). Leaf thickness is determined by mesophyll cell size and number, with larger cells containing more and larger chloroplasts that improve light use efficiency.

Thicker leaves also have thicker cuticles that reduce transpiration and enhance water storage capacity, along with higher heat capacity that prevents rapid temperature increases. Under drought conditions, both leaf thickness and area were relatively small because water deficit limited leaf water metabolism, reduced leaf water potential, decreased dry matter accumulation rates, and inhibited cell division and expansion, consistent with Jiao et al.

In hot desert climates, plants require transpirational cooling to reduce leaf temperature. Smaller leaves can more effectively lower surface temperature through higher surface thermal conductivity and convection rates, preventing heat damage. Therefore, tamarisk leaf area decreased under low soil water conditions. Similar patterns occurred under high soil water conditions, possibly because although larger leaf area implies higher net photosynthetic rates, whole-plant light capture largely depends on canopy coverage. High soil water conditions had the highest plant coverage (), affecting light interception and potentially leading to reduced leaf area to minimize mutual shading among leaves, consistent with Zhang et al.

### 3.3 Trade-offs Among Tamarisk Leaf Traits

Different leaf traits do not function independently but exhibit close trade-off relationships, making correlations among leaf traits common and reflecting plant ecological adaptation to environmental change. Nitrogen and phosphorus are key components of phospholipids, proteins, nucleic acids, and other important biomolecules, participating extensively in physiological and biochemical processes such as photosynthesis and respiration. Concentrations of these elements are typically closely correlated, as confirmed in numerous studies. However, this study found no significant correlation between tamarisk leaf nitrogen and phosphorus contents (), likely because phosphorus content showed no significant difference between medium and low water conditions while nitrogen content was significantly higher under low conditions, weakening their relationship.

C:N and C:P ratios reflect carbon fixation efficiency per unit of nitrogen and phosphorus absorbed. The highly significant negative correlations between total phosphorus and both C:P and N:P ratios ( $P < 0.01$ ) indicate that when soil water affects nitrogen and phosphorus uptake, it also interferes with carbon acquisition. However, carbon serves as the structural element of plants and generally does not directly participate in production processes, with stable leaf carbon content reflecting plant homeostasis mechanisms, consistent with Liu and Sun et al.

Additionally, tamarisk leaf tissue density showed a significant negative correlation with mean leaf thickness ( $P < 0.05$ ). Under extreme water deficit, increased leaf thickness reduces transpiration and improves water storage, but leads to looser cell arrangement, larger intercellular spaces, reduced palisade tissue density, and lower dry matter proportion, thereby decreasing tissue density. Unlike some studies, tamarisk showed positive correlation between leaf area and thick-

ness because leaves need to both reduce area to improve water use efficiency and decrease thickness to facilitate CO<sub>2</sub> diffusion. In this study, as C:N ratio increased, specific leaf area tended to decrease, reflecting trade-offs among nutrient absorption, specific leaf area, and leaf lifespan. Water stress can reduce leaf lifespan, while increased C:N ratio represents a strategy to extend leaf lifespan. Studies indicate that leaves with high specific leaf area grow rapidly but have short lifespans and low nutrient use efficiency, whereas leaves with low specific leaf area may allocate more resources to protective tissues and increase thickness. However, this also lengthens the CO<sub>2</sub> diffusion pathway from stomata to chloroplasts, increasing resistance and hindering photosynthesis. Therefore, specific leaf area is positively correlated with leaf nitrogen and phosphorus. These trade-offs enable tamarisk to form optimal functional combinations to adapt to harsh arid environments.

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## 4 Conclusion

This study examined *Tamarix ramosissima* under low, medium, and high soil water conditions at the northern edge of the Tarim Basin, measuring and analyzing its leaf structural and chemical traits. The main conclusions are:

1. Soil water conditions significantly affected tamarisk leaf traits. Under medium soil water conditions, tamarisk leaves showed maximum mean thickness and mean area but minimum total phosphorus and nitrogen contents, indicating non-linear responses of leaf traits to soil water content changes.
2. The mean N:P ratio of tamarisk leaves was greater than 16 under low and medium water conditions but less than 14 under high water conditions, indicating a shift from phosphorus-limited to nitrogen-limited growth with increasing soil water content.
3. Significant correlations existed among some leaf traits, such as total phosphorus with C:P and N:P ratios, and leaf tissue density with mean leaf thickness, demonstrating trait trade-offs. Tamarisk coordinates trait variation through resource allocation regulation to enhance environmental adaptation.

These findings enrich research on plant functional traits in arid regions, reveal tamarisk's adaptation mechanisms to soil water variation, and contribute to understanding plant ecological strategies in arid environments, providing a scientific basis for evaluating plant ecological adaptation during desert ecological conservation, restoration, and management.

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