Postprint: Functional Traits and Environmental Adaptation Characteristics of *Ammopiptanthus mongolicus*

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Abstract

To investigate the adaptive characteristics of the rare and endangered species *Ammopiptanthus mongolicus* in desert regions of northwestern China under climate change, we measured and analyzed functional traits of natural *A. mongolicus* populations in sandy and gravelly habitats across Inner Mongolia, Ningxia, and Gansu. Based on the self-calibrating Palmer Drought Severity Index (scPDSI), we examined drought conditions at the study sites, functional traits of *A. mongolicus*, and their adaptive responses to environmental factors. The results demonstrated that: (1) The intraspecific coefficient of variation for *A. mongolicus* ranged from 7.06% to 39.54%, with substantial variation in leaf morphology and structural composition. (2) The study region showed a trend toward humidification, with significant decreases in leaf dry matter content, leaf thickness, petiole length, petiole dry weight, petiole fresh weight, and transpiration rate ($P<0.05$), and significant increases in leaf fresh weight, leaf length, leaf shape index, and water use efficiency ($P<0.05$). (3) Leaf functional traits of *A. mongolicus* were significantly affected by environmental conditions, with primary environmental factors including soil sand content, mean annual wind speed, soil clay content, and mean annual potential evapotranspiration. (4) Plant trait networks (PTNs) of *A. mongolicus* adapted to sandy habitats through an overall loose but locally aggregated pattern, whereas in gravelly habitats they grew via trait coordination. In conclusion, *A. mongolicus* exhibited distinct trait characteristics and adaptive strategies under different environmental conditions, with its performance significantly influenced by environmental factors. This study provides a scientific basis for the environmental adaptation mechanisms of *A. mongolicus* and offers references for developing conservation and restoration strategies.

Full Text

Abstract

To investigate the adaptive characteristics of *Ammopiptanthus mongolicus*, a rare and endangered species endemic to desert regions of northwestern China, under climate change scenarios, we conducted a comprehensive analysis of functional traits in natural populations inhabiting gravelly habitats across Inner Mongolia, Ningxia Hui Autonomous Region, and Gansu Province. Using the self-calibrating Palmer Drought Severity Index (scPDSI), we assessed drought conditions at our study sites and examined how functional traits of *A. mongolicus* respond to environmental factors. Our findings reveal: (1) Intraspecific coefficient of variation ranged from 7.06% to 39.54%, with substantial variation in leaf morphology and structural composition. (2) The study region exhibited a trend toward humidification, with significant decreases in leaf dry matter content, leaf thickness, petiole length, petiole dry weight, petiole fresh weight, and transpiration rate ($P<0.05$), while leaf fresh weight, leaf length, leaf shape index, and water use efficiency increased significantly ($P<0.05$). (3) Leaf functional traits were significantly influenced by environmental conditions, with key factors including soil sand content, average annual wind speed, soil clay content, and average annual potential evapotranspiration. (4) Plant trait networks (PTNs) of *A. mongolicus* adapted to sandy habitats through a loosely structured yet locally clustered configuration, whereas traits were more synergistically coordinated in gravelly habitats. In conclusion, *A. mongolicus* exhibits distinct trait characteristics and adaptive strategies under different environmental conditions, with traits significantly shaped by environmental factors. This study provides scientific evidence for understanding the environmental adaptation mechanisms of *A. mongolicus* and offers a reference for developing conservation and restoration strategies for this endangered species.

Keywords: *Ammopiptanthus mongolicus*, drought stress, functional traits, environmental factors, plant trait networks

Introduction

Global change has led to uneven water resource distribution, with increasing frequency and intensity of extreme events such as drought and torrential rain. Palmer established the Palmer Drought Severity Index (PDSI) in 1965 to quantify drought, but its reliance on empirical parameters limited its applicability. Wells et al. (2004) subsequently developed the self-calibrating Palmer Drought Severity Index (scPDSI), which automatically calibrates empirical parameters based on historical climate data at each station, offering improved spatial comparability.

In desert regions, understanding plant adaptation mechanisms, particularly responses to extreme environmental changes, has become a critical scientific question and research focus. Plant functional traits characterize resource utilization capacity and environmental adaptation potential. As the most sensitive and adaptable aboveground organ, leaves exhibit functional traits that can be categorized as either structural or physiological. Structural traits, which are relatively easy to measure and have extensive environmental contact, are widely used to reveal plant adaptation patterns and include specific leaf area and leaf dry matter content. Physiological traits, including photosynthetic characteristics, reflect plant productivity. Functional traits exhibit complex correlations that jointly regulate plant growth and development. Plant trait networks (PTNs) represent a cutting-edge approach that uses network parameters to describe overall characteristics and reveal adaptation strategies to environmental change.

Ammopiptanthus mongolicus is a unique super-xerophytic evergreen broadleaf shrub endemic to desert ecosystems in northwestern China, classified as a national second-class protected species. It can adapt to low precipitation and nutrient-poor environments, exhibiting drought tolerance, windbreak and sand fixation, soil improvement, and water conservation properties that play crucial roles in maintaining ecosystem stability, vegetation restoration, and desertification control. However, severe pest and disease pressures, expanding aging populations, and poor self-repair capacity threaten its survival. Current research has focused on structural characteristics, physiological mechanisms, stress-resistance genes, and rhizosphere bacterial diversity. While some studies have examined leaf trait responses to climatic, topographic, and soil moisture conditions, regional-scale analyses of environmental change impacts remain limited, particularly integrated analyses of leaf functional traits with multiple environmental factors. Therefore, this study selected concentrated distribution areas in Otog Banner and Alxa Left Banner (Inner Mongolia), Zhongwei City (Ningxia), and Jingtai City (Gansu) as study regions. Using scPDSI and employing regression analysis and one-way ANOVA, we investigated trends in regional moisture conditions from 2001-2016 to address three questions: (1) What are the characteristics of *A. mongolicus* leaf traits? (2) Which environmental factors primarily influence *A. mongolicus*? (3) Do plant trait networks differ between sandy and gravelly habitats? Our objective is to reveal variation patterns in leaf functional traits and their relationships with environmental factors, providing scientific evidence for conservation and restoration strategies.

1.1 Study Area Description

The study area encompassed concentrated distribution regions of *A. mongolicus* within 37°26 36.3 –39°55 26.7 N and 104°44 08.3 –106°55 26.3 E. We established four study regions in Mengxi (Otog Banner), Alxa Left Banner, Zhongwei, and Jingtai, comprising eight sample plots across sandy and gravelly habitats [Figure 1: see original paper]. Located in arid and semi-arid climate zones at the transition between desert and semi-desert steppe, the region experiences a temperate continental arid climate characterized by large diurnal temperature variations, abundant sunshine, low precipitation, high evaporation, and frequent wind events. Mean annual temperature is approximately 8–9°C, with annual precipitation of 150–200 mm. Vegetation is dominated by xerophytic shrubs and semi-shrubs forming typical desert plant communities with relatively poor species composition and simple community structure. Soil types primarily include aeolian sandy soil, gray desert soil, and brown calcic soil.

1.2 Data Sources

This study utilized the self-calibrating Palmer Drought Severity Index (scPDSI) from the monthly global gridded drought dataset provided by the Climatic Research Unit, University of East Anglia (https://www.uea.ac.uk/groups-and-centres/climatic-research-unit/data), with 0.5°\$×\$0.5° spatial resolution covering 2001–2016. Precipitation and temperature data were obtained from the National Tibetan Plateau Data Center (https://data.tpdc.ac.cn/home), potential evapotranspiration from the National Earth System Science Data Center (http://www.geodata.cn/), sunshine duration and relative humidity from the China Ground Meteorological Data Daily Value Dataset V3.0, and wind speed from NOAA's National Centers for Environmental Information (https://www.ncei.noaa.gov/data/global-summary-of-the-day/archive/). Soil data were sourced from https://www.fao.org/soils-portal/en/. From these we calculated 16-year averages for mean annual precipitation (MAP), mean annual temperature (MAT), annual potential evapotranspiration (PET), mean annual sunshine duration (SUN), mean annual relative humidity (RH), and mean annual wind speed (WS).

Table 1 scPDSI grading standards

scPDSI Value	Level
\$ \$4.0	Extremely wet
3.0–3.99	Severely wet
2.0–2.99	Moderately wet
1.0–1.99	Slightly wet
-0.99–0.99	Normal
-1.99—1.0	Slightly dry
-2.99—2.0	Moderately dry
-3.99—3.0	Severely dry
≤-4.0	Extremely dry

1.3 Field Measurements

1.3.1 Topographic Factors and Soil Water Content We measured geographic coordinates and altitude using handheld GPS devices. Sample plots included three 10 m\$$\times 10 mquadratsinbothsandyandgravellyhabitatsinMengxiandAlxaLeftBanner, 30m\times 30m$
m transect in the Jingtai gravelly habitat located on a ridge. For each of three randomly selected target plants per plot, we collected soil samples at three points within 1 m of the root system at depths of 0–10 cm, 10–20 cm, and

20–30 cm. Samples were placed in aluminum boxes (W) and weighed with soil (W1), then oven-dried at 110°C to constant weight (W2). Soil water content (SWC, %) was calculated as:

$$SWC(\%) = \frac{W1 - W2}{W2 - W} \times 100\%$$

1.3.2 Leaf Structural Traits Measured leaf phenotypic traits included leaf area (LA, cm^2), leaf length (LL, cm), leaf width (LW, cm), leaf fresh weight (LFW, g), leaf dry weight (LDW, g), leaf thickness (LT, mm), petiole length (PL, cm), petiole dry weight (PDW, g), and petiole fresh weight (PFW, g). Derived traits included specific leaf area (SLA, $cm^2 \cdot g^{-1}$), leaf dry matter content (LDMC, $g \cdot g^{-1}$), leaf water content (LWC, %), leaf shape index (LSI), leaf volume (LV, cm^3), and leaf tissue density (LTD, $g \cdot cm^{-3}$). From each plot, we selected three healthy, intact mature plants and measured three fully expanded leaves from each plant using triangulation sampling. Leaves were photographed on A4 paper and analyzed using ImageJ software to determine LA, LL, LW, and PL. Fresh weights were measured using an electronic balance (0.001 g precision), then leaves were oven-dried at 80°C to constant weight for dry weight measurements.

1.3.3 Physiological and Ecological Indicators Photosynthetic physiological traits were measured on clear, sunny days. In each plot in Mengxi, Alxa Left Banner, and Zhongwei, we selected three healthy adult plants and measured at least three leaves per plant, with five replicates per leaf. To capture diurnal variation, measurements were taken at 10:00, 13:00, and 16:00 representing morning, midday, and afternoon periods using a Li-6400 portable photosynthesis system (LI-COR, USA). Measured parameters included net photosynthetic rate (Pn, $mol \cdot m^{-2} \cdot s^{-1}$), transpiration rate (Tr, $mmol \cdot m^{-2} \cdot s^{-1}$), and water use efficiency (WUE, $mol \cdot mmol^{-1}$), with values averaged across measurement times.

1.3.4 Growth Parameters We measured plant height (H, cm), long-axis crown diameter (D1, cm), vertical long-axis crown diameter (D2, cm), and ground diameter (D, mm) using tape measures and calipers.

1.4 Data Analysis

We analyzed interannual scPDSI trends using linear regression and visualized results in Excel. Relationships between drought index and leaf traits were examined through linear regression, while differences in leaf functional traits across drought levels were compared using one-way ANOVA with Origin 2024. Plant trait networks were constructed by designating all traits as nodes and correlations between traits as edges. Pearson correlation coefficients were calculated between all trait pairs, with significance thresholds set at $|R| > 0.2$ and $P <$

0.05. Networks were visualized using the igraph package in R, with edge density (ED), modularity (Q), and average clustering coefficient (AC) used to characterize network properties.

Trait calculations were performed as follows:

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

$$LDMC = \frac{LDW}{LFW}$$

$$LWC = \frac{LFW - LDW}{LFW}$$

$$LSI = \frac{LL}{LW}$$

$$LV = LA$$

$$LTD = \frac{LDW}{LV}$$

$$WUE = \frac{Pn}{Tr}$$

$$CV = \frac{\text{Standard Deviation}}{\text{Mean}} \times 100\%$$

Results

2.1 Interannual Variation in Drought Index

Based on mean scPDSI values, the eight sample plots were classified into six drought levels . Mean scPDSI values from highest to lowest were: Jingtai (-0.677), Zhongwei sandy (-1.673), Zhongwei gravelly (-1.725), Alxa Left Banner gravelly (-1.900), Mengxi (-2.195), and Alxa Left Banner sandy (-2.483), indicating increasing drought severity. According to Table 1, Jingtai was in normal condition, Zhongwei and Alxa Left Banner gravelly habitats were slightly dry, and Mengxi and Alxa Left Banner sandy habitats were moderately dry. From 2001–2016, scPDSI values showed an overall increasing trend across all plots [Figure 2: see original paper], indicating regional humidification.

Table 2 scPDSI and environmental characteristics of different sites

Sample plot	scPDSI mean value	Average annual precipitation	Annual potential evapotranspiration	Average annual temperature
Jingtai sandy habitat	-0.677			
Jingtai gravelly habitat				
Zhongwei sandy habitat	-1.673			
Zhongwei gravelly habitat	-1.725			
Alxa Left Banner gravelly habitat	-1.900			
Mengxi sandy habitat	-2.195			
Mengxi gravelly habitat				
Alxa Left Banner sandy habitat	-2.483			

2.2 Leaf Structural Trait Characteristics

Coefficients of variation for leaf structural traits ranged from 7.06% to 39.54% . Leaf water content, leaf dry matter content, specific leaf area, and leaf thickness showed weaker variation and remained relatively stable. Leaf volume exhibited the highest variation (39.54%), while petiole dry weight, petiole fresh weight, leaf fresh weight, and leaf dry weight showed substantial variation, suggesting that leaf morphology and structural composition respond preferentially to environmental changes with high plasticity.

Table 3 Leaf structural traits of *Ammopiptanthus mongolicus* in the study area

Trait	Average	CV (%)
Leaf fresh weight (LFW)		
Leaf dry weight (LDW)		
Leaf water content (LWC)		
Leaf dry matter content (LDMC)		
Leaf length (LL)		
Leaf width (LW)		
Leaf shape index (LSI)		
Leaf area (LA)		
Specific leaf area (SLA)		
Petiole length (PL)		
Petiole dry weight (PDW)		
Petiole fresh weight (PFW)		
Leaf thickness (LT)		
Leaf volume (LV)		
Leaf tissue density (LTD)		

2.3 Leaf Functional Traits Along Drought Gradients

Leaf structural traits responded differently to drought severity [Figure 3: see original paper]. As scPDSI increased from left to right (higher water availability, lower drought stress, toward humidification), leaf fresh weight, leaf length, and leaf shape index increased significantly ($P<0.05$), while leaf dry matter content, leaf thickness, petiole length, petiole fresh weight, and petiole dry weight decreased significantly ($P<0.01$). Leaf area, leaf dry weight, and leaf water content showed increasing trends, while leaf width, specific leaf area, leaf volume, and leaf tissue density showed decreasing trends, though these were not statistically significant. For physiological traits, transpiration rate decreased significantly ($P<0.01$) and water use efficiency increased significantly ($P<0.0001$) with increasing scPDSI, while net photosynthetic rate showed no significant change ($P>0.05$).

2.4 Environmental Factors Influencing Leaf Functional Traits

Multiple stepwise regression identified significant environmental predictors for each trait. Soil sand content and sunshine duration significantly influenced leaf fresh and dry weights. Longitude and soil pH significantly affected leaf water content and dry matter content. Leaf length was significantly influenced by soil organic carbon content, clay content, and altitude. Wind speed and soil gravel content significantly affected leaf width. Leaf shape index was influenced by multiple factors including soil organic carbon, wind speed, gravel content, and potential evapotranspiration. Leaf area was affected by wind speed, soil carbonate content, and sand content. Specific leaf area was significantly influenced by wind speed and soil pH. Petiole length was affected by soil clay and silt contents. Petiole dry weight was influenced by soil sand content, clay content, and air humidity. Petiole fresh weight was affected by sand content and latitude. Leaf thickness was influenced by precipitation and potential evapotranspiration. Leaf volume was affected by wind speed and sand content. Leaf tissue density was influenced by soil water content and carbonate content. Net photosynthetic rate was affected by annual precipitation and sand content. Transpiration rate was influenced by latitude and potential evapotranspiration. Water use efficiency was affected by scPDSI and wind speed. These results demonstrate that *A. mongolicus* leaf traits are shaped by a complex interplay of climatic, topographic, and edaphic factors.

Table 4 Regression equations of leaf functional traits and environmental factors of *Ammopiptanthus mongolicus*

Leaf trait	Regression equation	P value
Leaf fresh weight (LFW)	LFW = 0.262 + 0.000497Sand - 0.000064SUN	<0.01
Leaf dry weight (LDW)	LDW = 0.107 + 0.000207Sand - 0.000025SUN	<0.01
Leaf water content (LWC)	LWC = 1.791 - 0.011LON - 0.008pH	<0.01
Leaf dry matter content (LDMC)	LDMC = -0.791 + 0.011LON + 0.008pH	<0.01
Leaf length (LL)	LL = 1.968 - 1.109OC + 0.001ALT - 0.011Clay	<0.01
Leaf width (LW)	LW = 1.71 - 0.147WS + 0.019Gravel	<0.05
Leaf shape index (LSI)	LSI = 3.262 - 1.506OC - 0.001PET - 0.077Gravel + 0.3WS	<0.01
Leaf area (LA)	LA = 3.578 + 0.009Sand - 0.422WS + 0.022CACO3	<0.05
Specific leaf area (SLA)	SLA = 55.532 - 0.795pH - 1.969WS	<0.05
Petiole length (PL)	PL = 1.185 - 0.018Clay + 0.016Silt	<0.01

Leaf trait	Regression equation	P value
Petiole dry weight (PDW)	PDW = 0.022 + 0.000084Sand + 0.00039RH + 0.0001Clay	<0.01
Petiole fresh weight (PFW)	PFW = -0.035 + 0.000098Sand + 0.001LAT	<0.01
Leaf thickness (LT)	LT = 0.874 - 0.002MAP + 0.00012PET	<0.01
Leaf volume (LV)	LV = 0.217 + 0.001Sand - 0.028WS	<0.01
Leaf tissue density (LTD)	LTD = 0.053 + 0.002CACO3 - 0.222SWC	<0.01
Net photosynthetic rate (Pn)	Pn = -2.899 + 0.023Sand + 0.029MAP	<0.01
Transpiration rate (Tr)	Tr = -6.688 + 0.001PET + 0.179LAT	<0.01
Water use efficiency (WUE)	WUE = 4.075 + 1.573scPDSI + 0.583WS	<0.05

Note: LON = Longitude; LAT = Latitude; ALT = Altitude; scPDSI = Self-calibrating Palmer Drought Severity Index; MAP = Mean annual precipitation; PET = Annual potential evapotranspiration; MAT = Mean annual temperature; SUN = Mean annual sunshine hours; RH = Annual relative humidity; WS = Mean annual wind speed; SWC = Soil water content; Gravel = Percentage of gravel volume; Sand = Sand content; Clay = Clay content; Silt = Silt content; OC = Organic carbon content; pH = Soil pH; CACO3 = Carbonate or lime content.

2.5 Plant Trait Networks in Sandy and Gravelly Habitats

Based on functional trait measurements and correlation analyses across eight sample plots, we constructed plant trait networks [Figure 4: see original paper]. Analysis of soil water content revealed that gravelly habitats had higher network edge density, indicating better trait coordination and higher resource use efficiency . Sandy habitats showed higher modularity and average clustering coefficients, suggesting trait differentiation with tightly connected internal modules and loose external connections.

Table 5 Parameters of plant trait networks of *Ammopiptanthus mongolicus* in different habitat plots

Sample plot	Habitat	Soil water content (%)	Edge density	Modularity	Average clustering coefficient
Mengxi	Sandy				
Mengxi	Gravelly				

Sample plot	Habitat	Soil water content (%)	Edge density	Modularity	Average clustering coefficient
Alxa Left Banner	Sandy				
Alxa Left Banner	Gravelly				
Zhongwei	Sandy				
Zhongwei	Gravelly				
Jingtai	Sandy				
Jingtai	Gravelly				

The plant trait networks were divided into multiple modules, with nodes of the same color belonging to the same module. Black lines represent connections within modules, while red lines represent connections between different modules.

Discussion

3.1 Leaf Trait Characteristics of *Ammopiptanthus mongolicus*

Plant leaves typically modify their traits to adapt to spatial heterogeneity, with coefficient of variation reflecting trait plasticity. Investigating intraspecific variation in functional traits helps reveal plant responses to spatiotemporal environmental gradients and quantifies reactions to environmental change and resource competition. Our results show that leaf water content, leaf dry matter content, specific leaf area, and leaf thickness had low coefficients of variation, indicating stable traits. This aligns with previous findings that leaf dry matter content and specific leaf area characterize resource acquisition capacity and growth rate, reflecting stable resource uptake and nutrient storage. Leaf water content reflects tissue water status, and its relative stability in *A. mongolicus* likely represents an adaptive strategy or species characteristic for maintaining stable leaf water content in arid habitats, ensuring effective water acquisition and retention while avoiding drought damage. High variation in leaf volume, petiole dry weight, petiole fresh weight, leaf fresh weight, and leaf dry weight suggests that plants adapt by altering structural proportions. The petiole serves as mechanical support and a water transport pathway, with an allometric relationship to the leaf blade. Plants may adjust petiole investment to maintain leaf water demand, resist freezing-induced embolism and drought cavitation, and optimize light capture under different habitat conditions.

3.2 Leaf Functional Traits Along Drought Gradients

As leaves are highly exposed to the atmosphere, they exhibit strong phenotypic plasticity in response to environmental change. Our analysis of scPDSI trends from 2001–2016 revealed regional humidification, consistent with previous studies. As drought stress decreased and humidity increased, *A. mongolicus* increased leaf area and length to maximize light capture, while leaf shape index increased, indicating more elongated leaves that enhance water transport capacity through the leaf venation network. Consequently, leaf water content increased.

Under more severe drought, *A. mongolicus* tended to develop smaller, thicker, and denser leaves, consistent with previous research showing that such traits reduce light absorption and water loss. We found higher leaf tissue density and leaf dry matter content under drier conditions, indicating slower leaf turnover and greater investment in complex, energy-intensive protective tissues to store carbon and resist damage, thereby enhancing stress resistance and defense capacity. Higher leaf dry matter content reflects greater nutrient acquisition and retention capacity, producing tougher leaves that resist physical damage from rain, wind, and herbivory. Studies have shown that plants with high leaf dry matter content and tissue density typically exhibit high stress resistance and survival rates but lower growth rates, suggesting that *A. mongolicus* employs specific trait combinations to ensure survival under drought stress.

Previous research demonstrated that *A. mongolicus* can maintain or slightly increase photosynthetic and transpiration rates under moderate soil water deficit, indicating strong drought resistance. Our results align with these findings, though whether natural populations show declining Pn and Tr under severe drought requires further investigation. Increased water use efficiency under more humid conditions indicates improved adaptive capacity. While drought stress typically reduces petiole length in some species, we observed increased petiole length under drought, possibly to elevate leaves away from ground heat sources, reduce leaf temperature, and minimize water loss. Longer petioles may also reduce self-shading for more effective light capture and compensate for reduced transport efficiency and increased embolism risk under drought by greater investment in transport structures.

3.3 Leaf Trait Responses to Environmental Factors

Our study identified multiple influential environmental factors including soil sand content, wind speed, soil clay content, potential evapotranspiration, soil pH, latitude, precipitation, soil organic carbon, longitude, carbonate content, gravel content, and sunshine hours—representing soil water-holding capacity, nutrient status, and climatic aridity. In terms of climate, potential evapotranspiration, precipitation, and temperature are key regional factors, with precipitation being particularly critical in desert regions. These factors affect temperature and water availability for plant growth, consistent with previous findings that precipitation, temperature, and sunshine duration primarily influence *A. mongolicus* leaf traits. Topographic factors alter regional moisture conditions by affecting water, light, and heat distribution, with latitudinal patterns in leaf traits previously documented for this species. Soil properties represent fundamental controls on ecological processes, with soil nutrients and water content directly affecting plant growth and distribution. Soil pH influences enzyme activity, microbial processes, and organic matter decomposition, while soil texture (clay, sand, and gravel contents) affects water and nutrient retention. High wind speeds in desert regions can remove surface moisture and nutrient-rich fine particles, coarsening soil texture and increasing gravel content, creating harsher conditions that inhibit *A. mongolicus* growth. Overall, leaf trait expression in *A. mongolicus* represents a complex process shaped by multiple interacting environmental factors.

3.4 Differences in Plant Trait Networks Between Habitats

Plant trait networks partition traits into functional modules with high internal correlations. High edge density combined with low modularity and clustering coefficients indicates well-coordinated traits and high resource use efficiency, whereas high modularity and clustering coefficients suggest tightly connected internal modules with clear boundaries and weaker external connections. Previous studies found simpler leaf trait networks with lower modularity in drier climates, and stronger trait correlations in semi-arid compared to arid regions, as trait coordination facilitates growth under less severe drought. Our results align with these patterns. Sandy habitats, with coarser texture, rapid water infiltration, large pore spaces, poor water retention, and low fertility, present more challenging conditions that narrow trait variation ranges and reduce trait correlations under adverse conditions like drought and high temperature. Consequently, *A. mongolicus* adjusts trait modules to either coordinate traits globally or differentiate them into distinct modules to cope with water stress in different habitats. Future research should analyze the importance of individual traits and functional modules to identify hub traits and key modules for plant performance.

Conclusion

This study demonstrates that *Ammopiptanthus mongolicus* adjusts leaf morphology and structural proportions in response to drought severity. Under less severe drought and more humid conditions, the species maximizes leaf expansion for light capture and organic matter production. Under increased drought stress, leaves become smaller, thicker, and denser, with greater investment in protective tissues to resist adverse conditions, resulting in slower growth rates. Analysis of leaf functional trait responses revealed complex interactions among soil, climatic, and topographic factors, with key influences including soil sand content, wind speed, soil clay content, potential evapotranspiration, soil pH, latitude, precipitation, soil organic carbon, longitude, carbonate content, gravel content, and sunshine hours. *A. mongolicus* employs different plant trait network configurations to adapt to different habitats: a loosely structured yet locally clustered network in sandy habitats versus a more globally coordinated network in gravelly habitats.

References

Akram MA, Wang X, Shrestha N, et al., 2023. Variations and driving factors of leaf functional traits in the dominant desert plant species along an environmental gradient in the drylands of China [J]. Science of The Total Environment, 897(2): 165394.

Cavender-Bares J, Holbrook NM, 2001. Hydraulic properties and freezing-induced cavitation in sympatric evergreen and deciduous oaks with contrasting habitats [J]. Plant, Cell & Environment, 24(12): 1243-1256.

Chen FH, Xie TT, Yang YJ, et al., 2023. Discussion of the "warming and wetting" trend and its future variation in the drylands of Northwest China under global warming [J]. Science China Earth Sciences, 53(6): 1246-1262.

Chen L, Yang XG, Wang L, et al., 2024. Characteristics of evapotranspiration components of different plant communities in desert steppe and its relationship with environmental factors[J]. Acta Ecologica Sinica, 44(1): 330-342.

Dai A. 2011. Drought under global warming: a review [J]. WIREs Climate Change, 2(1): 45-65.

Dang XH, Meng ZJ, Gao Y, et al., 2020. Photosynthetic characteristics and ecological adaptability of desert shrubs in western Ordos [J]. Arid zone research, 37(2): 435-443.

Dijkstra P, Lambers H, 1989. Analysis of specific leaf area and photosynthesis of two inbred lines of *Plantago major* differing in relative growth rate [J]. New Phytologist, 113(3): 293-298.

Dong X, Xin ZM, Li YH, et al., 2019. Responses of *Ammopiptanthus mongolicus* Leaf Traits to Environmental Factors [J]. Journal of desert research, 39(6): 126-134.

Feng Y, Wang J, Wu BW, et al., 2023. Seasonal variation characteristics of phytoplankton community in Gucheng lake and the Influential environmental factors [J]. Journal of Ecology and Rural Environment, 39(8): 1042-1050.

Flores-Moreno H, Fazayeli F, Banerjee A, et al., 2019. Robustness of trait connections across environmental gradients and growth forms [J]. Global Ecology and Biogeography, 28(12): 1806-1826.

Gao F, Li H, Xiao Z, et al., 2018. De novo transcriptome analysis of *Ammopiptanthus nanus* and its comparative analysis with *A. mongolicus* [J]. Trees, 32(1): 287-300.

Gebauer R, Vanbeveren SPP, Volařík D, et al., 2016. Petiole and leaf traits of poplar in relation to parentage and biomass yield [J]. Forest Ecology and Management, 362: 1-9.

Guo WF, Chen MY, Gao F, et al., 2024. Traits of seven medicinal plants in Taihang Mountains and their responses to soil factors [J]. Journal of Environmental

Engineering Technology, 14(2): 612-621.

Han FR, 2017. Study on the vegetation and plant functional traits of *Ammopiptanthus mongolicus* [D]. Beijing: Minzu University of China.

He N, Li Y, Liu C, et al., 2020. Plant Trait Networks: Improved Resolution of the Dimensionality of Adaptation [J]. Trends in Ecology & Evolution, 35(10): 908-918.

Huang J, Yu H, Guan X, et al., 2016. Accelerated dryland expansion under climate change [J]. Nature Climate Change, 6(2): 166-171.

Huo JX, Ren L, Pan YP, et al., 2022. Functional traits of desert plants and their responses to environmental factors in Qaidam Basin, China [J]. Acta Ecologica Sinica, 42(11): 4494-4503.

Jiang S, Zhang L, Jing YS, et al., 2023. Spatial and Temporal Distribution Characteristics of Regional Extreme Climate Events in China from 1981 to 2015 [J]. Research of Soil and Water Conservation, 30(6): 295-306.

Jin XY, Gong L, Wang MT, et al., 2023. Differential covariation characteristics in functional traits of two ephemerals of Boraginaceae in the Gurbantunggut Desert, China [J]. Acta Prataculturae Sinica, 32(10): 58-70.

Kleyer M, Trinogga J, Cebrián-Piqueras MA, et al., 2018. Trait correlation network analysis identifies biomass allocation traits and stem specific length as hub traits in herbaceous perennial plants [J]. Journal of Ecology, 107(2): 829-842.

Kuppler J, Höfers MK, Wiesmann L, et al., 2016. Time-invariant differences between plant individuals in interactions with arthropods correlate with intraspecific variation in plant phenology, morphology and floral scent [J]. New Phytologist, 210(4): 1357-1368.

Lan YT, Wang SL, Li ZZ, et al., 2019. Research Advances in Proteomics of *Ammopiptanthus* in Responses to Abiotic Stresses [J]. Biotechnology Bulletin, 35(1): 112-119.

Lasky JR, Uriarte M, Boukili VK, et al., 2014. Trait-mediated assembly processes predict successional changes in community diversity of tropical forests [J]. Proceedings of the National Academy of Sciences, 111(15): 5616-5621.

Li G, Yang D, Sun S. 2008. Allometric relationships between lamina area, lamina mass and petiole mass of 93 temperate woody species vary with leaf habit, leaf form and altitude [J]. Functional Ecology, 22(4): 557-564.

Li HQ, Ma WY, Li HY, 2000. The resistant capability and prospects of *Ammopiptanthus* [J]. World Forestry Research, 5(5): 67-71.

Li L, Jin GZ, Liu ZL, 2022. Variations and correlations of lamina and petiole traits of three broadleaved species in a broadleaved Korean pine forest [J]. Chinese Journal of Plant Ecology, 46(6): 687-699.

Li S, Su P, Zhang H, et al., 2018. Distribution patterns of desert plant diversity and relationship to soil properties in the Heihe River Basin, China [J]. Ecosphere, 9(7): e02355.

Li SJ, Su PX, Zhang HN, et al., 2013. Characteristics and relationships of foliar water and leaf functional traits of desert plants [J]. Plant Physiology Journal, 49(2): 153-160.

Li Y, 2020. Variation of leaf trait network among different vegetation types and its influencing factors [D]. Beijing: Beijing Forestry University.

Li Y, Liu C, Sack L, et al., 2022. Leaf trait network architecture shifts with species-richness and climate across forests at continental scale [J]. Ecology Letters, 25(6): 1442-1457.

Li ZJ, Guo JY, Wang HJ, 2023. Differences in soil physical and chemical properties and quality under different land use types in the Yimeng mountainous region [J]. Journal of Shaanxi Normal University (Natural Science Edition), 51(2): 108-120.

Lin R, Zhou T, Qian Y, 2014. Evaluation of Global Monsoon Precipitation Changes based on Five Reanalysis Datasets [J]. Journal of Climate, 27(3): 1271-1289.

Liu T, Tang YY, Yang HY, et al., 2024. Responses of Functional Traits of *Ammopiptanthus mongolicus* to Soil Moisture [J]. Journal of MUC (Natural Sciences Edition), 33(1): 28-35.

Liu X, Zhang D, Luo Y, et al., 2013. Spatial and temporal changes in aridity index in northwest China: 1960 to 2010 [J]. Theoretical and Applied Climatology, 112(1-2): 307-316.

Liu XZ, Han WB, Gao RD, et al., 2021. Potential impacts of environmental types on geographical distribution of *Larix principis-rupprechtii* [J]. Acta Ecologica Sinica, 41(5): 1885-1893.

Lozano YM, Aguilar-Trigueros CA, Flaig IC, et al., 2020. Root trait responses to drought are more heterogeneous than leaf trait responses [J]. Functional Ecology, 34(11): 2129-2140.

Ma Q, Liang YL, Yu D, et al., 2024. Characteristics of leaf stoichiometry and the driving factors of *Ammopiptanthus mongolicus*, China [J]. Chinese Journal of Applied Ecology, 35(4): 909-916.

Ma XY, Fan K, 2023. Initial Examination of Interdecadal Shifts and Causes of Summer and Autumn Dryness and Wetness in Northwest China over Recent Decades [J]. Chinese Journal of Atmospheric Sciences, 47(4): 943-956.

Mao KZ, Gao MJ, Wu R, et al., 2024. Tree shape structure and leaf trait responses to habitat elements of *Bombax ceiba* [J]. Guihaia, 44(5): 863-872.

McGill BJ, Enquist BJ, Weiher E, et al., 2006. Rebuilding community ecology from functional traits [J]. Trends in Ecology & Evolution, 21(4): 178-185.

Meier IC, Leuschner C, 2008. Leaf size and leaf area index in *Fagus sylvatica* forests: competing effects of precipitation, temperature, and nitrogen availability [J]. Ecosystems, 11(5): 655-669.

Naud L, Måsviken J, Freire S, et al., 2019. Altitude effects on spatial components of vascular plant diversity in a subarctic mountain tundra [J]. Ecology and Evolution, 9(8): 4435-4446.

Niu XJ, Nie J, Yang ZY, et al., 2020. Leaf morphological responses of *Indigofera bungeana* to drought stress [J]. Acta Botanica Boreali-Occidentalia Sinica, 40(4): 613-623.

Scoffoni C, Chatelet DS, Pasquet-Kok J, et al., 2016. Hydraulic basis for the evolution of photosynthetic productivity [J]. Nature Plants, 2(6): 16072.

Sepaskhah AR, Tafteh A, 2013. Pedotransfer function for estimation of soil-specific surface area using soil fractal dimension of improved particle-size distribution [J]. Archives of Agronomy and Soil Science, 59(1): 93-103.

Siefert A, Violle C, Chalmandrier L, et al., 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities [J]. Ecology Letters, 18(12): 1406-1419.

Sun M, Tian K, Zhang Y, et al., 2017. Research on leaf functional traits and their environmental adaptation [J]. Plant Science Journal, 35(6): 940-949.

Tian YL, Yang H, Wang FL, et al., 2021. Differences of Leaf Functional Traits of *Pinus tabuliformis* and Its Response to Altitude Gradient in the Middle of Qinling Mountains [J]. Acta Botanica Boreali-Occidentalia Sinica, 41(2): 300-309.

Van der Schrier G, Barichivich J, Briffa KR, et al., 2013. A scPDSI-based global data set of dry and wet spells for 1901–2009 [J]. Journal of Geophysical Research: Atmospheres, 118(10): 4025-4048.

Vile D, Garnier É, Shipley B, et al., 2005. Specific leaf area and dry matter content estimate thickness in laminar leaves [J]. Annals of Botany, 96(6): 1129-1136.

Violle C, Navas M-L, Vile D, et al., 2007. Let the concept of trait be functional [J]. Oikos, 116(5): 882-892.

Wang R, Fan H, Li JR, et al., 2021. Leaf functional traits and water use characteristics of *Ammopiptanthus mongolicus* in west Ordos [J]. Journal of Inner Mongolia Forestry Science & Technology, 47(4): 7-12.

Wang X, Ji M, Zhang Y, et al., 2023. Plant trait networks reveal adaptation strategies in the drylands of China [J]. BMC Plant Biology, 23(1): 266.

Wang XY, Chen XS, Ding QP, et al., 2018. Vegetation and soil environmental factor characteristics, and their relationship at different desertification stages: a case study in the Minqin desert-oasis ecotone [J]. Acta Ecologica Sinica, 38(5): 1569-1580.

Wei LZ, Baiketuerhan Y, Yerken T, et al., 2024. Relationships among leaf structural characteristics and DBH growth of *Picea schrenkiana* var. *tianschanica* [J]. Guangxi Forestry Science, 53(1): 57-61.

Wells N, Goddard S, Hayes MJ. 2004. A Self-Calibrating Palmer Drought Severity Index [J]. Journal of Climate, 17(12): 2335-2351.

Wright IJ, Reich PB, Cornelissen JHC, et al., 2005. Assessing the generality of global leaf trait relationships [J]. New Phytologist, 166(2): 485-496.

Yang H, Li Y, Wu M, et al., 2011. Plant community responses to nitrogen addition and increased precipitation: the importance of water availability and species traits [J]. Global Change Biology, 17(9): 2936-2944.

Yang Q, Zhu RJ, Yang CY, et al., 2022. Variation in leaf functional traits of *Bombax ceiba* Linnaeus communities based on tree structure [J]. Acta Ecologica Sinica, 42(7): 2834-2842.

Yao JN, Dai JX, Liu X, et al., 2024. Analysis of bacterial community structure and function in rhizosphere soil of typical shrub in desert steppe of Ningxia [J]. Acta Ecologica Sinica, 44(20): 1-15.

Yu H, Pan ZT, Chen ZQ, et al., 2021. Effects of nitrogen addition on soil chemical properties and leaf functional traits of *Dicranopteris dichotoma* in the red soil erosion area of southern China [J]. Chinese Journal of Applied and Environmental Biology, 27(1): 46-53.

Zhang H, Hu HY, Li HX, et al., 2023. Physiological response and transcriptome analysis of the desert steppe dominant plant *Lespedeza potaninii* to drought stress [J]. Acta Prataculturae Sinica, 32(7): 188-205.

Zhang J, Ma YM, Wang SS, et al., 2023. Physiological responses of young *Ammopiptanthus mongolicus* to soil water loss and rehydration under different temperature [J]. Journal of Arid Land Resources and Environment, 37(3): 150-161.

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