



Convergent Variation in the Leaf Traits of Desert Plants in the Ebinur Lake Basin

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Elucidating the relationship between the variation of plant leaf functional traits and the environment is necessary for understanding the adaptation mechanism of plants and predicting changes in ecosystem structure. In this study, the leaf traits of desert plants in Ebinur Lake National Wetland Nature Reserve in Xinjiang, China were studied from the aspects of plant life forms (annuals, perennials and shrubs), phylogenetic signals, and relation to soil properties, using the principal component analysis, variance decomposition, and one-way analysis of variance. The results showed that: (1) There were significant differences in leaf carbon concentration (annuals>shrubs>perennials), leaf nitrogen concentration (shrubs \geq perennials \geq annuals), and leaf moisture content (perennials \geq annuals \geq shrubs) among the life forms, but there was no significant difference in leaf phosphorus concentration. Besides, soil nitrogen and phosphorus were significantly positively correlated with leaf carbon concentration and leaf nitrogen concentration. (2) There were significant differences in leaf carbon concentration, leaf nitrogen concentration, specific leaf area, and leaf moisture content between C3 and C4 plants, while the differences in P and leaf dry matter content were not significant. Besides, there were significant differences in leaf carbon concentration, leaf nitrogen concentration, specific leaf area, and leaf moisture content between leguminous and non-leguminous plants. Leguminous plants had higher leaf carbon concentration, leaf nitrogen concentration, and specific leaf area than non-leguminous plants, while non-leguminous plants had higher leaf moisture content than leguminous plants. (3) One way ANOVA analysis showed that taxonomy had a more significant effects on leaf carbon concentration, leaf nitrogen concentration, specific leaf area, and leaf moisture content than soil properties, and the coefficient of variation of leaf carbon concentration was greater than 50%. The phylogenetically independent contrasts analysis showed that the phylogenetic signal of all leaf traits was detected in all species and low (K value < 1 , $p > 0.05$), indicating that the functional traits were weakly affected by phylogenetics. Therefore, desert plants in the Ebinur Lake Basin evolved to adapt to arid environments, and leaf traits showed convergent variation.

Keywords: convergence, plant functional traits, desert plants, phylogenetic signals, Ebinur Lake Basin

INTRODUCTION

Plant functional traits are biological characteristics that directly affect the growth and reproduction of plants (Ackerly and Cornwell, 2007). Leaf traits are important ecological indicators that can directly reflect the characteristics of plants utilizing environmental resources and the survival strategies to adapt to complex environments (Bao and Liu, 2009). Convergence refers to the tendency of organisms (two or more) with low affinities to evolve to have similar structures, functions, and phenotypes in similar habitats (usually under extreme environmental conditions) (Losos, 2011). Similar habitat conditions produce similar environmental stresses on the morphophysiological characteristics of different plants, and plants develop similar traits to compete for environmental resources and adapt to the environment, leading to the occurrence of convergent evolution, although there are many differences between their lineages (Givnish, 2017). Studies have shown that plants are dwarfed, with thick leaves in phylogenetic development in high-altitude areas (Losos, 2011), and annual succulents have small, white downy, or spiny leaves in desert areas (Griffiths and Males, 2017). Plants in karst areas generally show the characters of low specific leaf area (SLA) and leaf area (LA) and high leaf dry matter content

(LDMC), indicating that plants tend to develop some traits to adapt to the drought caused by the shallow soil layer and soil water leakage in karst areas (Liu et al., 2014). Besides, studies in arid regions have shown that plants usually adapt to drought stress with thick and leathery leaves, low specific leaf area, small leaf size, increased leaf tissue density (LTD), and large specific root length (SRL) (Reich et al., 1998).

Environmental filtering can screen some species which can survive in a specific environment (Cui et al., 2022), especially in harsh environmental conditions (Botta-Dukát and Czúcz, 2016), and make their growth and abundance have convergent characteristics (Shipley et al., 2016). For example, under coastal environmental conditions, due to the influence of periodic tidal flooding, the leaf stomatal characteristics and photosynthetic function of plants up the tidal line showed convergent adaptation, while the leaf stomatal and morphological traits of plants below the tidal line showed co-evolution (Coyle et al., 2014). Besides, different plants have different levels of adaptation. For example, plants in the dune community in New Zealand have different water use patterns, thereby they can coexist, with a low competition between them. Convergence may be weakened by competition between functionally similar species, leading to differentiation. Harsh

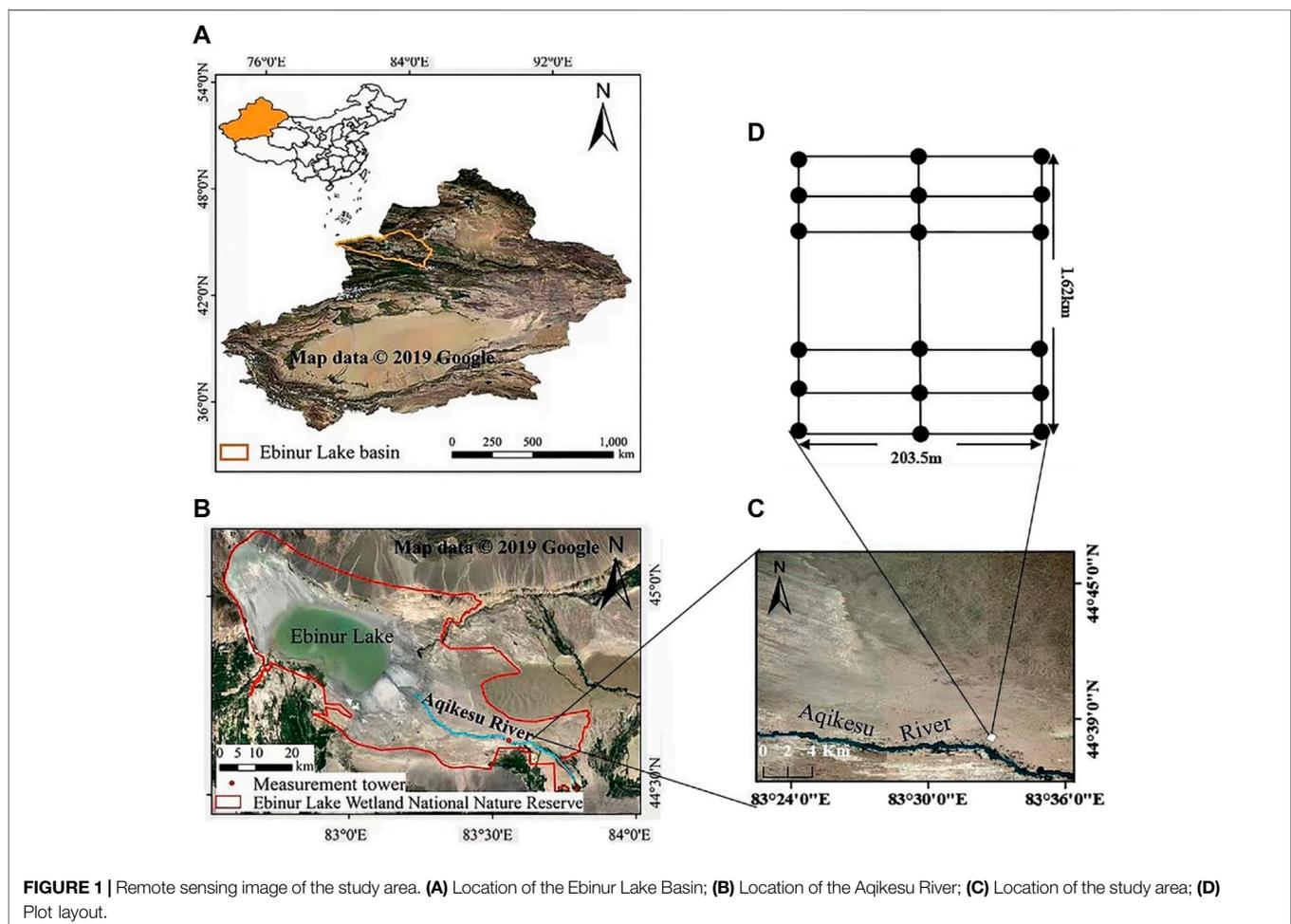


TABLE 1 | Determination method of plant functional traits.

Functional traits	Abbreviation	Measured method	Instrument
Specific leaf area	SLA	leaf area/leaf dry weight	—
leaf dry matter content	LDMC	dry leaf weight/fresh leaf weight	—
leaf moisture content	LMC	(leaf fresh weight - leaf dry weight)/leaf fresh weight	—
Leaf carbon concentration	LCC	Potassium dichromate external heating method Liu (2017)	Ultraviolet spectrophotometer (UV-6100, Shanghai Jinghua instruments, China)
Leaf nitrogen concentration	LNC	Nesslerization Crosby (1968)	Ultraviolet spectrophotometer (UV-6100, Shanghai Jinghua instruments, China)
Leaf phosphorus concentration	LPC	Molybdenum-antimony anti-colorimetric method Lu (2009)	Ultraviolet spectrophotometer (UV-6100, Shanghai Jinghua instruments, China)

TABLE 2 | Determination methods of soil physical and chemical properties.

Soil properties	Abbreviation	Measurement method	Instrument
Soil moisture content	SMC	Drying method	Oven
Soil salt concentration	SSC	Conductometric analysis	Electric conductometer (DDS-307A, Shanghai INESA & Scientific Instrument CO.LTD, China)
pH	PH	Glass electrode method	pH meter (DDS-307A, Shanghai INESA & Scientific Instrument CO.LTD, China)
Soil organic carbon	SOC	Potassium dichromate method Liu (2017)	—
Soil total nitrogen	STN	Kjeldahl method Saéz-Plaza et al. (2013)	Kjeldahl digestion apparatus (KDN-20C, Shanghai INESA & Scientific Instrument CO.LTD, China)
Soil total phosphorus	STP	Molybdenum blue method Murphy and Riley (1962)	Ultraviolet spectrophotometer (UV-6100, Shanghai Jinghua instruments, China)
Soil available phosphorus	SAP	Mo-Sb colorimetry Xu et al. (2020)	Ultraviolet spectrophotometer (UV-6100, Shanghai Jinghua instruments, China)

environmental conditions and physical factors may limit the survival and development of many plants. Study has found that plants in Alpine and desert have the patterns of convergence, differentiation, and diversification (Bao and Liu, 2009).

Based on convergence theory (McCoy-Sulentic et al., 2017), leaf traits are often used to elucidate the linkages between species traits, flora, habitats, and their roles in ecosystems in ecological researches (McCoy-Sulentic et al., 2017). The interspecific variation of leaf traits has the same trend in same environments at both small and large scales (Kattge et al., 2011), and this trend reinforces the plant strategy theories by illustrating the characteristics of plant traits developed in same environments (Westoby and Wright, 2006). As a basic framework for understanding species responses to ecological changes and their distribution differences, more and more researches have focused on the functional characteristics of plants.

Leaf traits of different plant taxa in different biomes have great ecological and evolutionary significance. Therefore, it is of great significance to examine the adaptation of leaf traits by phylogeny (Wang et al., 2017). The trait combination of plant species comes from trade-offs. In recent years, model studies have emerged to elucidate the leaf trait convergence and its influencing factors. However, the mechanisms underlying phylogenetic influences on leaf traits remain unclear.

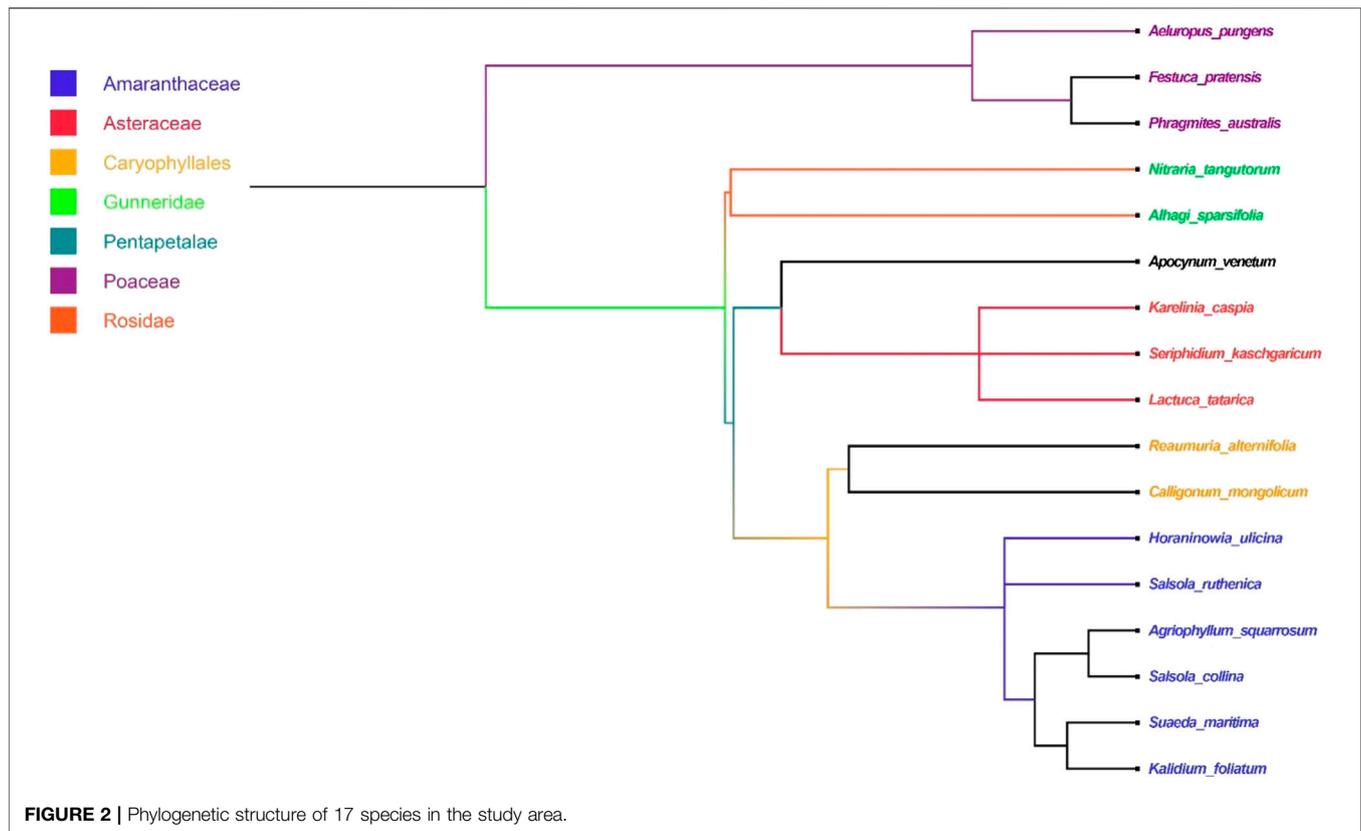
Arid zones are one of the most vulnerable ecosystems, with water being the most important influencing factor (Guo et al., 2003). At present, due to global climate change and

overexploitation, plants in arid desert areas are severely stressed in terms of growth, reproduction, and diversity. Ebinur Lake Basin has a typical arid desert ecosystem. Current studies mainly focus on the community characteristics, plant physiology and ecology, etc. in Ebinur Lake Basin, but there are few studies on the convergent evolution of desert plants. In this study, the desert plants with different life forms in the Ebinur Lake Basin were studied to explore their differences in functional traits and the relationship with phylogeny, aiming to clarify the changing trends of leaf traits among different desert plant species and taxa. We hypothesized that: (1) plants in the same environment might have a similar pattern of convergence in leaf morphology and physiological characteristics; and (2) the convergence pattern might be phylogenetically specific among different plant species. This study will improve our understanding of the variation of desert plant functional traits to similar environments in arid areas.

MATERIALS AND METHODS

Experimental Site

The study area is located in Ebinur National Wetland Nature Reserve in Jinghe County, Bortala Mongol Autonomous Prefecture, Xinjiang, China (44°31'05"-45°09'35"N, 82°33'47"-83°53'21"E). As the lowest depression in the Junggar Basin, Ebinur Lake wetland is mainly recharged by rivers and groundwater. The Ebinur Lake Basin has a typical temperate

**TABLE 3 |** Soil properties in the Ebinur Lake basin.

Soil properties								
Date	STP (g/kg)	STN (g/kg)	SAP (mg/kg)	SOC (g/kg)	SMC (%)	pH	SEC ($\mu\text{S}/\text{cm}$)	SSC (%)
Mean	0.28	0.06	18.25	1.64	2.02	7.76	2.47	2.48
SE	0.03	0.04	3.19	1.02	1.51	0.19	0.99	0.94
CV (%)	11.04	55.67	17.50	62.22	74.89	2.48	40.10	38.08

Note: SE, standard error; CV, coefficient of variation; SOC, soil organic carbon; STN, soil total nitrogen; STP, soil total phosphorus; SAP, soil available phosphorus; SMC, soil moisture content; SEC, soil electrical conductivity; SSC, soil salt concentration. The same below.

continental climate, with dry air, little rain, and large evaporation. The average daily temperature was 6–8°C, the accumulated temperature was 3,000–3,500°C, and the average annual precipitation was 90.9 mm. The soil types are gray desert soil and aeolian sandy soil. Plants are drought tolerant, including *Haloxylon ammodendron* Bunge, *Populus euphratica* Oliv., *Halimodendron halodendron* Pall., *Seriphidium kaschgaricum* Krasch., *Nitraria tangutorum* Bobr., *Kalidium foliatum* Pall., *Alhagi sparsifolia* Shap., *Aeluropus pungens* Pungens., *Apocynum venetum* L., *Sageretia pycnophylla* Ulicina., *Suaeda salsa* L., *Phragmites australis* Cav., *Calligonum mongolicum* Turcz., *Halimodendron halodendron* Pall., *Karelinia caspia* Caspia., etc.

Experimental Design and Data Acquisition

In the Ebinur Lake Basin, 5 km away from the Aqikesu River, three transects (1.62 km in length) with a distance of 100 m

from east to west were set in the direction perpendicular to the river. Then, plots (1.5 m \times 1.5 m) were set at an interval of 40 m from north to south in each transect, and there were 120 plots in total (Figure 1). Plant samples were collected from June to July 2017 (the most vigorous growth season for plants), and the geographic coordinates and elevation of each plot and plant species in the study area were recorded (Supplementary Table S1). For the plants in each plot, a total of 20 g of complete and mature leaves were collected from each plant in the direction of south, east, north, and west. The leaf samples of the same species in each plot were bagged. Leaf samples of 17 plant genera were collected finally, but only 14 genera were used for this study due to the low sample size of the other 3 genera (Supplementary Table S1). According to *Halophytes* in China (Zhao and Li, 1999), the plant samples were divided into 3 functional groups (4 annuals, 5

TABLE 4 | Leaf traits for plants with different life forms.

Life forms	Statistic	LCC (g·kg ⁻¹)	LNC (g·kg ⁻¹)	LPC (g·kg ⁻¹)	SLA (cm ² ·g)	LDMC (g·g ⁻¹)	LMC (%)
AG <i>n</i> = 4	Mean	217.67	10.04	2.65	34.57	0.16	78.74
	Max	323.00	25.39	3.93	88.09	0.45	86.15
	Min	135.50	0.93	1.62	1.29	0.01	65.78
	SE	4.00	0.46	0.04	1.69	0.01	0.30
	CV	20.56	50.70	16.62	54.66	51.79	20.56
PG <i>n</i> = 5	Mean	365.95	11.33	2.76	35.65	0.22	66.95
	Max	436.00	20.81	4.27	82.40	0.51	86.78
	Min	296.00	1.40	1.78	1.63	0.01	58.82
	SE	4.27	0.57	0.08	3.18	0.02	1.11
	CV	8.41	36.15	21.21	68.69	71.28	8.41
S <i>n</i> = 5	Mean	312.16	13.48	2.53	11.28	0.15	72.31
	Max	382.50	31.17	3.67	36.18	0.27	85.11
	Min	208.50	2.33	2.08	0.77	0.01	53.21
	SE	5.69	0.84	0.05	1.02	0.01	0.94
	CV	13.88	47.29	15.68	68.87	66.10	13.88
ALL <i>n</i> = 14	Mean	273.8	11.13	2.64	28.34	0.1528	74.55
	SE	4.91	0.35	0.03	1.34	0.01	0.49
	F	264.63	8.53	3.46	35.87	32.18	84.18
	P	0.00	0.00	0.03	0.00	0.00	0.00

Note: LCC, leaf carbon concentration; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; SLA, specific leaf area; LDMC, leaf dry matter content; LMC: leaf moisture content; SE, standard error; CV, coefficient of variation; n, number of samples.

TABLE 5 | Leaf traits for C3 plants, C4 plants, legumes, and nonlegumes.

Plant	Date	LCC (g/kg)	LNC (g/kg)	LPC (g/kg)	SLA (g/cm ²)	LDMC (g/kg)	LMC (%)
C3	Mean	345.70	12.16	2.66	22.09	0.14	69.28
	SE	3.98	0.54	0.06	2.10	0.01	0.80
	CV (%)	10.92	42.36	19.89	90.17	95.03	10.93
C4	Mean	229.18	10.56	2.64	32.57	0.16	77.91
	SE	4.61	0.46	0.04	1.64	0.01	0.42
	CV (%)	24.16	51.61	24.47	60.73	58.33	6.50
	F	306.60	4.92	0.12	15.54	1.61	109.49
	P	0.00	0.03	0.53	0.00	0.21	0.00
Legumes	Mean	337.68	14.31	2.53	16.71	0.09	71.34
	SE	4.54	1.19	0.08	1.71	0.01	0.90
	CV (%)	6.71	41.53	16.68	51.32	40.29	6.30
Nonlegumes	Mean	304.70	11.15	2.60	16.02	0.11	73.85
	SE	10.77	0.96	0.08	2.53	0.02	1.55
	CV (%)	21.50	52.27	17.78	95.99	98.33	12.73
	F	5.84	4.30	0.34	0.04	1.46	1.54
	P	0.02	0.04	0.56	0.84	0.23	0.22

Note: LCC, leaf carbon concentration; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; SLA, specific leaf area; LDMC, leaf dry matter content; LMC: leaf moisture content; SE, standard error; CV, coefficient of variation; n, sample size.

perennials, and 5 shrubs). Chemical analysis was conducted using the leaf samples in the lab after drying and grinding.

In this study, the leaf traits including leaf carbon concentration (LCC), leaf nitrogen concentration (LNC), leaf phosphorus concentration (LPC), specific leaf area (SLA), leaf dry matter content (LDMC), and leaf moisture content (LMC) were determined (**Supplementary Table S1; Table 1**).

In each plot, soils of the 0–30 cm layer were sampled using aluminum boxes (five replications), and mixed as the soil sample of the plot to measure the soil moisture content (SMC) in the lab. Besides, soils of 0–30 cm layer were also collected using shovel and packaged in ziplock bags, to determine soil properties

including salt concentration (SSC), pH, organic matter concentration (SOC), total nitrogen concentration (STN), total phosphorus concentration (STP), and available phosphorus concentration (SAP) in the lab after air drying (**Table 2**).

Data Analysis

To identify and explain the variation in leaf traits of each species, the data were analyzed from functional group and phylogeny. Firstly, the data for each functional group (such as annuals, perennials, and shrubs) were analyzed at the species level. In addition, the differences in C, N, P, SLA, LDMC, and LMC between functional groups were explored by one-way analysis of variance (ANOVA) using SPSS software (IBM, NY,

TABLE 6 | Pearson's correlation for plant leaf traits at the species level.

	LCC	LNC	LPC	SLA	LDMC	LMC
LCC	1					
LNC	0.090	1				
LPC	0.062	0.255**	1			
SLA	-0.187**	-0.081	0.180**	1		
LDMC	0.050	-0.037	0.255**	0.813**	1	
LMC	-0.672**	-0.075	-0.173**	0.013	-0.364**	1

Note: LCC, leaf carbon concentration; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; SLA, specific leaf area; LDMC, leaf dry matter content; LMC: leaf moisture content; ** significance at $p \leq 0.01$; * significance at $p \leq 0.05$.

USA). Principal component analysis (PCA) was used to analyze the correlations of the above 6 traits of plant leaves. The general linear model (GLM) was used to compute the contribution of soil and plant functional groups/family to the total variance of leaf traits.

Plant classification was performed using Angiosperm Phylogeny Group III (APG-III) (Twohey et al., 2019), and the phylogenetic tree was constructed by using the online tool Phylomatic (<http://www.phylodiversity.net/phylomatic/phylomatic.html>). The phylogenetic signal (PS) intensity of all leaf traits was confirmed by K statistics for leaf trait identification and phylogenetic preservation analysis. The trait-related phylogenetic errors were eliminated using phylogenetic independent contrasts (PIC), and PIC was calculated using the "Picante" package and the "Vegan" package in the R software (version 4.1.3, R core team, Vienna, Austria). Averages of LCC, LNC, LPC, SLA, LDMC, and LMC were plotted on a phylogenetic tree to determine their phylogenetic patterns. The binary relationship between leaf traits of various plant species and plant life forms (annuals, perennials, and shrubs) was evaluated using linear regression analysis. Statistical analyses of phylogenetic data were performed using R software (version 4.1.3, R core team, Vienna, Austria), and other relevant statistical analyses were performed using Origin 2018 (Origin Lab, Northampton, WA, USA) and SPSS software (IBM, NY, USA). The graphs were completed by using R software (version 4.1.3, R core team, Vienna, Austria) and Origin software, and the data sorting and statistics were completed by Office software (Microsoft, USA, 2016) and SPSS software.

RESULTS

Species Composition and Soil Properties

A total of 17 plant species belonging to 17 genera and 8 families (Amaranthaceae (7), Asteraceae (3), Poaceae (3), Apocynaceae (1), Fabaceae (1), Nitrariaceae (1), Tamaricaceae (1), Polygonaceae (1)) were recorded. Classification of functional groups of the species was as follows: (I) Annuals (5), perennials (6), and shrubs (6); (II) C3 species (9) and C4 species (8); (III) Legumes (1) and non-legumes (16). Perennials and shrubs were the dominants (**Figure 2**; **Supplementary Table S1**).

The soil in the study area was alkaline, and the coefficient of variations (CVs) of STN, SOC, and SMC were all greater than 50% (**Table 3**).

Patterns of Leaf Traits of Different Functional Groups

The One-way ANOVA analysis showed that the LCC and LNC in perennials and shrubs were higher than those in annuals, and there was no difference in the LPC. The SLA and LDMC in perennials were higher than that in annuals and shrubs (**Figure 2**; **Table 4**), and the LMC of annuals and shrubs was higher than that of perennials. The analysis of variance showed that there were significant differences in the LCC, LNC, LPC, SLA, LDMC, and LMC among different life forms (**Table 4**).

C3 plants had higher LCC, LNC, and LPC than C4 plants, while C4 plants had higher SLA, LDMC, and LMC than C3 plants. The one-way ANOVA analysis showed that there were significant differences in LCC, LNC, SLA, and LMC between C3 and C4 plants, but there was no difference in LPC and LDMC (**Table 5**). Leguminous plants had higher LCC, LNC, and SLA than non-leguminous plants, while non-leguminous plants had higher LMC than legumes. The ANOVA analysis showed that there were significant differences in LCC and LNC between legumes and non-leguminous plants, but there were no significant difference in LPC, SLA, LDMC, and LMC (**Table 6**).

Correlations Between Leaf Traits

Pearson correlation analysis showed that LCC was significantly negatively correlated with SLA and LMC. LNC was significantly positively correlated with LPC. LPC was significantly negatively correlated with SLA and LDMC and negatively correlated with LMC. SLA was significantly positively correlated with LDMC. LDMC was significantly negatively correlated with LMC (**Table 6**).

The PSs of functional traits were detected in all species (**Table 7**). However, the PSs of all leaf traits were low (K-value < 1 , $p > 0.05$), and that of LCC was the largest (K = 0.73).

In annuals, LCC was negatively correlated with LNC ($p < 0.05$) and LPC ($p < 0.05$), and LNC was positively correlated with LPC ($p < 0.05$). In perennials, LCC was positively correlated with LNC ($p < 0.05$) and LPC ($p < 0.05$), and LNC was positively correlated with LPC ($p < 0.05$). In shrubs, LCC was negatively correlated with LNC ($p < 0.05$) and LPC ($p > 0.05$), and LNC was positively correlated with LPC ($p > 0.05$) (**Figures 3, 4**).

Principal component analysis (PCA) showed that SLA and LDMC loaded on the PC1, C and LMC loaded on the PC2, and N

TABLE 7 | Phylogenetic signals of different leaf traits.

Traits	K	p
LCC	0.75	0.107
LNC	0.32	0.77
LPC	0.42	0.471
SLA	0.28	0.968
LDMC	0.31	0.84
LMC	0.58	0.384

Note: LCC, leaf carbon concentration; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; SLA, specific leaf area; LDMC, leaf dry matter content; LMC: leaf moisture content.

and P loaded on the PC3. PC1, PC2, and PC3 explained 32.3%, 27.5%, and 19.0% of the total variation, respectively (Figure 5; Supplementary Table S2).

Relationships Between Leaf Traits and Soil Properties

Only STN and STP were significantly positively correlated with LCC and LNC (Table 8).

Pearson correlation analysis showed that SOC was significantly positively correlated with STP, SAP, SMC, pH, and soil electrical conductivity (SCE). STN was significantly positively correlated with STP and SAP. STP was significantly positively correlated with SAP, SMC, pH, and SCE. SAP was significantly positively correlated with SMC, pH, and SCE. SMC was significantly positively correlated with pH and SCE. pH was significantly positively correlated with SCE (Table 9).

Taxonomy of Leaf Traits at Species and Family Levels

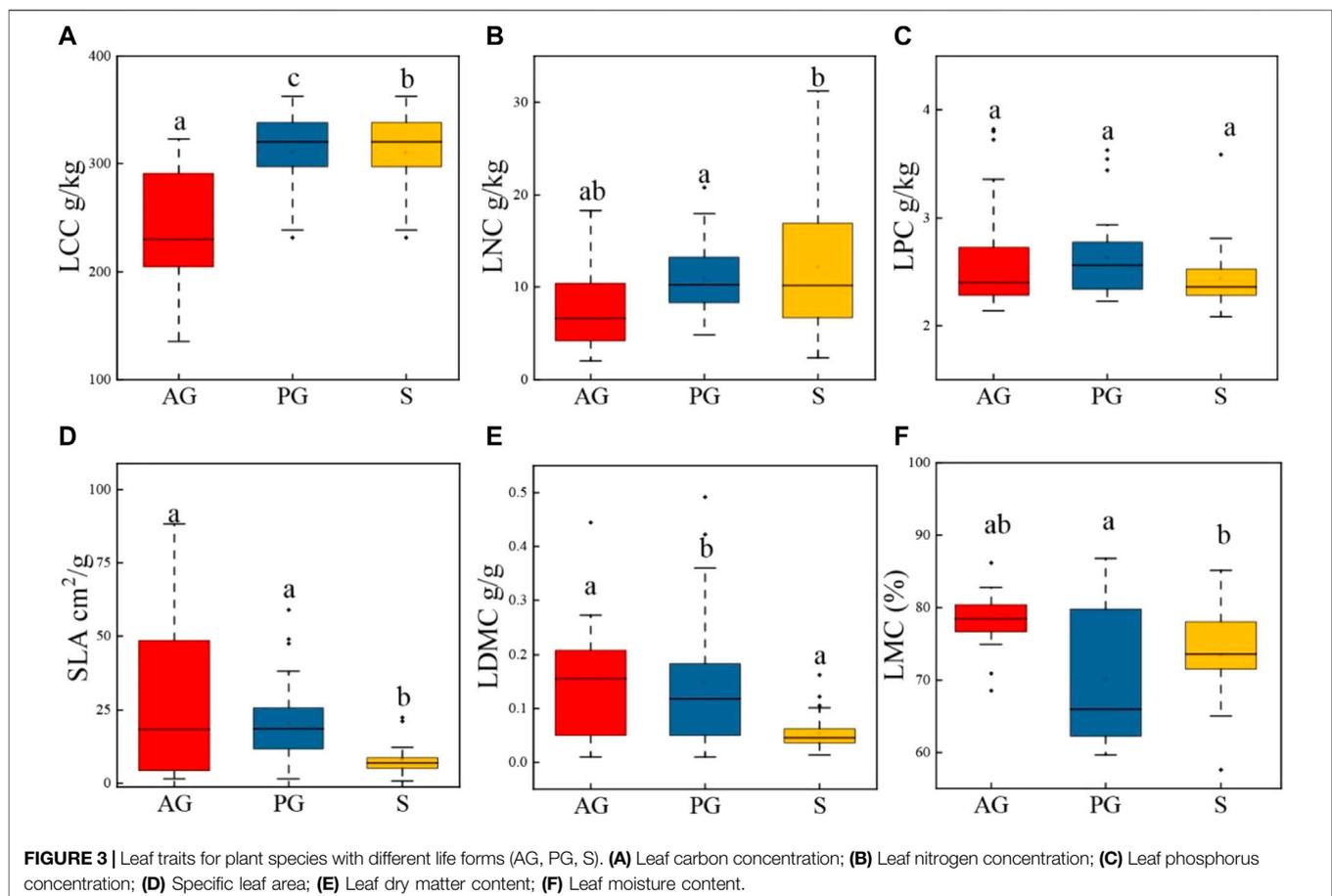
The leaf traits of different species varied greatly (Supplementary Table S3). At the species level, *Seriphidium kaschgaricum* and *Aeluropus pungens* had a higher LCC, *Kalidium foliatum* and

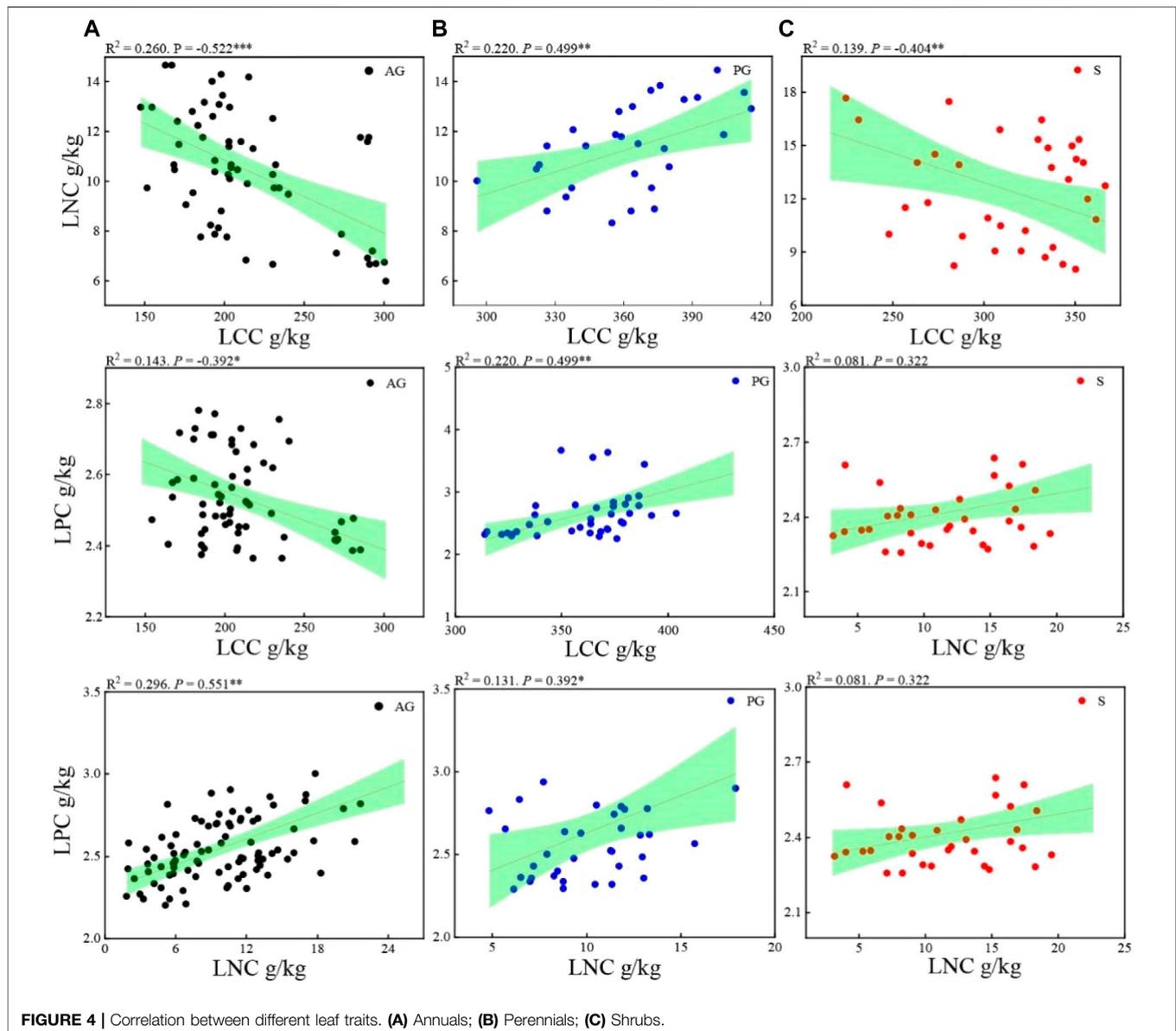
Nitraria tangutorum had a higher LNC, *Seriphidium kaschgaricum*, *Suaeda salsa*, and *Reaumuria alternifolia* had a higher LPC. *Suaeda salsa* and *Seriphidium kaschgaricum* had a higher SLA, *Suaeda salsa* and *Seriphidium kaschgaricum* had a higher LDMC, and *Karelinia caspia* and *Lactuca tatarica* had a higher LMC.

One-way analysis of variance showed that the six leaf traits varied widely among the 7 families (Supplementary Table S4). At the family level, Asteraceae had a higher LCC, Poaceae and Nitrariaceae had a higher LNC, and Asteraceae and Tamaricaceae had a higher LPC. Amaranthaceae and Asteraceae had a higher SLA. Asteraceae and Poaceae had a higher LDMC. Amaranthaceae and Nitrariaceae had a higher LMC.

Partitioning of Variance in Leaf Traits

The effects of taxonomy and soil properties on leaf traits were studied using general linear model (GLM). This model explained 13%–55% of the total variation. Among them, taxonomy explained 11%–43% of the variation, and soil properties explained 2.15%–12% of the variation. Therefore, taxonomy could better explain leaf trait variation. This is because taxonomy had a greater impact on LCC, LNC SLA, and LMC, while soil properties explained less variation in the same leaf trait (Table 10).





DISCUSSION

Differences in Leaf Traits of Different Functional Groups

Leaf is an important functional organ for plant photosynthesis, and it is also the organ that has the most contact with the surrounding environment. Using the change of leaf traits to study the adaptability of plants to the environment has become one of the important means to study the stress resistance of plants. Studies have found that species coexistence can be better elucidated only when functional trait differences are fully considered at the species level. In this study, leaf traits were investigated for 14 genera (Supplementary Table S1). The average LCC of the 14 plant genera (Table 4) was lower than that of plants in China (Tang et al., 2018) and herbs in

Yucatan, Mexico (Abdala-Roberts et al., 2018). The average LPC was significantly lower than that of global plants (Reich and Oleksyn, 2004) and plants in the terrestrial ecosystems in China (Tang et al., 2018). This indicates that the desert plants in the study area have a high degree of adaptation and tolerance to arid and barren environments. Leaf nutrient concentration plays a fundamental role in plant growth and physiological processes. During vigorous growth, plants may allocate most nutrients to leaves to improve the dry matter accumulation in the aboveground organs (Fernández-Martínez et al., 2019).

In terms of life form, perennials had the highest LCC, SLA, and LDMC, followed by shrubs and annuals. The higher LCC of perennials may be due to the difference in the ability of plants with different life forms to obtain light sources. Plants

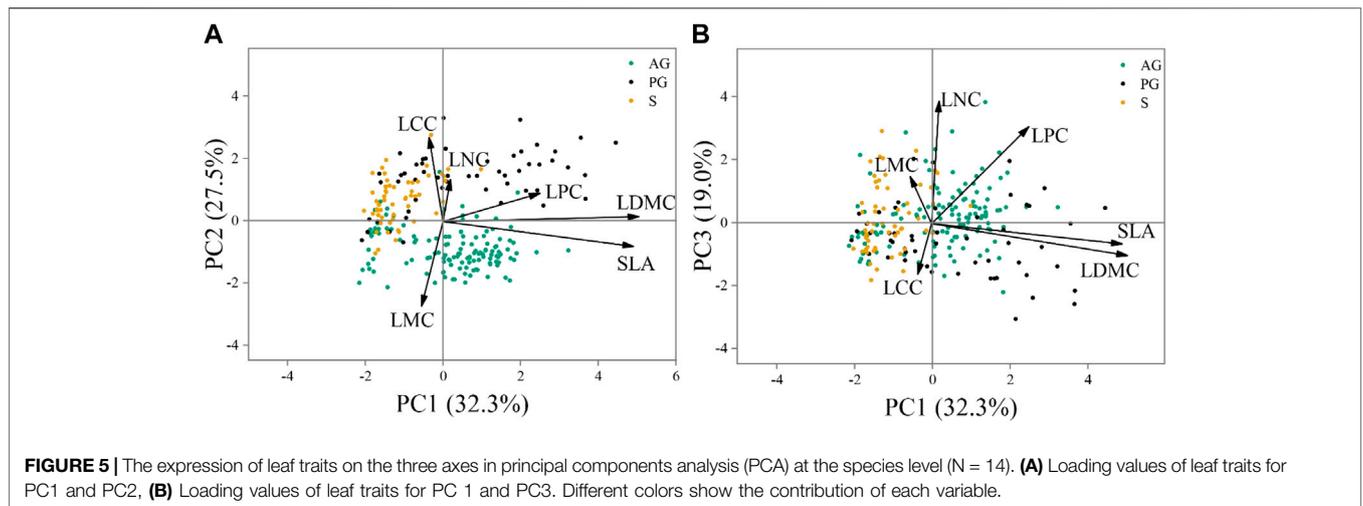


TABLE 8 | Correlation matrix for macro-elements of plant and soil.

	SOC	STN	STP
LCC	0.05	0.146*	0.141*
LNC	-0.11	0.195**	0.238**
LPC	-0.01	-0.02	-0.04

Note: LCC, leaf carbon concentration; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; SOC: soil organic carbon; STN: soil total nitrogen; STP: soil total phosphorus; Correlation is significant at ** $p \leq 0.01$ and * $p \leq 0.05$.

TABLE 9 | Correlation analysis of soil properties.

	SOC	STN	STP	SAP	SMC	pH	SCE
SOC	1						
STN	0.178	1					
STP	0.381**	0.228*	1				
SAP	0.525**	0.381**	0.458**	1			
SMC	0.413**	-0.005	0.408**	0.300**	1		
pH	0.365**	-0.029	0.451**	0.236**	0.511**	1	
SCE	0.473**	-0.001	0.460**	0.464**	0.686**	0.501**	1

SMC: soil moisture content; SSC: soil salt concentration; SOC soil organic carbon; STN soil total nitrogen; STP: soil total phosphorus; SAP: soil available phosphorus; SCE: soil electrical conductance. Correlation is significant at ** $p \leq 0.01$ and * $p \leq 0.05$.

TABLE 10 | General linear model (GLM) analysis of the effects of taxonomy and soil properties on leaf traits.

Leaf traits	Total effects (r^2 , %)		
	Full	Taxonomy	Soil properties
LCC	54.81	42.88	11.93
LNC	28.55	26.05	2.50
LPC	13.66	11.50	2.16
SLA	32.11	29.96	2.15
LDMC	19.17	14.94	4.23
LMC	28.48	26.18	2.30

Soil properties: pH, SCE, and SMC, of the 0–30 cm soil layer.

accumulate C through leaf photosynthesis, while perennials have a larger SLA ($35.65 \text{ cm}^2 \text{ g}^{-1}$) and higher photosynthetic capacity than annuals and shrubs (Chen et al., 2016). Díaz (Perez-Harguindeguy et al., 2016) found that plants with high SLA had higher photosynthetic capacity and growth rate, while plants with low SLA could better adapt to the water and nutrient insufficient environments. In this study, compared with low-height shrubs (*Apocynum venetum* and *Alhagi sparsifolia*), perennials (mainly *Karelinia caspia* and *Phragmites australis*) in the study area had stronger photosynthetic capacity and could quickly capture external resources, while slow-growing annuals had lower SLA value and tended to preserve internal resources better (Grassein et al., 2010). Similar to SLA, the analysis of LDMC also indicates the resource utilization strategies of plants at different heights with different life forms (Guo et al., 2003).

In this study, annuals had the highest LMC, followed by shrubs and perennials. In arid environments, water is the main limiting factor. As an “opportunist,” annuals can complete their seed germination and maintain their life cycle after spring rains (Zhang et al., 2006). The growth of annuals mainly depends on the environmental resources, while perennials have certain anti-interference and self-recovery capabilities (Alhamad and Alrababah, 2013). The results of this study showed that compared with plants in other types of habitats, desert plants in the study area had relatively low LPC and relatively high LNC. This indicates that P is the main limiting factor for the plants in the study area. The higher LNC may be due to that soil N is significantly positively correlated with leaf N. In this study, STN was higher than STP (Table 3). Previous studies have shown that the LPC in desert plants is higher in arid environment. Because P is very important for plants to maintain water use efficiency and growth, desert plants need to allocate a large amount of P-rich elements to meet their growth demands (Sardans and Peñuelas, 2007). This is contrary to our results. It may be due to the fact that under extreme drought conditions, plants require a large amount of N to enhance the activities of enzymes related to drought

tolerance of plants to adapt to the drought environment and maintain normal growth and development (Yuan and Tang, 2010).

In the study area, C3 plants had higher LCC, LNC, and LPC than C4 plants, and C4 plants had higher SLA and LDMC than C3 plants (Table 5). Under the same environmental conditions, C3 plants with lower photosynthesis rate need more C, N, and P to maintain photosynthesis to obtain energy, which reflects that plants adapt to environmental changes by increasing or reducing nutrient cycling (Guo et al., 2009). Compared with C3 plants, C4 plants had a larger SLA and are easier to receive light to promote photosynthesis. SLA reflects the ability of plants to acquire, preserve, and use resources. A larger SLA is more conducive to the capture and utilization of light by plants (Wright et al., 2005). The LDMC of C3 plants was lower than that of C4 plants in this study. The leaf dry matter reflects the plant's ability to retain nutrients. The larger the LDMC, the greater the leaf tissue density, the stronger the resistance and tolerance of plants (Sun et al., 2020). Previous research has shown that C4 plants are suitable to grow in the environment of high temperature and drought (Pau et al., 2013). To enhance the drought tolerance, C4 plants resist the adverse environments by accumulating more dry matter, leading to the higher LDMC compared with C3 plants.

This study showed the LCC, LNC, and SLA of legumes were higher than those of non-leguminous plants, and there was no significant difference in LPC and LMC (Table 5). The STP in desert environment was low in this study, which was insufficient for plant growth, while STN was sufficient for the growth of leguminous shrubs in this study. Legumes use soil nitrogen-fixing symbionts to exchange C into N (Rogers et al., 2009), resulting in higher LCC and LNC in legumes than in non-leguminous plants. Liu et al. showed that in addition to nitrogen fixation in legumes, plant acid phosphatase (APASE) can hydrolyze organic phosphates, thus improving P absorption by legumes (Liu et al., 2018). However, we did not find higher LPC in legumes in this study. This may be due to the different adaptation strategies of desert plants. The other reason may be that the relatively low soil P in China inhibit the uptake of P by legumes. When faced with P stress, legume nodules can redistribute P from root to nodules through internal P cycling and P retention mechanisms, rather than taking up P directly from soil (Vardien et al., 2016).

Relationship Between Leaf Traits, Phylogenetic Signals, and Soil Properties

PIC analysis showed that $K < 1$. This indicates that leaf traits of the desert plants in the study area were phylogenetically conserved. Whether or not phylogeny is considered, the relationship between leaf traits may be related to the chemical properties and biochemical functions (Zhang et al., 2012). It was found that the phylogenetic signal (PS) of C, N, P, SLA, LDMC, and LMC for all species was not significant. Therefore, the phylogeny may have a great influence on the functional traits (C, N, P, SLA, LDMC, and LMC), and these traits may be more phylogenetically conserved. The PS of all leaf traits were low ($K < 1$) in this study (Table 7). It indicates that leaf traits are predominantly influenced by climatic factors (Zhang et al., 2012). LDMC showed a significant negative correlation with

LMC (Table 6). This reflects the convergence in the leaf traits of desert plants related to nutrient absorption and light capture capacity. Therefore, these leaf traits have evolutionary changes. The SLA and LDMC loaded on PC1 are of great importance for plant nutrient retention and photosynthetic efficiency (Tang et al., 2018). The LCC, LMC, LNC, and LPC loaded on PCA 2 and 3 are of great importance for plant growth, physiological processes, photosynthesis, enzyme activity, and water use (Tang et al., 2018; Ratzmann et al., 2019).

SOC, STN, and STP reflects soil fertility and productivity. Among them, SOC directly affect the productivity of ecosystems (Ouyang et al., 2017), and STN and STP are necessary for plant growth and directly affect photosynthesis and the processes associated with productivity (Liu et al., 2013). In this study, correlation analysis showed that STN and STP were significantly positively correlated with LCC and LNC (Table 8). This indicates that when STN and STP increase, the C and N in leaf may be increased. STN can significantly promote the aboveground growth of desert plants. Liu et al. (Liu et al., 2014) found that in a certain range, the higher the STN, the higher the LCC of plants. This is consistent with our study results. SAP plays an important role in promoting plant growth and development (Du et al., 2009). In this study, SAP had a significant positive correlation with SMC and pH. However, the soils in the study area are mostly calcium carbonate-rich soils, and the soil particles are coarse, leading to the vast majority of P being fixed in the soil and low levels of SAP (Ja and Li, 2011). Wang et al. (Wang, 2010) investigated soils in northern China and found that in areas with generally low soil P concentrations, plants had higher P use efficiency. Besides, study has shown that the pH value of 7.76–8.89 can improve the bioavailability of soil P (Zhou et al., 2011). The soil pH in the study area is 7.76–8.39, which promotes the absorption of P by desert plants.

Partitioning of Variance of Leaf Traits by Taxonomy

Our results showed that there were significant differences in leaf traits at species (Supplementary Table S2) and family levels (Table 10) ($p < 0.05$). Taxonomy and soil properties jointly explained 19.17%–54.81% of the variation of leaf traits. Soil properties explained 2.15%–12% of the variation (Table 10). Besides, it was also found that taxonomy and plant phylogeny greatly affected plant leaf traits, resulting in great differences in the degree of variation between leaf traits. Due to the different survival strategies of plants caused by factors such as arid climate, less precipitation, and barren soil, the selective absorption of nutrients by plants leads to great variation of leaf traits, reducing the competition for resources and achieving convergent development (Zhang et al., 2012).

CONCLUSION

In the Ebinur Lake Basin, except for C and LMC, leaf traits (N, P, SLA, and LDMC) show a convergent pattern for all plant life forms. The plants have evolved and developed different survival strategies to adapt to the arid environment. The differences in leaf traits reflect the

differences of functional groups. Therefore, the plants in this study exhibit unique intrinsic characteristics. In addition, the leaf traits of desert plants tend to be consistent in adapting to the environment of the Ebinur Lake Basin, and the convergence pattern is not phylogenetically specific. All leaf traits are phylogenetically conserved ($K < 1$, $p > 0.05$). In addition, the convergence in leaf traits of the desert plants in Ebinur Lake Basin is most likely due to the environmental factors. This research may contribute to understanding the convergent adaptations and patterns of desert plants in arid regions.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

ZL provided field data for the paper; SN wrote the paper, and JL and LG contributed to writing—review and editing. All authors have read and agreed to the published version of the manuscript.

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SUPPLEMENTARY MATERIAL

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