

Relationships between *Artemisia ordosica* communities and environmental factors following sand-dune stabilization in the Mu Us desert, northwest China

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Abstract *Artemisia ordosica* is an excellent sand-fixing shrub for sand stabilization in northwestern China. Sand dune stabilization, a critically important process, leads changes in abiotic factors, such as soil structure and nutrient contents. However, the effects of factors on an *A. ordosica* community following sand stabilization remain unclear. In this study, we used canonical correspondence analysis (CCA) to examine the relationships between *A. ordosica* communities and environmental factors at three habitats: semi-fixed dune (SF), fixed dune with low-coverage biological soil crust (F), and fixed dune with high-coverage biological soil crust (FC) in Mu Us desert. The mean height and coverage of plants increased with sand stabilization, while species diversity and richness increased initially and then reduced significantly. Correlation analysis and CCA revealed that slope, soil organic carbon, and nutrient contents, proportion of fine soil particles, soil moisture, and thickness of biological soil crust were all

highly correlated with vegetation characteristics. These environmental factors could explain 40.42 % of the vegetation–environment relationships at the three habitats. The distribution of plant species was positively related to soil moisture in the SF dune. Soil moisture, soil nutrient, and fine-particle contents mainly affected plants distribution in the F dune. In the FC dune, distribution of plant species was positively and negatively correlated with the thickness of biological soil crust and soil moisture at a depth 0–20 cm, respectively. The dominance value of typical steppe species increased significantly following sand-dune stabilization and relations between species and samples in CCA ordination bi-plots showed that perennial grasses could invade the *A. ordosica* community on FC, indicating *A. ordosica* communities had a tendency to change into typical steppe vegetation with the further fixation. We conclude that the significant differentiation not only occurred in community characteristics, but also in the relationships between vegetation and environmental factors among the three stages of dune fixation. So, restoration of degraded dune ecosystems should be based on habitat conditions and ecological needs.

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Introduction

The interaction between plants and the environment generates plant communities, and multiple environmental factors affect the spatial distribution of those communities (Borcard et al. 1992). Studies of the relationship between sand-dune vegetation and environmental factors have

shown that soil properties, topography, and underground water level are the main factors leading to changes in vegetation (Qian et al. 2007; Stavi et al. 2008; Sang 2009). However, the distribution of vegetation is often associated with corresponding environmental conditions (Beyer et al. 1998). For plant communities on sand dunes with the same climatic conditions, differences in habitat conditions following sand-dune stabilization may be the main cause of differences in the species composition and spatial distribution of plant communities (Li et al. 2010, 2011a).

Whether the relationships between distribution of plant species and environmental factors remain constant under different habitat conditions is still unclear. In addition, vegetation coverage and species diversity are two important features of plant communities. Many studies have shown that the impact of environmental factors on these two features is rather complex (Kerley et al. 2004; Song et al. 2011). In-depth analysis of the relationships between the vegetation characteristics (including vegetation distribution, vegetation coverage, and plant-species diversity) and environmental factors during sand stabilization can provide important information related to the management of desert vegetation communities, and protection and restoration of arid and semi-arid sand dune ecosystems.

China is a country that suffers from serious desertification: some 27.33 % of China's total land area has become desert (State Forestry Administration 2011). A wide range of vegetation restoration programs have been carried out to control desertification in northwest China (Li et al. 2004). The Mu Us desert is situated in the arid and semi-arid ecotones of northern China. This special ecogeographic location is the key region where preventative work on desertification is highlighted (Yang et al. 2012). In the Mu Us desert, *Artemisia ordosica* is an excellent sand-binding shrub that grows on dunes with various degrees of sand mobility (Li 2001; Li et al. 2011a).

However, it is difficult to determine the stability of an *A. ordosica* community, which is important for vegetation management and ecological security maintenance (Li et al. 2011a). Current studies have mainly emphasized the composition of plants and their dynamics in *A. ordosica* communities, and have not comprehensively considered the variations in soil physical and chemical properties, soil moisture, the physiological and ecological characteristics of the *A. ordosica* community, and the dynamic characteristics of the population following sand-dune fixation (Gao et al. 1999; Li 2005; Li et al. 2011a). Differences in plant responses to environmental factors lead to changes in community distribution. Therefore, the changes in the relationship between the *A. ordosica* community and the environment still require further study.

Quantitative analysis provides an important method for ecological research related to vegetation, and gradient

analysis is the most widely used method in plant ecological studies (Song et al. 2009; Kent 2011; Khan et al. 2013). Gradient analysis is a technique of ordination, in which the quadrats (or plant species) are arranged in a certain space, so that the ordination axis can reflect certain ecological gradients. These gradients are used to explain the relationship between the vegetation conditions, including species composition and spatial distribution, and environmental factors.

In this study, basic characteristics of the *A. ordosica* communities and environmental factors at sites with different degrees of dune stabilization were investigated, and the relationships between plant distribution within the communities and environmental factors were analyzed using gradient analysis. Our objectives were to: investigate which environmental factors primarily affect the coverage and species composition of plants within *A. ordosica* communities; identify the main environmental factors affecting the distribution of plant species within the communities at different stages of sand fixation; and understand the effects of the environmental driving forces on the succession of *A. ordosica* communities. We hypothesized that the dominant environmental factors affecting the *A. ordosica* community vary following sand stabilization. Quantitative analysis to characterize *A. ordosica* communities shows that they tend to change into typical steppe vegetation following sand-dune stabilization.

Materials and methods

Study area

The study area was located in the Yanchi Research Station of Beijing Forestry University, in Ningxia, northwest China. The area lies on the southern edge of the Mu Us desert (37°42' N, 107°14' E; 1400–1800 m above sea level) and is characterized by a mid-temperate semi-arid continental monsoon climate. The mean annual precipitation (1954–2013) is 275 mm, the mean annual temperature is 8.1 °C (Wang et al. 2014), and the mean annual potential evapotranspiration is 2024 mm (Jia et al. 2014). The soil is aeolian sandy soil with a pH range of 8.5–8.8.

Vegetation in the station mainly comes from air seeding and afforestation for desertification control in the 1980s. After nearly 30 years, the dominant vegetation on the sand dunes is *A. ordosica* communities with some desert leguminous shrubs, xeric grass, and herbs.

Vegetation survey and soil sampling analysis

From July to August 2013, three 100 m × 100-m plots were established in the study area. All the plots were

covered by *A. ordosica* communities without anthropogenic interference. One plot was located in a semi-fixed sand dune (SF), one in a fixed dune with low coverage of biological soil crust (<20 %, F), and one in a fixed dune with high coverage biological soil crust (>50 %, FC). In each plot, 50 1 m × 1-m survey quadrats were randomly established, totaling 150 quadrats. The number of plant species, abundance of each species, and plant height and coverage were determined in each survey quadrat.

A geological compass was used to measure the degree and direction of slope. Thickness of biological soil crust on the land was measured using calipers, and biological soil-crust coverage was measured with a 10-pin point sampling frame (Li et al. 2005). Soil bulk densities (γ_s) were measured using a soil-cutting ring (diameter, 5 cm), within each quadrat at a soil layer of 0–20-cm depth. Then soil samples were collected within each quadrat at a depth of 0–20 cm by using a soil auger (diameter, 3 cm). Additional soil cores were taken with the same soil auger in each quadrat to measure soil water content (SW) at depths of 0–20 cm (SW1), 20–40 cm (SW2), and 40–60 cm (SW3). Soil samples were air-dried and hand-sieved through a 2 mm screen to remove roots and other debris. The pretreated soil samples were analyzed with a laser diffraction technique using Malvern (MS 2000) to measure the topsoil particles and fractal characteristics (Gao et al. 2014). Each sample was measured five times and the mean value was used. The soil particle size distribution (PSD) results were output by U.S. Soil Taxonomy in the following size grades: 0–2, 2–50, 50–100, 100–250, 250–500, 500–1000, and 1000–2000 μm . Soil pH was measured using a pH-3C laboratory pH meter (Dazhong Analytical Instruments Factory, Shanghai, China). Soil electrical conductivity was measured using a DDS-11A laboratory conductivity meter (Shanghai Lida Instrument Co., Shanghai, China), soil organic carbon (SOC) was measured using the potassium dichromate oxidation–external heating method, and soil total nitrogen (TN) content and total phosphorus (TP) content were measured using a Kjeldahl apparatus (FOSS 2200) and a Shimadzu UV-2550 UV spectrophotometer (Shimadzu Corp. Kyoto, Japan), respectively. All field sampling and measurements were repeated three times.

Data analysis

Calculation of dominance of species

The dominance value of each species was calculated using Formula (1) (Zuo et al. 2009):

$$DV = (RA + RH + RC)/3 \quad (1)$$

where *DV* is the dominance of a species; *RA* is the species relative abundance (%); *RH* is the species' relative height (%); and *RC* is the species relative coverage (%).

Calculation of species diversity index

Species richness (*R*) was defined as the number of species in each survey quadrat (*s*).

The Shannon–Wiener Index (*H*) was calculated using Formula (2) (Li 2001):

$$H = - \sum_{i=1}^S P_i \ln P_i \quad (2)$$

where *S* is the total number of species, and *P_i* is the proportion of individual plants belonging to species *i* in all individual plants.

The Simpson index was calculated using Formula (3):

$$\text{Simpson index} = 1 - \sum_{i=1}^S P_i^2 \quad (3)$$

where *S* is the total number of species, and *P_i* is the proportion of individual plants belonging to species *i* in all individual plants.

Calculation of fractal dimension

Fractal dimension of soil PSD was calculated based on the volume distribution of soil particle size. The equation (Gui et al. 2010) is expressed using Formula (4):

$$\frac{V(r < R_i)}{V_T} = \left(\frac{R_i}{R_{\max}} \right)^{3-D} \quad (4)$$

where *r* is the soil particle size, *R_i* is the soil particle size of grade *i*, *R_{max}* is the maximum value of soil particle size, *V(r < R_i)* is the volume of soil particle size less than *R_i*, *V_T* is the total volume of soil particles, and *D* is the volume-based fractal dimension.

Canonical correlation analysis

Canonical correlation analysis (CCA) was performed to examine the relationships between plant distribution and environmental factors in the three plots. To avoid the effect of redundant variables, the significance of species–environment correlation was tested by a Monte Carlo test (*P* < 0.05), then the significant environmental factors were used for CCA. A matrix composed of 150 quadrats and 12 environmental factors was constructed to analyze the relationships between the quadrat distribution and environmental factors. Another matrix composed of 24 species and 12 environmental factors was constructed to analyze the relationship between the distribution of plant species and environmental factors.

In general, the coordinates (scores) of ordination objects (quadrat, species, and environmental factors) are only relative; they do not have absolute meanings. When interpreting ordination plots, the relative distance, relative direction, and the relative order of projection points were used to explain the relationships between the objects. An arrow denotes the direction of maximum environmental factor change, and the length of the arrow represents the degree of the influence of the environmental factor on the species data (explanatory power).

The angle between the arrows represents the correlations between the factors. A smaller angle indicates a stronger correlation. If the angle is close to a right angle, the correlation is very small. Two arrows pointing in the same direction represent a positive correlation between factors, while arrows pointing in opposite directions represent negative correlation (ter Braak 1986).

Species are denoted using triangles and the corresponding acronyms. The relative distance between the species and quadrat was used to assess changes in the relative abundance of a species within the quadrat. Closer distances between the species and the quadrat indicated a higher relative abundance of the species in that particular quadrat. Projections were made from the quadrat points to the environmental factor arrows, and the positions of the projection points approximately represent the rank of the environmental factors in these quadrats. The relative positions of the projection of the species point to environmental factor arrows that represent the rank of the optimum value of the species for the corresponding environmental factors.

Statistical analysis

After a homogeneity of variance test ($P > 0.05$), univariate analysis of variance (ANOVA) and multiple comparison tests ($P < 0.01$) were performed to compare the community characteristics of species diversity in different stages of sand-dune stabilization. Univariate ANOVA and least-significant difference (LSD) multiple comparisons were performed using SPSS 18.0 for Windows. Shannon–Wiener (H) and Simpson indices, Monte Carlo test and CCA were calculated using the R 3.0.1 Vegan package (2.0–10).

Results

Vegetation characteristics of *A. ordosica* communities

Table 1 showed the differences in species number, average height, vegetation cover, Shannon–Wiener index, Simpson

index, and biological soil crust among the three dune plots ($P < 0.01$). The average height and coverage of plants within the communities increased from SF to FC dunes. The Shannon–Wiener and Simpson indices of the communities were lower on the FC dune than on the SF and F dunes. The biological soil-crust conditions differed significantly following sand stabilization, and the biological soil crust thickness gradually increased with dune fixing.

Table 2 showed the plant species dominance values in the three sand stabilization stages. Within the communities, dominant species were *A. ordosica* and *Chenopodium aristatum* on the SF dune, and *A. ordosica* and *Leymus secalinus* on the F and FC dunes. The dominance value of *A. ordosica* increased from 25.60 % on the SF dune and 26.64 % on the F dune to 30.45 % on the FC dune. The dominance of *C. aristatum* and *Corispermum puberulum* was relatively high on the SF dune (18.97 %). With sand fixing, the dominance value of *C. aristatum* and *C. puberulum* fell to 0.95 % on the F dune and 3.27 % on the FC dune. *Pennisetum centrasiaticum* and *L. secalinus* had rather high dominance values on the FC dune, and those species occurred in addition to *A. ordosica*.

Relationships between vegetation characteristics and environmental factors within *A. ordosica* communities

Correlation analysis among vegetation characteristics, soil factors, and topography are shown in Table 3. Vegetation coverage was significantly correlated with all soil factors, aside from soil pH and electrical conductivity. Species richness and surface-soil crust thickness was negatively correlated ($P < 0.01$). Vegetation coverage and species richness were both positively correlated with soil-particle structure factors (soil clay content, soil silt content, soil PSD) and soil nutrient factors, including TN, TP, and SOC, and were both negatively correlated with soil moisture.

Canonical correspondence analysis on plant distribution and environmental factors within *A. ordosica* communities

The relationships between distribution of plant species and environment factors (excluding uncorrelated environment factors) following sand-dune stabilization were obtained by performing CCA analysis (Fig. 1a, b). Species–environmental relationships (Table 4; Fig. 1) revealed that the correlation was relatively high on the first two canonical axes, where all environmental factors could explain 40.42 % of the species–environmental relationships.

Using partial CCA analysis the explanatory powers of topographical factors, soil factors, and the interaction

Table 1 Vegetation characteristics of *Artemisia ordosica* communities following sand dune stabilization

Dune type	Species number	Average height (cm)	Vegetation cover (%)	Shannon index (H)	Simpson index	Thickness of biological soil crust (mm)
SF	16	34.90 ± 0.02 ^a	36.60 ± 0.01 ^a	1.34 ± 0.05 ^a	0.66 ± 0.02 ^a	0.81 ± 0.25 ^a
F	20	65.40 ± 0.13 ^b	50.10 ± 0.01 ^b	1.40 ± 0.04 ^a	0.68 ± 0.01 ^a	2.43 ± 0.16 ^b
FC	13	80.40 ± 0.02 ^c	66.20 ± 0.01 ^c	1.12 ± 0.05 ^b	0.60 ± 0.02 ^b	6.73 ± 0.37 ^c

SF semi-fixed sand dune, F fixed dune with little biological soil crust, FC fixed dune with much biological soil crust

Values are mean ± SE; Values with different letters within columns are significantly difference at $P < 0.01$

Table 2 Species dominance values in the different stages of dune stabilization

Species	Ab.	Life-form	SF	F	FC
<i>Artemisia ordosica</i>	Aro	S	25.60	26.64	30.45
<i>Hedysarum mongolicum</i>	Hem	S	7.52	5.36	6.06
<i>Leymus secalinus</i>	Les	P	11.40	23.50	24.42
<i>Pennisetum centrasiaticum</i>	Pec	P	3.63		12.70
<i>Ixeridium graminifolium</i>	Ixg	P	3.68	2.15	2.72
<i>Setaria viridis</i>	Sev	A	4.30	2.68	7.56
<i>Heteropappus altaicus</i>	Hea	P	2.09	2.55	2.46
<i>Cynanchum thesioides</i>	Cyt	S	2.12	2.84	3.60
<i>Euphorbia humifusa</i>	Euh	A	1.32	0.83	1.07
<i>Chenopodium aristatum</i>	Cha	A	13.97	0.95	1.45
<i>Corispermum puberulum</i>	Cop	A	5.00		1.82
<i>Cynanchum komarovii</i>	Cyk	S	4.14		
<i>Sophora alopecuroides</i>	Soa	S	2.80	4.42	
<i>Caragana korshinskii</i>	Cak	S		3.37	
<i>Astragalus melilotoides</i>	Asm	P		5.25	
<i>Stipa breviflora</i>	Stb	P	2.16	2.17	4.21
<i>Cleistogenes squarrosa</i>	Cls	P	1.75	1.58	1.48
<i>Eragrostis minor</i>	Erm	A	0.92	0.74	
<i>Thermopsis lanceolata</i>	Thl	P	2.16	4.36	
<i>Hedysarum scoparium</i>	Hes	S		3.33	
<i>Phragmites australis</i>	Pha	A	2.50	4.47	
<i>Salsola collina</i>	Sac	A	1.34		
<i>Agriophyllum squarrosum</i>	Ags	A	1.60		
<i>Cynanchum chinense</i>	Cyc	P		2.81	

SF semi-fixed sand dune, F fixed dune with little biological soil crust, FC fixed dune with much biological soil crust, A annual grass and herbs, P perennial grass and herbs, S shrub (subshrub); Dominance values are presented as percent values

between the two on species distribution were 13.03, 19.43, and 7.96 %, respectively (Fig. 2).

The CCA ordination biplots characterize how plant coverage and species richness are simultaneously distributed along the quadrats and species (Fig. 1a, b). Most F and FC quadrats were associated with the direction of plant coverage that increased, in which the characteristic species are *A. ordosica*, *L. secalinus*, and *P. centrasiaticum* *Agriophyllum*. Species richness was correlated with most F quadrats and the characteristic species are *Astragalus melilotoides*, *Thermopsis lanceolata*, and *Sophora alopecuroides*.

Discussion

Changes in vegetation coverage and species richness within *A. ordosica* communities

Our results showed that vegetation coverage and species richness within the *A. ordosica* communities are significantly correlated with soil factors. The vegetation coverage increased as the sand dune was stabilized, whereas species richness first increased and then decreased (Table 3; Fig. 1). Many studies have found vegetation coverage increases following sand-dune stabilization in arid and

Table 3 Pearson's correlation among vegetation characteristics, soil factors, and topographical factors

Item	Coverage	R	Slope	Aspect	γ_s	pH	EC	Clay	Silt	BSC	D	TN	TP	SOC	SW1	SW2	SW3
Coverage	1.00																
R	0.23**	1.00															
Slope	0.29**	-0.06	1.00														
Aspect	0.17*	0.05	0.50**	1.00													
γ_s	0.46**	0.15	0.27**	0.09	1.00												
pH	-0.05	0.04	-0.09	0.01	-0.09	1.00											
EC	0.02	-0.02	0.12	0.14	0.08	0.21*	1.00										
Clay	0.65**	0.18*	0.21*	0.17*	0.54**	-0.04	0.12	1.00									
Silt	0.62**	0.19*	0.17*	0.17*	0.53**	-0.08	0.13	0.98**	1.00								
BSC	0.56**	-0.18*	0.38**	0.15	0.29**	-0.10	-0.12	0.39**	0.31**	1.00							
D	0.67**	0.30**	0.20*	0.17*	0.55**	-0.13	0.15	0.83**	0.82**	0.39**	1.00						
TN	0.47**	0.18*	0.12	0.16	0.39**	-0.07	0.15	0.49**	0.49**	0.26**	0.56**	1.00					
TP	0.64**	0.23**	0.19*	0.18*	0.45**	-0.17*	0.14	0.66**	0.66**	0.35**	0.71**	0.64**	1.00				
SOC	0.37**	0.32**	0.07	0.15	0.29**	-0.14	0.15	0.46**	0.48**	-0.01	0.53**	0.55**	0.81**	1.00			
SW1	-0.51**	0.07	-0.16*	-0.12	-0.33**	0.11	0.03	-0.37**	-0.33**	-0.51**	-0.41**	-0.25**	-0.55**	-0.24**	1.00		
SW2	-0.40**	-0.03	-0.04	-0.05	-0.37**	0.19*	-0.03	-0.44**	-0.43**	-0.19*	-0.48**	-0.40**	-0.45**	-0.34**	0.21*	1.00	
SW3	-0.62**	-0.27**	-0.26**	-0.03	-0.44**	0.07	-0.12	-0.61**	-0.57**	-0.35**	-0.63**	-0.46**	-0.57**	-0.41**	0.40**	0.28**	1.00

Coverage vegetation coverage, R species richness, γ_s soil bulk densities, pH soil pH, EC soil electrical conductivity, BSC thickness of biological soil crust, D fractal characteristics, TN soil total nitrogen content, TP soil total phosphorus content, SOC soil organic carbon content, SW soil water content: SW1 0–20 cm, SW2 20–40 cm, SW3 40–60 cm

* Correlation significant at the 0.05 level (2-tailed)

** Correlation significant at the 0.01 level (2-tailed)

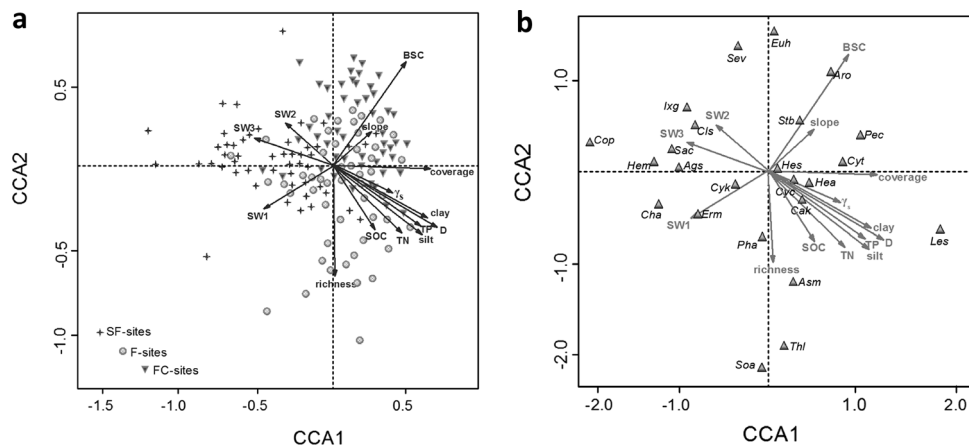


Fig. 1 CCA two-dimensional ordination diagram of the first two axes. This diagram addresses, includes the coordinates of quadrats and environmental factors in the ordination space (a); the overall correlation between the environmental factors and species distribution (b). The diagram a shows that there is a notable separation of sampling quadrats depending on the dune fixation stage associated with environmental factors, which can be combined together with (b), which shows a separated distribution of plant species with environmental factors. Most SF quadrats were associated with the soil water content, in which the relative abundances of *Agriophyllum squarrosum*

and *Corispermum puberulum* were high. Most F quadrats were associated with soil water content, soil nutrient factors, and structure of fine soil particles, in which the relative abundances of *Astragalus melilotooides*, *Thermopsis lanceolata*, and *Leymus secalinus* were high. Most FC quadrats were associated with the thickness of the surface soil crust and the slope, in which *A. ordosica*, *Stipa breviflora*, and *Pennisetum centrasiticum* had relatively high abundances. The species abbreviations and environmental variables can be seen in Tables 2 and 3

Table 4 Monte Carlo test for the significance of environmental factors and species distribution

Items	CCA1	CCA2	r ²	P
Coverage	1.00	0.04	0.15	0.001
R	0.01	-1.00	0.12	0.001
Slope	0.72	0.69	0.06	0.001
Aspect	0.98	-0.18	0.01	0.129
γ _s	0.91	-0.42	0.07	0.001
pH	-0.53	-0.85	0.02	0.067
EC	0.03	-1.00	0.01	0.121
Clay	0.89	-0.46	0.18	0.001
Silt	0.79	-0.61	0.20	0.001
BSC	0.57	0.82	0.30	0.001
D	0.87	-0.50	0.23	0.001
TN	0.71	-0.71	0.15	0.001
TP	0.83	-0.56	0.18	0.001
SOC	0.53	-0.85	0.10	0.001
SW1	-0.83	-0.56	0.11	0.001
SW2	-0.73	0.69	0.06	0.001
SW3	-0.95	0.30	0.10	0.001

Abbreviations as in Table 3; Monte Carlo tests to select significant environmental variables (P < 0.05); Monte Carlo permutation test simulation is run 999 times

semi-arid regions (Li 2005; Song et al. 2011; Li et al. 2014). With sand fixation, Liu et al. (2004) observed plant species richness would first increase and then decrease or would simply remain unchanged, whereas Baniya et al. (2009) reported that species richness gradually increases.

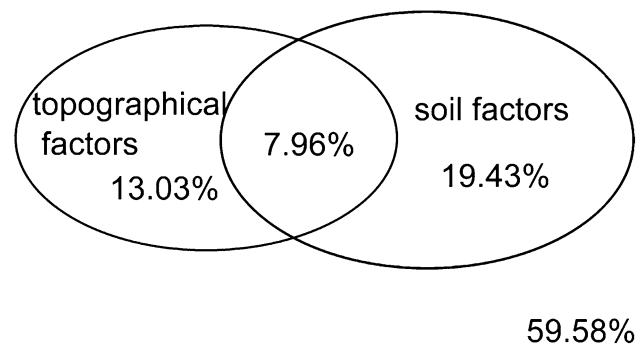


Fig. 2 Venn diagram of contributions of different environmental factors to the distribution of species

We found that the highest plant species richness within the *A. ordosica* community occurred at the F stage, rather than at the FC stage. Why did this occur? In the F dunes, there were moderate soil moisture and nutrient conditions, and soil heterogeneity following sand fixation, which were similar to intermediate disturbance habitats (Connell 1978; Catford et al. 2012). This kind of habitat could provide adequate opportunities and suitable environmental conditions for the colonization and survival of plants with different types and life forms (Bever 2003; Li 2005; Zuo et al. 2009; Song et al. 2011).

The balance of vegetation and soil moisture is very important to the formation of a stable vegetation system (Li et al. 2014). Our study shows that vegetation coverage increased and soil moisture decreased with the sand-dune

fixing. This suggests that, during sand-dune stabilization, increased vegetation coverage could lead to reduced soil moisture. Soil moisture was relatively high and soil nutrient contents were relatively low at the early stage of sand dune stabilization.

However, the converse conditions occurred in the fixed sand dune with high coverage and large thickness biological soil crusts at the late stage of sand dune stabilization. This suggests that there exists a threshold of vegetation coverage of *A. ordosica* communities during sand-dune stabilization, within which soil moisture and nutrient contents will both be sustainable. CCA ordination biplots shows that the threshold should appear during the transition from semi-fixed dunes to fixed dunes with high coverage biological soil crust. Therefore, we suggest that the threshold of vegetation coverage of *A. ordosica* communities may be about 50 % in the study areas. However, accurately determining the carrying capacity thresholds of vegetation in different bioclimatic zones may still need long-term investigation on the relationships between vegetation conditions and soil resources.

Changes in relationships between vegetation and environmental factors within *A. ordosica* communities

At the early stage of sand dune stabilization, the distribution of plant species was positively correlated with soil moisture and negatively correlated with soil nutrient contents. In the latter stage of sand-dune stabilization, the correlations between vegetation and these two factors reversed.

On the SF dune, the low-coverage vegetation mainly consisted of annual sandy herbs (such as *C. puberulum*, *Agriophyllum squarrosum*) and pioneer perennial shrubs (such as *A. ordosica*), because there was sufficient soil moisture for plant growth (Li et al. 2014). The distribution of plant species was significantly positively correlated with soil moisture on the SF dune ($P < 0.05$). As the sand dune stabilized, plant coverage, soil texture, and nutrient contents within *A. ordosica* communities rose, and the distribution of plant species was significantly positively correlated with soil texture and nutrient contents on the F dune ($P < 0.05$). At this stage, in the dune with low-coverage lichen or moss soil crusts, vegetation within *A. ordosica* communities consisted of sandy shrubs (such as *S. alopecuroides*, *Hedysarum mongolicum*), and xeric herbs and grass (such as *T. lanceolata*, *Cleistogenes squarrosa*), and coverage and species richness both increased. The plant community can improve the soil environment by capturing wind-driven fine soil materials and by increasing soil fertility through litterfall (Chapin et al. 2011), which would promote the growth of plants within the community

by increasing water-holding capacity and nutrient availability of the soil on sand dunes. That is, the vegetation community co-develops with the soil environment following sand dune stabilization. In the late stage of dune stabilization, vegetation coverage of *A. ordosica* community tended to stabilize, and the biological soil crust expanded and thickened gradually. The distribution of plant species was correlated with soil moisture, proportion of fine soil particles, soil nutrient contents, and the thickness of biological soil crust. At this stage, the biological soil crust affected the distribution of plant species significantly in the dune with high coverage biological soil crusts, due to its special hydrophysical characteristics and tough crust construction. Biological soil crust can reduce the rainfall infiltration to the subsoil and improve soil moisture in the topsoil, which is conducive to the survival and reproduction of shrubs and herbaceous plants with shallow roots (Li et al. 2011b); next, biological soil crust can also reduce seed germination, by preventing seeds from becoming covered with soil (Li et al. 2005), which will reduce the update ability of *A. ordosica* community. These reasons together led to more perennial and typical steppe grasses were distributed in the *A. ordosica* community in the dune with high coverage biological soil crusts.

CCA ordination biplots (Fig. 1) showed that, following sand stabilization, the relative abundances of pioneer herbs (*A. squarrosum*, *C. puberulum*, etc.) decreased, whereas the relative abundance of perennial grass and other perennial herbs increased. A 50-year long-term study on the introduction of sand-fixing vegetation and rehabilitation of the soil environment in Shapotou of Ningxia showed that the sand-fixing plant community formed a complete community composed of sparse shrubs and many herbs (Li 2005). This study revealed that, in the fixed sand dunes with extensive biological soil crust, the *A. ordosica* community tended to develop into an autochthonic community with many perennial grasses and herbs. This suggests that, with the interaction between artificial sand-fixing vegetation and the environment, the habitat in the sand dunes would be restored to the original habitat that existed before desertification. Therefore, shrub-planting for sand dune fixation is an effective approach to ecosystem restoration in the semi-arid Mu Us desert.

Conclusion

The relationships between community characteristics (species diversity, species composition, and vegetation cover) and environmental factors show strong variation along stages of dune fixation, supporting our conclusion that restoration of degraded dune ecosystems should consider habitat conditions and ecological needs. This study

also offers further evidence that *A. ordosica* communities tend to change into typical steppe vegetation following sand-dune stabilization, which helps us to apply these findings to management of semi-arid ecosystems.

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