Spatial pattern and heterogeneity of soil organic carbon and nitrogen in sand dunes related to vegetation change and geomorphic position in Horqin Sandy Land, Northern China

X. A. Zuo · X. Y. Zhao · H. L. Zhao · Y. R. Guo · T. H. Zhang · J. Y. Cui

Received: 12 September 2008 / Accepted: 10 March 2009 / Published online: 8 April 2009 © Springer Science + Business Media B.V. 2009

Abstract To assesses the effect of geomorphology, topography, and vegetation changes on spatial pattern of soil organic carbon (C) and total nitrogen (N) in sand dunes, we used the quantitative methods to examine the spatial heterogeneity of vegetation cover, soil organic C, and total N in an 11-year naturally restored mobile dune (RMD11) and a 20-year naturally restored mobile dune (RMD20) that had been fenced to exclude grazing in Horqin Sandy Land, northern China. Our results showed that the vegetation cover, plant density, species number and diversity, soil organic C, and total N increased from RMD11 to RMD20 and increased from the 50×50 -m plot (crest) to the 100×100 -m plot (slope) in each dune. Geostatistical analysis showed that the spatial structural variance accounted for the largest

X. A. Zuo · X. Y. Zhao · H. L. Zhao · Y. R. Guo · T. H. Zhang · J. Y. Cui Naiman Desertification Research Station, Cold and Arid Regions of Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou, 730000, People's Republic of China

X. A. Zuo (🖂)

proportion of the total sample variance in vegetation cover, soil organic C, and total N in each dune plot. Calculated spatial autocorrelation ranges of vegetation cover, soil organic C, and total N increased from RMD11 to RMD20, indicating that longer time since vegetation restoration results in a more homogeneous distribution of vegetation cover, soil organic C, and total N in sand dunes. In addition, the spatial continuity of vegetation cover, soil organic C, and total N decreased from the 50 \times 50-m plot (crest) to the 100 \times 100-m plot (slope) in each dune. These results suggest that the spatial distribution of soil organic C and total N in sand dunes is associated closely with geomorphic position related to the dune crest and slope, relative elevation of sampling site, and vegetation cover. Understanding the principles of this relationship between them may guide strategies for the conservation and management of semiarid dune ecosystems.

Keywords Geomorphic position • Mobile dune • Soil properties • Topographic feature • Vegetation restoration

Introduction

Spatial heterogeneity is considered as a ubiquitous feature of natural ecosystems (Palmer 2003) and is one of the major drivers of biological processes

Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, 320 Donggang West Road, Lanzhou, 730000, People's Republic of China e-mail: xazuo@126.com, zuoxa@cern.ac.cn

(Kumar et al. 2006). Not only has it a central place in theoretical framework of ecology (Legendre and Fortin 1989), but also it provides ecological practices such as land management and ecological restoration with basic guidance (Brosofske et al. 1999). Spatial heterogeneity of soil nutrient pools at scales from the sizes of individual plants to extensive fields is a general characteristic of arid and semiarid grassland ecosystems (Hook et al. 1991; Schlesinger et al. 1996). There are mutual relationships between plant distribution and spatial heterogeneity of soil properties in semiarid areas (Hook et al. 1991; Jackson and Caldwell 1993). Many studies have shown that soil heterogeneity is a basic element for competitive or facilitative interactions between plants in semiarid habitats (Chapin et al. 1994; Fowler 1986) and consequently may determine the plant distribution pattern.

Soil properties frequently exhibit spatial structure as the outcome of the combined interaction of biological, chemical, and physical processes acting at multiple scales (Parkin 1993). Spatial heterogeneity of soil resources often results from grazing disturbance (Robertson et al. 1993), topography (Burke et al. 1999), and the presence and composition of plants (Milchunas and Lauenroth 1993; Vinton and Burke 1995). The analysis of spatial heterogeneity in soil properties under different effective factors can permit a deeper understanding of the ecological relationship between soil and environment (Rossi et al. 1992).

Many studies suggest that spatial heterogeneity of soil nutrients is often associated with variation in plant distribution (Schlesinger et al. 1990; Gross et al. 1995). Lane and BassiriRad (2005) have indicated that vegetation changes resulting from habitat restoration affect the spatial pattern and heterogeneity of soil nutrients through plantsoil feedbacks. An island of fertility that forms under shrub canopies in arid regions is a welldocumented example of soil nutrient heterogeneity (Wezel et al. 2000). The "resource islands" under plant canopy not only act as hot spots of soil nutrients, microbial activity, and mycorrhizal inoculums (Titus et al. 2002) but also are focal points for plant interactions and seedling establishment (Aguilar and Sala 1999). In addition, at the landscape scale, a catena concept has been

used as a model to explain the pattern of variability in soil organic matter and nutrient distribution along toposequences (Gerrard 1981). The catena concept suggests that the downhill movement of material as a result of gravity and water movement results in a predictable sequence of soil characteristics from summits to toeslopes. Moreover, the rapid soil erosion can cause the topographic changes which can be partly attributed to the soil redistribution resulting from erosion of bare soil openings and from the trapping of windblown soil by grasses (depositional process) as plant growth occurs (Martinez-Turanzas et al. 1997). Hence, in order to implement conservation or restoration measures on semiarid dune ecosystem, it is meaningful to study the changes in pattern of vegetation and soil related to topographic features and geomorphic position in dunes.

Horqin Sandy Land lies in the semiarid area of southeast Inner Mongolia, China. Primary landscape is the scattered tree grassland on interdune lowlands alternated with sand dunes. Due to longterm and extensive fuelwood gathering, overgrazing, and heavy reclamation, it has become one of the most severe regions of desertification in northern China (Zhu and Chen 1994; Zhao et al. 2005). Sandy grassland in Horqin Sandy Land is ecologically fragile and is subject to desertification. A rapidly growing human population within the last 50-100 years has produced increasing impacts from grazing and cultivation and threatens desertification of the grassland. In particular, accelerated wind erosion induced by poorly regulated grazing has resulted in the occurrence of bare sand patches and has increased degree of spatial heterogeneity of the sandy grassland landscape. Moreover, reactivation of formerly stabilized dunes occurs to differing degrees due to the long-term overgrazing and vegetation disruption by fuelwood gathering, resulting in a fragmented landscape having mobile dunes and semimobile dunes with stabilized dunes in alternation (Su et al. 2006). However, thanks to the annual precipitation of 350 to 500 mm, some mobile dunes can be gradually restored to semifixed or fixed dunes after excluding destructive land uses. Desertification area gradually decreased due to the vegetation restoration since 2000 (Wang et al. 2004).

In recent years, many studies of desertification and its impact on changes in vegetation and soil have been carried out in the Horqin region (Su et al. 2006; Zhao et al. 2005; Liu et al. 2006; Zeng et al. 2008; Zuo et al. 2008a). However, few published reports describe the spatial pattern and heterogeneity of soil properties related to vegetation changes and geomorphic position in this area. To fully understand spatial patterns of soil properties in sand dune systems, the relationships between vegetation restoration, soil properties, topographic features, and geomorphic position need to be ascertained. Information on these changes is required for a better understanding of the restoration mechanisms and the interactions between soil and plant communities and for appropriate management and conservation of the environment in the Horqin region.

The overall purpose of this paper was to study the scale and magnitude of spatial heterogeneity in soil organic C and total N related to vegetation changes, topography features, and geomorphic position in sand dune ecosystems prone to wind erosion.

Materials and methods

Study area description

This study was conducted in southwestern Horqin Sandy Land, Inner Mongolia, China (42° 55' N, 120° 42' E; elevation approximately 360 m). The climate in this area is temperate, semiarid continental monsoonal, receiving average annual precipitation of 360 mm, with 75% of this in the growing season of June-September. The annual mean open-pan evaporation is about 1,935 mm. The annual mean temperature is around 6.4°C, with the minimum monthly mean temperature of -13.1°C in January and the maximum 23.7°C in July. The annual mean wind velocity is in the range of 3.2 to 4.1 m s⁻¹, and the prevailing wind is northwest in winter and spring and southwest to south in summer and autumn (Zhu and Chen 1994). The zonal soils are identified as degraded sandy chestnut soils, which are mostly equivalent to the Orthi-Sandic Entisols of sand origin in terms of the Food and Agriculture Organization–United Nations Educational, Scientific, and Cultural Organization system. These soils characterized by their coarse texture and loose structure with high proportion of sand (85– 95%) and low organic matter content (0.15– 0.5% soil organic C) are highly susceptible to wind erosion (Su et al. 2006). Dunes are covered with native plants, including grasses (e.g. *Cleistogenes squarrosa, Setaria viridis, Phragmites australis, Digitaria ciliaris, Leymus chinensis*), forbs (*Mellissitus ruthenicus, Salsola collina, Agriophyllum squarrosum, Artemisia scoparia*), shrubs (e.g., *Caragana microphylla, Lespedeza davurica*), and subshrubs (e.g., *Artemisia halodendron, Artemisia frigida*).

Experiment design

Research was carried out in mid-August 2006. In our experiment, one 11-year recovery site (2.2 ha) and one 20-year recovery site (5.6 ha), 1.5 km apart, were selected within two mobile dune areas that had been fenced to exclude grazing. Then, one mobile dune naturally restored for 11 years (RMD11) and another mobile dune naturally restored for 20 years (RMD20), with almost similar topography and size, were chosen in the two sites, respectively. Considering the size and extent of sand dunes in this area, a 100×100 -m plot covering the whole dune was chosen for sampling, oriented northwest-southeast. In order to examine the spatial pattern of soil organic C and total N in different plots and geomorphic positions on sand dunes, one 50×50 -m subplot on the dune crest with the exposure to wind erosion was selected in each 100×100 -m plot (slope). Then, in each 100×100 -m plot, four 50-m sampling transects were established from dune top to bottom, all intersecting at the sand dune apex in the plot center, oriented the northwest (prevailing wind direction in winter and spring), southwest (prevailing wind direction in summer and autumn), southeast, and northeast directions (Fig. 1). Along each of the four transects, sampling was done at 1-m intervals, giving a total of 200 1-m² quadrats in each 100 \times 100-m plot and 100 1-m² quadrats in each 50 \times 50-m plot, respectively. In each 1-m² quadrat, soil samples were collected and the vegetation cover, abundance, height, and cover of every species



Fig. 1 Layout of the location for sampling plot, transect, and quadrat $(A, 100 \times 100 \text{-m plot}; B, 50 \times 50 \text{-m plot}; dots sampling quadrat; dashed lines sampling transect)$

were recorded. The cover of vegetation and every species was visually estimated as percent canopy cover.

Three replicate soil samples were collected with each quadrat at 0-20-cm depth using a 3-cmdiameter soil auger. In order to carry out geostatistical analysis, additional soil samples were collected at within plots, with 80 1-m² and 40 1-m² sampling quadrats selected at random from within the 10,000 and the 2,500 1-m² grid cell defined in each 100 \times 100-m and 50 \times 50-m plots, respectively. Soil samples were hand-sieved through a 2-mm screen to remove roots and other debris (discarded). Soil organic carbon (C) was measured by the dichromate oxidation method of Walkey and Black (Nelson and Sommers 1982) and total nitrogen (N) was determined by the Kjeldahl procedure (ISSCAS 1978). In addition, a hand clinometer was used to measure the slope of each sand dune plot, and the relative elevation at the center of each quadrat along each transect was calculated through trigonometric functions.

Data analysis methods

The distributions of vegetation cover and soil properties were tested for normality by the

Kolmogorov-Smirnov test at the 0.05 significance level. For those variables not passing the normal distribution test, we used data transformation (e.g., log-transformation or square root transformation). The spatial pattern and heterogeneity for vegetation cover, soil organic C, and total N in each dune site were analyzed using geostatistical techniques. Geostatistical techniques evaluate the autocorrelation commonly observed in spatial data, where data values from locations close to each other are more similar than data values from locations far apart (Isaaks and Srivastava 1989; Wallace et al. 2000). Spatial autocorrelation analysis provides a quantitative estimate of the spatial correlation between the two samples as a function of their separation distance (Isaaks and Srivastava 1989). This spatial analysis used the semivariance estimated by:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} \left[z(x_i) - z(x_i + h) \right]^2$$

where N(h) is the number of sample pairs at each distance interval h, and $z(x_i)$ and $z(x_i + h)$ are values of the variable at any two places separated by a lag distance h. The experimental variogram is calculated for several lag distances. The lag h is defined as a vector with both distance and direction. In practice, the direction effect is considered by computing experimental variograms according to different directions of the h vector. The spatial structure of the data is determined by fitting a mathematical model to the experimental semivariogram, such as a spherical or exponential model. These models provide information about the structure of the spatial variation, as well as the input parameters for kriging by means of a least squares method (Cannavacciuoloa et al. 1998).

The specie dominance (DV) in each plot was calculated using the ordinary formula DV = (RA + RH + RC)/3, where RA is the relative abundance; RH is the relative height and RC the relative cover of the species. RA, RH, and RC were all represented as percent values. Species diversity was calculated by the Simpson index (*D*; Zhang et al. 2005). The parameters of the modeled variogram include: (a) spatial autocorrelation range or *A*, the separation distance at which spatial dependence is evident; (b) nugget value or Co,

Table 1 Characteristics of vegetation restoration in mobile dunes

	RMD11		RMD20			
	$50 \times 50 \text{ m} (n = 100)$	$100 \times 100 \ (n = 200)$	$50 \times 50 \text{ m} (n = 100)$	$100 \times 100 \ (n = 200)$		
Cover (%)	$25.55 \pm 22.40a$	$37.02\pm20.81\mathrm{b}$	$30.10\pm20.80\mathrm{b}$	$45.10\pm22.01\mathrm{c}$		
Average height (cm)	$22.33 \pm 16.78 \mathrm{a}$	$22.02\pm12.65a$	$19.79 \pm 9.83a$	$20.46\pm7.83a$		
Density (plant per square meter)	$22.82\pm34.80a$	$32.52\pm38.53ab$	$41.61 \pm 46.95b$	$65.20\pm60.05\mathrm{c}$		
D	$0.49\pm0.28a$	$0.59\pm0.23b$	$0.62\pm0.20\mathrm{b}$	$0.70\pm0.16\mathrm{c}$		

Value represents the mean \pm SE. The different letters in each vegetation characteristics indicate statistical difference between-dune plots at P < 0.01

RMD11 11-year restored mobile dune, RMD20 20-year restored mobile dune

which is the level of random variation within the data; (c) structural component or Cs, which is the level of structured variation within the data; and (d) sill or (Co + Cs), the total variation present. An especially important parameter, relative structural variance, was calculated as Cs/(Co + Cs). RSS or residual sums of squares provided an exact measure of how well the model fit the variogram data, with lower RSS indicating better model fits. The GS+ software (version 5.3b, Gamma Design software) used RSS to choose parameters for each of the variogram models by determining the com-

bination of parameter values that minimized RSS for any given model.

Differences of vegetation characteristics between the different plots were compared with Tukey's test when the analysis of variance showed significant (P < 0.01) treatment effects. In these analyses, data values at all quadrats within one plot are polled together as a single population. An independent-sample t test was used to compare the differences in mean values of soil organic C and total N for RMD11 vs. RMD20 plots (P < 0.01). The descriptive statistical parameters and

Table 2 Species	Species	Life form	RMD11		RMD20	
the vegetation restoration			50×50 m	$100 \times 100 \text{ m}$	50×50 m	$100 \times 100 \text{ m}$
of mobile dunes			(n = 100)	(n = 200)	(n = 100)	(n = 200)
	Artemisia halodendron	PS	36.70	38.40	29.30	22.50
	Lespedeza davurica	PS	0	0.80	0.10	2.00
	Caragana microphylla	PS	0	0	0.80	1.10
	Caragana microphylla	PS	1.80	1.20	4.40	4.70
	Melissitus ruthenicus	PL	3.10	7.40	5.90	4.90
	Cleistogenes squarrosa	PG	0	0	0.20	2.00
	Corispermum elongatum	AF	11.40	13.70	14.10	14.20
	Euphorbia humifusa	AF	0	0	2.90	4.00
	Cynanchum thesioides	PF	1.60	1.60	3.00	2.00
	Setaria viridis	AG	13.70	16.20	17.00	20.40
	Euphorbia esula	PF	1.00	1.60	0.80	0.70
	Aristida adscensionis	AG	0	0	1.20	2.10
	Agriophyllum squarrosum	AF	23.10	11.70	8.60	4.40
	Bassia dasyphylla	AF	0.10	0.10	0.20	0.50
AF annual forbs,	Chenopodium glaucum	AF	0	0.10	0.70	0.70
AG annual grass,	Ixeris chinensis	AF	0.50	1.60	3.50	2.40
PF perennial forbs,	Salsola collina	AF	0.10	0.20	0.60	1.70
PG perennial grass,	Linaria vulgaris	PF	0	0.10	0.20	0.80
<i>PL</i> perennial legume,	Phragmites australis	PG	7.70	5.60	0	0.20
<i>PS</i> perennial shrub,	Allium mongolicum	PF	0	0	0.10	0.10
RMD11 11-year restored	Thalictrum minus	PF	0	0	5.10	2.70
20-year restored mobile	Artemisia lavandulaefolia	PF	0	0	0	0.80
dune	Total number of species		12	18	25	32

significance test were calculated by SPSS (version 13.0).

Results

Changes in vegetation characteristics

The values of cover, density, and *D* in the 50 × 50-m plot or the 100 × 100-m plot in RMD11 were less than those at the corresponding plots in RMD20, and the differences were significant (P < 0.01; Table 1). The values of cover, density, and *D* increased from the 50 × 50-m plot to the 100 × 100-m plot for both sites, suggesting that lower amount of vegetation characteristics associated with the exposed dune apices (Table 1). In addition, the average height presented no significant difference (P > 0.05) between the different plots in both of the dunes.

Species number increased from the 50 \times 50-m plot to the 100 \times 100-m plot for both sites, and



Fig. 2 Changes in soil organic carbon (C) and total nitrogen (N) in two dunes. *Vertical bars* indicate standard errors of means

species numbers of herbaceous plants were higher in RMD20 than in RMD11 (Table 2). A. halodendron shrub and A. squarrosum herb were a dominant and subdominant species in 50×50 -m plot in RMD11, respectively. A. squarrosum is a pioneer plant on mobile dunes, whose dominance decreased from the 50 \times 50-m plot to the 100×100 -m plot and from RMD11 to RMD20. The dominance of A. halodendron increased with plot size increase in RMD11 and a reverse trend in RMD20. In addition, A. halodendron and S. viridis herb were dominant species in 100 \times 100-m plot in RMD20, accounting for 22.50% and 20.4% of the total dominance, respectively. Moreover, the dominance of other herbaceous plant increased with plot size increase, which indicates that most herbaceous plants mainly distribute in the slope of dunes.

Changes in soil organic C and total N

The differences in soil organic C and total N between two dunes are shown in Fig. 2. The average value of soil organic C and total N in the 50 \times 50-m plot and 100 \times 100-m plot in RMD11 was consistently less than those of the corresponding plot in RMD20, respectively; and significant differences were evident in soil organic C (t = -2.88, P = 0.005) and total N (t = -3.58, P = 0.001) in 50 \times 50-m plot for sample means between RMD11 and RMD20, as well as in soil organic C (t = -4.94, P = 0.000) and total N (t =-4.75, P = 0.000) in 100×100 -m plot for sample means between RMD11 and RMD20. In addition, the average values of soil organic C and total N in RMD11 increased with the plot from 50×50 -m to 100×100 -m, as well as in RMD20, and significant differences were evident in soil organic C (t = -2.17, P = 0.032) and total N (t = -2.76, P = 0.007) between the two plots in RMD11, as well as soil organic C (t = -2.35, P = 0.020) and total N (t = -2.33, P = 0.021) between the two plots in RMD20.

Semivariance analysis of vegetation cover, soil organic C, and total N

The parameters of the model-variogram-based geostatistical analysis for vegetation cover, soil

RMD11

RMD20

RMD11

RMD20

 $C(g kg^{-1})$

 $N(g kg^{-1})$

0.01

0.01

0.00

0.00

total N									
Variables	Dune type	Model	Со	Co + Cs	Cs / (Co + Cs)	<i>A</i> (m)	RSS		
$50 \times 50 \text{ m} (n =$	159)								
Cover (%)	RMD11	Spherical	0.01	6.47	0.99	21.63	17.73		
	RMD20	Spherical	0.01	4.46	0.99	26.12	0.01		
$C (g kg^{-1})$	RMD11	Spherical	0.01	0.06	0.88	23.92	0.00		
	RMD20	Spherical	0.001	2.46	0.90	64.28	0.00		
$N (g kg^{-1})$	RMD11	Spherical	0.00	0	0.79	25.50	0.00		
	RMD20	Exponential	0.00	0.01	0.99	61.05	0.00		
$100 \times 100 \text{ m} (n$	= 280)								
Cover (%)	RMD11	Spherical	0.00	0.08	0.99	20.60	0.01		
	RMD20	Spherical	0.00	0.07	0.99	22.60	0.01		

Table 3 Descriptive statistical characters, semivariogram model and parameters of vegetation cover, soil organic C, and

C soil organic carbon, N total nitrogen, H relative elevation of sample on dune, A spatial autocorrelation range, Co nugget value, Cs structured variation, (Co + Cs) the total variation, Cs / (Co + Cs) relative structural variance, RSS residual sums of squares, RMD11 11-year restored mobile dune, RMD20 20-year restored mobile dune

0.17

0.52

0.11

0.03

0.01

0.04

0.02

0.00

Spherical

Spherical

Spherical

Spherical

organic C, and total N in the two plots of each dune are summarized in Table 3. The spherical or exponential model was fitted to these variables, which showed that they had a spatial autocorrelation in their effective range. The degree of spatial autocorrelation was evaluated with the method of Jia et al. (2004), which calculates the proportion of relative structural variance as Cs/(Co + Cs);

21.70

70.00

24.40

76.10

0.94

0.94

0.83

0.99





Fig. 3 Sample semivariograms for vegetation cover in different dune plots (a vegetation cover in 50×50 m of RMD11; **b** vegetation cover in 50×50 m of RMD20;

c vegetation cover in 100×100 m of RMD11; **d** vegetation cover in 100×100 m of RMD20)





0.24

0.18

0.12

C2

Fig. 4 Sample semivariograms for soil organic C and total N in different dune plots (C_1 , soil organic C in 50 × 50 m of RMD11; C_2 , soil organic C in 50 × 50 m of RMD20; N_1 , total N in 50 × 50 m of RMD11; N_2 , total N in 50 × 50 m

of RMD20, C_3 , soil organic C in 100 × 100 m of RMD11; C_4 , soil organic C in 100 × 100 m of RMD20; N_3 , total N in 100 \times 100 m of RMD11; N₄, total N in 100 \times 100 m of RMD20)

values over 75%, between approximately 75% and 25%, and less than 25% correspond to strong, moderate, and lower spatial autocorrelation, respectively. The proportions of relative structural variance Cs/(Co + Cs) of vegetation cover, soil organic C, and total N in each plot were over 78%, which suggests that they had a strong spatial autocorrelation in their respective effective ranges

Table 4 Pearson's correlation among soil organic C and total N, geographic features, and vegetation cover in each dune plot

	RMD 11				RMD 20					
	C	Ν	Cover	Н	Slope	C	Ν	Cover	Н	Slope
$\overline{50 \times 50}$ m	, n = 100									
С	1.00					1.00				
Ν	0.78 ^a	1.00				0.94 ^a	1.00			
Cover	0.70 ^a	0.64 ^a	1.00			0.62 ^a	0.68 ^a	1.00		
Н	-0.49^{a}	-0.50^{a}	-0.88^{a}	1.00		-0.51^{a}	-0.51^{a}	-0.82^{a}	1.00	
Slope	-0.14	-0.11	-0.12	0.14	1.00	-0.19	-0.21	-0.01	0.22	1.00
100×100	m, <i>n</i> = 200									
С	1.00					1.00				
Ν	0.81 ^a	1.00				0.92 ^a	1.00			
Cover	0.65 ^a	0.57 ^a	1.00			0.50 ^a	0.43 ^a	1.00		
Н	-0.40^{a}	-0.44^{a}	-0.76^{a}	1.00		-0.38^{a}	-0.36^{a}	-0.66^{a}	1.00	
Slope	-0.29^{a}	-0.33^{a}	-0.31^{a}	0.40 ^a	1.00	-0.06	-0.07	-0.21^{a}	0.20 ^b	1.00

C soil organic carbon, N total nitrogen, H relative elevation of sample on dune, RMD11 11-year restored mobile dune, RMD20 20-year restored mobile dune

^aCorrelation is significant at the 0.01 level (two-tailed)

^bCorrelation is significant at the 0.05 level (two-tailed)

in each plot. These results reveal that the spatial structural variance accounted for the largest proportion of the total sample variance in vegetation cover, soil organic C, and total N in each plot.

Calculated ranges of spatial autocorrelation (A), in the 50 \times 50-m plot, for vegetation cover were 21.63 m in RMD11 and 26.12 m in RMD20, which were more than that in the 100×100 -m plot in the two dunes (20.60 and 22.60 m, respectively; Fig. 3, Table 3). In addition, the spatial autocorrelation ranges were 23.92 m for soil organic C and 25.58 m for total N in the 50 \times 50-m plot in RMD11, which were less than that in RMD20 (64.28 and 61.05 m, respectively; Fig. 4, Table 3). In the 100×100 -m plot, the spatial autocorrelation ranges were 21.70 m for soil organic C and 24.40 m for total N in RMD11 less than that in RMD20 (70.00 and 76.10 m, respectively; Fig. 4, Table 3). Moreover, our results showed that the spatial autocorrelation ranges for soil organic C and total N in RMD11 decreased from 50×50 -m plot to 100×100 -m plot, which indicated that the spatial dependence of soil organic C and total N was higher in 50 \times 50-m plot than in 100 \times 100-m plot. Meanwhile, although the spatial autocorrelation ranges for soil organic C and total N in RMD20 increased to 8.90% and 24.65% from 50 \times 50-m plot to 100 \times 100-m plot, their spatial dependence was still higher in 50×50 -m plot than in 100×100 -m plot.

Correlation analyses among soil organic C, total N, vegetation cover, relative elevation of sampling site, and slope at the two plot sizes in each dune are shown in Table 4. Correlation analyses indicated that, at the two plot sizes, there were significantly positive correlations among soil organic C, total N, and vegetation cover (P < 0.01) and significantly negative correlations between relative elevation of sampling site and soil organic C, total N, and vegetation cover (P < 0.01). These results indicate that the changes and distributions in soil organic C and total N in each dune plot size are related to the vegetation condition and topographic features.

Discussion

The order of restorative succession of plant community from mobile dunes to fixed dunes in Horqin Sandy Land could be divided into four major phases, namely the pioneer plant phase dominated by *A. squarrosum* (mobile dune), the prephase of *A. halodendron* (semimobile dune), the postphase of *A. halodendron* (semifixed dune, dominant species was *S. viridis*), and the fixed dune phase (dominant species was *A. scoparia* herb; Zhang et al. 2004). Our results suggest that the plant community composition of RMD11 and RMD20 is similar to that of semimobile dune stage and semifixed dune stage, respectively. In addition, the spatial heterogeneity of vegetation cover decreased with vegetation restoration of dunes, indicating that longer time since vegetation restoration results in a more homogenous distribution of vegetation cover of dunes. However, although the vegetation cover, species number, and diversity increased from the 50×50 -m plot to the 100×100 -m plot for both sites, the spatial heterogeneity of vegetation cover increases from the 50×50 -m plot to the 100×100 -m plot in each dune. This result suggests that the geomorphic position and sampling plot size have an important influence on vegetation pattern and distribution of dunes.

Soil organic C and total N appear to be very variable in semiarid area ecosystems in general (Schlesinger et al. 1996) and many variables interact and contribute to the spatial distributions of soil organic C and total N (Su et al. 2006). Our results showed that the degree of spatial heterogeneity of soil organic C and total N was lower in RMD11 than in RMD20, suggesting that longer time since vegetation restoration results in a more homogenous distribution of soil organic C and total N in mobile dunes. The study by Zuo et al. (2008a) showed that, in 100×100 -m scale, the spatial autocorrelation ranges were 66.30 m for soil organic C and 50.80 m for total N in a 5-year grazed dune more than that in RMD11 (21.70 and 24.40 m) and less than that in RSD20 (70.00 and 76.10 m). These results suggest that long-time grazing also results in a more homogenous distribution of soil organic C and total N in dunes. However, plant-induced heterogeneity in soil properties has been recognized in many types of ecosystems (Boettcher and Kalisz 1990; Schlesinger and Pilmanis 1998). Plant species forming the aboveground vegetation cover are considered to have differential effects on local soil properties. The research results of Su et al. (2005) indicated that, after the establishment of A. halodendron shrub on mobile dune in Horqin Sandy Land, higher levels of soil organic C and total N were found under its shrub canopies in comparison with their openings, exhibiting the classic "islands of fertility." The presences of shrubs result in higher soil nutrient levels and promote the heterogeneity of soil nutrients (Whitford et al. 1997; Zheng et al. 2008). Our results also showed that the dominance of *A. halodendron* shrub decreased with vegetation restoration from RMD11to and RMD20 and a reverse trend for *S. viridis* herb and other herbaceous plants. Therefore, due to the effect of *A. halodendron* shrub on soil nutrient, the spatial distribution of soil organic C and total N is more heterogeneous in RMD11 than in RMD20.

When plant recruitment does not occur in bare mobile sand, seedling establishment is often possible under the shade of existing "nurse" shrub plants, allowing the colonization and rejuvenation of some herbaceous species (Shumway 2000; Holmgren and Scheffer 2001). Furthermore, reduced soil erosion and improved soil properties associated with the development of shrubs created a nutrient-rich water-retaining substrate, thus providing a better environment for germination of seeds and establishment of seedlings (Su et al. 2005). All these changes in dune habitat resulted ultimately in the population decrease of A. halodendron, because A. halodendron is a sand plant and its growth is promoted by sand burial on mobile dunes, and also resulted in spread and restoration of herbaceous species from dune bottom to top. At the same time, following vegetation restoration of mobile dunes, the development of herbaceous species has an important role in soil development through the greater accumulation of organic litter, which can further improve the physical and chemical properties of the soil and decrease soil nutrients' spatial heterogeneity. Perennial grasses are capable of accumulating nutrients beneath plants (Derner et al. 1997; Schlesinger et al. 1996), e.g., the increase in soil organic C and total N beneath caespitose grasses was demonstrated by Hook et al. (1991), Vinton and Burke (1995), and Kelly et al. (1996).

Topography is a major factor controlling soil processes at the landscape scale (Seibert et al. 2007). Many studies in semiarid regions have shown a significant topographic influence on soil organic matter accumulation, with toeslope positions frequently having the largest pools and fastest rates of N mineralization (Schimel et al. 1985; Aguilar et al. 1988). Pierson and Mulla (1990) found that soils on foot slope and toeslope positions had higher organic C content. These changes may be interpreted as being the result of the process of downslope movement of fine soil materials that acts to stabilize soil organic matter (Burke et al. 1999). In this explanation, wind erosion results in a change in soil texture, which is the proximal control over soil organic matter accumulation. In concert with the movement of mineral materials, organic matter may be redistributed downslope through erosion (Aguilar and Heil 1988). Our results showed that soil organic C and total N increased with the decline of relative elevation of sampling site on each dune, supporting that the topography affects the distribution of soil nutrients at the dune scale (Zuo et al. 2008b).

Spatial change is closely related to scale and shifts of scale may even result in alternation between heterogeneity and homogeneity. The variability of soil properties is also large in complex hills, and soil organic C has been shown to vary with slope position (Miller et al. 1988). Geomorphic position is discriminating factors for spatial variability of soil organic C (Wei et al. 2006). Our result suggests that the contents of soil organic C and total N increase with vegetation restoration or the spatial-scale enlargement from 50×50 -m plot to 100×100 -m plot, and the spatial heterogeneity of soil organic C and total N in the dune crest (50 × 50-m plot) displays a more homogeneous spatial pattern than the slope $(100 \times 100 \text{-m plot})$, indicating that the scale and geomorphic position have an important effect on the distribution and pattern of soil nutrients in sand dunes. The study on the scaling effects on soil nutrients in desertified area of northeastern Tanzania showed that the desertified microlandscapes had an overall lower soil organic matter and total nitrogen (Oba et al. 2008). The different scales or landscapes could reflect an unequal spatial distribution of soil nutrients related to the vegetation and topographic and geomorphic variations (Ludwig et al. 2000; Zuo et al. 2008b). In our study, the exposure of dune crest to wind erosion and an overall more barren/sparse landscape are due to difficulty in establishing vegetation which enrich the soil on the crest. Vegetation cover has major effects on soil resources in semiarid areas (Jackson and Caldwell 1993; Vinton and Burke 1995; Schlesinger et al. 1996). The vegetation cover and litter cover increasing from dune top to bottom also promote

the accumulation of soil organic C, total N, and their spatial heterogeneity in toeslope positions of the dunes.

Moreover, the levels of soil organic C and total N and their spatial variability may have profound effects on vegetative restoration in sand dune ecosystems prone to wind erosion. The distribution patterns of soil organic C and total N have significant feedbacks to plant establishment, growth, and survival (Hook et al. 1991). Zuo et al. (2008b) used the canonical correspondence analysis to study the relationship between the plant distribution and soil properties in RMD11 and RMD20, which showed that the distribution of sand pioneer plant, A. squarrosum, was positively related to the relative height of sampling site and soil water content, while that of other herbaceous plants was positively related to soil nutrients in each dune. Our results showed that significant differentiation occurred in the plant species composition, life form, and vegetation cover between the two naturally restored mobile dunes (Tables 1 and 2), supporting the conclusion that changes in the magnitude and scale of spatial dependence in soil nutrients may reflect changes in the vegetation cover or composition over a successional period (Gross et al. 1995).

Conclusions

Because of the computational limitation in geostatistical analysis, our study was conducted using non-replicated plots over a relatively restricted area. This deficiency in experimental design may cause some degree of bias in the resulting data. Nonetheless, it is clear in this study that the heterogeneity of soil organic C and total N in the studied sand dunes was most strongly related to geomorphic position, topography features, and vegetation changes. The restoration and establishment of shrubs promoted the heterogeneity of soil nutrients of dunes. Longer time since vegetation restoration had a strong influence on total pools of soil nutrients and resulted in an increase in soil organic C and total N, as well as a decrease in spatial variability of soil organic C and total N. Topography affected the amount of soil organic C and total N at sites from dune top to bottom and partly contributed to the distribution of soil properties in the dune ecosystem. Geomorphic position influences the distribution and pattern of soil organic C and total N in dune due to the changes of exposure of dune, topography feature, and vegetation cover. These results also suggest some mechanistic explanations for the observed spatial patterns of organic C and total N and the relationships between soil, vegetation, and geographical features at the different geomorphic position. Understanding the principles of the relationship between them may provide some help for making decisions about plot size and shape and location of dune restoration and management. So, for the practice of restoration process, much effort should be made to manage mobile dunes according to different geomorphic position, to enhance the protection of larger-area mobile dunes and, to promote the establishment of native shrubs on mobile dunes in semiarid area.

Acknowledgements Authors thank all the members of the Naiman Desertification Research Station, China Academy of Sciences (CAS), for their help in field work. We also wish to thank two anonymous reviewers for valuable comments on the manuscript. This paper was financially supported by the "Xibuzhiguang" Project of Chinese Academy of Sciences, National Basic Research Program of China (973 Program; 2009CB421303), the National Nature Science Foundation of China (40601008), and the Knowledge Innovation Programs of the Chinese Academy of Sciences (KZCX2-YW-431).

References

- Aguilar, M. R., & Sala, O. E. (1999). Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends in Ecology & Evolution*, 14, 273– 277. doi:10.1016/S0169-5347(99)01612-2.
- Aguilar, R., & Heil, R. D. (1988). Soil organic carbon, nitrogen, and phosphorus quantities in northern Great Plains rangeland. Soil Science Society of America Journal, 52, 1076–1081.
- Aguilar, R., Kelly, E. F., & Heil, R. D. (1988). Effect of cultivation on soils in Northern Great Plains Rangeland. *Soil Science Society of America Journal*, 52, 1081–1085.
- Boettcher, S. E., & Kalisz, P. J. (1990). Single-tree influence on soil properties in the mountains of eastern Kentucky. *Ecology*, 71, 1365–1372. doi:10.2307/ 1938273.
- Brosofske, K. D., Chen, J., Crow, T. R., & Saunders, S. C. (1999). Vegetation responses to landscape structure

at multiple scales across a Northern Wisconsin, USA, pine barrens landscape. *Plant Ecology*, *143*, 203–218. doi:10.1023/A:1009768115186.

- Burke, I. C., Lauenroth, W. K., Riggle, R., Brannen, P., Madigan, B., & Beard, S. (1999). Spatial variability in soil properties in the shortgrass steppe: The relative importance of topography, grazing, microsite, and plant species in controlling spatial patterns. *Ecosystems (New York, NY)*, 2, 422–438. doi:10.1007/ s100219900091.
- Cannavacciuoloa, M., Bellidoa, A., Cluzeaua, D., Gascuelb, C., & Trehen, P. (1998). A geostatistical approach to the study of earthworm distribution in grassland. *Applied Soil Ecology*, 9, 345–349. doi:10. 1016/S0929-1393(98)00087-0.
- Chapin, F. S. III, Walker, L. R., Fastie, C. L., & Sharman, L. C. (1994). Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs*, 64, 149–175. doi:10.2307/2937039.
- Derner, J. D., Briske, D. D., & Boutton, T. W. (1997). Does grazing mediate soil carbon and nitrogen accumulation beneath C4, perennial grasses along an environmental gradient? *Plant and Soil*, 19, 147–156. doi:10.1023/A:1004298907778.
- Fowler, N. (1986). The role of competition in plant communities in arid and semiarid regions. Annual Review of Ecology and Systematics, 17, 89–110. doi:10. 1146/annurev.es.17.110186.000513.
- Gerrard, A. J. (1981). *Soils and landforms*. London: George, Allen and Unwin.
- Gross, K., Regitzer, K., & Burton, A. (1995). Spatial variation in nitrogen availability in three successional plant communities. *Journal of Ecology*, 83, 357–367. doi:10.2307/2261590.
- Holmgren, M., & Scheffer, M. (2001). El Niño as a window of opportunity for the restoration of degraded arid ecosystems. *Ecosystems (New York, NY)*, *4*, 151–159. doi:10.1007/s100210000065.
- Hook, P. B., Burke, I. C., & Lauenroth, W. K. (1991). Heterogeneity of soil and plant N and C associated with individual plants and openings in North American shortgrass steppe. *Plant and Soil*, 138, 247– 256. doi:10.1007/BF00012252.
- Institute of Soil Sciences. Chinese Academy of Sciences (ISSCAS) (1978). Physical and chemical analysis methods of soils (pp. 7–59). Shanghai: Shanghai Science Technology Press (in Chinese).
- Isaaks, E., & Srivastava, R. (1989). *Applied geostatistics* (p. 561). New York: Oxford University Press.
- Jackson, R. B., & Caldwell, M. M. (1993). Geostatistical patterns of soil heterogeneity around individual perennial plants. *Journal of Ecology*, 81, 683–692. doi:10.2307/2261666.
- Jia, Y. P., Su, Z. Z., & Duan, J. N. (2004). Spatial variability of soil organic carbon at small watershed in gully region of Loess Plateau. *Chinese Journal of Soil Water Conservation*, 18, 31–34.
- Kelly, R. H., Burke, I. C., & Lauenroth, W. K. (1996). Soil organic matter and nutrient availability responses to reduced plant inputs in shortgrass steppe. *Ecology*, 77, 2516–2527. doi:10.2307/2265750.

- Kumar, S., Stohlgern, T. J., & Chong, G. W. (2006). Spatial heterogeneity influences native and nonnative species richness. *Ecology*, 87, 3186–3199. doi:10.1890/ 0012-9658(2006)87[3186:SHINAN]2.0.CO;2.
- Lane, D. R., & BassiriRad, H. (2005). Diminishing spatial heterogeneity in soil organic matter across a prairie restoration chronosequence. *Restoration Ecology*, 13, 403–412. doi:10.1111/j.1526-100X.2005.00050.x.
- Legendre, P., & Fortin, M. J. (1989). Spatial pattern and ecological analysis. *Vegetatio*, 80, 107–138. doi:10.1007/ BF00048036.
- Liu, Z. M., Yan, Q. L., Baskin, C. C., & Ma, J. L. (2006). Burial of canopy-stored seeds in the annual psammophyte *Agriophyllum squarrosum* Moq. (Chenopodiaceae) and its ecological significance. *Plant and Soil*, 288, 71–80. doi:10.1007/s11104-006-9090-7.
- Ludwig, J. A., Wiens, J. A., & Tongway, D. J. (2000). A scaling rule for landscape patches and how it applies to conserving soil resources in savannas. *Ecosystems* (*New York*, *NY*), 3, 84–97. doi:10.1007/s100210000012.
- Martinez-Turanzas, G. A., Coffin, D. P., & Burke, I. C. (1997). Development of microtopography in a semiarid grassland: effects of disturbance size and soil texture. *Plant Soil*, 191, 163–171.
- Milchunas, D. G., & Lauenroth, W. K. (1993). Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, 63, 327–366. doi:10.2307/2937150.
- Miller, P. M., Singer, M. J., & Nielsen, D. R. (1988). Spatial variability of wheat yield and soil properties on complex hill. *Soil Science Society of America Journal*, 52, 1133–1141.
- Nelson, D., & Sommers, L. (1982). Total carbon, organic carbon and organic matter. In A. L. Page, et al. (Eds.), *Methods of soil analysis, part 2, no. 9* (2nd ed., pp. 539– 577). Madison: ASA Publication.
- Oba, G., Weladji, R. B., Msangameno, D. J., Kaitira, L. M., & Stave, J. (2008). Scaling effects of proximate desertification drivers on soil nutrients in northeastern Tanzania. *Journal of Arid Environments*, 72, 1820– 1829. doi:10.1016/j.jaridenv.2008.04.009.
- Palmer, T. M. (2003). Spatial habitat heterogeneity influences competition and coexistence in an African acacia ant guild. *Ecology*, 84, 2843–2855. doi:10.1890/ 02-0528.
- Parkin, T. B. (1993). Spatial variability of microbial processes in soil: A review. *Journal of Environmental Quality*, 22, 409–417.
- Pierson, F. B., & Mulla, D. J. (1990). Aggregate stability in the Palouse region of Washington: Effect of landscape position. *Soil Science Society of America Journal*, 54, 1407–1412.
- Robertson, G. P., Crum, J. R., & Ellis, B. G. (1993). The spatial variability of soil resources following long-term disturbance. *Oecologia*, 96, 451–456. doi:10. 1007/BF00320501.
- Rossi, R. E., Mulla, D. J., Journel, A. G., & Franz, E. H. (1992). Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecological Mono*graphs, 62, 277–314. doi:10.2307/2937096.

- Schimel, D. S., Coleman, D. C., & Horton, K. A. (1985). Soil organic matter dynamics in paired rangeland and cropland toposequences in North Dakota. *Geoderma*, 36, 201–214. doi:10.1016/0016-7061(85)90002-3.
- Schlesinger, W. H., & Pilmanis, A. M. (1998). Plant-soil interactions in deserts. *Biogeochemistry*, 42, 169–187. doi:10.1023/A:1005939924434.
- Schlesinger, W. H., Raikes, J. A., Hartley, A. E., & Cross, A. F. (1996). On the spatial pattern of soil nutrients in desert ecosystems. *Ecology*, 77, 364–374. doi:10.2307/2265615.
- Schlesinger, W. H., Reynolds, J. F., Cunningham, G. L., Huenneke, L. F., Jarrell, W. M., Virginia, R. A. et al. (1990). Biological feedbacks in global desertification. *Science*, 247, 1043–1048. doi:10.1126/science.247. 4946.1043.
- Seibert, J., Stendahl, J., & Sørensen, R. (2007). Topographical influences on soil properties in boreal forests. *Geoderma*, 141, 139–148. doi:10.1016/j.geoderma. 2007.05.013.
- Shumway, S. W. (2000). Facilitative effects of a sand shrub on species growing beneath the shrub canopy. *Oecologia*, 124, 138–148. doi:10.1007/s004420050033.
- Su, Y. Z., Li, Y. L., & Zhao, H. L. (2006). Soil properties and their spatial pattern in a degraded sandy grassland under post-grazing restoration, Inner Mongolia, northern China. *Biogeochemistry*, 79, 297– 314. doi:10.1007/s10533-005-5273-1.
- Su, Y. Z., Zhang, T. H., Li, Y. L., & Wang, F. (2005). Changes in soil properties after establishment of *Artemisia halodendron* and *Caragana microphylla* on shifting sand dunes in semiarid Horqin Sandy Land, Northern China. *Environmental Management*, 36, 272–281. doi:10.1007/s00267-004-4083-x.
- Titus, J. H., Nowak, R. S., & Smith, S. D. (2002). Soil resource heterogeneity in the Mojave Desert. *Journal of Arid Environments*, 52, 269–292. doi:10.1006/jare.2002.1010.
- Vinton, M. A., & Burke, I. C. (1995). Interactions between individual plant species and soil nutrient status in short-grass steppe. *Ecology*, 76, 1116–1133. doi:10.2307/1940920.
- Wallace, C. S. A., Watts, J. M., & Yool, S. R. (2000). Characterizing the spatial structure of vegetation communities in the Mojave Desert using geostatistical techniques. *Computers & Geosciences*, 26, 397–410. doi:10.1016/S0098-3004(99)00120-X.
- Wang, T., Wu, W., Xue, X., Han, Z. W., Zhang, W. M., & Sun, Q. W. (2004). Spatial-temporal changes of sandy desertified land during last 5 decades in Northern China. *Acta Geographica Sinica*, 9, 203–212 (in Chinese).
- Wei, J. B., Xiao, D. N., Zhang, X. Y., Li, X. Z., & Li, X. Y. (2006). Spatial variability of soil organic carbon in relation to environmental factors of a typical small watershed in the black soil region, northeast China. *Environmental Monitoring and Assessment*, 121, 597–613.
- Wezel, A., Rajot, J. L., & Herbrig, C. (2000). Influence of shrubs on soil characteristics and their function in Sahelian agro-ecosystems in semi-arid Niger.

Journal of Arid Environments, 44, 383–398. doi:10. 1006/jare.1999.0609.

- Whitford, W. G., Anderson, J., & Rice, P. M. (1997). Stemflow contribution to the 'fertile island' effect in creosote bush, *Larrea tridentata. Journal of Arid Envi*ronments, 35, 451–457. doi:10.1006/jare.1996.0164.
- Zeng, D. H., Hu, Y. L., Chang, S. X., & Fan, Z. P. (2008). Land cover change effects on soil chemical and biological properties after planting Mongolian pine (*Pinus sylvestris* var. *mongolica*) in sandy lands in Keerqin, northeastern China. *Plant and Soil*. doi:10. 1007/s11104-008–9793-z.
- Zhang, T. H., Zhao, H. L., Li, S. G., Li, F. R., Shirato, Y., Ohkuro, T. et al. (2004). A comparison of different measures for stabilizing moving sand dunes in the Horqin Sandy Land of Inner Mongolia, China. *Journal of Arid Environments*, 58, 203–214. doi:10.1016/ j.jaridenv.2003.08.003.
- Zhang, J. Y., Zhao, H. L., Zhang, T. H., Zhao, X. Y., & Drake, S. (2005). Community succession along a chronosequence of vegetation restoration on sand dunes in Horqin Sandy Land. *Journal of Arid Environments, 62*, 555–566. doi:10.1016/j.jaridenv.2005. 01.016.

- Zhao, H. L., Zhao, X. Y., Zhang, T. H., & Zhou, R. L. (2005). Desertification processes of sandy rangeland due to over-grazing in semi-arid area, Inner Mongolia, China. *Journal of Arid Environments*, 62, 309–319. doi:10.1016/j.jaridenv.2004.11.009.
- Zheng, J., He, M., Li, X., Chen, Y., Li, X., & Liu, L. (2008). Effects of Salsola passerina shrub patches on the microscale heterogeneity of soil in a montane grassland, China. *Journal of Arid Environments*, 72, 150–161. doi:10.1016/j.jaridenv.2007.05.010.
- Zhu, Z. D., & Chen, G. T. (1994). *The sandy desertification in China* (pp. 7–268). Beijing: Science Press (in Chinese).
- Zuo, X. A., Zhao, H. L., Zhao, X. Y., Zhang, T. H., Guo, Y. R., Wang, S. K. et al. (2008a). Spatial pattern and heterogeneity of soil properties in sand dunes under grazing and restoration in Horqin Sandy Land, Northern China. *Soil & Tillage Research*, 99, 202–212. doi:10.1016/j.still.2008.02.008.
- Zuo, X. A., Zhao, H. L., Zhao, X. Y., Guo, Y. R., Li, Y. L., & Luo, Y. Y. (2008b). Plant distribution at the mobile dune scale and its relevance to soil properties and topographic features. *Environmental Geology*, 54, 1111–1120. doi:10.1007/s00254-007-1104-0.