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Spatial relationships among species, above-ground biomass, N, and P in degraded grasslands in Ordos Plateau, northwestern China

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Abstract

We chose five communities, representing a mild to severe gradient of grassland desertification in a semi-arid area of Ordos Plateau, northwestern China, to explore the spatial relationships among plant species, above-ground biomass (AGB), and plant nutrients (N and P). Community 1 (C1) was dominated by *Stipa bungeana*; Community 2 (C2) by a mix of *S. bungeana* and the shrub *Artemisia ordosica*; Community 3 (C3) by *A. ordosica*; Community 4 (C4) by a mix of *Cynanchum komarovii* and *C. komorovii*; and Community 5 (C5) by *C. komorovii*. Quantitative methods, including geostatistics, were used to compare community composition, structure, and indicators of ecosystem function (i.e. AGB, plant N and P) in five 16-m^2 plots. The highest AGB, plant nitrogen (N) and plant phosphorus (P) were found in lightly degraded community C2. With increasing desertification effects from C3 to C5, the AGB, N, and P decreased significantly while plant density remained unchanged. The spatial variations of AGB were higher in shrub-dominated communities (C1 and C5) than in grass-dominated communities (C2–C4). Strong spatial relationships were detected within and among the communities, with stronger relationships between AGB and density than between AGB and species richness. Spatial patterns of plant N and P were different from those of AGB, reflecting different N and P contents of individual plants and different species that can redistribute soil

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resources in these communities. The AGB was positively correlated with soil nutrients (TOC, TN, TP, and IN), except for soil AP. We concluded that several specific aspects of ecosystem properties were directly associated with the conversion of the grass and shrub "functional types" in these degraded grasslands.
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Keywords: Spatial heterogeneity; Desert vegetation; Plant nutrients; Disturbed prairie; Geostatistics

1. Introduction

Desertification associated with human activities has been recognized over the past 2 decades as one of the important facets of ongoing global environmental change (Jain, 1986; Verstraete and Schwartz, 1991; UNEP, 1997; Huenneke et al., 2002). Recent studies have also directed ecologists to prioritize the following important ideas in ecological research: (1) changes in ecosystem structure and function (e.g. production) are cohesively related (Jain, 1986; Verstraete and Schwartz, 1991); (2) for many desert ecosystems, shrub invasion and displacement of grasslands play important roles in determining ecosystem structure, function, and dynamics, as well as relationships among these (Schlesinger et al., 1990; Gibbens et al., 1992; Van Auken, 2000); and (3) communities are spatially heterogeneous, and the degree of heterogeneity often plays a critical role in community function and stability (Levin, 1992; Schlesinger et al., 1996).

For many semi-arid grassland ecosystems, scientists have reported a general trend of increasing dominance of shrub species as desertification becomes more frequent and intensive (Schlesinger et al., 1990; Schlesinger et al., 1996; Facelli and Temby, 2002). Several studies suggested that increase in shrub dominance in a community is responsible for elevating the spatial variability of both above- and belowground properties (Schlesinger et al., 1990; Huenneke et al., 2002; Parizek et al., 2002). In many desert landscapes, for example, 'islands of fertility' have developed with desertification when clustered shrubs emerge as new ecosystem components (Garner and Steinberger, 1989; Schlesinger et al., 1996; Kieft et al., 1998; Facelli and Temby, 2002). Formation of fertility islands, which accelerates desertification, has been credited with an increase in spatial variation of soil resources (Huenneke et al., 2002). Schlesinger et al. (1990) and Katherinel et al. (1995) reported that the spatial variation of soil nutrients is often associated with variation in plant distribution. Shrub invasion or replacement of grasses speeds up the loss of soil organic matter, nitrogen, and other resources, leading to a progressive degradation of the productive capacity of the ecosystem (Schlesinger et al., 1990; Reynolds et al., 1999). This suggests that research focusing on the spatial distribution of plants, nutrients, and ecosystem functions (e.g. production) is essential to understand the desertification process. Furthermore, it is equally important to understand how these structural changes in ecosystems have altered the magnitude of biomass and its spatial distribution. Yet very few efforts have been made to quantitatively explore those spatial relationships in degraded grasslands.

The above-ground vegetation can be a good indicator of an ecosystem's overall function in arid and semi-arid areas (Ludwig and Tongway, 1995). Alterations in the above-ground vegetation patches over time can result in changes in the distributions of both living organisms and soil resources. Soil organic matter (SOM), nitrogen (N) and phosphorus (P)

are among the most important measures of ecosystem function because of their direct roles in many ecosystem processes (e.g. plant growth, carbon cycle; Robertson et al., 1988). In recent years, substantial effort has been made to explicitly quantify variation in plant species composition and structure, which are spatially related to the rate of and variability in nutrient cycling along a successional sere (Vitousek et al., 1982; Katherinel et al., 1995). Even at very small scales, the spatial variation in nutrient availability was found to be associated with individual plants (Schlesinger et al., 1990). However, the specific mechanisms controlling belowground resources (e.g. plant N content) under different degraded regimes remain unclear (e.g. whether the spatial variability of soil resources is closely related to the above-ground biomass (AGB)). For grasslands, many efforts have been made to investigate the changes in spatial heterogeneity between grass and shrub-dominated communities (Schlesinger et al., 1990, 1996; Valone et al., 2002). These studies found that soil resources did in fact become increasingly spatially heterogeneous with increasing duration of shrub dominance at a site (Schlesinger et al., 1996; Reynolds et al., 1999). The shrub-dominated ecosystems are predicted to become increasingly patchy (i.e. greater spatial heterogeneity), with respect to the distribution of both living organisms and soil resources. However, few studies have quantitatively described the relative patchiness of biomass or of ecosystem function in grass- vs. shrub-dominated semi-arid systems along degraded gradients.

Climate changes and human activities have influenced and altered a wide variety of semi-arid and arid ecosystem functions. In the past 50 years, the climate in northern China has been predominantly dry and warm, creating conditions favorable for the desertification process (Lin and Tang, 2002). Similarly, drought and over-grazing have been the major casual factors leading to the loss of dominant grass species, or replacement of a desirable grass species by undesirable shrubs or alien weeds with poor forage quality (Zhang, 1994). *Stipa bungeana* (STBU), *Artemisia ordosica* (AROR) and *Cynanchum komarovii* (CYKO) are three dominant species representing a series of communities along a degraded gradient in Ordos Plateau, northwestern China. STBU is a perennial meso-xerophytic grass, with the STBU community being typical steppe vegetation in the region; AROR is a xerophyte shrub (the dominant species in the Ordos Plateau) and can be used as an indicator for mid-level desertification; and CYKO is a member of the milkweed family and a strong xerophyte whose presence indicates serious desertification (Zheng and Huang, 1992; Yang et al., 1994; Cheng et al., 2001a). Drought and over-grazing lead first to the STBU community, then to an AROR community, and finally to a CYKO community (Zheng and Huang, 1992; Yang et al., 1994). In our previous studies, we found that vegetation characteristics (e.g. flora, lifeform, biomass and hydro-ecological group) varied substantially among the five degraded communities (Cheng et al., 2001a, b) and were associated with the micro-scale spatial distribution and loss of soil nutrients (TOC, TN, TP, IN, and AP) (Cheng et al., 2004). However, changes in the spatial relationships among community structure, function, and nutrients in these degraded communities remain to be identified.

In this study, we hypothesized that the spatial associations among community composition, structure, plant nutrients (N and P), and AGB would significantly change along a gradient of five degraded grassland communities (i.e. C1–C5) in a semi-arid area of the Ordos Plateau of northwestern China. Specifically, our objectives were to: (1) compare the community composition, structure (e.g. density, plant nutrients), and function (i.e. AGB) in five communities along a desertification gradient; (2) quantify the spatial

distribution patterns of AGB, plant N and P in these communities using spatial statistics; and (3) further explore the relationships among AGB, soil nutrients (total organic carbon (TOC), total nitrogen (TN), inorganic nitrogen (IN), total phosphorus (TP), and available phosphorus (AP), and species composition to identify potential underlying mechanisms determining the distributions of soil resources in these ecosystems.

2. Methods

2.1. Study area and species

The study area (39°02′ N and 109°51′ E) is located in the Ordos Plateau in the northeast of the Mu Us Sand-land (37°27′–39°22′ N and 107°20′–111°30′ E) in Northwestern China. The elevation of the study site is about 1355 m. The continental semi-arid climate is characterized with an annual precipitation of 250–440 mm, 60–80% of which occurs between June and August. The annual mean temperature varies from 6.0 to 8.5 °C, with monthly means of 22 °C for July and −11 °C for January. Shrubs are the dominant vegetative growth forms, and shrub-land is the most important vegetation type of the region (Li, 2001). The other important vegetation types of the study area include steppes and meadows. In addition, there are farmlands and forest plantations distributed along the rivers and scattered in sandy grassland (Zhang, 1994).

Three dominant species, *Stipa bungeana*, *Artemisia ordoscia* and *Cynanchum komorovii*, represent different stages of vegetation degradation in the Mu Us sandland. *S. bungeana* is a typical mild desertification; *A. ordoscia* can be used as an index of mid-level desertification; while *C. komarovii* indicates severe desertification (Cheng et al., 2001a, 2004). We conducted our study within five communities chosen along a gradient of mild to severe desertification occurring following repeated disturbances. Community 1 (C1) was dominated by *S. bungeana*; Community 2 (C2) by a mix of *S. bungeana* and the shrub *A. ordosica*; Community 3 (C3) by *A. ordosica*; Community 4 (C4) by a mix of *A. ordoscia* and *C. komorovii*; and Community 5 (C5) by *C. komorovii*. Other species common in communities C1–C5 included *Cleistogenes squarrosa* (CLSQ), *Lespedeza davurica* (LEDA), *Oxytropis psammochans* (OXPS), *Astragalus melilotodes* (ASME), *Heteropapus altaicus* (HEAL), and *Bassia dasyphylla* (BADA) (Appendix 1 electronic version only).

2.2. Field sampling

Twenty-five $2 \times 2\,m^2$ plots (total 125) were placed in each of the successional community from July to September (Cheng et al., 2001a, b) to measure cover, height, and biomass by species but no spatial information was recorded. Multivariate analyses based on these data showed that five communities differed significantly in species richness; density, lifeform spectrum and biomass in each community among five communities (see Cheng et al., 2001a, b). However, within each community, the species composition and biomass were relatively homogeneous (Cheng et al., 2001a, b).

For spatial analysis of species distribution and ecosystem functional measures, we established a representative $4 \times 4\,m^2$ plot in each of the five communities (C1–C5) in 2001. To avoid potential anisotropic effects and to meet the stationarity assumption when analyzing our field data using geostatistical methods (Cressie, 1993), we carefully placed our plots in flat areas with minimal micro-topographic variation (e.g. homogeneous soil

surface). Each $4 \times 4\,m^2$ plot was marked with the (0, 0) at its southwestern corner and (4, 4) at the northeastern corner. The 4-m plot frame was marked every 10 cm to assure the accuracy of mapping to be less than a centimeter. We recorded the spatial coordinates of the center of each plant individual by species, and harvested all the above-ground parts of each plant included dead branches of shrub and dry leave of grasses within each plot. At same time, we collected soil samples at 0–20 cm depth in each plot for soil nutrients (TOC, TN, IN, TP, and AP) analysis. Thirty soil samples from the root-spheres and 60 soil samples from bare soil were taken randomly in 3 selected transect (30 m × 100 m) in each plot for quantifying soil properties (Cheng et al., 2004). Plant and soil samples were stored in plastic bags in a cooler ($< 5\,^{\circ}C$) for immediate transportation to a laboratory at Nanjing University.

2.3. Laboratory analysis

All plant samples included dead branches and dry leaves were oven-dried at 80 °C until a stable weight was reached. These samples then were weighed for above-ground biomass (AGB). We randomly selected six replicated samples for each species for plant N and P analysis. A portion of each sample was clipped, ground, and sieved through 2 mm mesh. A small amount of the each ground sample was weighed and analysed for its N concentration. The total N content was determined using micro-Kjeldahl digestion followed by colorimetric analysis for NH_3. For total phosphorus analyses, three 5 g sub-samples were taken and extracted in 50 ml of Bray's P-1 extractant and then subjected to flow injection analysis (Robertson et al., 1993). Finally, we calculated the plant N and P content of each sample based on its AGB. The soil nutrients (TOC, TN, IN, TP, and AP) laboratory analysis was mentioned in detail in the previous paper (Cheng et al., 2004). Briefly, TOC was estimated using the wet oxidation–diffusion technique. The TN and TP were determined using the same method as plant N, and P mentioned above. IN was taken to be the sum of NH_4-N and NO_3-N. NH_4^+ and NO_3^- were analysed using standard methods on a Traacs 800 auto-analyzer. AP was taken as the PO_4^{-3}, which was measured in a 0.5 M $NaHCO_3$ extract on the auto-analyzer (Cheng et al., 2004).

2.4. Data analysis

The spatial distributions of individual AGB, and total plant N and P are associated with each individual plant, resulting in a discrete distribution (i.e. point pattern). We adopted the approach developed by Chen et al. (2004) to convert a point pattern to a continuous variable (Cressie, 1993). Random circular plots with predefined radius were placed within the $4 \times 4\,m^2$ plot. Any individuals falling within the circular plot were used for calculating the average AGB, and plant N and P of the plot. These calculated values represented the AGB, N, and P of the plot center. With these procedures, the calculated variables are spatially continuous because random circular plots overlap. Two parameters, the number of sampling plots and plot size (i.e. radius), are crucial to assure a statistically sound conversion of the data. We varied plot size (i.e. radius) from 5 to 50 cm and the number of plots from 50 to 1000; the mean and variation of each sampling strategy were compared graphically by plotting changes in the means with plot radius and sampling size. Based on the results of these exploratory analyses, we used 500 25-cm radius plots per community.

We performed semivariance and kriging analyses for the converted databases using the GS+ software (Gamma Design Software, Plainswell, Michigan, Version 3.1). We set the maximum lag distance as 200 cm (i.e. half of the maximum dimension) and compared various models for predicting changes in semivariance with scale (i.e. distance). Based on calculated sum square of error (SSR) and R^2, we changed models of semivariances with distance and found that the spherical model (Cressie, 1993) was the best choice for most data sets. For the sake of compatibility among different data sets, we used the spherical model for interpolation in kriging analysis. We set 1 cm as the grid size to calculate predicted values, which were subsequently exported in Excel format for analyzing the spatial correlations between AGB and other community features (i.e. density, plant N and P) within the ArcView geographic information system (GIS).

Predicted AGB, N and P (continuous variables) were imported into ArcView in grid format with a cell size of 0.25 m, and the original plant distribution (point pattern) was imported as point coverage. The Kriged AGB map was categorized into four equal biomass zones between the minimum and maximum values of AGB. This spatial contour map was used as a cookie-cutter to intersect with other spatial databases of plant N and P. A new combined database of individual plant N and P, overlaid with the position within each AGB zone, was finally created. Importance value (IV) was calculated as the mean of relative density, relative height, and relative biomass. Species composition, density, IV of each species, and total plant N and P were calculated for each AGB zone for all five communities (C1–C5). Regression analysis was employed to explore the effects of richness and density on AGB, and further, to explore the effect of AGB on soil nutrients (TOC, TN, TP, IN, and AP) (Cheng et al., 2004) among the five communities.

3. Results

3.1. Community composition, structure, and function

The major species in the five communities were STBU, AROR, CYKO, CLSQ, LEDA, OXPS, ASME, HEAL, and BADA. Each species had substantially different total N and P concentrations among the five communities (Table 1), ranging from 9.15 to 28.42 g kg^{-1} and 1.25 to 5.18 g kg^{-1}, respectively. The five communities differed in species composition with a clear transition of species from C1 to C5 (Fig. 1). STBU had a high importance

Table 1
Nitrogen and phosphorus content (mean ± standard deviation; $n = 6$) of major 9 plant species in five degraded communities in Ordos grasslands of northwestern China

Species	Species code	N (g kg^{-1})	P (g kg^{-1})
Stipa bungeana	STBU	11.65 ± 1.12	1.45 ± 1.04
Artemisia ordosica	AROR	9.15 ± 1.08	1.25 ± 0.89
Cynanchum komarovii	CYKO	12.91 ± 1.43	1.88 ± 0.94
Cleistogenes squarrosa	CLSQ	14.13 ± 1.37	1.62 ± 1.10
Lespedeza davurica	LEDA	17.86 ± 1.56	1.66 ± 1.24
Oxytropis psammochans	OXPS	15.91 ± 1.29	2.28 ± 1.33
Astragalus melilotodes	ASME	13.61 ± 1.03	5.18 ± 1.78
Heteropapus altaicus	HEAL	9.71 ± 0.94	1.73 ± 0.86
Bassia dasyphylla	BADA	28.42 ± 1.79	2.92 ± 1.27

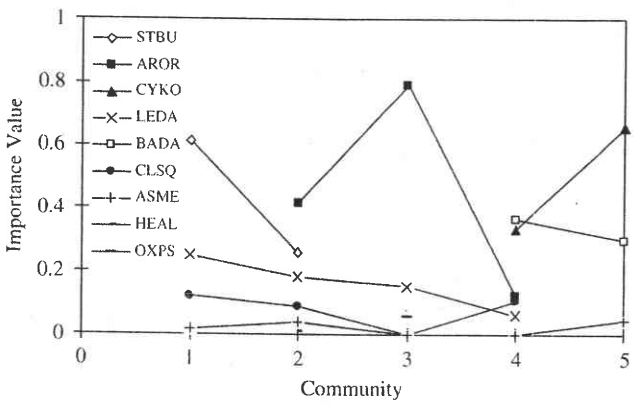

Fig. 1. Shifts of species importance values (IV) along five degraded grasslands communities (C1–C5) of increasing desertification in Ordos grasslands in northwestern China.

value (IV) in communities C1–C2, AROR in communities C2–C4, and CYKO and BADA in communities C4–C5. LEDA and CLSQ were common in communities C1–C4, with a decreasing trend (Fig. 1).

Communities C1, C3, and C5 were dominated by a single species (STBU, AROR, and CYKO, respectively) and had lower numbers of species than communities C2 and C4. Community C1 was dominated by STBU (IV = 0.613), with three companion species (i.e. CLSQ, LEDA, and ASME). STBU and LEDA contributed 60.35% and 23.32% of the density (total = 83.57%), respectively. They were also responsible for 63.16% and 28.19% of the total AGB. Community C2 was co-dominated by STBU and AROR (IV = 0.258 and 0.416, respectively) with four companion species (CLSQ, LEDA, ASME, and HEAL). STBU and AROR were responsible for 80.47% of the total density and 96.49% of the total biomass. Community C3 was dominated by AROR (IV = 0.791) and accompanied by LEDA and OXPS. About 69.87% of the total density and 97.46% of the total biomass in C3 were contributed by AROR. Community C4 was co-dominated by CYKO and BADA (IV = 0.335 and 0.368, respectively) and accompanied by CLSQ, LEDA and AROR. The densities of BADA and CYKO were 42.34% and 24.70%, and the biomass of BADA and CYKO was 25.60% and 51.00% of the total, respectively. Community C5 was dominated by CYKO (IV = 0.655), with ASME and BADA existing as companion species. CYKO contributed 54.85% of the density and 87.27% of total biomass (Appendix 1 electronic version only). A decreasing trend in AGB, total N, and total P occurred from C2 to C5 (Appendix 1 electronic version only), but C2 had higher values of these variables than C1 (lower grazing frequency/intensity). Species richness did not appear to be linearly correlated with community AGB ($R^2 = 0.2753$, $P = 0.3641$) (Fig. 2a), but density significantly increased with biomass ($R^2 = 0.7611$, $P < 0.0001$) (Fig. 2b).

3.2. Spatial distributions of biomass, N, and P

Clear patch patterns of AGB, total N, and total P existed in all five communities (Fig. 3), as indicated by high R^2, low SSR, and relatively low nugget values in changes of modeled semivariance with distance (Table 2). However, the patch patterns of AGB, total N, and total P content within the same plot did not match very well, except for the island clusters

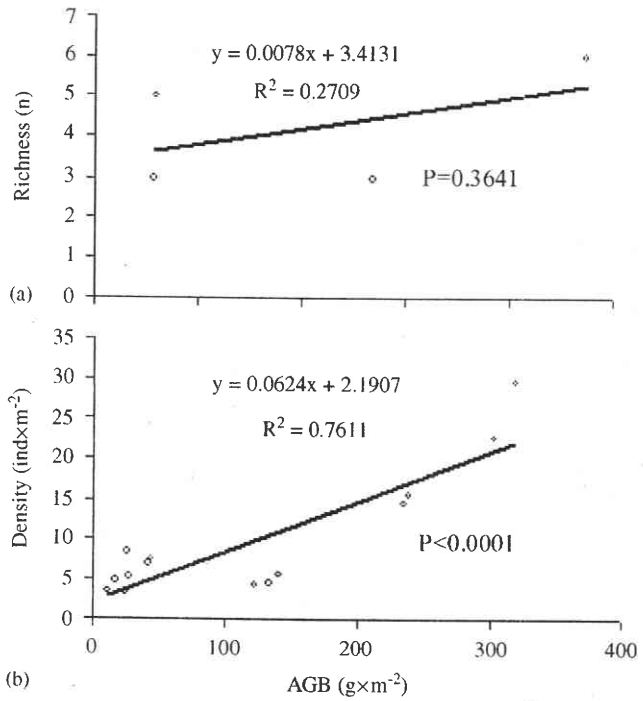

Fig. 2. Correlations between community diversity (richness and density) and above-ground biomass (AGB) in five degraded grasslands communities in Ordos grasslands of northwestern China. *Note*: In the regression equations, "*y*" represents richness (a), and density (b), respectively; "*x*" represents AGB.

measured by N and P content in C3 and C5 (Fig. 3). In C1, for example, AGB was moderate for most of the plot, with a few extreme patches, yet N clearly increased from the left to the right side of the plot. There appeared to be a similar increasing trend for P, but from the bottom to the top (Fig. 3a). In C4, spatial variations across the plot were relatively small for AGB and P, but were greater for N (Fig. 3d).

Average patch sizes for AGB, total N, and total P ranged from 47.5 to 87.7 cm, 49.5 to 83.8 cm, and 47.5 to 68.7 cm, respectively (Table 2). C1 and C5, the two degradation extremes (weakest and strongest), were more homogeneous (i.e. larger patch sizes, Fig. 3 and Table 2). Obvious "islands" of high plant N and P existed in the C2 and C3 communities (Fig. 3), but not in the C4 community (Fig. 3d).

3.3. Relationships among the variables

The spatial patterning of AGB did not match that of total plant N or P (Fig. 3). First, the proportion of AGB zones differed among communities (Appendix 2 electronic version

Fig. 3. Spatial isopleths of above-ground biomass (AGB), plant N and P based on Kriging of spherical models (Table 2) in five degraded grasslands communities (C1–C5) in Ordos Plateau of northwestern China. *Note:* The spatially interpolated distributions are equally divided into 4 zones between the minimum and maximum for each variable. The "darker color" represents the higher biomass, N and P; the "lighter color" represents the lower biomass, N and P.

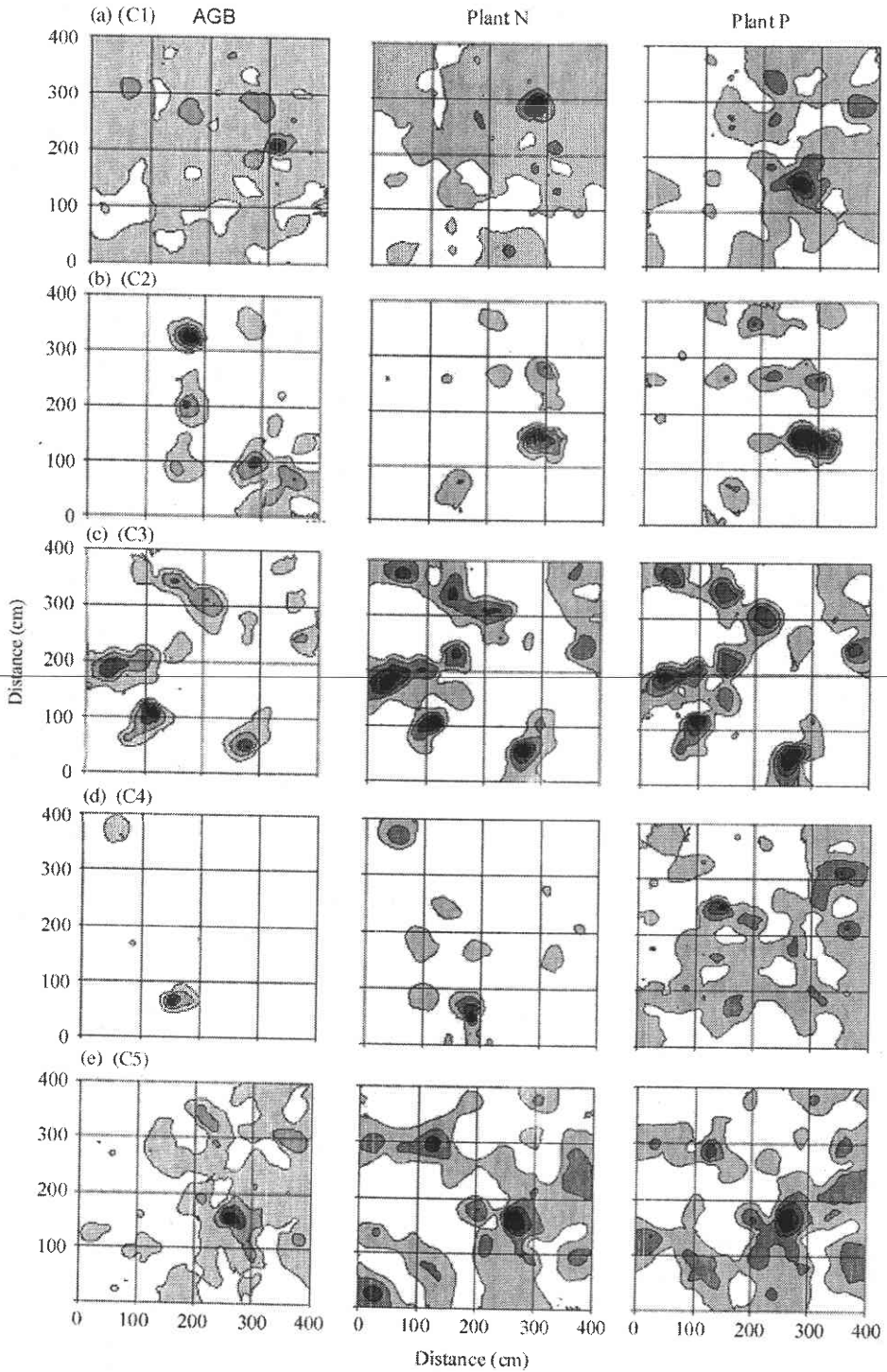
(a) (C1) AGB
Plant N
Plant P
(b) (C2)
(c) (C3)
(d) (C4)
(e) (C5)
Distance (cm)
0
100
200
300
400
Distance (cm)

Table 2
Coefficients and statistics estimated in semivariance analyses of above-ground biomass (AGB), total plant nitrogen (N), and total plant phosphorus (P) in the five degraded communities in Ordos grasslands

Variable	Community	C_0	C_0+C	A_0 (cm)	$C_0/(C_0+C)$	r^2	RSS
AGB ($g\,m^{-2}$)	C1	0.064	1.019	47.500	0.937	0.935	0.015
	C2	0.145	1.020	72.700	0.858	0.985	0.005
	C3	0.219	0.985	54.900	0.778	0.979	0.003
	C4	0.001	1.002	57.100	0.999	0.915	0.032
	C5	0.188	1.013	87.700	0.814	0.958	0.013
N ($g\,m^{-2}$)	C1	0.101	1.130	83.800	0.911	0.956	0.024
	C2	0.118	1.147	60.700	0.897	0.868	0.055
	C3	0.093	1.016	61.900	0.908	0.964	0.011
	C4	0.201	1.019	49.500	0.803	0.905	0.015
	C5	0.184	1.099	80.100	0.833	0.954	0.019
P ($g\,m^{-2}$)	C1	0.110	0.934	62.200	0.882	0.859	0.038
	C2	0.069	1.132	47.500	0.939	0.953	0.093
	C3	0.270	1.002	59.000	0.731	0.938	0.011
	C4	0.125	0.975	50.300	0.872	0.935	0.013
	C5	0.232	1.066	68.700	0.782	0.983	0.005

Note: The spherical model was used in predicting changes of semivariance (γ) with distance (h). C_0 = nugget variance, C_0+C = sill variance, $C_0/C_0+C=$ nugget variance C_0 as proportion of model sample variance $[C_0+C]$, and A_0 = range (cm).

only). C1 was dominated by AGB zones 2 and 3, while degraded communities (C2–C5) were mostly contained within AGB zone 1 (the lowest) and zone 2, with very small portions of the plot occupied by higher AGB zones (Appendix 2 electronic version only). Secondly, the community composition, density, total plant N, and total plant P were clearly different among the four AGB zones (Appendix 2 electronic version only). However, generally positive relationships between AGB and soil nutrients (TOC, TN, TP, IN, and AP) existed (Fig. 4). Soil nutrients (TOC, TN, TP, and IN) were positively correlated with community AGB, with R^2 of 0.3915 ($P = 0.0008$), 0.4472 ($P = 0.0003$), 0.2563 ($P = 0.0098$) and 0.2691 ($P = 0.0098$), respectively (Fig. 4a–d); meanwhile, soil AP was negatively correlated with community AGB ($R^2 = 0.6142$, $P<0.0001$) (Fig. 4e).

4. Discussion

Spatial heterogeneity is a common feature of natural plant communities, and the degree of heterogeneity may significantly affect plant community structure, ecosystem processes and function (Robertson et al., 1993; Robertson and Gross, 1994). Understanding the spatial relationships between vegetation heterogeneity and ecological processes is essential for predicting the potential community dynamics under environmental change and different degradation regimes. Robertson et al. (1997) reported that spatial distribution of soil elements (TC, TN, IN) varies with changes in plant species distributions. In turn, changes in spatial distribution of soil nutrients would alter both vegetative productivity and structure, and provide feedback that aggravates soil further desertification (Fisher

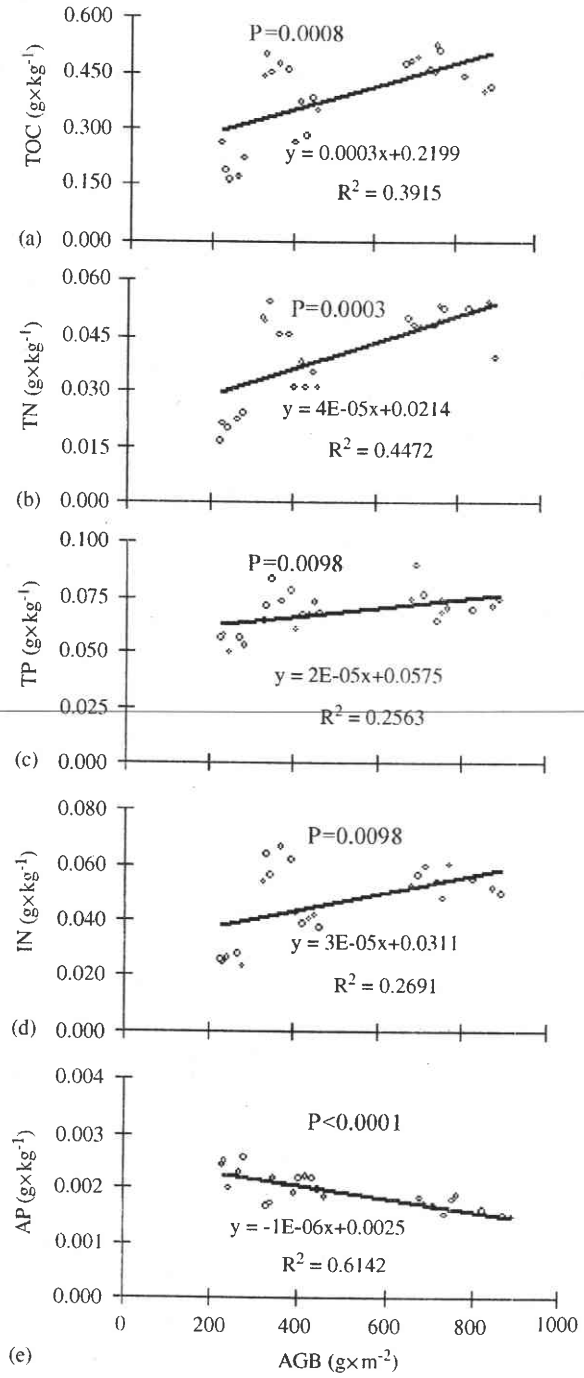

Fig. 4. Correlations between above-ground biomass (AGB) and soil nutrients (total organic carbon (TOC), total nitrogen (TN), inorganic nitrogen (IN), total phosphorus (TP), and available phosphorus (AP) in five degraded grassland communities in Ordos grasslands of northwestern China. *Note*: In the regression equations, "*y*" represents TOC (a), TN (b), IN (c), TP (d), and AP (e), respectively; "*x*" represents AGB.

et al., 1987; Breshears and Barnes, 1999). Such a degradation process occurs in our study area in the grasslands of northern China. More importantly, we found that the spatial relationships or interactions between species composition and indicators of ecosystem function such as biomass and nutrients became more complex as species composition shifted along the degraded gradient from C1 to C5 (Fig. 1 and Appendix 1 electronic version only).

The Ordos plateau is a relatively independent physiographic unit and a complex, sensitive ecotone in the semi-arid zone of north China (Li, 2001). Historically, Ordos Plateau was covered by productive grassland (i.e. C1), yet about 60% of the landscape is currently classified as shrub land because of intensive over-grazing and water stress (Zheng and Huang, 1992; Zhang, 1994). Consequently, ecosystem biomass and nutrients have decreased significantly. Our results suggest that repeated disturbances have significantly changed the species composition and structure, and ultimately, ecosystem biomass and nutrient availability (Fig. 1 and Appendix 1 electronic version only). Specifically, ecosystem composition and structure have coevolved to unique spatial patterns (Fig. 3) that drive spatial allocation of production. Although previous studies had concluded that prairie communities with light desertification supported higher biomass and net productivity than those of shrub-dominated communities created by intensive disturbances (Huenneke et al., 2001, 2002), our studies in Ordos Plateau showed that shrub invasion (AROR) was the key process leading to higher above-ground biomass, vegetative nitrogen, and vegetative phosphorus in light desertification community C2 (Appendix 1 electronic version only). In an previous study, we found that soil nutrients did not change significantly from community C1 to C2 (Cheng et al., 2004); but shrub invasion in community C2 promoted competition for soil nutrients between the dominant species STBU and AROR, which consequently increased plant growth (Guo and Wade, 1998). Therefore, the beginning of grassland desertification did not simply promote a decline but an increase in biomass of the degraded grasslands in Ordos plateau, China. With progressive desertification, the ecological replacement of shrub communities is obvious (Li, 2001). Following the AROR community degradation, CYKO replaced AROR and eventually became dominant with increasing disturbance frequency and intensity (Zheng and Huang, 1992; Cheng et al., 2001a). As desertification continued, the community shifted from C3 to C5 and the AGB, N, and P decreased significantly while density remained at similar levels (Appendix 1 electronic version only). The shrublands are vulnerable to losses of soil nutrients, leading to a progressive degradation of productive capacity of the ecosystem over a long period (Schlesinger et al., 1990; Huenneke et al., 2002). Thus, the decline of biomass is probably related to drought and the loss of soil nutrients from these ecosystems with progressive desertification (Shachak et al., 1998).

An interesting result of this study was high variation in AGB, N, and P distribution among the degraded grasslands. The distribution of AGB was more variable in shrub-dominated communities than in the grass-dominated, as indicated by the relatively greater homogeneity within communities C1 and C5 than within communities C2 and C3; C4, C1, and C5 seemed more homogeneous with only a few small patches where shrub biomass was high (Fig. 3). Huenneke et al. (2002) reported that the distributions of above-ground biomass and net ecosystem productivity (NEP) were more heterogeneous when grassland undergoes desertification to shrub-land and develops the "fertility islands" that are common in shrub-dominated landscapes. Our results also showed that the AGB became more spatially heterogeneous with increasing desertification as shrub invasion progressed

(from C1 to C3). Following the AROR community along the desertification gradient, the AGB became more spatially homogeneous with longer and more intensive desertification as AROR moved out of the community from C4 to C5. These results were consistent with other studies that indicated that vegetative conversion could be used as an index for the degree of spatial heterogeneity in AGB at the scale of individual plants (Cross and Schlesinger, 1999; Huenneke et al., 2002). More interestingly, the patch structure of N and P appeared to be different from those of AGB (Table 2 and Fig. 3), likely because the N and P contents (Table 1) among species were greatly different and, additionally because of difference in plant species composition prior to disturbances. Previous studies have primarily focused on the heterogeneity of soil resources (Schlesinger et al., 1990, 1996; Cross and Schlesinger, 1999; Hirobe et al., 2001). Few have studied the spatial variation of AGB and associated nutrient contents of plants in grassland or shrub-lands in any comparable way. The distribution pattern and patch size have been associated with species composition and spatial locations of individual plants (Schlesinger et al., 1996; Huenneke et al., 2002). Our results suggested that the spatial distribution of species (i.e. composition) reflected the spatial pattern of the AGB, and plant N and P in degraded grassland communities in Ordos (Appendix 2 electronic version only and Fig. 3). The spatial distribution of nutrients constitutes a critical component of the structure of plant communities.

The spatial distributions of AGB and plant N and P are linked with spatial heterogeneity in soil resources. The "soil resource redistribution" hypothesis (Schlesinger et al., 1990; Reynolds et al., 1999) has generated mounting interest in the spatial patterns of plant biomass and productivity. Primary productivity, the fixation of carbon dioxide into organic molecules by photosynthesis, is a key feature of ecosystem function (Huenneke et al., 2002). As intensive drought changes the plant communities in the study area, different plant materials with different biomass and nutrient characteristics are available as input to the soil. Our results clearly demonstrated that the soil nutrients TOC, TN, TP, and IN were positively correlated with AGB in all five degraded communities (Fig. 4a–d). Additionally, we found that the soil nutrient AP decreased with AGB (Fig. 4e). Our earlier study showed that the dynamics of soil phosphorus were different from the other elements in five degraded communities—notably that the mean AP concentration showed no significant change from C1 to C4 in mid-level desertification, and then increased from C4 to C5 in progressive desertification (Cheng et al., 2004). Soil TOC is derived mainly from decomposed plant material; soil TN is provided by nitrogen in dead plant material, which was either taken up by the plants from the soil N pool or fixed biologically or chemically from the atmosphere; and soil TP comes mainly from the soil. Thus, desertification changed the spatial above-ground vegetation associated with the soil resources in our landscape. Based on our previous work in similar grasslands (Cheng et al., 2001a, b, 2004), we concluded that several specific aspects of ecosystem properties (e.g. loss of soil nutrients, spatial heterogeneity, density, AGB, N, and P) were directly affected by the conversion of the grass and shrub "functional types" in these frequently, and intensively degraded grasslands.

5. Conclusions

The spatial variations of AGB were higher in shrub-dominated communities than in grass-dominated communities, i.e. C1 and C5 had more homogeneous AGB than did C2,

C3, and C4. The highest AGB, plant nitrogen (N) and plant phosphorus (P) were found in lightly degraded community C2. With increasing desertification effects from C3 to C5, the AGB, N, and P decreased significantly while community density remained unchanged. Strong spatial relationships were detected within and among the communities, with stronger relationships between AGB and density than between AGB and species richness. Spatial patterns of plant N and P appeared to be different from those of AGB, while the AGB was positively correlated with soil nutrients (TOC, TN, TP and IN), except for soil AP. Our results suggested that N and P distribution did not reflect patterns of above-ground biomass, but did not recognize that these patterns might be relicts from previous plant distribution patterns.

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Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jaridenv.2006.07.006.

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