

Phytomass and plant functional diversity in early restoration of the degraded, semi-arid grasslands in northern China

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Abstract

We analysed vegetation data recorded in the degraded lowland grasslands in Otindag Sandland during the first 4-years of restoration (2001–2004) to investigate: (1) the contribution of individual plant functional type (PFT) to PFT diversity of community and (2) the relationships between primary productivity and biodiversity both at species and PFT levels. Sixteen PFTs were distinguished based on the following traits: (1) life-span (annual vs. perennial); (2) photosynthetic pathway (C_3 vs. C_4); (3) reproductive mode (clonal vs. non-clonal); and (4) growth form (grass vs. forb). Analysis of data indicates that density, coverage, number of species, phytomass, and relative importance of PFTs depended strongly on life-span, photosynthetic pathway, reproductive mode and growth form. Phytomass was significantly correlated with PFT diversity, but not species diversity. However, the relationship between phytomass and PFT diversity varied greatly with year, with a positive relationship in 2001 and 2004 and a negative one in 2002 and 2003. As the restoration proceeds, the perennial C_3 clonal grass became the greatest contributor to PFT diversity.

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Keywords: Biodiversity and ecosystem functioning; Otindag sandland; Primary productivity; Semi-arid sandy grassland; Species diversity

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1. Introduction

Although primary productivity is generally correlated with species richness (Schulze and Mooney, 1993), ecosystem functions and services are also likely to be related to the distribution of species among functional groups (Leps et al., 1982; MacGillivray and Grime, 1995; Wardle et al., 1997; Naeem, 1998). Plant functional type (PFT) is a group of species which share similar traits (morphological and physiological attributes), function in similar ways and show similar responses to environmental conditions. Using PFT, plant communities can be described in the way that it is simple enough to be understood and detailed enough to convey useful information about the structural and functional components (Robert and Dethier, 1994). PFT also provides a logical link between physiological and life-history strategies at the individual level and those ecological processes that operate at the ecosystem level (Walker, 1992; Chapin, 1993; Noble and Gitay, 1996; Paruelo and Lauenroth, 1996; Diaz and Cabido, 1997; Gitay and Noble, 1997). Therefore, PFT has been used as a means to overcome the limitations of species-based descriptions on ecosystem structure at regional to global scales (Smith and Shugart, 1996; Diaz Barradas et al., 1999; Pillar and Sosinski, 2003) and to summarize the enormous complexity of individual species and populations into a relatively small number of general recurrent patterns (Walker, 1992).

Literature on PFT is more concerned with the prediction of plant type distributions or the persistence of different plant species in different ecosystems, rather than the impact of functional-type diversity on ecosystem functioning (Walker et al., 1999). Recently, however, Tilman et al. (1997) found that functional diversity had greater impact on ecosystem processes than did species diversity in Cedar Creek grasslands; Hector et al. (1999) found that above-ground biomass decreased with decreasing functional groups in European grasslands. The knowledge relating to plant productivity and PFTs is limited, especially the changes in PFTs and plant productivity in the natural restoration process have been rarely reported (Forys and Allen, 2002; Godefroid et al., 2003).

Otindag Sandland is a temperate, semi-arid area in Inner Mongolia, China. It is a major resource for the local economic developments, and also a natural regulator of local and regional environments. Water shortage and infertility are the common features in this area due to low precipitation, sandy substrate, strong solar radiation and strong wind. This area is highly sensitive to environmental changes such as global climate change, natural fire and disturbances by human activities like over-grazing and the conversion of grassland into farmland. In Otindag Sandland and also in other semi-arid areas of China, it is a common phenomenon that human disturbances cause a reduction in grass cover, and an increase in bare soil and soil erosion, leading to land desertification (Wang and Guo, 1993; Sugiura et al., 1998; Ni, 2003).

In this paper, we study changes in PFTs during the early restoration stage of the degraded grasslands in Otindag Sandland. We investigate: (1) effects of life-span (annual versus perennial), photosynthetic pathway (C_3 versus C_4), reproductive mode (clonal versus non-clonal) and growth form (grass versus forb) on community traits, including density, number of species, coverage, relative importance (RI), and phytomass; (2) contribution of the PFT traits to PFT diversity; and (3) relationships between phytomass and diversity at both species and PFT levels.

2. Materials and methods

2.1. Study area

The study was conducted at Otindag Sandy Grassland Ecological Station (OSGES; 42°53'N, 116°01'E) of Institute of Botany, Chinese Academy of Sciences, which is located in the hinterland of Otindag Sandland in Zhenglanqi of Inner Mongolia, China. It is a semi-arid area with a mean annual temperature of 1.8 °C and a mean annual precipitation of 367.1 mm (unpublished data based on Annual Reports (1960–2000) of the Weather Bureau of Zhenglanqi). Due to serious desertification caused by human disturbances such as mining, herding and land reclamation, the major part of the present vegetation is dominated by sparse trees, shrubs and herbs such as *Ulmus pumila*, *Caragana microphylla*, *Hedysarum laeve* *Polygonum divaricatum*, *Potentilla acaulis*, *Cleistogenes squarrosa*, *Carex duriuscula*. The landscape is mainly composed of stable, semi-moving or moving sand dunes as well as lowland grasslands. The habitat is highly patchy on a broad range of spatial (and temporal) scales due to desertification and sand dune dynamics. The lowland grasslands are dominated by herbs such as *Leymus secalinus*, *Calamagrostis epigejos*, *Bromus inermis* and *Leymus chinensis*. In summer, the lowland areas were frequently grazed by livestock.

2.2. Methods

In October of 2000, an area of 2700 hm² was fenced against grazing in the study site and six 50 m × 50 m permanent plots were set up in the lowland meadows within the fenced area. In 2001, 2003 and 2004, six randomly located 1 m × 1 m quadrats in each plot were investigated between 26 and 28 August. In August 2002, we surveyed only four 1 m × 1 m quadrats in each plot. In each quadrat, we recorded the occurrence of each vascular species and measured its coverage, density and mean height. Above-ground plant parts were then harvested and sorted into species. They were oven-dried at 80 °C and weighed. In this paper, community primary productivity referred to the dry weight of above-ground plant parts (i.e. phytomass). Relative coverage (RC_{*i*}), relative height (RH_{*i*}) and relative density (RD_{*i*}) of species *i* were the proportion of the cover, mean height and density of species *i* to the sum of the plant cover, mean height and density of all species within a quadrat, respectively. Relative importance (RI_{*i*}) of species *i* was the average of RC_{*i*}, RH_{*i*} and RD_{*i*}. Based on the RI, Shannon–Wiener index of species diversity (*H*_{iv}) was determined using the following equation (Barbour et al., 1999):

$$H_{iv} = - \sum RI_i \ln(RI_i) \quad (i = 1, 2, 3, \dots, S),$$

where *S* is the number of species.

Based on the RI of each PFT, we also calculated Shannon–Wiener index of PFT diversity (*H*_{iPFT}) using the following equation:

$$H_{iPFT} = - \sum RI_{iPFT} \ln(RI_{iPFT}) \quad (i = 1, 2, 3, \dots, S),$$

where RI_{iPFT} is the sum of RI of all species in PFT *i*. Relative importance (RI_{iPFT}) of PFT *i* was the average of RC_{iPFT}, RH_{iPFT} and RD_{iPFT} of PFT *i*. RC_{iPFT}, RH_{iPFT} and RD_{iPFT} were the proportion of coverage, mean height and density of all species in PFT *i* to the sum

of coverage, height and density of all species (i.e. all PFTs) of community, respectively. Shrubs were not present in the study grasslands. All plant species were, therefore, classified into 16 PFTs based on life-span (annual vs. perennial), photosynthetic pathway (C_3 vs. C_4), reproductive mode (clonal vs. non-clonal) and growth form (grass vs. forb, Tables 1 and 2). Information on photosynthetic pathway was obtained from previous studies (Yin and Li, 1997; Yin and Wang, 1997; Tang, 1999; Wang, 2002; Niu et al., 2003; Liu et al., 2004). Information on life-span, reproductive mode and growth form were extracted from Flora of Inner Mongolia (The Editorial Committee of Flora of Inner Mongolian, 1989–1998). During the 4-year investigations, only two *Ulmus pumila* seedlings of 0.5 cm tall were observed in the plots and they were thus included in the PFT3 (Table 2).

A four-way ANOVA with repeated measures was used to examine the effects of life-span, photosynthetic pathway, reproductive mode, growth form and their interactions on density, number of species, coverage, phytomass and the RI of PFTs. To examine the contribution of the RI of different PFTs (RI_{PFT}) to PFT diversity (H_{PFT}), a stepwise regression analysis was carried out for PFT diversity against the RI of PFTs. The regression analysis (curve estimation) was also performed to investigate the correlations of primary productivity with species diversity (H_{iv}) and with PFT diversity (H_{PFT}), respectively. SPSS10.0 software package was used for all analyses.

3. Results

Life-span, photosynthetic pathway, reproductive mode, growth form and their two-factor interactions had significant effects on density, number of species, coverage, RI and phytomass of PFTs (Table 3). Measuring date also significantly affected density, number of species, coverage, RI and phytomass of PFTs (Table 3), namely, there were significant changes in the structural features including the density, the number of species, the coverage

Table 1

Plant functional types (PFTs) based on life span, photosynthetic pathway, reproductive mode, and growth form in the Otindag Sandland and their codes

PFTs	Code
Annual C_3 non-clonal forb	PFT1
Annual C_3 clonal forb	PFT2
Perennial C_3 non-clonal forb	PFT3
Perennial C_3 clonal forb	PFT4
Annual C_3 non-clonal grass	PFT5
Annual C_3 clonal grass	PFT6
Perennial C_3 non-clonal grass	PFT7
Perennial C_3 clonal grass	PFT8
Annual C_4 non-clonal forb	PFT9
Annual C_4 clonal forb	PFT10
Perennial C_4 non-clonal forb	PFT11
Perennial C_4 clonal forb	PFT12
Annual C_4 non-clonal grass	PFT13
Annual C_4 clonal grass	PFT14
Perennial C_4 non-clonal grass	PFT15
Perennial C_4 clonal grass	PFT16

Table 2
Plant species, plant family and plant functional types (PFTs) based on the six plots in the Otindag Sandland

No.	Species	Family	Plant functional types (PFTs)
1	<i>Chenopodium glaucun</i> L.	Chenopodiaceae	PFT1
2	<i>Chenopodium aristatum</i> L.	Chenopodiaceae	PFT1
3	<i>Salsola collina</i> Pall.	Chenopodiaceae	PFT9
4	<i>Corispermum stauntonii</i> Mop.	Chenopodiaceae	PFT1
5	<i>Chenopodium acuminatum</i> Willd.	Chenopodiaceae	PFT1
6	<i>Artemisia scoparia</i> Waldst. et Kit.	Compositae	PFT3
7	<i>Saussurea amara</i> (L.) DC.	Compositae	PFT3
8	<i>Taraxacum dissectum</i> (Ledeb.) Ledeb.	Compositae	PFT4
9	<i>Artemisia intramongolica</i> H.C.FU	Compositae	PFT4
10	<i>Artemisia rubripes</i> Nakai	Compositae	PFT4
11	<i>Artemisia mongolica</i> (Fisch. ex Bess.) Nakai	Compositae	PFT3
12	<i>Artemisia frigida</i> Willd.	Compositae	PFT4
13	<i>Heteropappus altaius</i> (Willd.) Novopokr.	Compositae	PFT3
14	<i>Artemisia sieversiana</i> Ehrhart ex Willd.	Compositae	PFT9
15	<i>Carex duriuscula</i> C.A. Mey.	Cyperaceae	PFT8
16	<i>Bromus inermis</i> Leyss.	Gramineae	PFT8
17	<i>Puccinellia</i> Parl. <i>tenuiflora</i> (Griseb.) Scribn.	Gramineae	PFT8
18	<i>Setaria viridis</i> (L.)Beauv.	Gramineae	PFT13
19	<i>Cleistogenes squarrosa</i> (Trin.) Keng	Gramineae	PFT16
20	<i>Agropyron cristatum</i> (L.) Gaertn.	Gramineae	PFT8
21	<i>Digitaria ischaemum</i> (Schreb.) Schreb.ex Muhl.	Gramineae	PFT13
22	<i>Leymus chinensis</i> (Trin.) Tzvel.	Gramineae	PFT8
23	<i>Stipa grandis</i> P.Smirn.	Gramineae	PFT8
24	<i>Poa annua</i> L.	Gramineae	PFT5
25	<i>Koeleria crictata</i> (L.)Pers.	Gramineae	PFT8
26	<i>Leymus secalinus</i> (Georgi)Tzvel.	Gramineae	PFT8
27	<i>Calamagrostics epigejos</i> (L.) Roth	Gramineae	PFT8
28	<i>Agrostis sibirica</i> V.Petr.	Gramineae	PFT8
29	<i>Potentilla tanacetifolia</i> Willd. ex Schlecht	Rosaceae	PFT4
30	<i>Potentilla bifurca</i> L.	Rosaceae	PFT4
31	<i>Potentilla ansetina</i> L.	Rosaceae	PFT4
32	<i>Potentilla supina</i> L.	Rosaceae	PFT4
33	<i>Silene repens</i> Patr.	Caryophyllaceae	PFT4
34	<i>Medicago falcata</i> L.	Leguminosae	PFT4
35	<i>Oxytropis gracillima</i> Bunge	Leguminosae	PFT4
36	<i>Iris lactea</i> Pall. var. <i>chinensis</i>	Iridaceae	PFT4
37	<i>Ulmus pumila</i> L.	Ulmaceae	PFT3
38	<i>Halerpestes sarmentosa</i> (Adams) Kom.	Ranunculaceae	PFT12
39	<i>Polygonum angustifolium</i> Pall.	Polygonaceae	PFT1
40	<i>Polygonum sibiricum</i> Laxm.	Polygonaceae	PFT1
41	<i>Polygonum aviculare</i> L.	Polygonaceae	PFT1
42	<i>Lepidium apetalum</i> Willd.	Cruciferae	PFT1
43	<i>Allium tenuissimum</i> L.	Liliaceae	PFT4
44	<i>Euphorbia fischeriana</i> Steud.	Euphorbiaceae	PFT1

PFTs are coded as in Table 1.

and the phytomass of different PFTs on a temporal scale (Fig. 1). Density, coverage, phytomass, number of species, and RI in the fourth year are the greatest in perennial, clonal C₃ grasses (PFT8) among the 16 PFTs (Fig. 1).

Table 3

F-value of repeat measurement four-way ANOVA for the effects of growth form (*G*), reproductive mode (*R*), photosynthetic pathway (*P*), life span (*L*) and repeated measure time (*T*) and their interactions on PFTs characters such as density, number of species, coverage (%), phytomass (g m^{-2}) and relative importance

Effects	Density	Number of species	Coverage (%)	Phytomass (g m^{-2})	Relative
Growth form (<i>G</i>)	52.229***	129.555***	176.729***	157.127***	222.93***
Reproductive mode (<i>R</i>)	40.936***	20.729***	129.703***	144.557***	128.655***
Photosynthetic pathway (<i>P</i>)	108.65***	357.665***	417.19***	325.251***	526.993***
Life span (<i>L</i>)	59.4**	201.186***	317.843***	283.091***	408.052***
Repeated measure time (<i>T</i>)	6.636**	7.29***	4.855**	7.646***	0.192 ^{ns}
<i>G</i> × <i>R</i>	15.338***	0.376 ^{ns}	21.437***	50.337***	28.512***
<i>G</i> × <i>P</i>	72.268***	279.663***	217.626***	194.465***	304.991***
<i>R</i> × <i>P</i>	43.088***	66.303***	135.339***	160.816***	164.473***
<i>G</i> × <i>R</i> × <i>P</i>	13.636***	7.85**	16.879***	39.75***	14.439***
<i>G</i> × <i>L</i>	33.462***	143.883***	147.746***	162.197***	216.324***
<i>R</i> × <i>L</i>	86.128***	165.655***	202.51***	192.952***	242.759***
<i>G</i> × <i>R</i> × <i>L</i>	41.076***	3.71*	44.964***	56.463***	42.98***
<i>P</i> × <i>L</i>	81.765***	498.482***	397.853***	345.641***	582.185***
<i>G</i> × <i>P</i> × <i>L</i>	20.345***	44.279***	114.424***	128.27***	148.226***
<i>R</i> × <i>P</i> × <i>L</i>	83.074***	86.135***	195.602***	175.101***	198.772***
<i>G</i> × <i>R</i> × <i>P</i> × <i>L</i>	43.994***	16.934***	52.23***	68.96***	65.541***
<i>G</i> × <i>T</i>	2.756 ^{ns}	10.274***	8.621***	11.188***	9.152***
<i>R</i> × <i>T</i>	0.552 ^{ns}	2.696*	3.627*	9.097***	0.43 ^{ns}
<i>P</i> × <i>T</i>	4.492*	11.013***	4.134**	8.627***	2.154 ^{ns}
<i>L</i> × <i>T</i>	0.366 ^{ns}	9.87***	6.47***	11.027***	3.546*
<i>G</i> × <i>R</i> × <i>T</i>	0.029 ^{ns}	11.26***	4.119**	11.249***	2.608 ^{ns}
<i>G</i> × <i>P</i> × <i>T</i>	5.507**	7.875***	9.095***	10.402***	6.289***
<i>R</i> × <i>P</i> × <i>T</i>	0.465 ^{ns}	3.486*	4.233**	10.678***	0.211 ^{ns}
<i>G</i> × <i>R</i> × <i>P</i> × <i>T</i>	0.774 ^{ns}	2.807*	1.559 ^{ns}	8.487***	3.287*
<i>G</i> × <i>L</i> × <i>T</i>	1.276 ^{ns}	5.186**	11.199***	12.688***	7.573***
<i>R</i> × <i>L</i> × <i>T</i>	5.138*	0.714 ^{ns}	2.975*	8.253***	0.428 ^{ns}
<i>G</i> × <i>R</i> × <i>L</i> × <i>T</i>	1.495 ^{ns}	0.522 ^{ns}	0.487 ^{ns}	6.439***	3.058*
<i>P</i> × <i>L</i> × <i>T</i>	1.141 ^{ns}	3.375*	6.657***	9.98***	0.92 ^{ns}
<i>G</i> × <i>P</i> × <i>L</i> × <i>T</i>	0.016 ^{ns}	9.578***	11.464***	13.587***	11.34***
<i>R</i> × <i>P</i> × <i>L</i> × <i>T</i>	3.309*	1.275 ^{ns}	2.971*	6.999***	1.067 ^{ns}
<i>G</i> × <i>R</i> × <i>P</i> × <i>L</i> × <i>T</i>	2.552 ^{ns}	4.169**	2.214 ^{ns}	8.791***	1.49 ^{ns}

Significant levels: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; and ns, $p > 0.05$.

Primary productivity was not correlated with species diversity in any year (Fig. 2A–D), but was significantly positively correlated with PFT diversity in 2001 and 2004 (Fig. 2E and H) and significantly negatively correlated with PFT diversity in 2002 and 2003 (Fig. 2F and G).

4. Discussion

In Otindag Sandland, productivity was significantly correlated with biodiversity at PFT level, but not at species level (Fig. 2). This finding supports the notion that PFT diversity is a better predictor of ecosystem functioning than species diversity (Tilman et al., 1997).

The absence of a significant correlation between plant species diversity and productivity was also found in grassland ecosystems in Tanzania and Kenya (McNaughton, 1983).

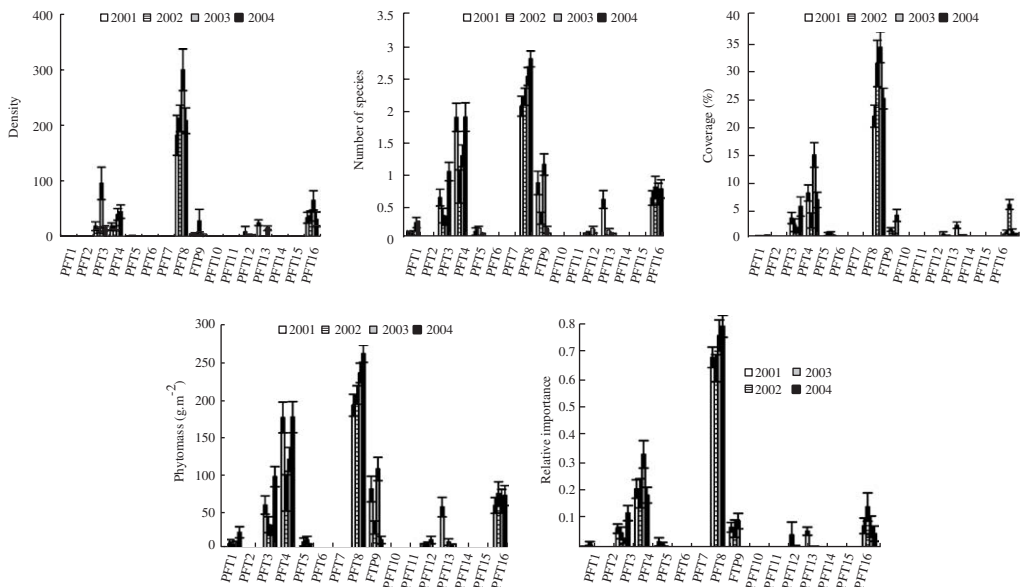


Fig. 1. Effects of life-span, photosynthetic pathway, reproductive mode and growth form on the community traits during the four consecutive years (2001–2004). Mean \pm 1 SE is indicated. PFTs are coded as in Table 1.

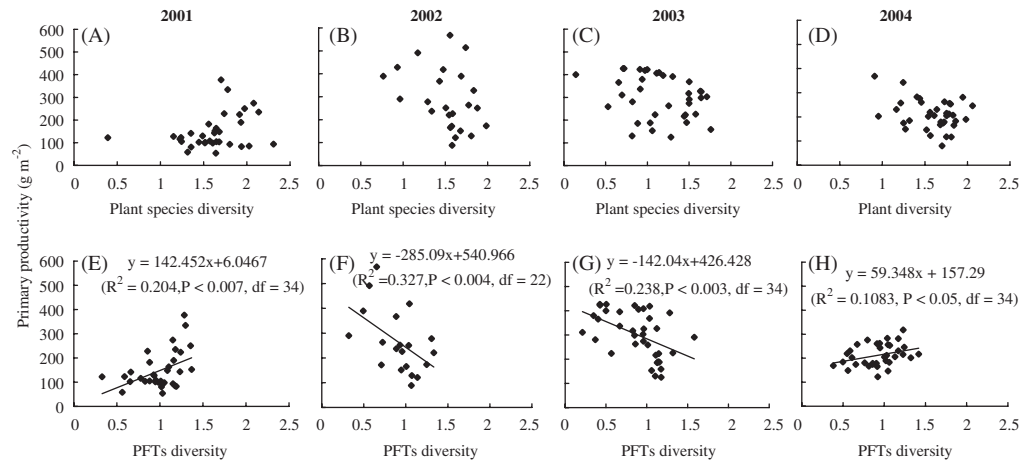


Fig. 2. Relationships between primary productivity and biodiversity at both species (A–D) and PFT levels (E–H) in Otindag Sandland in China during the four consecutive years (2001–2004).

Recent research proposed that the lack of a relationship between the diversity and productivity depends on the scale of observation (Zobel and Liira, 1997; Mackey and Currie, 2001; Mittelbach et al., 2001). In our study, it is likely that the relationship between the diversity and productivity varied with the stages of succession.

A positive relationship between plant functional diversity and ecosystem functioning has been demonstrated in many natural and artificially assembled communities (Hooper and Vitousek, 1997, 1998; Tilman et al., 1997). In the present study, however, the relationships between PFT diversity and primary productivity varied markedly with year (Fig. 2): PFT diversity had a positive effect on primary productivity in 2001 and 2004, but a negative effect in 2002 and 2003. These findings suggest that primary productivity in Otindag grasslands is likely correlated also with factors other than biodiversity (Auclair and Goff, 1971). In the first year (2001) of the restoration, there were enough space and resources for plants to develop because grazing was stopped. The communities with more PFTs showed stronger production capability than those with less PFTs. Human-influenced reductions in small-scale plant diversity, in this case evenness, will lead to indirect reductions in total primary productivity. In the converse case, when the disturbance by human or grazing vanished, it seems likely that productivity increases even without the number of species increasing (Wilsey and Potvin, 2000).

It is well known that density-dependence is likely to be important in natural systems. Population density may be a main factor that affects productivity of the community (Hassel and Varley, 1969). Productivity of the community probably to a varying extent depends on the nature and the relative strengths of species' intra- and interspecific interactions (Micael and Bjorn, 2003). We propose that density-dependence may depend on both intra- and inter-PFT interactions. PFT-rich communities with higher inter-PFT interference may slow down ecological processes (for instance the diffused process of the species) because encounter rates with inter-PFTs are higher as compared to communities with PFT-poor. Within PFTs, the species have a similar ability to persist, compete and regenerate under different environmental constraints (Walker, 1992; Paruelo and Lauenroth, 1996; Diaz and Cabido, 1997; Gitay and Noble, 1997). Higher densities and hence higher levels of interference induce the severe competition. Thus, in 2002 and 2003 resource competition between inter- and intra-PFT may be stronger in PFT-rich communities than that in PFT-poor ones. In 2004, because of the massive accumulation of litter many above-ground plant parts produced in 2003 were not decomposed, the growth of the plant were affected, the productivity of the communities were decreased than those of the past 2 years and the positive relationship was showed.

Moreover, Aarssen (1997) proposes that interspecific differences in primary productivity, combined with the greater probability of having a primary productivity to increase with a high diversity plot, might cause primary productivity to increase with diversity. In grasslands, strong inter-PFTs differences in attributes exist between forbs and grasses, which may significantly affect the productivity variables under studies. In our study, we found that the greatest contribution to the community characters was the groups of perennial, C₃ clonal grass (PFT8; Fig. 1). The density, the coverage, the RI and the primary productivity of PFT8 were bigger than those of other PFTs. This result agrees with the findings of a previous study, in which it was found that the number of C₃ species was the largest in the temperate grasslands in south-east Inner Mongolia as compared to that in the other areas of China (Ni, 2003). Different PFTs may represent different strategies of adaptation to the local habitats, and therefore, play different roles in communities (Song and Dong, 2002). In general, PFT8 seems to adapt to the environment of Otindag Sandland much better and played a more important role than other PFTs. Along with the restoration process, the PFT8 become dominant PFTs, so that the communities with PFT8 had greater phytomass than those without PFT8.

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