Biodiversity *versus* stability: the biological effect of plant functional traits on ecosystem functioning in grasslands dominated by *Leymus chinensis*

Na ZHAO[1, 2], Xinqing SHAO[2], Kun WANG[2,*]

[1] Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810008, P.R. China

[2] Department of Grassland Science, China Agricultural University, Beijing 100193, P.R. China
  * e-mail: wangkun@cau.edu.cn (*corresponding author*)

ARTICLE INFO

ABSTRACT

Although diversity-ecosystem theory predicts that ecosystem functioning is strongly determined by species number, species traits play an important role in regulating ecosystem-level dynamics. We analyze responses of species attributes to diversity level and resource availability, and explore their consequences for ecosystem functioning and ultimately assess the contributions of five traits (vegetative plant height, clonal growth, root depth, cespitose habit and seed mass) to ecosystem functioning defined by spatial stability of community biomass. We found that functional traits disproportionately affected spatial stability. Relationships between species functional traits and spatial stability of community biomass indicated that diversity of vegetative plant height facilitated stability of a nitrogen fertilized undisturbed natural community (NAT), and that of a phosphorus fertilized forb, legume and bunchgrass community (FLB). The clonal growth form was also identified as a stabilizing trigger for a unfertilized undisturbed natural community (NAT), whereas diversity in root depth, cespitose habit and seed mass were related to destabilization of a nitrogen fertilized rhizomatous grass community (RRR). Studies quantifying interactions among plant traits, community structure and ecological functioning will contribute much more to understanding of the effects of the ecological behavior of specific traits on the ecosystem functioning.

INTRODUCTION

The role of biological characteristics of plants in the vegetation changes (Hobbs 1997) has become a topic of growing interest. Suites of morphological and physiological characteristics at species level have been frequently used in models of vegetation change (Kleyer 1999) and in the definition of plant functional groups (Lavorel *et al.* 1999). However, in earlier studies, some research groups advocated protocols involving the exploration of both trait-community and trait-environment associations (Leishman and Westoby 1992). For example plant growth would be stimulated by the presence of deciduous habit (Hunt *et al.* 1993) and root architecture and reserve organs would strongly determine species survival and species existence, especially in severe drought and frosty environments (Schulze 1982). The capacity of plants to cope with changing conditions was associated with high dispersal ability and rapid establishment and maturation (Grime *et al.* 1988). Seed characteristics (shape and mass) were also predominant indicators for persistence of seeds in soil banks (Thompson *et al.* 1993).

Several studies have demonstrated the significant role of plant functional attributes in identifying the dominant ecosystem processes (Kelly 1996, Diaz and Cabido 2001,

Ernest and Brown 2001). However, the main focus of earlier experiments was to consider the relationship between species traits and community net primary productivity. As shown by Hector *et al.* (1999), legumes have a marked effect and their occurrence or omission could contribute a large variation of productivity of approximately 360 g m^{-2} on average. Additionally, Thompson *et al.* (2005) found that canopy height, related to competitive dominance (Hodgson *et al.* 1999), appeared to be the best predictor of community biomass. Schumacher and Roscher (2009) also found that there were significantly positive relationships between such functional traits as life history, leaf area, vegetative height of species and aboveground biomass. Although there has been considerable progress with respect to trait-productivity relationship, only a small proportion of the studies have explicitly addressed the effect of plant functional attributes on ecosystem stability (Weigelt *et al.* 2008). Ecosystem stability indicates ecological dynamic characteristics and also the self-adjusting ability of ecosystem and so need to be urgent to study.

Land management is a major factor determining species dynamics of grassland vegetation (Duru *et al.* 2005). Numerous studies have reported responses of plant functional traits to land use practices. Earlier ecologists also found that the fertility level determined the pattern of biomass allocation (Campbell and Grime 1989) and the response of species to fertilizer was closely associated with their plasticity in above and below-ground morphology. In the case of nitrogen fertilizer, deficiency of nitrogen tended to favor the development of branched root systems and promoted the length of tertiary roots (Berendse and Elberse 1990). In brief, traits at the species level tended to be used as direct predictions of environmental conditions (Olff *et al.* 1994) because of obvious differences in some specific attributes along environmental gradients (Diaz and Cabido 1997). The contribution of each species to the community varied with environmental changes because of idiosyncratic trait responses of individual species, and thus resulted in corresponding shifts among population dynamics.

The nature of community response to fertilization was realized through change of plant functional traits. Plants formed different ecological strategies under fertilization gradients through the changes of species functional traits, which could objectively express species fitness. Meanwhile fertilization could produce strong selection pressure on plant traits, and caused further species behavioral change (Miao and Bazzaz 1990). Plant functional traits are the basis of the studies of population and community structure and are also a bridge among population, community and ecosystem. Species biological properties could better reflect plant adaptability to external environments (Peco *et al.* 2005). This is conducive to understanding the decisive mechanism of ecosystem functioning, and moreover analyzing community particular response pattern to disturbance (Lavorel and Garnier 2002). On the basis of significance of the relationship among species attributes, population dynamics and community structure, the predictions of particular traits to ecosystem functioning in various environments should be given more attentions (McIntyre *et al.* 1995).

Most of biodiversity experiments have been based on synthesized communities of a gradient of plant species richness, which were established by sowing of seed, and mainly excluded environmental heterogeneity (Thompson *et al.* 2005). Much of the experimental evidence has continued to document striking discrepancy between artificial and natural assemblages. Thompson *et al.* (2005) showed that immature synthesized communities were of limited use in exploring the relationship between biodiversity and ecosystem functioning. Additionally, community properties are subject to wide variation because different species, owing to functional trait differentiation, are expected to play different roles in terms of matter and energy processes in ecosystems (Huston 1997). In view of the enormous complexity and instability of individual species, plant functional types were considered to bridge the gap among plant ecological behavior, species existence and ecosystem processes (Diaz and Cabido 1997).

With these considerations we carried out a biodiversity experiment to investigate the changes of species attributes with both varying diversity levels and fertilization gradients,

and to explore the possible consequences for ecosystem functioning in some communities modified by species removal. The natural community, *Leymus chinensis* (Trin.) Tzvel. dominant grassland, was modified by removal of different plant functional types rather than the removal of plant species. Through response patterns of species attributes, an objective of the present study was to better understand the role of the specific trait expression in maintaining of ecosystem functioning and to identify its contribution to the interference resistance and recovery mechanism. Further this could offer information about community ecological adaptability in an extreme environment, and would ultimately promote the generalization of the ecological pattern.

MATERIALS AND METHODS

Study site

The study was carried out at the National Key Grassland Experiment Station located in the typical agro-pastoral transition region of Hebei Province, northern China (41°46′N, 115°40′E, 1,380 m above sea level). Dry and cold winter and rainfall heavily concentrated to the warm season are characteristic to the whole region, with an average annual temperature of 1°C. Mean annual rainfall amounts to about 350 mm and is highly seasonal (Huang *et al.* 2007). Annual precipitation was 331 mm in 2008, 382 mm in 2009 and 376 mm in 2010. A potential growing season is from Late-April to Mid-October. This mature natural community has been excluded from grazing for more than 10 years. The biomass and species richness are therefore likely to be at or near equilibrium. The study began in May 2008 and continued to May 2011.

The soil of the site is classified as Cambids (US soil taxonomy classification system), young soil prone to desertification. No fertilizer has been applied to the area before the study commenced. The plant community was predominantly dominated by the rhizomatous grass *Leymus chinensis* (Trin.) Tzvel. The other dominant species and their allocation to functional groups are presented in Appendix 1, together with the proportion of the

peak biomass of each functional group forming the natural community.

Experimental design and treatments

The experimental layout had three large replicate blocks, each containing three functional group mixtures. These three functional group mixtures were randomly assigned within each block. Each functional group mixture had an area of 43.5 square meters (3 m × 14.5 m) and represented a particular diversity-level community of given functional group combination. The functional group mixtures were: i) An undisturbed natural community containing forbs, legume, bunchgrass and rhizomatous grasses functional groups (NAT); ii) Forbs, legume and bunchgrass functional groups (FLB); iii) Rhizomatous grass functional group alone (RRR). To establish these functional group mixtures, plants that did not belong to the functional group community were selectively trimmed aboveground and their roots were dug out 5 cm deep belowground. This removal was repeated approximately half-monthly from early May to early October in 2008 and 2009. Further, five fertilizer plots, each 3 m × 2.5 m in area, were assigned to each functional group mixture. The fertilizer treatments were 6 g N for N_{Low}, 35 g N for N_{High}, 0.4 g P for P_{Low}, 6 g P for P_{High} m^{-2} year^{-1} and no fertilizer for CK. All these plots were separated by 0.5 m wide aisles to reduce potential edge effects. Fertilizer was applied in early May in experimental years by application of $CO(NH_2)_2$ for nitrogen and $Ca(H_2PO_4)_2$ for phosphorus treatments. With three replications, the experimental layout of three diversity levels and five fertilizer treatments had a total of 45 plots.

Data collection

Previous study has shown that one-time static measurement of particular functional traits for a mature plant is unsatisfactory (Dyer *et al.* 2001). Therefore, species relevant traits were observed every 10 days from May to October in 2010 (Appendix 2). We mainly studied morphological, regenerative and

reproductive traits, as previous studies have shown that the correlations between these traits are weak (Grime *et al.* 1988, Leishman and Westoby 1992). Moreover, they have some functional associations with vegetation dynamics (Hobbs 1997, Weiher *et al.* 1998, Lavorel *et al.* 1999).

In order to truly reflect intra-species variation in each combination of diversity and fertilizer treatment, the traits were observed for each 3 m × 2.5 m plot because there were different responses of traits to micro-environment (Chapin 1991, Dyer *et al.* 2001). The variation in intra-species traits was primarily due to plasticity of plant species (Huston 1997). Species responses to the conditions were more sensitively expressed by the morphological changes. In choosing key traits, therefore, we selected cespitose habit, clonal growth, vegetative plant height, root depth, and mean seed mass (Appendix 2). Trait variables were expressed as either nominal or ordinal because of their different measurement scales and standards. Before analysis, all traits were square-root transformed to produce more symmetric distribution and simultaneously standardized to have a mean of 0 and variance of 1.

In each of the 45 plots, we harvested all above-ground vegetation from four 0.5 m × 0.5 m quadrats from 15 to 17 August 2010. All harvested vegetation was sorted into species, and oven-dried and weighed (80°C, 48 h). Additionally, two cuboids sized 0.5 m × 0.5 m × 1 m were dug in each plot in late August 2010. We classified sampled plants into aboveground and belowground parts and their relevant functional attributes were recorded (Appendix 2).

Data analyses

The coefficient of variation (*CV*) is used as an opposite assessment of spatial stability (McCann 2000).

$$CV = \delta/\mu$$

So the spatial stability (*SS*) was calculated as follows:

$$SS = \mu/\delta$$

Where *SS* is the spatial stability of community biomass, μ is the mean of biomass

and δ is the standard deviation of biomass (Lehman and Tilman 2000).

Additionally, specific functional trait *m* diversity was calculated as:

$$D_m = \sum_{i=1}^{s} \sum_{j=1}^{s} (X_{im} - X_{jm})^2$$

Where D_m is specific functional trait *m* diversity in a given community, and *s* is the total numbers of species in a community, *i* and *j* are discretionary two species in a community, and *m* refers to certain functional trait at the species level between species *i* and *j*. X_{im} and X_{jm} are the trait values of specific traits *m* for species *i* and *j* in a community.

The biomass response of different functional communities to the fertilizer treatment was analyzed by univariate analysis of variance. In order to test the predictive power of different functional traits to spatial stability, the relationship between plant traits and the CV of community biomass was analyzed by regression of curve estimation to determine the respective contribution of each trait. Standardized regression coefficient (ß′) is used to explain the magnitude of contribution of trait *m* to the spatial stability. Data was analyzed using SPSS 20.0.

RESULTS

Particular trait variables

Diversity in plant vegetative height was found to increase the spatial stability of the N fertilized NAT community and the P fertilized FLB community. Diversity in clonal growth was also found to increase the spatial stability of the unfertilized NAT community. However, diversity in root depth, cespitose habit, and seed mass were instability triggers for the N fertilized RRR community (Table 1).

Community biomass

As shown by univariate analysis of variance, the NAT community biomass averaged for all the fertilizer treatments was significantly higher and RRR community was secondly significantly higher than the FLB community. The overall fertilizer effect was significant and the

Table 1. Regression relationships of curve estimation between plant traits and the coefficient of variation (CV) of community biomass for each community. Codes see the text and Fig. 1. Values for standardized regression coefficient (ß′) and the probability of the significance (*P*) are shown. Bold font means statistical results reach significant level.

Trait	Community	Fertilizer treatments		
		CK	N	P
Plant vegetative height	NAT	ß′= - 0.031 **P=0.023**	**ß′= - 0.003 P=0.049**	ß′=0.054 P=0.261
	FLB	ß′=0.036 P=0.230	**ß′= - 0.009 P=0.001**	ß′=-0.336 P=0.686
	RRR	ß′=0.063 P=0.553	ß′=0.082 P=0.164	ß′=-0.036 P=0.553
Clonal growth	NAT	ß′= - 0.849 P=0.132	ß′= - 0.013 P=0.659	ß′=0.001 P=0.401
	FLB	ß′= - 0.003 P=0.658	ß′= - 0.536 P=0.197	ß′=0.006 P=0.606
	RRR	ß′=0.005 P=0.780	ß′=0.267 P=0.363	ß′= - 0.007 P=0.131
Root depth	NAT	ß′= - 0.006 P=0.054	ß′= - 0.042 P=0.775	ß′=0.001 P=0.513
	FLB	ß′=0.677 P=0.191	ß′= - 0.518 P=0.414	ß′= - 3.496 P=0.131
	RRR	ß′=0.008 P= 0.667	**ß′=0.158 P= 0.000**	ß′=0.005 P= 0.380
Cespitose habit	NAT	ß′=0.006 P=0.558	ß′=0.001 P=0.838	ß′=0.001 P=0.475
	FLB	ß′= - 0.006 P=0.627	ß′=-0.445 P=0.297	ß′=0.124 P=0.356
	RRR	-	**ß′=0.027 P=0.020**	-
Seed weight	NAT	ß′= - 1.046 P=0.200	ß′= - 0.006 P=0.432	ß′=0.001 P=0.562
	FLB	ß′=0.078 P=0.861	ß′= - 0.407 P=0.389	ß′= - 0.143 P=0.800
	RRR	ß′=0.012 P=0.368	**ß′=0.063 P=0.020**	ß′= - 0.004 P=0.549

"-" indicated that the independent variable diversity value was equal to 0, unable to regression analysis.

interaction between diversity and fertilization also indicated that there were different community biomass responses to fertilizer applications (Table 2). This response is clearly shown in Fig. 1. Application of P clearly increased the biomass of the FLB community, but decreased the biomass of the NAT community. Biomass increases occurred for the N fertilized NAT and RRR communities.

DISCUSSION AND CONCLUSIONS

There is a growing consensus that the effect of diversity on ecosystem processes was largely due to the functional traits of individual species (Grime 1997, Diaz and Cabido 2001, Naeem and Wright 2003, Mouillot *et al.* 2005). Our results are consistent with this consensus. For instance, diversity in vegetative plant height for both the P fertilized FLB community and the N fertilized NAT community enhanced stability. A combination of large-statured and small-statured vegetative plants might better exploit light niche in the plant canopy (Rüger *et al.* 2009). Finke and Snyder (2008) stated that differentiation in resource-use pattern was expected to intensify resource extraction. Development of a vegetative plant canopy that involved plants of differing stature could enhance the
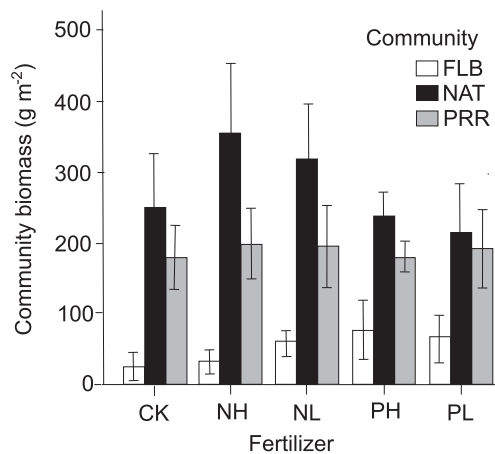
Fig. 1. Relationship between the biomass (mean ± SE) of different communities and fertilizer treatments. Functional group mixtures: NAT (undisturbed natural community containing forbs, legume, bunchgrass and rhizomatous grasses functional groups), FLB (Forbs, legume and bunchgrass functional groups), RRR (only the rhizomatous grass functional group). Fertilizer treatments: CK: no fertilizer applied; NH: $(CO(NH_2)_2)$ applied at the rate of 35 g N m^{-2} year^{-1}; NL: $(CO(NH_2)_2)$ applied at the rate of 6 g N m^{-2} year^{-1}; PH: $(Ca(H_2PO_4)_2)$ applied at the rate of 6 g P m^{-2} year^{-1}; PL: $(Ca(H_2PO_4)_2)$ applied at the rate of 0.4 g P m^{-2} year^{-1}.

photosynthetic fixation of C. The transfer of photosynthetic C to roots might promote the capture and exploitation of phosphate patches, a conversion process that was particularly demanding of photosynthetic C supply (Cui and Caldwell 1997). This facilitative action might have allowed the P fertilized FLB community to more comprehensively occupy above and below-ground niches to enhance biomass (Fig. 1; Table 1), and thus enhance stability.

Soil nitrogen supply markedly increased leaf nitrogen content and leaf area (Harpole *et al.* 2007, Gastine *et al.* 2003), allowing the

interception of more light for photosynthesis. Thus differences in height of vegetative plants and their leaf properties could have jointly enhanced photosynthetic C fixation when the NAT community was fertilized with nitrogen, leading to increased biomass production (Fig. 1; Table 1) and thus possibly increased stability. According to Lehman and Tilman (2000), increased stability can be achieved by either an increase in mean productivity or a decrease in variation of productivity.

Diversity in clonal growth was shown to enhance the stability of the unfertilized NAT community (Table 1). Clonal plants were able to distribute nutrients through all the ramets of a clone (Stuefer *et al.* 1996) and thus buffered local environmental heterogeneity by clonal division and physiological integration to ultimately stabilize a community. Non-clonal plant species might also quickly establish seedlings in small patches to increase their populations and decrease biomass variability, although seedling recruitment was supposed to be a rare but general event that influenced both species diversity and rejuvenation of populations (Thompson *et al.* 1996, Eriksson and Eriksson 1997). Our study indicated that diversity in clonal growth better stabilized the unfertilized NAT community because the unfertilized soil tended to have greater heterogeneity. The stability of the N fertilized RRR community was reduced by greater variation of cespitose habit, seed mass and root depth (Table 1). Cespitose species had larger individual plant size than other species and this habit was likely to generate high variability of community biomass by either largely occupying or being absent from sample quadrats. This agreed with observations by Weigelt *et al.* (2008) who indicated that large individual plant size tended to cause high variability of community biomass because of presence or absence in a given quadrat. Although the analysis of clonal structure demonstrated that

Table 2. Univariate analysis of variance of the biomass responses of different communities to fertilizer treatments. Statistically significant effect is given in bold.

Source of variation	Sum of squares	Df	Mean square	F	P
Fertilizer	27667.543	4	6916.886	2.626	**0.041**
Community	755365.474	2	377682.737	143.391	**0.000**
Fertilization ×Community	70270.977	8	8783.872	3.335	**0.003**

the spatial distribution pattern of *Leymus chinensis* clones was one of the 'guerilla' architecture, the increasing density and volume of tillering plants from the same tillering node could cause ramets to cluster behavior, and thus to increase light competition. Soil nitrogen improved the asexual reproduction ability of *Leymus chinensis* (Li 2014) and further aggravated light competition. Hence, cespitose habit acted to reduce the stability of the N fertilized rhizomatous grass community (RRR) because of competitive exclusion.

Ecologists have generally believed that seedlings from large-seeded species had higher probability of survival than those from small-seeded species in both natural conditions (Dalling and Hubbell 2002, Moles and Westoby 2004) and synthetic experimental conditions (Leishman and Westoby 1994, Turnbull *et al.* 1999). The RRR community had high tiller density. When N was applied to this community, a further increase of this density would reduce gaps for seedling establishment. Additionally, stressful conditions were further complicated by both an increase in shade as a result of leaf area index increase and a decrease in soil moisture, both resulting from application of N (Zavaleta *et al.* 2003, Harpole *et al.* 2007). Therefore, species with heavier seeds, rather than various seeds, were better colonizers of gaps under such intensively competitive situations and thus stabilized communities by a regeneration niche mechanism.

The evidence that diversity in root depth was a biomass-destabilizing driver for the N fertilized rhizomatous grass community (RRR), was not consistent with the idea that niche partitioning raised resource exploitation (Finke and Snyder 2008) and promoted species persistence in grasslands (Fargione and Tilman 2005). However, the negative pattern of spatial stability in response to different root depths was in this case possibly driven by the morphological properties of rhizomatous grass. Rhizomatous grass grew quickly after disturbance caused by the extraction of forbs, legumes and bunchgrasses and formed a continuously horizontal network of rhizomes when nutrient availability, particularly of N fertilizer, was increased (Harpole *et al.* 2007). The root web of thick and interweaved below-ground rhizomes had a stronger stabilizing effect than variation of root depth. So a role of variation of root depth in community stability might have been overwhelmed in the N fertilized rhizomatous grass community (RRR).

In summary, study about the adaptability of plant functional traits to fertilization and their ecological countermeasures to simulated diversity reduction is a breakthrough from describing surface to internal biological mechanisms in ecological study. Species trait assembly pattern could explain the process of species niche differentiation and the development of community building under different disturbance gradients (Diaz *et al.* 2007, de Bello *et al.* 2009). Such understanding would help predict vegetation distribution to future land use and further open up new area of exploration of community response patterns (Westoby and Wright 2006, Castro *et al.* 2010).

REFERENCES

Berendse F., Elberse W.T. 1990 – Competition and nutrient losses from the plant (In: Causes and consequences of variation in growth rate and productivity, Eds: H. Lambers, M.L. Cambridge, H. Konings, T.L. Pons) – SPB, Academic Publishing: The Hague, pp. 69–84.

Campbell B.D., Grime J.P. 1989 – A comparative-study of plant responsiveness to the duration of episodes of mineral nutrient enrichment – New Phytol. 112: 261–267.

Castro H., Lehsten V., Lavorel S., Freitas H. 2010 – Functional response traits in relation to land use change in the Montado – Agric. Ecosyst. Environ. 137: 183–191.

Chapin F.S. 1991 – Integrated responses of plants to stress – Bioscience, 41: 29–36.

Cui M., Caldwell M.M. 1997 – Shading reduces exploitation of soil nitrate and phosphate by *Agropyron desertorum* and *Artemisia tridentate* from soils with patchy and uniform nutrient distributions – Oecologia, 109: 177–183.

Dalling J.W., Hubbell S.P. 2002 – Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species – J. Ecol. 90: 557–568.

de Bello F., Buchmann N., Casals P., Leps J., Sebastia M.T. 2009 – Relating plant species and functional diversity to community [delta] C^{13} in NE Spain pastures – Agric. Ecosyst. Environ. 131(3–4): 303–307.

Diaz S., Cabido M. 1997 – Plant functional types and ecosystem function in relation to global change – J. Veg. Sci. 8: 463–474.

Diaz S., Cabido M. 2001 – Vive la difference: plant functional trait diversity matters to ecosystem processes – Trend. Ecol. Evol. 16: 646–650.

Diaz S., Lavorel S., de Bello F., Quetier F., Grigulis K., Robson T.M. 2007 – Incorporating plant functional diversity effects in ecosystem service assessments – Proc. Natl. Acad. Sci. USA. 104(52): 20684–20689.

Duru M., Tallowin J., Cruz P. 2005 – Functional diversity in lowinput grassland farming systems: characterisation, effect and management (In: Integrating efficient grassland farming and biodiversity, Eds: R. Lillak, R. Viiralt, A. Linke, V. Geherman) – EGF, Tartu, vol. 10, pp. 199–210.

Dyer A.R., Goldberg D.E., Turkington R., Sayre C. 2001 – Effects of growing conditions and source habitat on plant traits and functional group definition – Funct. Ecol. 15: 85–95.

Eriksson A., Eriksson O. 1997 – Seedling recruitment in semi-natural pastures: the effects of disturbance, seed size, phenology and seed bank – Nord. J. Bot. 17: 469–482.

Ernest S.K.M., Brown J.H. 2001 – Delayed compensation for missing keystone species by colonization – Science, 292: 101–104.

Fargione J.E., Tilman D. 2005 – Niche differences in phenology and rooting depth promote coexistence with a dominant C4 bunchgrass – Oecologia, 143: 598–606.

Finke D.L., Snyder W.E. 2008 – Niche partitioning increases resource exploitation by diverse communities – Science, 321: 1488-1490.

Gastine A., Scherer – Lorenzen M., Leadley P.W. 2003 – No consistent effects of plant diversity on root biomass, soil biota and soil abiotic conditions in temperate grassland communities – Appl. Soil Ecol. 24: 101–111.

Grime J.P., Hodgson J.G., Hunt R. 1988 – Comparative plant ecology: a functional approach to common British species – Unwin Hyman, London.

Grime J.P. 1997 – Biodiversity and ecosystem function: the debate deepens – Science, 277: 1260–1261.

Harpole W.S., Potts D.L., Suding K.N. 2007 – Ecosystem responses to water and nitrogen amendment in a Californian grassland – Global Change Biol. 13: 2341–2348.

Hector A.B., Schmid C., Beierkuhnlein M.C., Caldeira M., Diemer P.G., *et al.* 1999 – Plant diversity and productivity experiments in European grasslands – Science, 286: 1123–1127.

Hobbs R.J. 1997 – Can we use plant functional types to describe and predict responses to environmental change? (In: Their relevance to ecosystem properties and global change. Plant functional types, Eds: T.A. Smith, H.H. Shugard, F.I. Woodward) – Cambridge University Press, Cambridge, pp. 66–90.

Hodgson J.G., Wilson P.J., Hunt R., Grime J.P., Thompson K. 1999 – Allocating C–S–R plant functional types: a soft approach to a hard problem – Oikos, 85: 282–296.

Huang D., Wang K., Wu W.L. 2007 – Dynamics of soil physical and chemical properties and vegetation succession characteristics during grassland desertification under sheep grazing in an agro-pastoral transition zone in Northern China – J. Arid Environ. 70: 120–136.

Hunt R., Hand D.W., Hannah M.A., Neal A.M. 1993 – Further responses to CO_2 enrichment in British herbaceous species – Funct. Ecol. 7: 661–668.

Huston M.A. 1997 – Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity – Oecologia, 110: 449–460.

Kelly C.K. 1996 – Identifying plant functional types using floristic data bases: ecological correlates of plant range size – J. Veg. Sci. 7: 417–424.

Kleyer M. 1999 – The distribution of plant functional types on gradients of disturbance intensity and resource supply in an agricultural landscape – J. Veg. Sci. 10: 697–708.

Lavorel S., Rochette C., Lebreton J.D. 1999 – Functional groups for response to disturbance in Mediterranean old fields – Oikos, 84: 480–498.

Lavorel S., Garnier E. 2002 – Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail – Funct. Ecol. 16(5): 545–556.

Lehman C.L., Tilman D. 2000 – Biodiversity, stability and productivity in competitive communities – Am. Nat. 156: 534–552.

Leishman M.R., Westoby M. 1992 – Classifying plants into groups on the basis of associations of individual traits: evidence from Australian semi-arid woodlands – J. Ecol. 80: 417–424.

Leishman M.R., Westoby M. 1994 – The role of seed size in seedling establishment in dry soil conditions-experimental evidence from semi-arid species – J. Ecol. 82: 249–258.

Li Z.L. 2014 – Study on growth and development response of *Leymus chinensis* to main global climate change factors – Ph.D. Thesis, The northeast normal university.

McIntyre S., Lavorel S., Tremont R.M. 1995 – Plant lifehistory attributes: their relationship to disturbance response in herbaceous vegetation – J. Eco. 83: 31–44.

Miao S.L., Bazzaz F.A. 1990 – Responses to nutrient pulses of two colonizers requiring different disturbance frequencies – Ecology, 71: 2166–2178.

Moles A.T., Westoby M. 2004 – Seedling survival and seed size: a synthesis of the literature – J. Eco. 92: 372–383.

Mouillot D., Norman Mason W.H., Dumay O., Wilson J.B. 2005 – Functional regularity: a neglected aspect of functional diversity – Oecologia, 142: 353–359.

Naeem S., Wright J.P. 2003 – Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem – Ecol. Let. 6: 567–579.

Olff H., Pegtel D.M., van Groenendael J.M., Bakker J.P. 1994 – Germination strategies during grassland succession – J. Ecol. 82: 69–77.

Peco B., de Pablos I., Traba J., Levassor C. 2005 – The effect of grazing abandonment on species composition and functional traits: the case of dehesa grasslands – Basic Appl. Ecol. 6: 175–183.

Rüger N., Huth A., Hubbell S.P., Condit R. 2009 – Response of recruitment to light availability across a tropical lowland rain forest community – J. Ecol. 97: 1360–1368.

Schulze E.D. 1982 – Plant life forms and their carbon, water and nutrient relations – Encycl. Plant physiol. N. S. 12B: 615–676.

Schumacher J., Roscher C. 2009 – Differential effects of functional traits on aboveground biomass in semi-natural grasslands – Oikos, 118: 1659–1668.

Stuefer J.F., De Kroon H., During H.J. 1996 – Exploitation of environmental heterogeneity by spatial division of labour in a clonal plant – Func. Ecol. 10: 328–334.

Thompson K., Band S.R., Hodgson J.G. 1993 – Seed size and shape predict persistence in soil – Func. Ecol. 7: 236–241.

Thompson K., Hillier S.H., Grime J.P., Bossard C.C., Brand S.R. 1996 – A functional analysis of a limestone grassland community – J. Veg. Sci. 7: 371–380.

Thompson K., Askew A.P., Grime J.P., Dunnett N.P., Willis A.J. 2005 – Biodiversity, ecosystem function and plant traits in mature and immature plant communities – Func. Eco. 19: 355–358.

Turnbull L.A., Rees M., Crawley M.J. 1999 – Seed mass and the competition colonization tradeoff: a sowing experiment – J. Ecol. 87: 899–912.

Weigelt A., Schumacher J., Roscher C., Schmid B. 2008 – Does biodiversity increase spatial stability in community biomass? – Ecol. Let. 11: 338–347.

Weiher E., Clarke G.D.P., Keddy P.A. 1998 – Community assembly rules, morphological dispersion, and the coexistence of plant species – Oikos, 81: 309–322.

Westoby M., Wright I.J. 2006 – Land-plant ecology on the basis of functional traits – Trends Ecol. Evol. 21(5): 261–268.

Zavaleta E.S., Shaw M.R., Chiariello N.R., Thomas B.D., Cleland E.E., Field C.B., Mooney H.A. 2003 – Grassland responses to three years of elevated temperature, CO_2, precipitation, and N deposition – Ecol. Monogre. 73: 585–604.

Appendix 1.
Species occurring on the experimental site, dominant species (D), their classification into functional groups, and the percentage of peak above-ground biomass of each functional group (%).

Forbs (24%)	Legumes (7%)	Rhizomatous grasses and sedges (51%)	Bunch grasses (18%)
Androsace umbellate (Lour.) Merr.	Astragalus adsurgens Pall. (D)	Bromus inermis Leyss.	Elymus dahuricus Turcz.
Artemisia argyi Lévl. et Vant.	A. scaberrimus Bge.	Carex stenophylloides V. Krecz. (D)	Puccinellia distans (Jacq.) Parl. (D)
A. eriopoda Bge.	Medicago falcata L.(D)	Leymus chinensis (Trin.) Tzvel. (D)	P. tenuiflora (Griseb.) Scribn.et Merr. (D)
A. pectinata Pall.	Melissitus ruthenicus (L.) C. W. Chang	L. secalinus (Georgi) Tzvel.	Setaria viridis (L.) Beauv. (D)
A. sacrorum Ledeb.	Thermopsis lanceolata R. Br. (D)	Psathyrostachys juncea (Fisch.) Nevski	Stipa krylovii Roshev
A. scoparia Waldst. et Kit.			
A. sieversiana Wild. (D)			
Aster tataricus L. f.			
Chenopodium aristattum L. (D)			
C. glaucum L.			
Corispermum declinatum Steph. ex Stev. (D)			
Halerpestes ruthenica (Jacq.)Ovcz.			
Iris lactea Pall. var. chinensis (Fisch.) Koidz.			
Lepidium apetalum Wild. (D)			
Lxeris gracilis (Houtt.) Stebb. (D)			
L. sonchifolia (Bge.) Hance. (D)			
Myosotis sylvatica (Ehrh.) Hoffm.			
Plantago asiatica L.(D)			
Polygonum aviculare L.			
P. divaricatum Linn.			
P. sibiricum Laxm.			
Potentilla anserina L. (D)			
P. bifurca L.			
P. tanacetifolia Willd. ex Schlecht. (D)			
Saussurea glomerata Poir. (D)			
S. japonica (Thunb.) DC. (D)			
S. salsa (Pall.) Spreng (D)			
Scutellaria scordifolia Fisch. ex Schrenk.			
Serratula centauroides L. (D)			
Silene conoidea L. (D)			
Sonchus oleraceus L. (D)			
Stellera chamaejasme L.			
Taraxacum mongolicum Hand. – Mazz. (D)			
Ixeris chinensis (Thunb.) Nakai (D)			

Appendix 2.
The list of species traits expressed at the individual level.

Species traits	Variable type	Description of classes in matrix
Morphological traits		
(1) caespitose	nominal	(0) non caespitose; (1) caespitose
(2) height of vegetative plant	ordinal	(1) up to 10 cm; (2) up to 20 cm; (3) up to 30 cm; (4) up to 40cm; (5) >40cm
(3) root depth	ordinal	(1) <5 cm; (2) <10 cm; (3) <20 cm; (4) <40 cm; (5) <60 cm; (6) <100 cm; (7) >100 cm
Regenerative trait		
(4) capacity to lateral spread by vegetative growth	ordinal	(0) no lateral spread; (1) over short distances (short stolons rhizomes commonly <5cm); (2) over longer distances (creeping stems above- and below-ground stolons)
Reproductive trait		
(5) mean 1,000 seed weight (g)	ordinal	(1 <0.5 g; (2) <1 g; (3) <1.5 g; (4) <2 g; (5) >2 g