RESEARCH ARTICLE

The Influence of Historical Land Use and Water Availability on Grassland Restoration

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Abstract

The ecological role of historical land use has rarely been explored in the context of grassland restoration. We conducted a 4-year field experiment in a steppe and an old field in Inner Mongolia in northern China to examine the influence of historical land use and water availability on ecosystem restoration. Species richness, evenness, and plant cover were higher in the steppe than in the old field. The steppe was more temporally stable compared with the old field in terms of species richness, evenness, plant density, and cover. Water addition increased peak aboveground biomass, belowground net primary productivity, species richness, plant density, and cover in both the steppe

and the old field. Water addition also enhanced the stability of ecosystems and the restoration of grassland. Our findings suggested that historical land use determines community structure and influences the process of grassland restoration. Converting grasslands to farmland in semiarid areas can cause the long-term loss of biodiversity and instability of ecosystem with consequent impacts on ecosystem services. The amendment of limited resources is an effective practice to increase the success of ecosystem restoration.

Key words: community structure, diversity stability, historical land use, old field, steppe, water addition.

Introduction

The temperate steppe in the arid and semiarid regions in northern China constitutes an integral part of the Eurasian grassland and represents one of the typical vegetation types on the Eurasian continent (Kang et al. 2007). Because of historical overgrazing and agricultural conversion (Zhou et al. 2006), about 90% of the grasslands in northern China are currently degraded (Ding et al. 2006). Both intensive farming and overgrazing cause reductions in vegetation cover, loss of surface soil via wind erosion, and decreases in productivity and carrying capacity of the grasslands. Large-scale degradation and desertification of grasslands result in many eco-environmental and socio-economical problems, such as biodiversity loss, frequent sandstorms, and deteriorated ecosystem services, which threaten sustainable development of the local and regional community (Liu & Tong 2003; You et al. 2003). Since 2000, two kinds of practices (grazing exclusion and fallowing of cultivated land) have been widely adopted to combat land degradation and desertification in the western and northern China by restoring grasslands to higher vegetation cover, primary productivity, and biodiversity (Zhou et al. 2006).

Water availability can greatly influence community structure, productivity, and dynamics in grassland ecosystems (Knapp et al. 2002; Chen et al. 2007), and limit restoration of grassland, especially in semiarid areas (Zeng et al. 2005). Given that precipitation is a major factor for determining restoration success (Wilson et al. 2004), water amendment in semiarid ecosystems may play an important role in maintaining community structure and ecosystem productivity (Weltzin et al. 2003; Harpole et al. 2007) and may promote the process of grassland restoration (Suttle & Thomsen 2007). However, the influence of water addition on temporal stability (inversely related to temporal variability) in the restoration process of semiarid communities remains illusive. Because water addition stimulates plant growth, increases diversity (Dickson & Foster 2008), and decreases variability of community properties in unstable environments, it is reasonable to assume a

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Ecological restoration should take into consideration the historical context of ecosystem development. Understanding how current vegetation is related to previous land use has important implications for conservation and restoration of plant communities (Neill et al. 2007). Community structure (Foster et al. 2003), dominant life forms of plants (Knapp 1992), and responses of plant communities to environmental perturbation (Elmore et al. 2006) are commonly influenced by historical land use. Despite the fact that many arid and semiarid landscapes are currently in some stages of succession following anthropogenic disturbance, land use history is an often-overlooked component of land restoration and management (Knapp 1992; Stylinski & Allen 1999; Zhang et al. 2005; Elmore et al. 2006).

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positive effect of water addition on ecosystem stability and restoration.

One of the main purposes of ecological restoration is to establish a relatively mature and stable plant community in terms of community structure and ecosystem function under fluctuating environmental conditions (Seabloom 2007). Primary productivity, especially community productivity, is the most important ecosystem function. Temporal stability at the community level, an important objective of ecosystem restoration, is widely observed to increase with diversity (Dodd et al. 1994; Loreau et al. 2001; Tilman et al. 2006). Diversity-stability relationships have rarely been discussed in restoration studies, although it is clear that stability will increase the success of a restored community (Palmer et al. 1997; Young et al. 2005; Seabloom 2007). In addition, it is not clear whether the diversity-stability relationships change with initial community conditions of ecological restoration.

Here, we report the results of a field experiment conducted in a temperate steppe and an old field in Inner Mongolia since 2005. The different land use history in the steppe and the adjacent old field provides an opportunity to study the restoration process of grassland following disturbance. Water addition was applied to half of the plots to examine effects of resource amendment on ecological restoration of grassland ecosystems. The specific objectives were to determine how historical land use affects temporal stability of the restored plant communities and how water addition affects restoration in the two habitats.

Methods

Study Sites

Our experimental site was located in Duolun County (lat 116°17′E, long 42°02′N, 1,324 m a.s.l.), a semiarid area located in Inner Mongolia, China. This area occurs in an agropastoral ecotone with a temperate monsoon climate. Mean annual temperature is 2.1°C, with mean monthly temperatures ranging from-17.5°C in January to 18.9°C in July. Mean annual precipitation is 385.5 mm. The sandy soil in the study area is chestnut soil, based on Chinese classification, or Calcisorthic Aridisol in the U.S. Soil Taxonomy classification.

A steppe and an adjacent old field (with approximately 100 m distance between the two sites) were chosen as our experimental sites in 2005. Both sites were grazed freely before the old field was converted to farmland with plantings of Sesamum indicum L., Avena chinensis, Triticum aestivum L., and Fagopyrum sagittatum Gilib in the early 1980s. During the years of farming, the land was plowed in early April, and about 90 kg/ha diammonium phosphate fertilizer was applied to the soil at seeding time in May of each year. The old field was abandoned in 2000, and the steppe continued to be grazed until 2000. Plants in the study sites were classified as grasses or forbs on the basis of life form. Dominant plant species in the steppe were Artemisia frigida (C3 forb), Agropyron cristatum (C₃ grass), and Stipa krylovii (C₃ grass), whereas in the old

field, A. cristatum was the most dominant species followed by Artemisia scoparia Waldst. et Kit. (C3 forb).

Experimental Design

Fourteen 8 m \times 8 m plots were set up in each site with 1 m buffer zone between adjacent plots. From June to August, 15 mm of water was added weekly to half the plots in both sites via sprinkling irrigation, resulting in a total precipitation amount of 180 mm, approximately 50% of mean annual precipitation in the study area, supplied each year (12 weeks by 15 mm/week) from 2005 to 2008. The remaining seven plots served as controls receiving no sprinkling irrigation.

In middle July from 2005 to 2008, species richness (number of species) and plant density (the summed number of individuals of every species) were measured within a permanent quadrat of $1 \text{ m} \times 1 \text{ m}$ in each plot. In the same quadrat, plant cover at the community level was determined using a 1 $m \times 1$ m metal pane with 100 grids, by counting the junctions of the grids whose vertical projections overlapped with plants. Species evenness (Pielou index) was used to describe the diversity traits of plant communities. Pielou index (E) was calculated as:

$$E = \frac{\left(-\sum P_i \ln P_i\right)}{\ln S} \tag{1}$$

where P_i is the relative importance value of species i and S the total number of species.

Species gain rate (G_p) , loss rate (L_p) , and turnover rate (T_p) were determined in each quadrat to describe the community change rate during succession. They are expressed as a proportion of the average number of species present during the measurement period (Anderson 2007):

$$G_p = \frac{100 \times G}{[(1/2)(S_1 + S_2)]} \tag{2}$$

$$G_p = \frac{100 \times G}{[(1/2)(S_1 + S_2)]}$$

$$L_p = \frac{100 \times L}{[(1/2)(S_1 + S_2)]}$$

$$T_p = \frac{100 \times (G + L)}{(S_1 + S_2)}$$
(4)

$$T_p = \frac{100 \times (G+L)}{(S_1 + S_2)} \tag{4}$$

where G is the rate at which previously absent species appear in the community; L the rate at which species disappear from the community; S_1 and S_2 are species richness at the beginning and end of the sampling interval, respectively.

In early September of 2007 and 2008, aboveground biomass (AGB) was determined by harvesting all living tissues within a quadrat of 0.15 m \times 2 m in each plot and oven-dried at 65°C to constant weight. Belowground net primary productivity (BNPP) was measured using the root in-growth method (Xu & Wan 2008). From May to October, a 3-cm diameter soil core from the top 10 cm of soil was collected weekly in each plot, and then dried for 48 hours at 105°C to determine soil moisture. In August 2007, four soil cores (15 cm in depth and 5 cm in diameter) were collected from each plot. The four soil cores were mixed completely and roots and organic debris were removed by hand. The soil samples were sieved

Table 1. Results (*F*-values) of multiple ANOVA on the effects of historical land use (HL), water addition (W), and their interactions with year (Y) on species richness, evenness, plant density, cover, peak AGB, and BNPP.

Variation Source	df	Species Richness	Evenness	Density	Cover	AGB	BNPP
Y	3	4.28**	13.62***	23.59***	32.22***	35.08***	72.43***
HL	1	79.55***	14.89***	1.37 n.s.	23.48***	14.49***	5.64*
W	1	21.30***	0.17 n.s.	18.55***	98.33***	32.19***	4.75*
$Y \times HL$	3	4.20**	11.87***	11.61***	1.15 n.s.	12.08**	2.88 n.s.
$Y \times W$	3	3.61*	1.04 n.s.	2.52 n.s.	16.47***	0.38 n.s.	10.48**
$HL \times W$	1	2.89 n.s.	0.07 n.s.	2.15 n.s.	9.35**	7.72**	0.41 n.s.
$Y \times HL \times W$	3	0.15 n.s.	2.39 n.s.	1.36 n.s.	0.85 n.s.	2.14 n.s.	0.0008 n.s.

Degree of freedom (df) of variation source is 1 for AGB and BNPP, error df is 42 for AGB and BNPP and 96 for other variables. *, **, and ***: statistically significant at p < 0.05, 0.01, and 0.001, respectively; n.s.: statistically insignificant.

with a mesh (2 mm) and air-dried. The air-dried soil samples were ground and sieved with a mesh (0.25 mm) to measure soil organic carbon (potassium dichromatevitriol oxidation method), total nitrogen (Kjeldahl digestion), inorganic nitrogen (alkalisable diffusion method), and total phosphorus contents (H₂SO₄-HCIO₄ digestion colorimetry), respectively (Institute of Soil Science, Chinese Academy of Sciences [ISSCAS], 1978). The soil bulk density was calculated from the dry mass of soil per volume collected in the metal ring.

Data Analysis

A general linear model was used to examine the main effects of historical land use, year, water addition, and their possible interactions on species richness, evenness, plant density, and cover. Two-way analyses of variance ANOVAs were used to test the effects of water addition on community structure in each site. The effects of water addition on ecosystem stability were examined using t-test within each site. To test whether compensatory effects existed in the communities, we explored the relationship between plant cover both at species and life form group levels using Pearson's correlation analysis. To explore potential community level stabilizing mechanisms, linear regressions were conducted to determine the relationship of coefficient of variation (CV; temporal variability) in plant density and cover with species richness as well as the relationship of summed variance and covariance of plant density with diversity. Repeated measures ANOVAs were performed to examine effects of historical land use and water addition on soil moisture. All statistical analyses were performed using SPSS 13.0 (SPSS, Inc., Chicago, IL, U.S.A.).

Results

Differences in Soil Characteristics, Community Structure, and Stability between the Steppe and the Old Field

The prior farming practices depleted nutrients and decreased the humus content in the old field soil, resulting in significant differences in soil characteristics between the two habitats. Soil organic carbon content was greater in the steppe than the old field (15.68 and 12.92 mg/g, respectively; p < 0.05). The

steppe had higher (p < 0.01) values of soil total phosphorus, total nitrogen and inorganic nitrogen content, and soil moisture (0.32, 1.63 mg/g, 13.17 mg/kg, and 5.28%, respectively) compared with the old field (0.26, 1.24 mg/g, 10.03 mg/kg, and 6.38%, respectively). The soil bulk density was lower (p < 0.001) in the steppe (1.21 g/cm³) than the old field (1.39 g/cm³).

The effects of historical land use were significant for species richness, evenness, plant cover, AGB, and BNPP, but not for plant density (Table 1). The steppe had higher species richness (14.5), evenness (0.75), and plant cover (56.7%) than the old field (9.9, 0.69, and 47.4%, respectively) across the 4 years (p < 0.001; Fig. 1a, 1b, & 1d). Both AGB and BNPP were higher in the old field than the steppe (p < 0.05, < 0.001, respectively; Table 1, Fig. 2a & 2b). CV in species richness, evenness, plant density, and cover were significantly higher in the old field than in the steppe (p < 0.05; Fig. 4a-d). Summed variance and covariance of species density of all the plots in the 4 years were greater in the old field (17,971.1 and 3,691.5, respectively) than those in the steppe (5,931.9 and 758.9, respectively). Overyielding effects (plant density increases with species richness) were found in the steppe $(r^2 = 0.11, p < 0.05)$, but not in the old field.

Effects of Water Addition on Community Structure and Stability

Water addition significantly enhanced species richness, plant density, cover, AGB, and BNPP across the two sites and the sampling years (p < 0.05 for AGB and p < 0.001 for others; Table 1). However, no effects of water addition were found on species evenness (Table 1). Mean species richness across the two habitats increased from 13.1 in the unwatered plots to 14.0 in the watered plots in 2005, and from 11.1 to 13.4 in 2006, 8.4 to 13.6 in 2007, and 11.4 to 12.5 in 2008 (Fig. 1a). Water addition stimulated plant cover, density, AGB, and BNPP by 45.0, 39.4, 56.5, and 24.5%, respectively, across both sites and the measurement years (p < 0.05 for BNPP and p < 0.001 for others; Figs. 1d, 2a & 2b). We examined the effects of water addition on community structure within each site. Across the 4 years, species richness increased from 12.9 to 16.1 in the steppe and from 9.1 to 10.6 in the old field (p < 0.001 for both sites) under water addition in comparison with the control. Water addition enhanced plant cover, density,

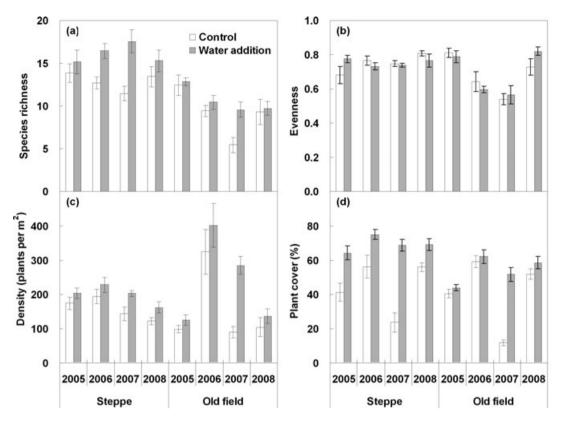


Figure 1. Species richness, evenness, plant density, and cover (mean ± SE) response to water treatments in steppe and old field.

AGB, and BNPP by 56.6 (p < 0.001), 25.6 (p < 0.01), 32.9 (p < 0.001), and 38.3% (p < 0.05), respectively, in the steppe and by 32.4 (p < 0.01), 53.5 (p < 0.001), 86.0 (p < 0.001), and 14.8% (p = 0.307) in the old field across the sampling years. In the steppe, the increases in plant cover caused by water addition were largely attributable to *Artemisia frigida*, *Potentilla acaulis*, and *Melilotoides ruthenica* (increased 21.0, 7.4, and 8.0%, respectively; p < 0.001), whereas the increases in the old field could be ascribed to *A. scoparia Waldst. et Kit.* and *Potentilla bifurca* (increased 3.4 and 2.7%; p < 0.05; Fig. 3a &3b). Water addition also altered the composition of plant life forms, reducing the proportion of grass cover and increasing the proportion of forbs cover by 23.0 and 6.8% in the steppe and the old field, respectively (Fig. 3c).

Water addition significantly increased soil moisture across two sites (F = 117.12, p < 0.001). All the measured variables (p < 0.05) except for BNPP showed strong linear dependence on soil moisture. Across the two habitats, water addition decreased the CV in plant cover by 33.0%, plant density by 11.6%, species richness by 8.6%, and evenness by 0.7% (p < 0.05 for species richness and plant cover; Fig. 4a–d). Influences of water addition on ecosystem stability were examined within each site. Under water addition, CV in plant cover decreased from 45.1 to 11.3% in the steppe (p < 0.001), CV in species richness and plant cover decreased from 37.4 and 51.7% to 21.7 and 19.5%, respectively, in the old field (p < 0.001).

Relationship between Diversity and CV of Plant Density and Cover, the Correlations between Plant Cover of Species or Functional Groups

CV of plant density and cover across the 4 years was linearly and negatively correlated with mean species richness (p < 0.01; Fig. 5a & 5b) across all the plots in the two ecosystems. At the life form level, results of Pearson correlation showed a significantly negative correlation (r = -0.319, p < 0.05) between the covers of grasses and forbs in the steppe. At the species level, correlation analyses for species cover of 45 most common species pairs, both in the steppe and the old field, showed that there were four pairs of negative correlation in the steppe (p < 0.05). No significantly negative correlation was found both at the species and functional group level in the old field (Appendices 1 and 2).

Plant Cover CV of Most Common Species and Community Change Rate

From the species consecutively present for 4 years, the first 10 species were selected according to species cover from high to low both in the steppe and the old field. We compared the species cover CV of these species between the two sites. The results showed that mean species cover CV was higher in the old field (124.6%) than the steppe (80.5%) across all the species. Water addition decreased the mean cover CV of these species from 119.8 to 85.2%. In terms of community change rate, the old field had significantly higher (p < 0.001)

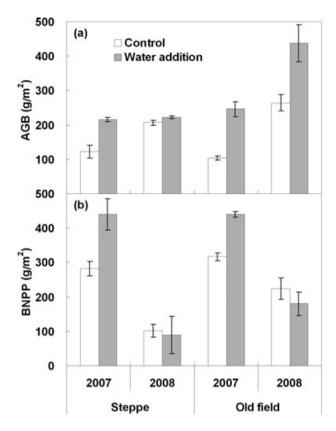


Figure 2. Peak AGB and BNPP (mean \pm SE) response to water treatments in steppe and old field.

values of species gain rate, loss rate, and turnover rate (35.2, 60.0, and 47.6%, respectively) than the steppe (17.6, 18.6, and 18.1%, respectively; Fig. 6) from 2005 to 2008.

Discussion

Historical land use influenced soil traits and community structure in the study sites. The higher contents of soil nutrients, soil moisture, and lower soil bulk density in the steppe compared with the old field presumably provided more favorable conditions for germination and growth, a pattern consistent with Steenwertha et al. (2002) and Evrendilek et al. (2004). Nevertheless, the steppe had lower AGB and BNPP than the old field. It can be mainly ascribed to the different species composition between the two sites. In the old field, Agropyron cristatum is the absolutely dominant species and its species biomass accounts for about 67.3% of AGB. As a perennial bunchgrass, A. cristatum has high stature (approximately 45 cm on average), abundant branches and dense roots, and very high species biomass. While in the steppe, the most dominant species is Artemisia frigida (accounts for 30.6% of AGB). However, the species is short in stature (about 18 cm), and has very small and light leaves and small root mass. Agropyron cristatum and Stipa krylovii, other dominant species in the steppe, constituted lower proportions (15.9 and 12.6%, respectively) of AGB. Other species are

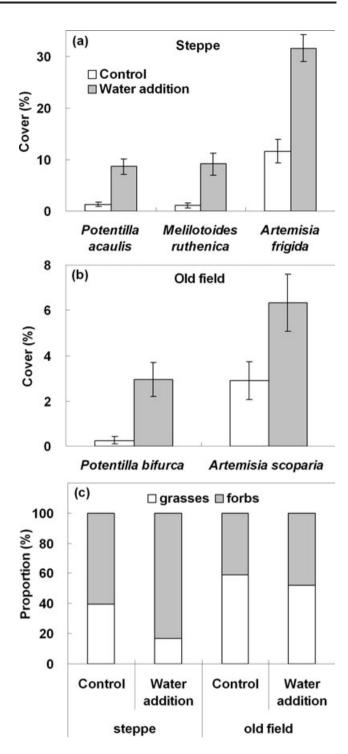


Figure 3. Effects of water addition on plant cover (mean \pm SE) at species level (a and b) and proportion of functional group cover (c) in steppe and old field.

relatively small in size or lower in quantity and contribute little to the community biomass. As a result, the summed biomass at community level is higher in the old field than the steppe. Significantly greater plant diversity in the steppe than the old field can be attributable to two reasons: (1) more resources

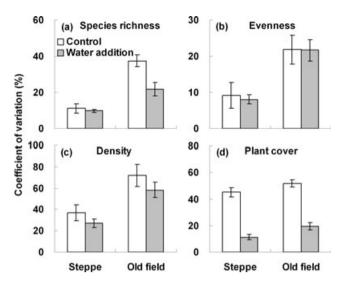


Figure 4. CV (mean \pm SE) in species richness, evenness, plant density, and cover across the 3 years for water treatment plots in steppe and old field.

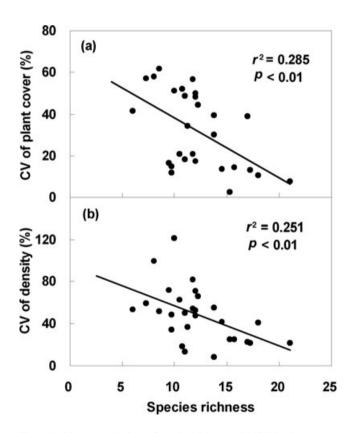


Figure 5. Linear correlations of species richness with CV in plant density and cover across all the plots in two sites.

are available in the steppe to support plant species (Morin 2000) and (2) the old field is in an early stage of secondary succession while the steppe is much more mature. Mature communities support co-occurring species that use different niches to maximize resource utilization and can thus support

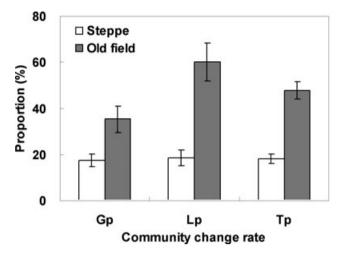


Figure 6. Species gain rate (G_p) , loss rate (L_p) , and turnover rate (T_p) (mean \pm SE) in steppe and old field.

more plant species than immature communities, even those with similar resource availability (Cook et al. 2005).

Revealing the possible effects of management techniques on biodiversity and ecosystem stability is the main issue to be addressed in ecosystem restoration (Aronsod et al. 1993). An understanding of diversity-stability relationships will help to improve management regimes and likely increase restoration success (Seabloom 2007). Theory (Yachi and Loreau 1999; Thebault and Loreau 2005) and most empirical studies (Dodd et al. 1994; Naeem & Li 1997; Tilman et al. 2006) suggest that plant diversity ensures ecosystems against declines in their functions because of the summed covariance effect (different species respond differently to environmental change; Ives et al. 2000) and overvielding effect (Hector et al. 2002; Jiang et al. 2008). In this study, the consistently negative correlation of CV of plant cover and density at community level with species richness suggest the positive relationship between community stability and diversity. The consistently lower CV of species richness, evenness, plant density, and cover in the steppe in our study indicated its higher stability compared with the old field under environmental (especially precipitation) fluctuation. Bai et al. (2004) suggested that community level stability arises from compensatory interactions among major components at both species and functional group levels. The compensatory effects, which can be explained as one species increase in response to the reduction or loss of another (Naeem & Li 1997), may take place in ecosystems under changing environment as negative correlations exist between some of the species. Significant negative correlations, both at species and life form levels, were found in the steppe (Appendix 1), indicating that compensatory effects occur in the steppe. However, no negative correlation was observed in the old field (Appendix 2). Disturbance increases community change through time, and the system with relatively higher species change rate was less stable (McIntyre and Lavorel 1994; Woodward et al. 2002). The higher community change rate in the old field indicates its lower stability in comparison

with the steppe. The diversity-stability hypothesis and the compensatory effects together with the community change assumption explained the difference in stability between the steppe and the old field.

Seabloom (2007) proposes that a restored community will not persist unless it is robust to the variability in the environment. Because of the complexity and variability of climate, maximizing stability of ecosystems to a wide range of conditions should be one of the important goals for restoration.

Grassland restoration in arid and semiarid areas is mainly limited by water availability (Roundy et al. 2001; Ma et al. 2004; Banerjee et al. 2006). Species composition, richness, abundance, and primary productivity have been documented to be improved by water addition in grassland ecosystems (Hobbs & Mooney 1991; Harpole et al. 2007; Dickson & Foster 2008). Weaver and Albertson (1940) have reported the deterioration of grassland from stability to denudation with decreasing soil moisture in the United States. In the arid valley of the Minjiang River of China, soil moisture is an important factor in restoration of grassland (Ma et al. 2004). Shifts in precipitation regimes can change the structure and functioning of semiarid grassland and affect the restoration of community. Water addition at appropriate times can be critical to restoration of native species (Suttle & Thomsen 2007). Similar results were documented by Roundy et al. (2001) and Banerjee et al. (2006) in studies on abandoned farmland restoration.

January-July precipitation is the primary climatic factor causing fluctuations in community biomass production in the Inner Mongolia grassland (Bai et al. 2004). January-July precipitation varied substantially from 2005 to 2008 in the study area. Precipitation in 2005 was 216.5 mm, which is close to the long-term mean (225.1 mm), and precipitation in 2008 was 175.5 mm. Precipitation in 2006 and 2007 was the highest (357.8 mm) and lowest (93.2 mm), respectively, for the past five decades. Weekly water addition altered the dry period pattern, increased species richness, and decreased the variation in both precipitation (from 55.3 to 37.6%) and community structure, which suggested the positive effect of water addition on ecosystem stability. Our observations are in agreement with those reported by Noy-Meir (1973) and Sala et al. (1988) that supplementing a restricted resource can increase the stability of ecosystems. However, our results seem to be inconsistent with those observed in a Kansas tallgrass prairie (Knapp et al. 2002), where greater variability, rather than amount of soil water availability, promoted species diversity. The difference in diversity response to water addition in the semiarid grassland and the tallgrass prairie might be partly attributable to the difference in initial water conditions (Weltzin et al. 2003). The semiarid grassland in northern China is predominantly constrained by water availability; improved water resources allow more species to coexist, thus higher plant diversity maintains greater ecosystem stability. Water availability in the Kansas tallgrass prairie, with mean annual precipitation approximately 833 mm, is relatively abundant compared with the grassland in our research sites. Other factors such as temperature, N availability, and/or light availability may be more critical in limiting plant growth than water availability in the Kansas tallgrass prairie. Greater variability in soil water availability may provide wider niche ranges for more plants to coexist, leading to greater plant diversity and consequent ecosystem stability (Knapp et al. 2002).

Since the summer precipitation in the northern China is predicted to increase in the future (Cholaw et al. 2003), empirically based information on how climate change (precipitation) will impact habitats in this area is urgently required. Our findings have important implications for both improving our understanding of the potential effects of climate change and guiding the current practices on grassland restoration and management in agro-pastoral ecotones in northern China. These could also be significant for restoration and conservation in other places or other ecosystem types experiencing similar problems. Historical land use must be considered in ecological restoration as it determines the most important aspects of structure and functions of community which influence the success of ecosystems restoration.

Implications for Practice

- It is imperative to restore degraded grasslands to productive, biologically diverse and high vegetation cover ecosystems with greater capability to improve the ecological environment and serve socio-economics in northern China.
- Water addition is effective for semiarid ecosystem restoration because it improves primary productivity, community structure, and ecosystem stability. We therefore recommend water addition in semiarid areas to accelerate grassland restoration.
- Historical cultivation greatly affects various ecosystem aspects, including soil condition, vegetation structure, and ecosystem functioning. Conversion of grassland to cultivated farmland causes the long-term loss of biodiversity and instability of ecosystem.
- Maintenance of high diversity and stability should be taken into consideration as an important goal in ecosystem restoration and criteria in evaluation of the success of restoration.
- Long-term observation is required to study the development of ecosystems following disturbance.

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Appendix 1. Pearson's correlation matrix of most common species in steppe.

	Agropyron cristatum	Stipa krylovii	Artemisia frigida	Carex korshinskyi	Melilotoides ruthenica	Potentilla acaulis	Potentilla tanacetifolia	Potentilla bifurca	Allium bidentatum
Stipa krylovii	0.039								
Artemisia frigida	-0.044	-0.383**							
Carex korshinskyi	-0.121	-0.301*	0.350**						
Melilotoides ruthenica	0.243	-0.211	0.026	-0.029					
Potentilla acaulis	-0.161	-0.201	0.291*	0.083	0.345***				
Potentilla tanacetifolia	-0.217	-0.081	0.091	-0.001	0.057	0.563***			
Potentilla bifurca	0.087	-0.009	-0.195	0.294*	-0.145	-0.336*	-0.118		
Allium bidentatum	0.057	0.347**	-0.232	-0.165	-0.180	-0.199	-0.207	0.121	
Artemisia scoparia Waldst. et Kit.	-0.109	0.005	-0.269*	0.124	-0.130	-0.178	0.027	0.162	0.076

^{*, **,} and ***: statistically significant at p < 0.05, 0.01, and 0.001, respectively.

Appendix 2. Pearson's correlation matrix of most common species in old field.

	Agropyron cristatum	Potentilla tanacetifolia	Potentilla bifurca	Leymus chinensis	Artemisia scoparia Waldst. et Kit.	Leymus secalinus (Georgi)Tzvel.	Medicago sativa L.	Erodium stephanianum Willd.	Artemisia argyi L.
Potentilla tanacetifolia	0.073								
Potentilla bifurca	0.255	0.035							
Leymus chinensis	0.063	-0.086	-0.098						
Artemisia scoparia Waldst. et Kit.	0.051	-0.113	0.269*	0.054					
Leymus secalinus (Georgi)Tzvel.	0.019	-0.102	0.149	0.121	0.263				
Medicago sativa L.	-0.116	-0.238	-0.189	-0.030	-0.171	-0.108			
Erodium stephanianum Willd.	0.047	0.004	-0.029	-0.057	0.036	-0.102	-0.216		
Artemisia argyi L.	-0.114	0.376**	-0.144	-0.084	-0.133	-0.085	-0.172	-0.088	
Setaria viridis Beauv.	-0.043	-0.042	0.057	-0.046	0.540***	-0.114	0.084	0.329*	-0.151

^{*, **,} and ***: statistically significant at p < 0.05, 0.01, and 0.001, respectively.