

Increasing nitrogen deposition enhances post-drought recovery of grassland productivity in the Mongolian steppe

Toshihiko Kinugasa · Atsushi Tsunekawa ·
Masato Shinoda

Received: 24 June 2011 / Accepted: 26 April 2012
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Abstract Arid regions are prone to drought because annual rainfall accumulation depends on a few rainfall events. Natural plant communities are damaged by drought, but atmospheric nitrogen (N) deposition may enhance the recovery of plant productivity after drought. Here, we investigated the effect of increasing N deposition on post-drought recovery of grassland productivity in the Mongolian steppe, and we examined the influence of grazing in this recovery. We added different amounts of N to a Mongolian grassland during two sequential drought years (2006 and 2007) and the subsequent 3 years of normal rainfall (2008–2010) under grazed and nongrazed conditions. Aboveground biomass and number of shoots were surveyed annually for each species. Nitrogen addition increased grassland productivity after drought irrespective of the grazing regime. The increase in grassland productivity was associated with an increase in the size of an annual, *Salsola collina*, under grazed conditions, and with an increase in shoot emergence of a perennial, *Artemisia adamsii*, under nongrazed conditions. The addition of low N content simulating N deposition around the study area by the year 2050 did not significantly increase grassland

productivity. Our results suggest that increasing N deposition can enhance grassland recovery after a drought even in arid environments, such as the Mongolian steppe. This enhancement may be accompanied by a loss of grassland quality caused by an increase in the unpalatable species *A. adamsii* and largely depends on future human activities and the consequent deposition of N in Mongolia.

Keywords Arid region · *Artemisia adamsii* · Grazing · Palatability · Precipitation

Introduction

Drought is an extreme climatic event that occurs in virtually all climatic zones, and its frequency and severity are projected to increase (IPCC 2007; Mishra and Singh 2010; Dai 2011). Arid regions are particularly prone to drought because annual rainfall accumulation depends on a few rainfall events. Drought reduces the emergence of annual plants—and ground cover and primary productivity of arid grasslands—while perennials are less affected owing to their deeper root systems (Le Houèrou 1996; Loeser et al. 2007; Shinoda et al. 2010a). Reduced plant cover expands land degradation and dust transport as a result of wind erosion (Wolfe and Nickling 1993; Breshears et al. 2009; Shinoda et al. 2010b), and decreased grassland productivity negatively affects livestock production (Le Houèrou 1996; Aklilu and Wekesa 2001). When a normal weather pattern returns after drought, vegetation cover and grassland productivity recover mainly due to the re-emergence of annuals (Le Houèrou 1996; Loeser et al. 2007).

As the availability of nitrogen (N) also limits productivity of plant communities (Gough et al. 2000; Vitousek et al. 2002; LeBauer and Treseder 2008), increasing

Communicated by Mercedes Bustamante.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-012-2354-4) contains supplementary material, which is available to authorized users.

T. Kinugasa (✉)
Faculty of Agriculture, Tottori University,
4-101 Koyama-Minami, Tottori 680-8553, Japan
e-mail: kinugasa@muses.tottori-u.ac.jp

A. Tsunekawa · M. Shinoda
Arid Land Research Center, Tottori University,
1390 Hamasaka, Tottori 680-0001, Japan

atmospheric N deposition would enhance post-drought recovery of grassland productivity. Increasing atmospheric N deposition, which largely results from N emissions from anthropogenic sources such as chemical fertilizers, fossil-fuel combustion, and N₂-fixing crop cultivation (Galloway et al. 2004, 2008; Gruber and Galloway 2008), generally enhances grassland productivity while reducing species richness (Vitousek et al. 1997; Aerts and Bobbink 1999; LeBauer and Treseder 2008; Bobbink et al. 2010). The increase in plant productivity with N addition is found even in arid ecosystems, although the increase is sometimes restricted by water availability (Hooper and Johnson 1999; Rao and Allen 2010; Gao et al. 2011; Gong et al. 2011). However, the effect of increasing N deposition on grassland recovery following a drought has not been demonstrated.

In this study, we investigated the effect of increasing N deposition on post-drought recovery of grassland productivity in the Mongolian steppe. The emission of N oxides has been increasing in Mongolia as a result of an increased number of motor vehicles (Asian Development Bank 2005). The Mongolian steppe has historically been used as grazing land, and about half the Mongolian population depends directly or indirectly on livestock production (Johnson et al. 2006). Because drought occurs frequently in Mongolia and has severe consequences for livestock production (Asian Development Bank 2005; Johnson et al. 2006; Sternberg 2008), rapid recovery of grassland productivity after a drought is essential for the Mongolian economy. Grassland productivity was found to increase with NPK fertilization even under ambient precipitation levels in the Mongolian steppe (Wesche and Ronnenberg 2010; Ronnenberg and Wesche 2011), implying that grassland productivity is no longer under water limitation after a drought. However, no study has investigated the sole effect of N addition on the productivity of the Mongolian steppe. As N and P are colimiting factors for plant productivity in most terrestrial ecosystems (Elser et al. 2007), N addition without P may not increase grassland productivity even without drought stress.

To simulate post-drought recovery of grassland productivity under future levels of N deposition, we added N to the grassland in two sequential drought years and 3 years of normal rainfall. Our experiment was performed in grasslands with and without livestock grazing because grazing can affect grassland productivity and species composition and therefore may influence the response of grassland to N. In general, perennials decrease and annuals increase with higher grazing intensity (Pettit and Froend 2001; Bartolome et al. 2004; Diaz et al. 2007; Loeser et al. 2007). As the increase in plant biomass due to high N levels is greater in annuals than in perennials (Xia and Wan 2008), N-induced enhancement of post-drought grassland productivity may be greater under a grazing regime.

Materials and methods

The study site, Bayan-Unjuul (47°02.77'N, 105°57.08'E), is located in a moderately dry steppe (Vostokova and Gunin 2005), about 130 km southwest of Ulaanbaatar, the capital of Mongolia. A meteorological monitoring station located approximately 700 m southeast of the center of the study site (provided by the Institute of Meteorology and Hydrology of Mongolia) recorded an annual mean temperature and precipitation from 1996 to 2010 of 0.4 °C and 159 mm, respectively. Annual precipitation in 2006–2010 was 94, 101, 162, 198, and 143 mm, respectively. Growth of vegetation usually begins in May and ends in September, and about 85 % of annual precipitation falls during that period. Because the precipitation from May to September in 2006 and 2007 was far lower than the 15-year average (see Electronic supplementary material 1), we treated these 2 years as drought years and the following 3 years as normal rainfall years. Monthly mean temperatures during the experimental period (2006–2010) were 11.6, 18.2, 20.9, 17.9, and 12.5 °C for May to September, respectively.

The study site is regularly grazed by large livestock herds dominated by goats and sheep, in addition to horses and cattle. The vegetation of the study site in June 2006 prior to the start of our study was dominated by perennial grasses (*Agropyron cristatum*, *Cleistogenes squarrosa*, and *Stipa krylovii*), perennial forbs (*Artemisia adamsii*), and fabaceous shrubs (*Caragana stenophylla*). Soils at the study site are classified as Kastanozems with a calcic horizon more than 40 cm below the surface. Total C and N contents of the soils at 0–15 cm depth prior to the start of the study were 7.57 and 0.88 mg g⁻¹, respectively. Soil pH at 0–10 cm depth was 6.6–6.9.

Present and future levels of N deposition around the study site were calculated using global grid estimates of atmospheric deposition of total inorganic N for 1993 and 2050 (Dentener 2006). Assuming a linear increase in annual N deposition during that period, annual N deposition around the study site in 2006, the first year of our experiment, and 2050 was calculated to be 298 and 587 mg N m⁻² year⁻¹.

We used a split-plot experimental design with four replications. Four experimental blocks were randomly established within an area of 150 × 100 m in August 2006. Each block had two experimental plots, grazed and non-grazed (12 × 12 m each). Nongrazed plots were surrounded by wire netting to exclude grazing livestock. In each experimental plot, three treatments (4.5 × 4 m each) with different levels of N application were established: control (C; 0 mg N m⁻² year⁻¹), low N (LN; 300 mg N m⁻² year⁻¹), and high N (HN; 1,500 mg N m⁻² year⁻¹). To simulate N deposition in 2050, N application in the LN treatment corresponded approximately to the increase in N

deposition around the study site predicted for the period from 2006 until 2050. To evaluate the potential response of grassland productivity to N application, the HN treatment in 2009 and 2010 received five times more N than that until 2008 ($7,500 \text{ mg N m}^{-2} \text{ year}^{-1}$). One nongrazed plot was heavily disturbed by burrowing mice, and we abandoned that plot in 2009 and its corresponding grazed plot within the same experimental block in 2010. For N treatment, an ammonium nitrate (NH_4NO_3) solution containing the required amount of N was sprayed in July and September every year. Only water without NH_4NO_3 was applied to control plots. The annual amount of water sprayed during the addition of N corresponded to 2.6 mm of precipitation, which was less than 3 % of annual precipitation in drought year 2006.

Vegetation surveys were carried out each year in late August. During each survey, a $0.5 \times 0.5 \text{ m}$ quadrat was randomly set in each N treatment. The number of shoots of each species was recorded, and shoots were then harvested by species. In 2010, the vegetation survey was repeated two times in 10 days to provide adequate replications for statistical analysis. Harvested shoots were dried at 70°C for more than 3 days and then weighed. Dried samples were ground in a mill and their N content was measured by an elemental analyzer (JM1000CN; J-Science, Kyoto, Japan).

We assessed the effects of N addition, grazing, and rain regime (drought years and normal years) on aboveground biomass, species richness, and the proportion of annual species to aboveground biomass using generalized linear models (GLM) with normal distribution (link function: identity), Poisson distribution (link function: log), and binomial distribution (link function: logit), respectively. Effects of N addition on aboveground biomass, number of shoots, and shoot biomass were tested by paired t tests followed by sequential Bonferroni adjustment when necessary. The difference in the proportion of annual species to aboveground biomass between treatments was tested by U test with sequential Bonferroni adjustment. Statistical tests were performed using the software JMP 7 (SAS Institute, Cary, NC, USA).

Results

Aboveground biomass was affected by grazing, N addition, and rainfall regime (drought years and normal years), and a significant interactive effect of grazing and rainfall regime was found (Table 1). Aboveground biomass was low during drought years compared to normal rainfall years (Fig. 1). HN treatment significantly increased aboveground biomass in 2009 and 2010 in grazed plots and in 2010 in nongrazed plots. No significant effect of LN addition was found.

We recorded 27 species, including 7 annuals, 18 perennials, and 2 shrubs, during the study period (Electronic supplementary material 2). Species richness was not affected by N addition or rainfall regime, whereas a significant effect of grazing and a significant interactive effect of grazing and rainfall regime was found (Table 1). Species richness was lower in 2007 compared with other years (Fig. 2). We found no effect from the addition of N to species number.

The proportion of annuals to total aboveground biomass was not affected by N addition or rainfall regime but was affected by grazing (Table 1). An interactive effect of grazing and rainfall regime was found. The proportion of annuals to total aboveground biomass was less than 0.35 in drought years but increased to more than 0.8 in 2008 (Fig. 3). During normal rainfall years, the proportion of annuals was maintained at a high level in grazed plots. In contrast, the proportion of annuals in nongrazed plots decreased to less than 0.05 by 2010. We found no effects from N addition in grazed or nongrazed plots.

Figure 4 shows the effects of N addition on aboveground biomass of annuals and perennials in normal rainfall years after a drought. As LN addition did not significantly affect aboveground biomass (Fig. 1), LN treatment was excluded hereafter. In the grazed plots, aboveground biomass of annuals increased with the addition of N in 2009 and 2010 (Fig. 4a), whereas N addition had no effect on perennials (Fig. 4c). In nongrazed plots, aboveground biomass of annuals decreased every year and was not affected by the addition of N (Fig. 4b). In contrast, aboveground biomass of perennials in nongrazed plots increased yearly and was significantly increased by the addition of N in 2010 (Fig. 4d).

In grazed plots, three *Chenopodium* species accounted for more than 85 % of the aboveground biomass of annuals during the early recovery from drought in 2008 (Fig. 5a). Similar results were found in the nongrazed plots (data not shown). The contribution of the three *Chenopodium* species to the aboveground biomass of annuals in grazed plots decreased rapidly in 2009 and was less than 5 % in 2010. In contrast, the contribution of *Salsola collina* increased rapidly to more than 80 % in 2009 and exceeded 95 % in 2010. Significant effects of survey year on the contribution of three *Chenopodium* species and *S. collina* to the aboveground biomass of annuals were found (GLM with binomial distribution using N and year as independent variables, $P < 0.001$). In nongrazed plots, *A. adamsii* accounted for about 40 % of the aboveground biomass of perennials in 2008, increasing to more than 55 % in 2010 (Fig. 5b). A significant effect of year on the contribution of *A. adamsii* to the aboveground biomass of perennials was found (GLM with binomial distribution using N and year as independent variables, $P < 0.05$).

Table 1 Generalized linear model of the effects of grazing (grazed and nongrazed), nitrogen (control, low nitrogen, and high nitrogen), and rainfall regime (drought years and normal years) on aboveground biomass (Fig. 1), species richness (Fig. 2), and proportion of annuals in aboveground biomass (Fig. 3)

Source	<i>df</i>	Aboveground biomass	Species richness	Proportion of annuals
Grazing (G)	1	2.843 [†]	4.428*	24.427***
Nitrogen (N)	2	4.892 [†]	0.082	0.251
Rainfall (R)	1	75.295***	1.464	0.135
G × N	2	0.197	1.041	0.220
G × R	1	6.906**	7.197**	20.996***
N × R	2	3.905	0.376	0.868
G × N × R	2	0.476	0.345	0.046

Aboveground biomass is based on a normal distribution, species richness on a Poisson distribution, and proportion of annuals in aboveground biomass on a binomial distribution

[†] $P < 0.1$

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

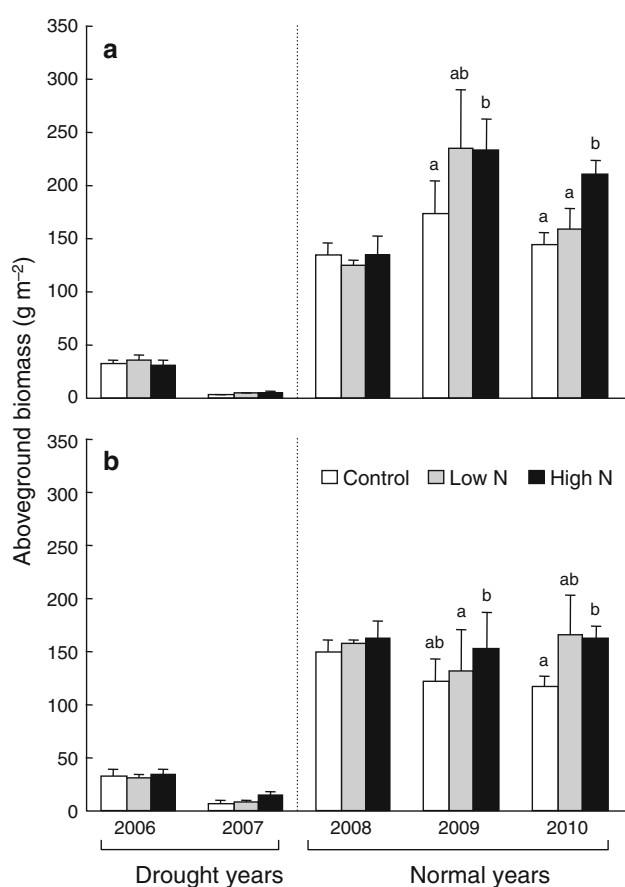


Fig. 1 Aboveground biomass with different levels of N addition in **a** grazed and **b** nongrazed plots during drought years (2006 and 2007) and normal rainfall years (2008–2010). Within each year, different lowercase letters above the bars indicate statistically significant differences between N treatments (paired *t* test with sequential Bonferroni adjustment; $P < 0.1$). Error bars +1SE ($n = 6$ for 2010, $n = 3$ for nongrazed plots in 2009, $n = 4$ for all other plots)

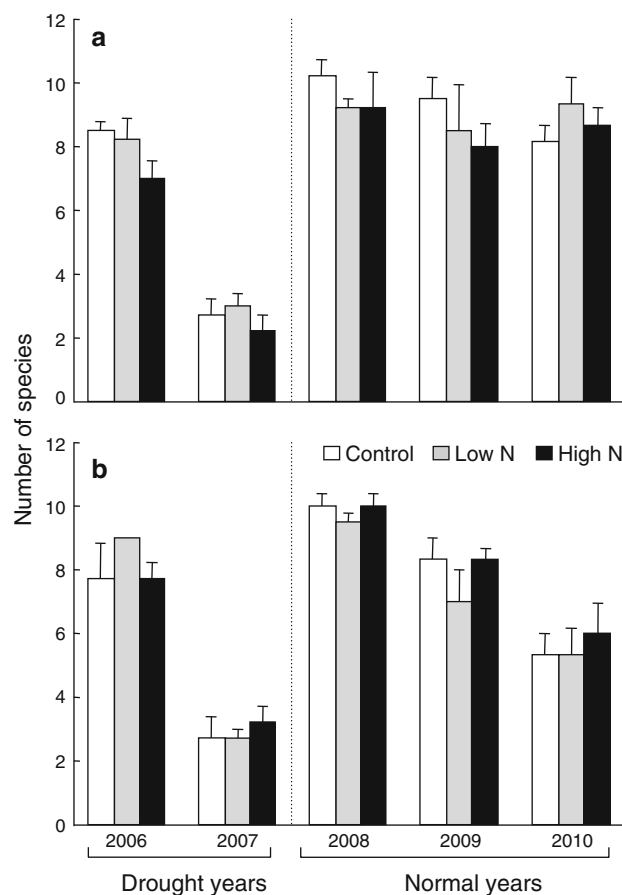


Fig. 2 Species richness with different levels of N addition in **a** grazed and **b** nongrazed plots during drought years (2006 and 2007) and normal rainfall years (2008–2010). No statistically significant difference was found between N treatments within each year (paired *t* test with sequential Bonferroni adjustment; $P < 0.1$). Error bars +1SE ($n = 6$ for 2010, $n = 3$ for nongrazed plots in 2009, $n = 4$ for all other plots)

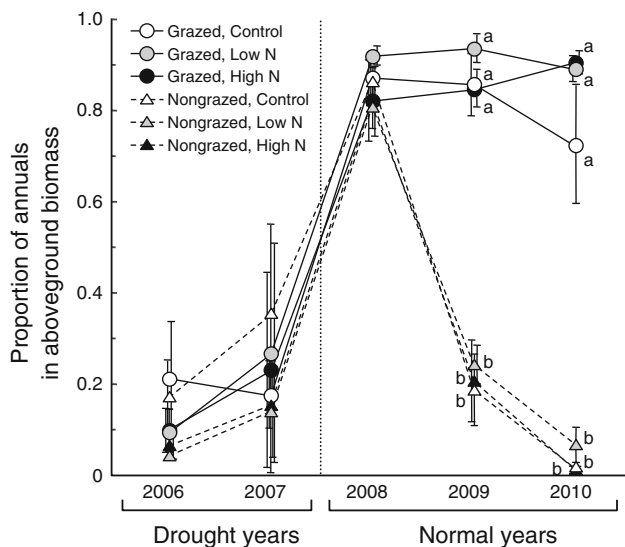


Fig. 3 Proportion of annual species in aboveground biomass during drought years (2006 and 2007) and normal rainfall years (2008–2010). Within each year, *different lowercase letters* indicate a statistically significant difference between plots and treatments (*U* test with sequential Bonferroni adjustment; $P < 0.1$). Error bars +1SE ($n = 6$ for 2010, $n = 3$ for nongrazed plots in 2009, $n = 4$ for all other plots)

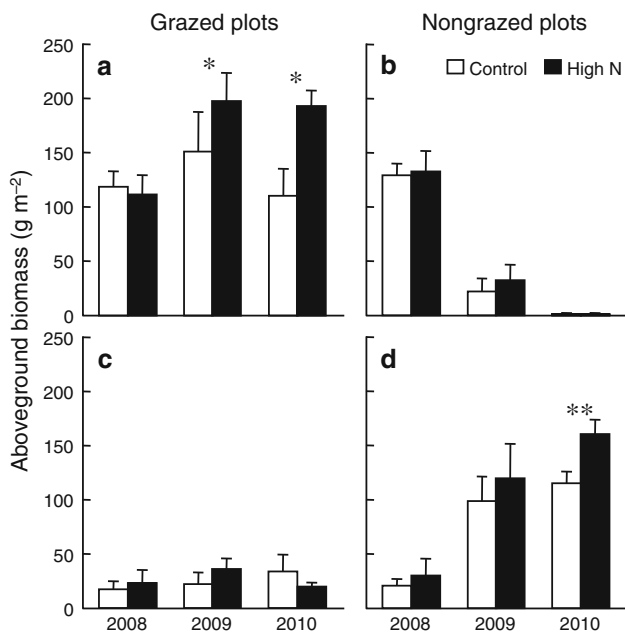


Fig. 4 Aboveground biomass of annuals at **a** grazed and **b** nongrazed plots and of perennials at **c** grazed and **d** nongrazed plots in normal rainfall years. Error bars +1SE ($n = 6$ for 2010, $n = 3$ for nongrazed plots in 2009, $n = 4$ for all other plots). * $P < 0.05$, ** $P < 0.01$ (paired *t* test)

In 2009 and 2010, the aboveground biomass of *S. collina* in grazed plots significantly increased with the addition of N (Fig. 6a). The number of shoots of *S. collina* more than doubled in 2009 and 2010 and was not affected

by N treatment (Fig. 6c). Shoot biomass of *S. collina* was less in 2010 than in 2009, and the addition of N significantly increased shoot biomass in 2010 (Fig. 6e). Nitrogen concentration of *S. collina* shoots significantly increased with the addition of N in 2010 (Fig. 6g). The aboveground biomass of *A. adamsii* in nongrazed plots increased with N treatment, although it was not statistically significant (Fig. 6b). The number of *A. adamsii* shoots showed a significant increase with the addition of N (Fig. 6d), whereas the shoot biomass of *A. adamsii* was not affected (Fig. 6f). The shoot N concentration of *A. adamsii* was significantly higher in HN than in control plots in 2010 (Fig. 6h).

Discussion

Nitrogen addition to soils of the Mongolian steppe increased grassland productivity during normal rainfall years after a 2-year drought (Fig. 1). Positive effects to grassland productivity in northeastern Asia from the addition of N have also been reported in recent studies (Bai et al. 2010; Chen et al. 2011; Gong et al. 2011; Li et al.

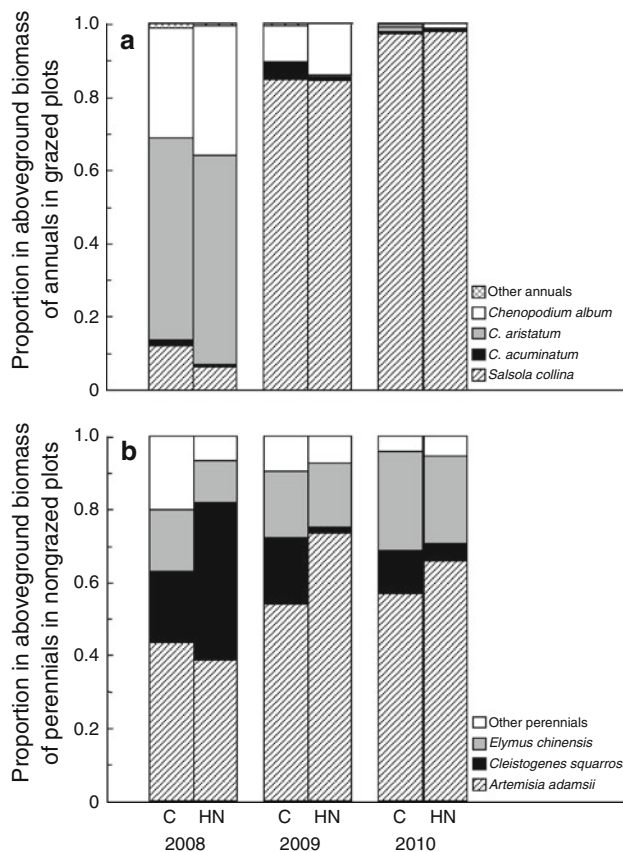


Fig. 5 Relative biomass composition of **a** annual communities in grazed plots and **b** perennial communities in nongrazed plots in normal rainfall years. C control, HN high N treatment

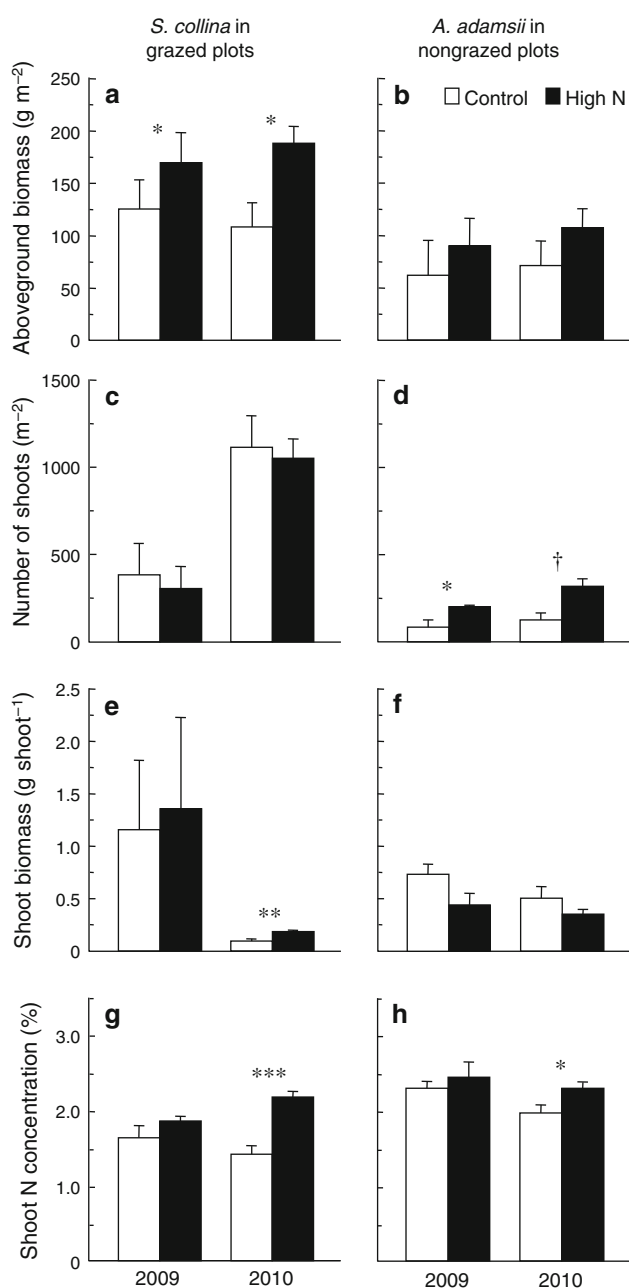


Fig. 6 **a, b** Aboveground biomass, **c, d** number of shoots, **e, f** shoot biomass, and **g, h** shoot N concentration of the annual *Salsola collina* in grazed plots and the perennial *Artemisia adamsii* in nongrazed plots in 2009 and 2010. Error bars +1SE ($n = 6$ for 2010, $n = 4$ for *S. collina* in 2009, $n = 3$ for *A. adamsii* in 2009). † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ (paired t test)

2011). Increased grassland productivity with the addition of N is generally accompanied by a loss of species richness as a result of the heterogeneous response to N among species and interspecific competition (Newman 1973; Aerts and Bobbink 1999; Gough et al. 2000; Bai et al. 2010). In our study, however, a significant reduction in species richness was not found (Fig. 2). This may be because the vegetation in our study area was sparse (plant cover was

less than 50 % even in the HN treatment in 2010) and therefore interspecific competition was low. In Inner Mongolia, the magnitude of species loss with N addition was reported to be small in degraded grassland with low aboveground biomass compared with mature grassland with large amounts of aboveground biomass (Bai et al. 2010). Vegetation density may be a key factor that causes the loss of species richness with increasing N deposition.

We expected that the increase in grassland productivity with the addition of N would be more obvious in grazed than in nongrazed plots because grazing generally favors annuals over perennials and annuals are more sensitive to N content than perennials. However, because N addition increased the biomass of both annuals in grazed plots and perennials in nongrazed plots (Fig. 4), the relative response of grassland productivity to N treatment did not differ between grazed and nongrazed plots (no interactive effect of N and grazing regime on grassland productivity was found; Table 1). The increase in both aboveground biomass of *S. collina*, the dominant annual of grazed plots, and *A. adamsii*, the dominant perennial of nongrazed plots, was accompanied by an increase in shoot N concentration, implying improvement of photosynthetic ability. Increased aboveground biomass of *A. adamsii* resulted from increased shoot emergence, indicating the possible enhancement of clonal expansion, which can lower grassland quality because *A. adamsii* is unpalatable to most livestock (Fernandez-Gimenez and Allen-Diaz 2001; Jigjidsuren and Johnson 2003; Yoshihara et al. 2009).

During post-drought recovery, dominant annuals of the grazed plots shifted from two *Chenopodium* species, *C. aristatum* and *C. album*, to *S. collina* (Fig. 5a). Shifts in dominant annuals during post-drought recovery have also been observed in semi-arid grassland in Arizona (Loeser et al. 2007). The decrease in the *Chenopodium* species during the recovery may be attributed to their high light requirement at germination (Karssen 1967; Vincent and Roberts 1977, 1979). In 2009, the second year after the drought, grassland productivity from the previous year most likely led to an increase in litter, which would have shaded the soil surface and may have reduced the germination of the *Chenopodium* seeds. Litter accumulation can improve soil moisture due to soil shading (Goldberg and Werner 1983), and this may have contributed to an increase in the biomass of *S. collina*, which is known to prefer wetter conditions (Li et al. 2011).

Our results may underestimate the response of grassland productivity to increasing N deposition because shoot emergence can increase beyond what we were able to observe. Larger plant size and/or more shoots with a greater addition of N (Fig. 6) can increase seed production and consequently plant emergence in subsequent years. Nitrogen addition enhanced flowering activity of a

grassland community in Mongolia (Wesche and Ronnenberg 2010) and increased seed production and seed viability of *S. krylovii*, a nutritious grass for livestock, in grasslands in central Asia (Ronnenberg et al. 2011). In our study, it would have been difficult to determine increased grassland productivity through increased seed production because seeds are easily dispersed off site by strong winds. To determine the effects of increased N on seed production, more focused investigations on seed production in response to N content are needed, specifically for species in the study fields. Another possibility is to study natural spatial gradients of N deposition (e.g., Stevens et al. 2004, 2010, 2011a), but continuous observation of N deposition in multiple spots is necessary.

Ammonium nitrate (NH_4NO_3) has commonly been used as an N additive to simulate increasing N deposition. However, the ratio of reduced N (NH_x) to oxidized N (NO_y) with N deposition differs spatially because of differences in their source, atmospheric transformation, and deposition velocity (Galloway et al. 2004; Dentener 2006; van den Berg et al. 2008). While NO_y emissions result primarily from fossil fuel combustion, NH_x emissions mainly result from agricultural activities, and most deposition of NH_x is relatively near to the emission source (Vitousek et al. 1997; Hornung and Langan 1999; Galloway et al. 2004). In our study area, increased NH_x deposition from 1993 to 2050 was estimated to be about five times greater than NO_y deposition (Dentener 2006). It is well known that foliar uptake of NH_x generally exceeds that of NO_y (Stevens et al. 2011b), while plant species vary in their preference for the form of inorganic N (NO_3^- or NH_4^+) by root uptake (Pearson and Stewart 1993; de Graaf et al. 1998; van den Berg et al. 2008). Thus, it is difficult to speculate how the $\text{NH}_x:\text{NO}_y$ ratio in N deposition affects grassland productivity in our study area.

A simulation of N deposition (LN , $300 \text{ mg N m}^{-2} \text{ year}^{-1}$) around the study area did not indicate that there would be a significant increase in grassland productivity caused by increasing N deposition by the year 2050 (Fig. 1). However, world N deposition estimated by Dentener (2006), on which our N addition is based, has an error of $\pm 50\%$ because of uncertainties in emission inventories, chemical transformation, the deposition process, and atmospheric transport of NH_x and NO_y (cf. Galloway et al. 2004). If human activities rapidly increase in Mongolia and N deposition increases above the estimation of Dentener (2006), grassland productivity could potentially increase. An increase in grassland productivity may occur in grasslands on the Mongolian plateau with a higher N deposition, such as northeastern Inner Mongolia (Dentener 2006; Lu and Tian 2007).

In summary, the addition of N increased grassland productivity of the Mongolian steppe after a drought, irrespective

of grazing. This greater productivity might be attributed to enhanced photosynthesis due to the increase in plant N with N addition; this was accompanied by an increase in plant size of the annual *S. collina* under grazed conditions and an increase in shoot emergence of the perennial *A. adamsii* under non-grazed conditions. The simulation of N deposition around the study area by 2050 did not significantly increase grassland productivity. Our results imply that increasing N deposition can enhance grassland recovery after a drought even in arid environments, such as the Mongolian steppe. In the Mongolian steppe, post-drought recovery of grassland productivity may be accompanied by the loss of grassland quality due to an increase in an unpalatable species (*A. adamsii*). The quality and extent of recovery largely depends on future human activities and the level of N deposition in Mongolia.

Acknowledgments We thank T. Ganbold, T. Batoyun, G.U. Nanchinshonhor, Y. Purevdorj, E. Nishihara, T. Kawai, T. Nakano, Y. Suzuyama, and N. Tsuchihashi for their kind help during the field survey. Comments of Dr. T. Hirose, Tokyo University of Agriculture, helped improve this manuscript. We thank two anonymous reviewers for constructive comments on an earlier version of the manuscript, as well as Dr. C. Körner, University of Basel, and Dr. M. Bustamante, University of Brasilia, for useful comments and for editing the manuscript. This work was supported in part by a Grant-in-Aid for Young Scientists (B) by the Ministry of Education, Culture, Sports, Science and Technology, Japan [18770016].

Conflict of interest None.

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