

Impact of drought on vegetation dynamics of the Mongolian steppe: A field experiment

M. Shinoda^{a,*}, G.U. Nachinshonhor^b, M. Nemoto^c

^a *Arid Land Research Center, Tottori University, 1390 Hamasaka, Tottori 680-0001, Japan*

^b *National Museum of Ethnology, Osaka 565-0826, Japan*

^c *National Agricultural Research Center for Hokkaido Region, Sapporo 062-8555, Japan*

ARTICLE INFO

Article history:

Received 11 July 2008

Received in revised form

13 July 2009

Accepted 19 July 2009

Available online 6 August 2009

Keywords:

Climate change

Ecosystem resilience

Ecosystem sensitivity

Grassland

Rain shelter

Sustainability

ABSTRACT

Drought has become widespread in the Northern Hemisphere and has affected the specific Mongolian steppes both quantitatively and qualitatively. To simulate vegetation responses to drought, we conducted a drought experiment in the Mongolian steppe during a rainy summer growing season. A 30 × 30 m rain shelter excluded natural precipitation during the 2005-growing season, simulating a drought with a return interval of 60–80 years. We examined the effects of the drought on aboveground phytomass (AGP) of each species, total belowground phytomass (BGP), and soil water. The drought drastically reduced AGP and soil water but did not substantially affect BGP. AGP recovered quickly in the late summer of 2006, likely because BGP (which was several times AGP) was not severely damaged by the drought. However, the poorly resilient species did not recover to pre-drought levels, suggesting that the response time scales differed among species. Despite the intense drought, the large root system provided a basis for quick recovery of AGP to pre-drought levels without a shift to a drier equilibrium community. We propose new drought sensitivity and resiliency indices to measure the ecosystem's sustainability and identify species with low sensitivity (i.e., high drought tolerance) that form the baseline of AGP.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

Recent widespread and intense droughts have become likely manifestations of large-scale climate change, including global warming. Droughts have become widespread in the Northern Hemisphere, including Asia, and particularly in Mongolia (e.g., Barlow et al., 2002; Dai et al., 1998; Hoerling and Kumar, 2003; Lotsch et al., 2005). In Mongolia, the increasing drought frequency has had more and more important effects on animal husbandry and pasturing (e.g., Natsgadorj, 2003). The effects of drought on Mongolian grasslands have been both quantitative, such as decreases in phytomass (Erdenetsetseg et al., 2004; Miyazaki et al., 2004; Munkhtsetseg et al., 2007; Zhang et al., 2005), and qualitative, such as changes in phenology (Kondoh et al., 2005; Shinoda et al., 2007). On the other hand, there have been no comprehensive studies of the impacts of drought on Mongolia's grassland ecosystem, including the effects on plant species composition and root system distributions.

Aboveground primary production in North American grasslands is characterized by the highest interannual variability among different biomes combined with moderate precipitation variability (Knapp and Smith, 2002). Considerable evidence derived from field measurements in grassland ecosystems has accumulated on plant responses to drought (e.g., Bai et al., 2004; Haddad et al., 2002; Lauenroth and Sala, 1992; O'Connor et al., 2001; Wiegand et al., 2004). Some studies have shown that drought, as a disturbance, had negative impacts on plant production in subsequent years (Haddad et al., 2002; Lauenroth and Sala, 1992; Oesterheld et al., 2001; Wiegand et al., 2004). However, years of moderate drought at burned sites are sometimes followed by years with higher production than would be expected from the increased precipitation alone, probably owing to greater nitrogen availability (Briggs and Knapp, 1995). In contrast, Snyman (2005a) reported that over a short term, burning in a semi-arid grassland tended to decrease plant susceptibility to drought by impeding root development.

Several field experiments based on controlled precipitation treatments have been conducted in North American dryland ecosystems (e.g., Bates et al., 2006; English et al., 2005; Knapp et al., 2002; Reynolds et al., 1999; Schwinning et al., 2005). In these ecosystems, precipitation was rather evenly distributed

* Corresponding author. Tel./fax: +81 857 21 7030.

E-mail address: shinoda@alrc.tottori-u.ac.jp (M. Shinoda).

among the seasons, providing a basis for growth of different types of life forms and species with different phenologies, rooting patterns, and physiological responses to soil water. Thus, manipulating drought conditions during the different seasons imposed different influences on each type of life form and species (Bates et al., 2006; Reynolds et al., 1999; Schwinning et al., 2005). Moreover, the impacts of potential changes in rainfall intensity on ecosystems under projected future climate scenarios have been simulated in sophisticated field experiments (Bates et al., 2006; Knapp et al., 2002).

The experiment described here is the first attempt to examine the impacts of drought treatment on an Asian dryland. Mongolia exhibits marked seasonality in precipitation, with rainfall concentrated during a few months of the summer growing season, accompanied by high evapotranspiration. This seasonality differs from those of wide areas of the North American drylands, providing a valuable opportunity to study the responses of rapidly growing plants to a summer drought. Our study site is among the driest of the world's grassland ecosystems, with an annual mean precipitation of less than 200 mm, with values lower than 100 mm occurring in recent drought years and allowing only limited plant growth. In fact, the aboveground primary production (typically no more than 100 g m⁻²) at this site is among the lowest productivities recorded among arid and semi-arid communities (Noy-Meir, 1973). We designed our study to examine the directions of ecosystem response to a severe drought, with a return interval of 60–80 years. Would the ecosystem cross a dry threshold and shift into another drier (or desertified) equilibrium condition, or would it recover to the pre-drought conditions over a long or short time period?

2. Materials and methods

2.1. Site description

Within Mongolia there is a latitudinal gradient of climate and vegetation, with the climate becoming increasingly dry towards the south. The drought experiment (DREX) site at Bayan Unjuul (47°02'37.2"N, 105°57'04.9"E, 1200 masl) is characterized by its semi-arid climate, defined on the basis of the aridity index (UNEP,

1992) between 0.20 and 0.50, and its steppe vegetation (Yunatov, 1976). Meteorological observations have been obtained approximately 400 m southeast of the center of the DREX site by the Institute of Meteorology and Hydrology of Mongolia (IMH) monitoring station. Data from the IMH station reveal that annual precipitation (1995–2005) averaged 163.0 mm, concentrated in the summer months of May to August (124.4 mm). The annual mean temperature is 0.1 °C, ranging from a maximum of 20.6 °C in July to a minimum of –24.0 °C in January, with soil freezing during the 6-month winter (October to March). In this investigation, the precipitation from May to August was most important, because this period generally coincides with the period of plant growth in the Mongolian grasslands (Shinoda et al., 2007). This region has experienced a reduction in summer precipitation since the mid-1990s, with severe droughts (less than 90 mm of annual precipitation) occurring in 2002, 2005, and 2006.

The Mongolian steppe is part of the Eurasian steppe that extends from Hungary in the west to Manchuria in the east; it covers 26.1% of Mongolia. It is characterized by the frequent occurrence of *Caragana* shrubs and *Artemisia* annual forbs, and this differentiates it from other steppe regions (Yunatov, 1976). In general, this steppe is dominated by perennial grasses such as *Stipa*, *Cleistogenes*, *Elymus*, and *Agropyron* species. This species composition also characterizes the study site, which was co-dominated by perennial grasses such as *Stipa krylovii*, *Agropyron cristatum*, and *Cleistogenes squarrosa*, by forbs such as *Artemisia adamsii* and *Chenopodium aristatum*, and by small shrubs such as *Caragana* spp. (Table 1). The soil at the site was classified as a Kastanozem (FAO/ISRIC/ISSS, 1998), which is widely distributed in the plains steppes of Mongolia (Dorjgotov, 2003).

2.2. Experimental design

A 300 × 300 m area at the DREX site has been surrounded by a fence since June 2004 to protect this area from grazing by livestock. The Bayan Unjuul county (*soum*) including our site was grazed with a stocking rate of approximately 0.4 sheep equivalent ha⁻¹ for four years (2000–2003) before establishing the enclosure. This stocking rate was classified as a light to moderate grazing in

Table 1
Plant species and their aboveground phytomass and belowground phytomass in the drought treatment plot at the DREX site at the time of peak phytomass production (August) from 2004 to 2006. SD indicates the standard deviation. The phytomass data represent the means ± SD for four quadrats (n = 4), except where measurements are missing for one or more quadrats. NA indicates that values for three of the four quadrats were zero; thus the SD could not be calculated.

Life form	Species	Life cycle	23 Aug. 2004		19 Aug. 2005		21 Aug. 2006	
			Aboveground phytomass (g m ⁻²)	SD	Aboveground phytomass (g m ⁻²)	SD	Aboveground phytomass (g m ⁻²)	SD
Grass	<i>Agropyron cristatum</i>	Perennial	8.5	9.9	3.3	1.1	1.1	0.7
	<i>Cleistogenes squarrosa</i> ^a	Perennial	44.2	9.7	6.7	2.5	14.4	10.0
	<i>Elymus chinensis</i>	Perennial	7.4	9.7	—	—	—	—
	<i>Stipa krylovii</i>	Perennial	4.0	2.3	3.3	3.8	5.8	3.7
Sage	<i>Carex</i> spp.	Perennial	7.9	1.0	1.1	0.4	2.1	1.3
Forb	<i>Artemisia adamsii</i>	Perennial	0.7	NA	2.0	2.2	0.0	NA
	<i>Bassia dasyphylla</i>	Annual	—	—	—	—	0.2	0.2
	<i>Chenopodium acuminatum</i>	Annual	—	—	—	—	2.3	0.3
	<i>Chenopodium album</i>	Annual	—	—	—	—	0.3	0.3
	<i>Chenopodium aristatum</i>	Annual	40.7	15.6	—	—	11.2	2.1
	<i>Dontostemon integrifolia</i>	Perennial	0.1	0.1	—	—	—	—
	<i>Draba integrifolia</i>	—	0.0	NA	—	—	—	—
	sp.	—	—	—	0.0	NA	0.0	NA
	<i>Salsola ruthenica</i>	Annual	—	—	—	—	4.4	3.0
	Shrub	<i>Caragana</i> spp.	Perennial	1.9	1.7	2.6	1.4	2.4
Aboveground phytomass			115.4	28.3	19.0	1.7	44.3	5.6
Belowground phytomass			301.2	67.2	183.4	94.1	227.6	102.7
Total phytomass			416.6	—	202.4	—	271.9	—

^a Species with the C4 photosynthetic pathway. All other plants are C3 species.

a similar steppe region of Mongolia (Sugita et al., 2007). Inside the fenced area, we established two kinds of no-grazing plot: a control, with unmodified natural precipitation, and a drought treatment. The drought treatment was conducted using a rain shelter with a transparent polyethylene roof, with an average height of 1.5 m above the ground, open on all sides, during the growing season from 23 May to 3 August 2005. The size of the drought plot was 30 × 30 m, with a 2 m buffer strip bordering the plot. At the center of the buffer strip, we dug a 30-cm-deep, 60-cm-wide trench to drain water from the rain shelter and to prevent lateral movement of soil water between the two types of plot.

Aboveground phytomass (AGP) measurements were conducted approximately monthly during the growing season from June to August by clipping all plants within four 1 × 1 m quadrats that were randomly located within each plot. In general, the AGP of the grasslands reaches its yearly maximum in late August. The locations of the quadrats were moved every month so that no area was clipped twice. The clipped plant materials were sorted into phytomass and litter, and the phytomass was separated by species. All the plant materials were oven-dried at 80 °C for more than 75 h, and were then weighed to determine their dry weights.

In the same four quadrats, belowground phytomass (BGP) was measured immediately after the AGP sampling by excavating all roots in the top 20 cm of the soil within a 25 × 25 cm quadrat. This layer was within the 24-cm A-horizon, which represents the major rooting zone in the study area. In a typical steppe of eastern Mongolia, the top 20-cm layer of the soil includes 57.9% and 80.7% of the total BGP for *Elymus* and *Stipa* communities, respectively (Jargalsaikhan, 2008), which are among the dominant species at our site. The BGP measurement quadrats were increased to 50 × 50 cm in July 2006 to improve the precision of the measurements. The sampled materials were sieved through a 0.3 × 0.3 cm mesh and the soil was washed away. The roots were then oven-dried at 80 °C for more than 75 h and weighed to provide their dry weights. We calculated average AGP and BGP values and their standard deviations for the four quadrats at each measurement time in both the control and drought plots.

We compared the initial conditions for the control and drought plots in September 2003 and August 2004 to examine systematic differences in AGP, BGP, species diversity, and physical or chemical soil properties. During the drought treatment, we measured air and ground-surface temperatures, relative humidity, and photosynthetically active radiation (PAR) inside and outside the rain shelter to examine the effect of the shelter on microclimate. The observation point outside the shelter was located inside the fenced area. In this study, we assumed that all the precipitation from 1 May to the day before destructive sampling of the plants was available to the plants (hereafter referred to as the plant-available precipitation). We used the daily precipitation data observed at the IMH station for this parameter. Since the top 30 cm of the soil includes the majority of the rooting zone, as explained above, we measured the volumetric soil water content at 10-cm (in the center of the rooting zone) and 30-cm depths (below the rooting zone) inside and outside the shelter from 2004 to 2006, including the drought treatment period, by using time-domain reflectometry (TRIME-EZ, IMKO, Germany). This method can provide fast, precise, and nondestructive in situ measurements. Furthermore, to evaluate the drought-derived water stress imposed on the plant, we calculated the rooting-zone soil water content at three levels: field capacity, the lentic-capillary point, and the permanent wilting point (Fig. 1). These values were estimated on the basis of soil texture by the method of Saxton et al. (1986). The lentic-capillary point is defined as the soil water at which a plant starts to experience significant water stress because the movement of capillary water has been interrupted.

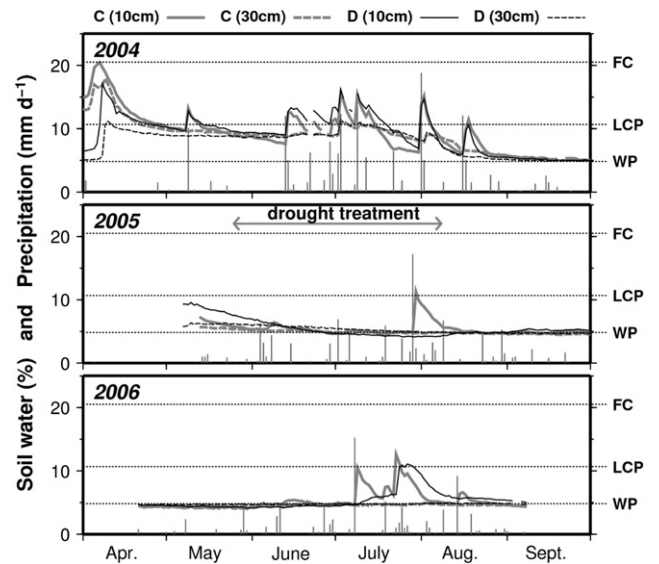


Fig. 1. Time series of daily precipitation and volumetric water content in the drought plot (black lines) and the control plot (gray lines) at depths of 10 cm (solid lines) and 30 cm (broken lines) from 2004 to 2006. The drought treatment period in 2005 is indicated by the horizontal arrow. FC, LCP, and WP denote the field capacity ($pF \approx 2.0$), lentic-capillary point ($pF \approx 3.0$), and permanent wilting point ($pF \approx 4.2$), respectively.

2.3. Statistical analysis

The experimental layout was a fully randomized design, consisting of two treatments (control and drought plots) with four replicates (quadrats). We calculated mean AGP and BGP values (and standard deviations) for the four quadrats. Statistically significant differences in phytomass between the two types of plot were determined by the Tukey–Kramer test.

We used precipitation data collected for the Mandalgovi station from 1944 to 2002 to estimate the probability of occurrence of the drought produced by the rain shelter. We used the data for this station because long-term data from the Bayan Unjuul station of IMH are not available and because the Mandalgovi station has similar climatic conditions. We fitted a gamma distribution to the year-to-year data for the yearly maximum number of days without precipitation from May to August from 1944 to 2002. In this analysis, we defined dry spells as the longest continuous period without precipitation exceeding 3 mm d^{-1} (a value much smaller than the minimum potential evaporation) between May and August.

2.4. Sensitivity and resilience analyses of phytomass

Tilman and Downing (1994) proposed the relative rate of phytomass change (dM/Mdt , yr^{-1}) between pre-drought and drought years to quantify the sensitivity of a plant community to a drought. In this parameter, M denotes the AGP in the pre-drought year. We modified this index by replacing M with M_m , the multi-year average, and by considering the quantitative effects of precipitation change (dP/P_mdt , yr^{-1}), which has the strongest influence on the phytomass of drylands, all else being equal. The resulting sensitivity index (SI) is thus expressed as:

$$SI = \frac{dM_{pre}/dP_{pre}}{M_m/P_m} \quad (1)$$

where dM_{pre} and dP_{pre} denote changes in phytomass and precipitation, respectively, from the pre-drought year to the drought year, and M_m and P_m denote the multi-year averages of phytomass and

precipitation, respectively. Moreover, the resilience index (*RI*) can be expressed similarly:

$$RI = \frac{dM_{\text{post}}/dP_{\text{post}}}{M_m/P_m} \quad (2)$$

where dM_{post} and dP_{post} denote changes in phytomass and precipitation from the drought year to the post-drought year, respectively. We calculated these indices for changes between two consecutive years. The drought-related changes in phytomass and precipitation between consecutive years (dM and dP) were calculated by using the phytomass data from the drought plot, measured at the end of the growing season (in August, when the phytomass reaches its yearly maximum), and the data for plant-available precipitation in the drought plot from 1 May to the previous dates of phytomass sampling. The value of M_m/P_m ($\text{g m}^{-2} \text{mm}^{-1}$) was calculated by using the phytomass and plant-available precipitation data from the control plot during the three years (2004, 2005, and 2006).

The value of M_m/P_m corresponds to the climatological site-specific rain-use efficiency (Huxman et al., 2004), if we assume that AGP is a good approximation of warm-season aboveground net primary production for the grassland ecosystem, because there is only negligible living aboveground phytomass in the spring after the 6-month winter. With the addition of M_m/P_m , we are able to compare the ecosystem's sensitivity and resilience with those of other regions. The normalizing procedure provided by adding this parameter is necessary because the values of $dM_{\text{pre}}/dP_{\text{pre}}$ and $dM_{\text{post}}/dP_{\text{post}}$ differ among regions, depending on the degree of aridity.

3. Results

3.1. Effect of the rain shelter on microclimate

During the drought treatment, air and ground-surface temperatures were higher inside the shelter than outside by 0.8 °C and 2.3 °C, respectively. PAR inside the shelter averaged 78% of the levels outside the shelter. Relative humidity was slightly lower inside (by 0.1%). The plant-available precipitation was identical in the drought and control plots in 2004 (137.6 mm) and in 2006 (71.7 mm), but during the 2005 drought treatment it decreased from 69.8 mm in the control plot to 9.5 mm in the drought plot (Fig. 1). Our statistical analysis of the long-term precipitation data from the Mandalgovi station indicate that the return interval for a dry spell as intense as the one created during the 2005 drought treatment would be once every 60–80 years.

3.2. Soil water responses

In general, the soil water content was higher at 10 cm depth than at 30 cm depth, rarely reaching field capacity except in April 2004 (Fig. 1). During the summer of 2004, the soil water content frequently exceeded the lentic-capillary point in both plots owing to the relatively frequent and intense precipitation, whereas during the summers of 2005 and 2006 the soil water content remained low, mostly between the lentic-capillary point and the permanent wilting point, because of lower precipitation in both years. The drought treatment most strongly affected soil water content at 10 cm depth. The difference between the drought and control plots was manifested shortly after precipitation events of about 5 mm d^{-1} during June and July 2005; in late July there was no response to the intense rainfall event in the drought plot. On the other hand, the increased soil water content in the control plot rapidly declined to the permanent wilting point. We observed no

substantial difference between the drought and control plots after late August 2005. In 2006, soil water responses to high precipitation during July and August were delayed in the drought plot compared with those in the control plot.

3.3. Plant phytomass responses

We compared the initial conditions for the control and drought plots in September 2003 and August 2004 and found no significant differences ($P > 0.05$) in AGP, BGP, species diversity, and physical or chemical soil properties. Before the drought treatment in 2004, AGP and BGP did not differ significantly ($P > 0.05$) between the two types of plot, and both parameters gradually increased as the rainy season progressed (Fig. 2). During the drought treatment, AGP in the drought plot did not increase, whereas it showed the normal seasonal increase in the control plot. AGP was significantly greater ($P < 0.05$) in the control plot during June, July, and August 2005. The difference persisted until July 2006, although the difference was not statistically significant ($P > 0.05$), and it disappeared entirely in August 2006. The effect of the drought on BGP was not dramatic; although BGP was smaller in the drought plot in June and July 2005, the difference was not statistically significant ($P > 0.05$).

3.4. Sensitivity and resilience of phytomass

The value of M_m/P_m was $0.81 \text{ g m}^{-2} \text{mm}^{-1}$ for the study site, and *SI* and *RI* were 0.93 and 0.50, respectively. In 2005, the effect of drought was evident in four species (although the clear decrease from 2004 to 2006 was not statistically significant ($P > 0.05$) for *A. cristatum*) but not in *S. krylovii* and *Caragana* spp. (Fig. 3). We only presented data for 6 of the 14 species in Table 1, because those species appeared for 2004 and 2006. We did not include data for *A. adamsii* because it has only a small amount of AGP in all three years. We categorized the species into two major groups in terms of their drought sensitivity and resilience: species with low sensitivity and resilience (*S. krylovii* and *Caragana* spp.) and species with high sensitivity and resilience (*C. squarrosa*, *Carex* spp., and *C. aristatum*). Values of *SI* and *RI* in

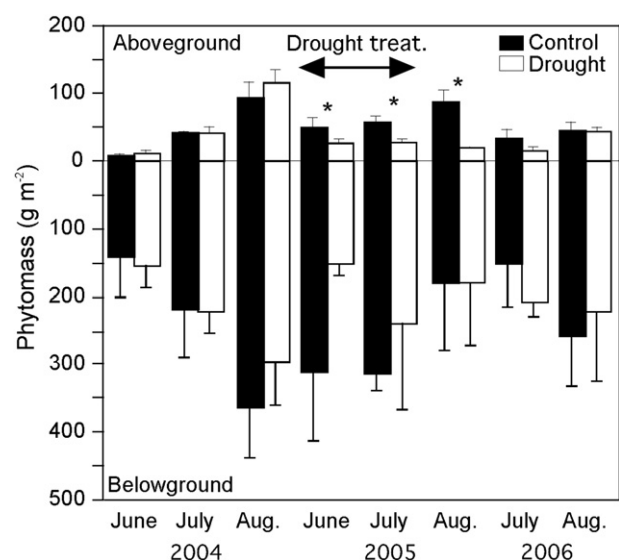


Fig. 2. Aboveground and belowground phytomass values in the control and drought plots from 2004 to 2006. Values represent means \pm SD ($n = 4$). The drought treatment was conducted from May to August 2005. Asterisks indicate statistically significant differences in phytomass between the control and drought plots (Tukey–Kramer test, $P < 0.05$).

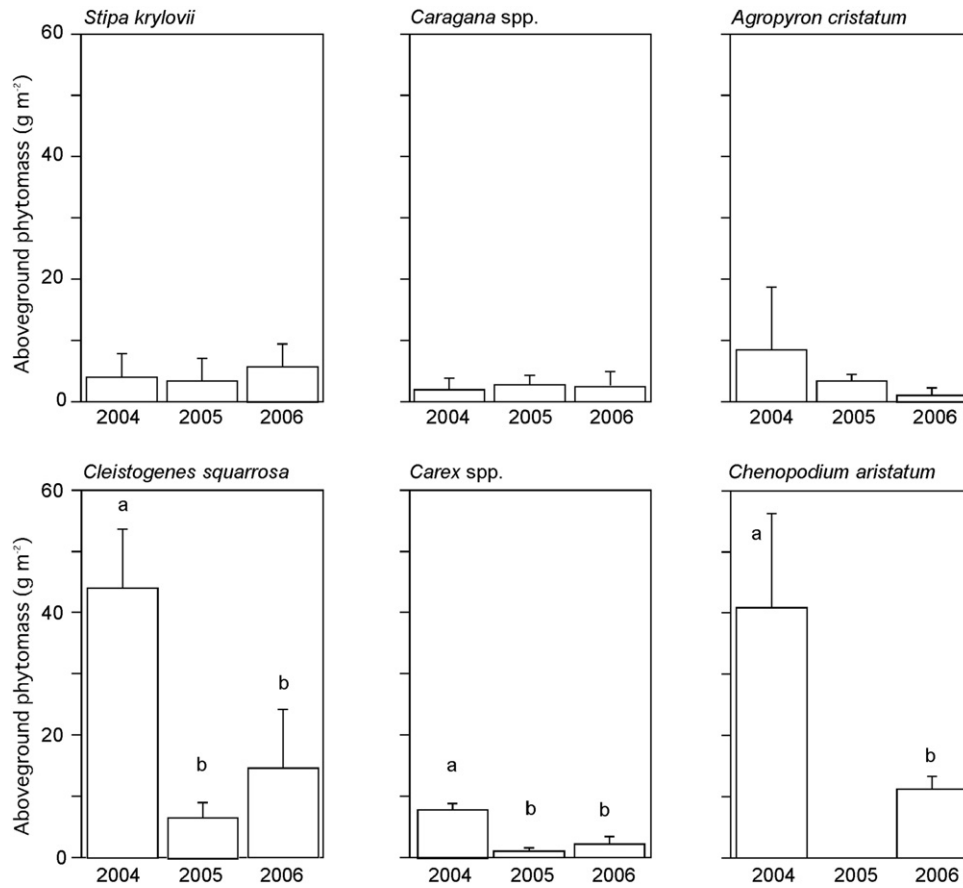


Fig. 3. Aboveground phytomass for six species in the drought plot during August from 2004 to 2006. Bars for a species labeled with different letters differ significantly ($P < 0.05$) among years.

the first group averaged 0.00 and 0.04, respectively, versus values of 0.82 and 0.40 in the second group. *A. cristatum* had low resilience ($SI = 0.05$, $RI = -0.04$), and AGP for this species did not recover in 2006.

4. Discussion and conclusions

4.1. Effect of the rain shelter on microclimate

The drought treatment produced by the rain shelter resembled drought conditions with a return interval of 60–80 years. During the drought treatment, the air and ground-surface temperatures inside the shelter increased by amounts comparable to the increases in air temperature (0.5–2 °C) and ground-surface temperature (2.5–4 °C) that were observed in similar treatments by Schwinning et al. (2005) and Svejcar et al. (1999). The PAR reduction under the shelter (22%) was smaller than that (about 50%) observed by Svejcar et al. (1999), and comparable to those in previous studies (22%, Fay et al., 2000; 24%, English et al., 2005). Our shelter had a minimal impact on relative humidity. These results indicate that, except for the interception of precipitation, our rain shelter increased temperature and decreased PAR by values similar to those in previous research. In the natural droughts that occur in southern Mongolia, decreased precipitation and increased temperature occur simultaneously, and the combination of these changes was strongly correlated with pasture yield in a previous study (Munkhtsetseg et al., 2007). Thus, the microclimate produced by our rain shelter resembled the natural drought conditions that are experienced in Mongolia, except for the

reduction in PAR. (During a drought, PAR would be expected to increase because of reduced cloudiness.)

4.2. Soil water and plant responses

It is likely that the relatively high soil water content in April 2004 (Fig. 1) resulted from snowmelt water after snow accumulation during the preceding winter. In the summer of 2004, the soil water content exceeded the lentic-capillary point, thereby providing conditions favorable for plant growth, whereas during the summers of 2005 and 2006 soil water ranged mostly between the lentic-capillary point and the permanent wilting point, and this suppressed plant growth (Fig. 2). This is because plant-available precipitation in 2005 and 2006 was only about half that in 2004 (Section 3.1).

Although no difference in soil water between the two types of plot at a depth of 10 cm appeared from June to mid-July 2005 (Fig. 1), the impact of the decreased soil water on AGP was significant in both months (Fig. 2). This suggests that the major portion of the soil water in the control plot remained in the top 10 cm of the soil and that it was utilized efficiently to support plant growth. The intense rainfall that occurred in late July 2005 was prevented from affecting the drought plot, where AGP did not increase in August, whereas AGP increased significantly in the control plot after this rain. Thus, the plants in the drought plot experienced severe water stress during the summer season. No substantial drought effect was observed at the 30-cm depth. Since potential evaporation is far larger than precipitation in the study area (data not shown), most of the soil water provided by precipitation did not reach that depth,

and instead evaporated or was transpired quickly from the upper layers of the soil. The soil depth to which precipitation penetrated is similar to that observed at Mandalgovi by Yamanaka et al. (2007).

In late August 2005, the increased soil water in the control plot decreased rapidly to the permanent wilting point as a result of evapotranspiration. As Shinoda et al. (2004) reported, there was no clear “drought memory effect” between the drought treatment in 2005 and the following year. That is, the difference between the two types of plot was minimal before the onset of the main rainy season in July 2006, whereas the responses to the first intense rainfall in early July differed substantially at 10 cm depth, in that water content did not respond quickly in the drought plot. This difference appears to have been caused by the changes in soil properties produced by the drought treatment. Highly compacted and extremely dry soil was observed near the ground surface, preventing precipitation from infiltrating to a depth of 10 cm. This tendency was also seen in the delayed response to intense rainfall (with daily precipitation of nearly 5 mm or more) in July and mid-August 2006. As mentioned above, precipitation and evaporating water are present in the top soil layer (Yamanaka et al., 2007), and the soil water at a depth of 30 cm did not exhibit a clear response to the precipitation. This suggests that soil water deeper than 30 cm has a negligible influence on the variation in soil water at shallower depths.

Despite the lack of a difference in soil water contents between the two types of plot after late August 2005 (Fig. 1), a difference in AGP could be seen in the next growing season until July 2006, though the difference was not significant (Fig. 2). On the other hand, there was no significant difference in BGP during and after the drought experiment. AGP was 38% of BGP in August 2004, before the drought (Fig. 2, Table 1). During the drought, AGP decreased to 10% of the corresponding BGP, but it recovered to 19% of BGP in the year after the drought. BGP in August 2005 decreased to 61% of its pre-drought value (in August 2004), versus a decrease to 16% of its pre-drought value for AGP. This relative stability of BGP likely accounts for the quick recovery in AGP. In brief, the results support our second hypothesis, namely that the ecosystem would recover quickly to its pre-drought conditions in terms of AGP and BGP.

As mentioned in Section 2.2, the top 20-cm layer of the soil includes the majority of the total BGP at our site. This suggests that the shallower roots are largely responsible for the observed biomass production. However, we do not rule out the possibility that roots that penetrate deeper than 20 cm improve survival during drought conditions, as has been pointed out by Snyman (2005b).

4.3. Sensitivity and resilience of phytomass

The value of M_m/P_m ($0.81 \text{ g m}^{-2} \text{ mm}^{-1}$) for the study site falls within the range between 0.5 and $2.0 \text{ g m}^{-2} \text{ mm}^{-1}$ that was determined by Noy-Meir (1973) on an annual basis for dryland ecosystems. The value also lies in the range from less than 0.05 to 1.00 for rangelands of arid and semi-arid zones around the world (Le Houérou, 1984; Le Houérou et al., 1988). The normalizing procedure that we used for M_m/P_m in equations (1) and (2) produces values such that SI (or RI) greater than 1.0 denotes sensitivity (or resilience) higher than the site-specific multi-year average. Conversely, values less than 1.0 indicate lower sensitivity (or resilience). Judging from the fact that SI and RI were 0.93 and 0.50 , respectively, AGP responded to the drought as quickly as expected from the multi-year data, but the recovery was slower than expected on the basis of these data.

The group of plants with low sensitivity to drought (*S. krylovii* and *Caragana* spp.) forms the baseline AGP and stabilizes Mongolian grasslands, despite the drastic changes caused by drought. In

2006, even some species in the second group (*C. squarrosa*, *Carex* spp., and *C. aristatum*) had high resilience but still did not recover to the AGP level that existed in 2004. This is probably because the plant-available precipitation in 2006 (71.7 mm) was only about half that in 2004 (137.6 mm). Most seriously, the impact of the drought remained obvious, even in the year after the drought, in the low-resilience species *A. cristatum*. Given that a multi-year memory effect resulting from past droughts has been reported in previous studies (Haddad et al., 2002; Lauenroth and Sala, 1992; Oesterheld et al., 2001; Wiegand et al., 2004), this species should be observed continuously for several more years to learn the time scale over which its recovery from drought is delayed.

The potential for compensation among species or functional groups has been suggested as a way for plant productivity to stabilize in regions where climate, and particularly precipitation, varies among years (e.g., Bai et al., 2004; O'Connor et al., 2001; Tilman and Downing, 1994), but no such compensating effect has been reported in other studies (e.g., Pfisterer and Schmid, 2002). Our results indicated that, under extreme drought conditions in one of the world's driest grassland ecosystems, no compensation was evident in terms of AGP because of consistent reductions in AGP among the species.

In conclusion, we demonstrated that despite the severity of the drought (a return interval of 60–80 years), the root system of the plants retained a phytomass (BGP) that was several times the AGP value, and this permitted a quick recovery of AGP to pre-drought conditions, without shifting the plant community to equilibrium conditions for a drier climate. Given the background of global climate change and recent widespread droughts in the world's drylands, the sensitivity and resilience indices described in this paper will be useful tools for comparing the sustainability of dryland ecosystems in different regions in response to drought disturbance.

Acknowledgements

This research was supported by Grants-in-Aid for Scientific Research from the Japanese Ministry of Education, Science, Sports, and Culture (Nos. 16405002, 20255001).

References

- Bai, Y., Han, X., Wu, J., Chen, Z., Li, L., 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature* 431, 181–183.
- Barlow, M., Cullen, H., Lyon, B., 2002. Drought in central and southwest Asia: La Niña, the warm pool, and the Indian Ocean precipitation. *Journal of Climate* 15, 697–700.
- Bates, J.D., Svejcar, T., Miller, R.F., Angell, R.A., 2006. The effect of precipitation timing on sagebrush steppe vegetation. *Journal of Arid Environments* 64, 670–697.
- Briggs, J.M., Knapp, A.K., 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. *American Journal of Botany* 82, 1024–1030.
- Dai, A., Trenberth, K.E., Karl, T.R., 1998. Global variations in droughts and wet spells: 1900–1995. *Geophysical Research Letters* 25, 3367–3370.
- Dorjgotov, D., 2003. Soils of Mongolia. Admon, Ulaanbaatar, p. 287 (in Mongolian).
- English, N.B., Weltzin, J.F., Fravolini, A., Thomas, L., Williams, D.G., 2005. The influence of soil texture and vegetation on soil moisture under rainout shelters in a semi-desert grassland. *Journal of Arid Environments* 63, 324–343.
- Erdenetsetseg, D., Shinoda, M., Nemoto, M., 2004. Drought assessment in Mongolia. In: Nam, J.-C., Park, S.K. (Eds.), *Proceedings of International Conference on High-impact Weather and Climate: Understanding, Prediction and Socio-economic Consequences*, Seoul, Korea, 22–24 March 2004. Secretariat of ICHWC, Seoul, pp. 288–291.
- FAO/ISRIC/ISSS, 1998. World Reference Base for Soil Resources. World Soil Reference Reports 84. FAO, Rome, p. 88.
- Fay, P.A., Carlisle, J.D., Knapp, A.K., Blair, J.M., Collins, S.L., 2000. Altering rainfall timing and quantity in a mesic grassland ecosystem: design and performance of rainfall manipulation shelters. *Ecosystems* 3, 308–319.
- Haddad, N.M., Tilman, D., Knops, J.M.H., 2002. Long-term oscillations in grassland productivity induced by drought. *Ecology Letters* 5, 110–120.

- Hoerling, M., Kumar, A., 2003. The perfect ocean for drought. *Science* 299, 691–694.
- Huxman, T.E., Smith, M.D., Fay, P.A., Knapp, A.K., Shaw, M.R., Loik, M.E., Smith, S.D., Tissue, D.T., Zak, J.C., Weltzin, J.F., Pockman, W.T., Sala, O.E., Haddad, B.M., Harte, J., Koch, G.W., Schwinning, S., Small, E.E., Williams, D.G., 2004. Convergence across biomes to a common rain-use efficiency. *Nature* 429, 651–654.
- Jargalsaikhan, L., 2008. Dynamics of Natural Pasture Plant Communities in the Eastern Mongolian Grassland Ecosystem. PhD dissertation, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, pp. 16–17 (in Russian).
- Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S., McCarron, J.K., 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* 298, 2202–2205.
- Knapp, A.K., Smith, M.D., 2002. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291, 481–484.
- Kondoh, A., Kaihotsu, I., Hirata, M., Azzaya, D., 2005. Interannual variation of phenology and biomass in Mongolian herbaceous vegetation. *Journal of Arid Land Studies* 14, 209–218 (in Japanese with English abstract).
- Lauenroth, W.K., Sala, O.E., 1992. Long-term forage production of North American shortgrass steppe. *Ecological Applications* 2, 397–403.
- Le Houérou, H.N., 1984. Rain use efficiency: a unifying concept in arid-land ecology. *Journal of Arid Environments* 7, 213–247.
- Le Houérou, H.N., Bingham, R.L., Skerbek, W., 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *Journal of Arid Environments* 15, 1–18.
- Lotsch, A., Friedl, M.A., Anderson, B.T., Tucker, C.J., 2005. Response of terrestrial ecosystems to recent Northern Hemispheric drought. *Geophysical Research Letters* 32, L06705. doi:10.1029/2004GL022043.
- Miyazaki, S., Yasunari, T., Miyamoto, T., Kaihotsu, I., Davaa, G., Oyunbaatar, D., Natsagdorj, L., Oki, T., 2004. Agrometeorological conditions of grassland vegetation in central Mongolia and their impact for leaf area growth. *Journal of Geophysical Research* 109, D22106. doi:10.1029/2004JD005658.
- Munkhtsetseg, E., Kimura, R., Wang, J., Shinoda, M., 2007. Pasture yield response to precipitation and high temperature in Mongolia. *Journal of Arid Environments* 70, 94–110.
- Natsagdorj, L., 2003. Climate change. In: Batima, P. (Ed.), *Climate Change: Pasture and Animal Husbandry*. Institute of Meteorology and Hydrology of Mongolia, Ulaanbaatar, pp. 13–44.
- Noy-Meir, I., 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4, 25–51.
- O'Connor, T.G., Haines, L.M., Snyman, H.A., 2001. Influence of precipitation and species composition on phytomass of a semi-arid African grassland. *Journal of Ecology* 89, 850–860.
- Oosterheld, M., Loreti, J., Semmartin, M., Sala, O.E., 2001. Inter-annual variation in primary production of a semi-arid grassland related to previous-year production. *Journal of Vegetation Science* 12, 137–142.
- Pfisterer, A.B., Schmid, B., 2002. Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature* 416, 84–86.
- Reynolds, J.F., Virginia, R.A., Kemp, P.R., de Soyza, A.G., Tremmel, D.C., 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecological Monographs* 69, 69–106.
- Saxton, K.E., Rawls, W.J., Romberger, J.S., Papendick, R.I., 1986. Estimating generalized soil-water characteristics from texture. *Soil Science Society of America Journal* 50, 1031–1036.
- Schwinning, S., Starr, B.L., Ehleringer, J.R., 2005. Summer and winter drought in a cold desert ecosystem (Colorado Plateau) part I: effects on soil water and plant water uptake. *Journal of Arid Environments* 60, 547–566.
- Shinoda, M., Ito, S., Nachinshonhor, G.U., Erdenetsetseg, D., 2007. Phenology of Mongolian grasslands and moisture conditions. *Journal of Meteorological Society of Japan* 85, 359–367.
- Shinoda, M., Nemoto, M., Erdenetsetseg, D., 2004. Role of soil moisture memory in drought processes over the Asian–African arid region. In: Nam, J.-C., Park, S.K. (Eds.), *Proceedings of International Conference on High-impact Weather and Climate: Understanding, Prediction and Socio-economic Consequences*, Seoul, Korea, 22–24 March 2004. Secretariat of ICHWC, Seoul, pp. 308–311.
- Snyman, H.A., 2005a. Influence of fire on root distribution, seasonal root production and root/shoot ratios in grass species in a semi-arid grassland of South Africa. *South African Journal of Botany* 71, 133–144.
- Snyman, H.A., 2005b. Rangeland degradation in a semi-arid South Africa: 1. Influence on seasonal root distribution, root/shoot ratios and water-use efficiency. *Journal of Arid Environments* 60, 457–481.
- Sugita, M., Asanuma, J., Tsujimura, M., Mariko, S., Lu, M., Kimura, F., Azzaya, D., Adyasuren, Ts., 2007. An overview of the rangelands atmosphere–hydrosphere–biosphere interaction study experiment in northeastern Asia (RAISE). *Journal of Hydrology* 333, 3–20.
- Svejcar, T., Angell, R., Miller, R., 1999. Fixed location rain shelters for studying precipitation effects on rangelands. *Journal of Arid Environments* 42, 187–193.
- Tilman, D., Downing, J.A., 1994. Biodiversity and stability in grasslands. *Nature* 367, 363–365.
- UNEP, 1992. *World Atlas of Desertification*. Arnold, London, p. 69.
- Wiegand, T., Snyman, H.A., Kellner, K., 2004. Do grasslands have a memory: modeling phytomass production of a semiarid South African grassland. *Ecosystems* 7, 243–258.
- Yamanaka, T., Kaihotsu, I., Oyunbaatar, D., Ganbold, T., 2007. Summertime soil hydrological cycle and surface energy balance on the Mongolian steppe. *Journal of Arid Environments* 69, 65–79.
- Yunatov, A.A., 1976. *Fundamental Characteristics of the Vegetation of Mongolian People's Republic*. Mongolian Academy of Science, Ulaanbaatar (in Mongolian).
- Zhang, Y., Munkhtsetseg, E., Kadota, T., Ohata, T., 2005. An observational study of ecohydrology of a sparse grassland at the edge of the Eurasian cryosphere in Mongolia. *Journal of Geophysical Research* 110, D14103. doi:10.1029/2004JD005474.