

UC Davis

UC Davis Previously Published Works

Title

Differential response of alpine steppe and alpine meadow to climate warming in the central Qinghai-Tibetan Plateau

Permalink

<https://escholarship.org/uc/item/88k3v71b>

Authors

Ganjurjav, Hasbagan
Gao, Qingzhu
Gornish, Elise S
et al.

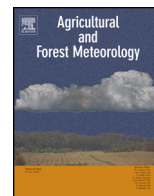
Publication Date

2016-06-01

DOI

10.1016/j.agrformet.2016.03.017

Peer reviewed



Differential response of alpine steppe and alpine meadow to climate warming in the central Qinghai–Tibetan Plateau



Hasbagan Ganjurjav^{a,b}, Qingzhu Gao^{a,b,*}, Elise S. Gornish^c, Mark W. Schwartz^d, Yan Liang^{a,b}, Xujuan Cao^{a,b}, Weina Zhang^{a,b}, Yong Zhang^e, Wenhan Li^{a,b}, Yunfan Wan^{a,b}, Yue Li^{a,b}, Luobu Danjiu^f, Hongbao Guo^f, Erda Lin^{a,b}

^a Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agricultural Sciences, Beijing 100081, China

^b Key Laboratory for Agro-Environment & Climate Change, Ministry of Agriculture, Beijing 100081, China

^c Department of Plant Sciences, University of California, Davis 95616, USA

^d Institute of the Environment, University of California, Davis 95616, USA

^e State Key Laboratory of Water Environment Simulation, School of Environment, Beijing Normal University, Beijing 100875, China

^f Nagqu Agriculture and Animal Husbandry Bureau, Tibet Autonomous Region, Nagqu 852100, China

ARTICLE INFO

Article history:

Received 9 November 2015

Received in revised form 6 March 2016

Accepted 30 March 2016

Available online 2 May 2016

Keywords:

Warming

Productivity

Community composition

Species diversity

Alpine grassland

ABSTRACT

Recently, the Qinghai–Tibetan Plateau has experienced significant warming. Climate warming is expected to have profound effects on plant community productivity and composition, which can drive ecosystem structure and function. To explore effects of warming on plant community productivity and composition, we conducted a warming experiment using open top chambers (OTCs) from 2012 to 2014 in alpine meadow and alpine steppe habitat on the central Qinghai–Tibetan Plateau. We measured above-ground net primary productivity (ANPP), community composition and species diversity under ambient and two levels of artificially warmed conditions across three years. Our results showed that warming significantly stimulated plant growth in the alpine meadow, but reduced growth on the alpine steppe. The increase of ANPP in alpine meadow was a result of an increase of plant height under warming. Warming-induced drought conditions were primarily responsible for the observed decrease of ANPP in an alpine steppe. Plant community composition and species diversity were not influenced by warming in alpine meadow. Alternatively, in alpine steppe, cover of graminoids and forbs significantly declined while legumes substantially increased under warming, subsequently resulting in rapid species losses. Changes in soil moisture were responsible for observed changes in graminoids and legumes in the alpine steppe. Overall, experimental results demonstrated that warming had a positive impact on plant community structure and function in alpine meadow and had a negative impact on these characteristics in an alpine steppe. This work highlights the important role of soil moisture for regulating plant productivity and community composition response to warming in the alpine steppe. In particular, the deep-rooted, drought resistant plants may increase in a warmer future in the central Qinghai–Tibetan Plateau. These changes may reduce habitat quality for the local community of grazers because many of the species that increased are also unpalatable to grazers.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

Recently, as a result of increase of greenhouse gases emissions, global temperature has been rapidly increasing (IPCC, 2014). Climate change has been shown to invoke dramatic impact on the structure and function of terrestrial ecosystems (Grimm et al.,

2013). Because grasslands occupy a considerable portion of the global terrestrial ecosystem (Saugier et al., 2001), subsequently providing enormous economic and ecological value, many studies have investigated the effects of warming on plant communities in these systems (Walker et al., 2006; Klein et al., 2008; Hudson et al., 2011).

Alpine grasslands, mainly distributed in high altitude regions, are particularly sensitive to the effects of global change. The cold climate in these areas is responsible for soil temperature, soil moisture and soil properties which directly regulate plant growth (Hudson et al., 2011). Climate warming can thaw frozen soil, which is expected to enhance nutrient cycling and increase plant productiv-

* Corresponding author at: Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agricultural Sciences, CAAS. No. 12 South Street Zhongguancun, Beijing 100081, China.

E-mail address: gaoqingzhu@caas.cn (Q. Gao).

ity (Klady et al., 2011). In grasslands, warming may actually induce water stress because of increased evapotranspiration and result in decreased ecosystem productivity (Peñuelas et al., 2007). This is supported by a meta-analysis by Wu et al. (2011) that summarized warming effects on terrestrial ecosystems on the global scale. The authors found that in cases where warming had a negative effect on ecosystems, productivity can be enhanced when warming and precipitation increase occur simultaneously (Wu et al., 2011). Clearly, conditions of ecosystem water supply are important for understanding the directional effect of warming on grassland ecosystems (Mowll et al., 2015).

Climate change can have a significant effect on plant community structure and composition, which will have feedbacks on ecosystem productivity (Polley et al., 2014). This is because species interactions are driven by many factors that are affected by warming, such as microclimates, ecosystem water level and nutrient availability (McCluney et al., 2012). Climate change effects on community structure and composition is dependent on species identity, the number of functional groups and community types, and geographical distributions (Sheldon et al., 2011; Yang et al., 2011; Frenette-Dussault et al., 2013). In regions with small seed banks and low invisibility, like arctic and alpine regions, climate change effects at community level can be considerable. In alpine tundra, for example, warming can induce an increase in the coverage of deciduous shrub and graminoids, and a decrease in the proportions of moss and lichens, resulting in an overall decrease in species diversity (Walker et al., 2006). Also, in alpine grasslands, researchers have found that warming induced sharp decreases of low stature forbs, bryophytes and lichens (Klanderud, 2008).

The Qinghai–Tibetan Plateau, a 2.5 million sq. km region dominated by alpine grassland ecosystems (Gao et al., 2014), is known as the ‘third pole’ on the world because of its high altitude and low temperature (Qiu, 2008) and has experienced continuous warming since the 1960s (Chen et al., 2013; Gao et al., 2013). The region supports domestic grazing by yak and Qinghai–Tibetan sheep as well as natural grazing by endangered ungulates, such as the Qinghai–Tibetan antelope and wild yak. Many studies have been conducted in this region to explore effects of warming on alpine grassland productivity and community structure, but results differ in the identification of a mechanism driving plant community response. Some studies have documented increased productivity under warming in Qinghai–Tibetan Plateau (Li et al., 2011; Peng et al., 2014; Wang et al., 2014). For example, Xu et al. (2009) found that warming stimulated shoot and leaf growth on the eastern plateau. But in northeastern Qinghai–Tibetan Plateau, warming has been found to significantly decrease alpine grassland productivity (Klein et al., 2008). The warming induced heat effects were responsible for decrease of plant productivity and proportion of palatable grasses (Klein et al., 2008). Therefore, it is also unclear how alpine grasslands should be expected to respond to warming in Qinghai–Tibetan Plateau.

We conducted a three-year warming experiment in alpine meadow and alpine steppe on the central Qinghai–Tibetan Plateau, by using open top chambers (OTCs). We collected data describing abiotic soil conditions (including moisture, temperature, organic carbon and nitrogen) and biotic aboveground conditions (such as aboveground net primary productivity (ANPP), composition, cover, and height of each species). We hypothesized that (1) warming would impact ANPP and that this effect may be contingent upon water availability and hence differ between meadows and steppe; (2) warming induced change of ANPP will be distributed differentially among species and alter the competition of species, resulting in changes of plant community structure and species diversity in alpine meadow and alpine steppe.

2. Materials and methods

2.1. Site description and experimental design

We conducted the warming experiment in Nagqu County (31.441°N, 92.017°E; 4460 m above sea level) and Baingoin County (31.389°N, 90.028°E; 4725 m above sea level), Nagqu Prefecture, Tibet Autonomous Region, China. The experimental site located in Nagqu County is characterized by alpine meadow habitat and the site in Baingoin County is characterized by alpine steppe habitat. The mean annual temperature is -1.2°C and -0.4°C in Nagqu County and Baingoin County, respectively. The annual precipitation is 431.7 mm in Nagqu County and 334.1 mm in Baingoin County. The dominant graminoids in the meadow site were *Kobresia pygmaea*, *Carex moorcroftii*, *Poa pratensis*; the dominant forbs were *Potentilla acaulis* and *Lancea tibetica*. The graminoids at the steppe site were *Stipa purpurea*, *Koeleria argentea*, *Festuca ovina*; the dominant forb was *Leontopodium nanum*; and the dominant legume was *Oxytropis microphylla*. The experimental area was grazed by yak before the experiment and fenced in 2010. The site was not grazed or mowed during the experimental period.

The open top chambers (OTCs) were deployed to simulate warming for the entire duration of the year. The OTCs were made of solar transmitting plastic and were cylindrical, with the height of 0.45 m, the diameter of 1.20 m at ground height, and the diameter of 0.65 m at the maximum height (Ganjurjav et al., 2015). Dominant vegetation averaged less than 10 cm in height providing air space above the plant canopy inside chambers. Two types of OTCs were used in this study. One is the typical type, as described above. A second modified type, which includes a fan to reduce the heating effect, was also used. We initiated the warming experiment in July 2011 with four replicates of each of three treatment types: control plots (control), low warming plots (LW, modified OTCs) and High warming plots (HW, use of general type of OTCs) for a 12 plots in both sites, with a total of 24 plots for the whole study.

2.2. Soil measurements

We used the EM50 Data Collection System (Decagon Devices, Inc., NE, USA) for microclimate measurements. We measured the soil temperature and soil water content at 5 cm, 15 cm and 30 cm depth because the roots were mainly distributed at 0–30 cm depth. Because there were no differences among the plots (Control, LW and HW) in soil temperature and moisture at 15 cm (12.4°C and $11.2\% \text{ cm}^3/\text{cm}^3$ in meadow; 13.0°C and $8.8\% \text{ cm}^3/\text{cm}^3$ in steppe) and 30 cm (11.3°C and $10.9\% \text{ cm}^3/\text{cm}^3$ in meadow; 12.3°C and $8.3\% \text{ cm}^3/\text{cm}^3$ in steppe), we only present the soil microclimates collected at 5 cm depth in this paper. The data were collected at 30 min intervals from June to August.

The total organic carbon (TOC), total nitrogen (TN) and available nitrogen were determined by standard methods (Soon and Hendershot, 2007). The availability of ammonium nitrogen (NH_4^+-N) and nitrate nitrogen (NO_3^--N) were measured by ion exchange resin membrane (IERM) as a plant root simulator. First, the IERM (area of $5 \times 2.5 \text{ cm}$) was inserted into the soil and laid at 0–5 cm soil depth in each plot in early June in 2014. After one month, we replaced the previous one. In total, we collected three (June–August) IERM per plot in 2014. The IERM were immersed in a KCl solution (2 mol l^{-1}) and then the NH_4^+-N and NO_3^--N content were measured with an autoanalyzer (BRAN+LUEBBE, AA3, Germany). The availability of NH_4^+-N and NO_3^--N were represented by absorption of NH_4^+-N and NO_3^--N per area per day ($\mu\text{g cm}^{-2} \text{ d}^{-1}$) by IERM.

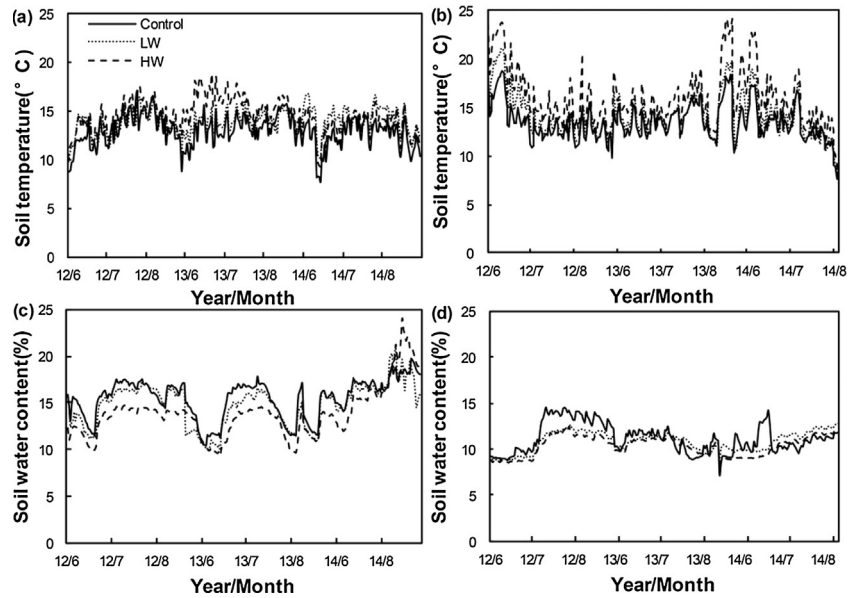


Fig. 1. Average soil temperature and soil water content in each treatment in (a and c) alpine meadow and (b and d) alpine steppe in growing season (June–August) from 2012 to 2014.

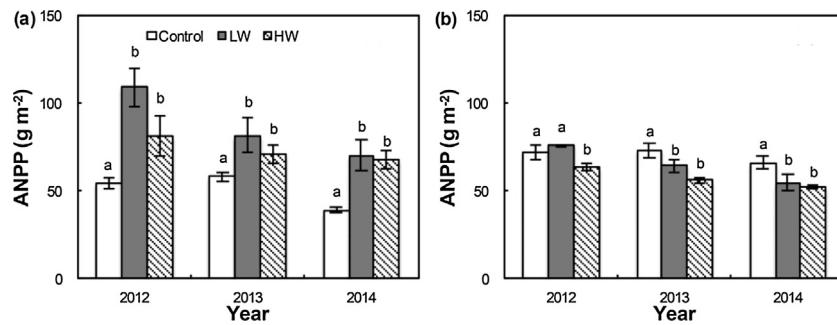


Fig. 2. Average aboveground net primary productivity (ANPP) from 2012 to 2014 (\pm SE) in (a) alpine meadow and (b) alpine steppe site. Different letters indicate significant difference ($P < 0.05$) among treatments.

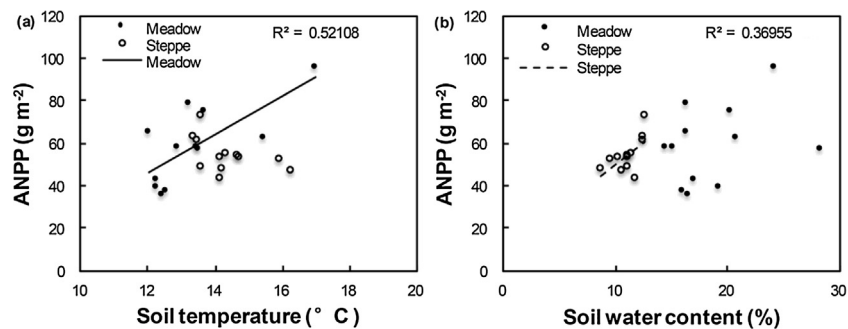


Fig. 3. Correlations between ANPP and (a) soil temperature and (b) soil moisture in alpine meadow and alpine steppe.

2.3. Vegetation measurements

We measured the aboveground net primary productivity (ANPP) at peak biomass in mid-August in 2012, 2013, and 2014. We set 30 calibration plots (0.5 × 0.5 m²) adjacent to the experimental plots. In mid-August, we recorded the cover and height of each plant species in both the experimental plots and the calibration plots. The leaves and stems of the plants in the calibration plots were cut,

sorted, and placed in envelopes. The envelopes were then placed in a drying oven for 30 min at 105 °C, after which the temperature was maintained at 70 °C until a constant weight was reached; the dried plants were then weighed. We then applied a nondestructive method, based on linear regression between aboveground biomass and vegetation height and cover for each species in calibration plots to estimate the total aboveground biomass in the experimental plots (Xia et al., 2009).

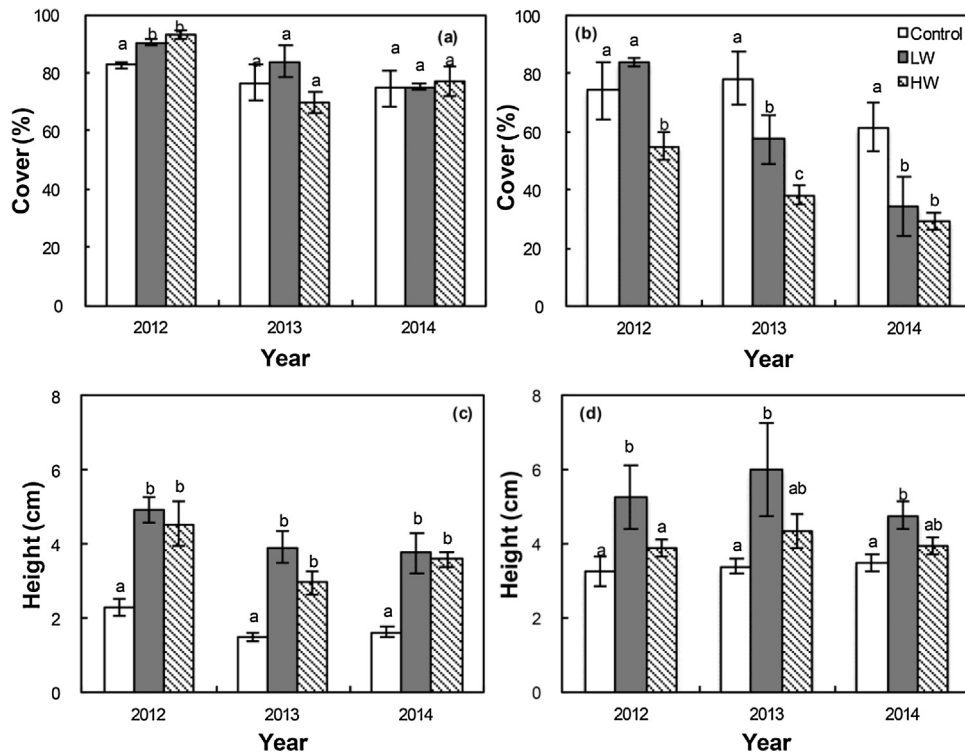


Fig. 4. Average plant cover and height (\pm SE) in (a and c) alpine meadow and (b and d) alpine steppe site from 2012 to 2014. Different letters indicate significant difference ($P < 0.05$) among treatments.

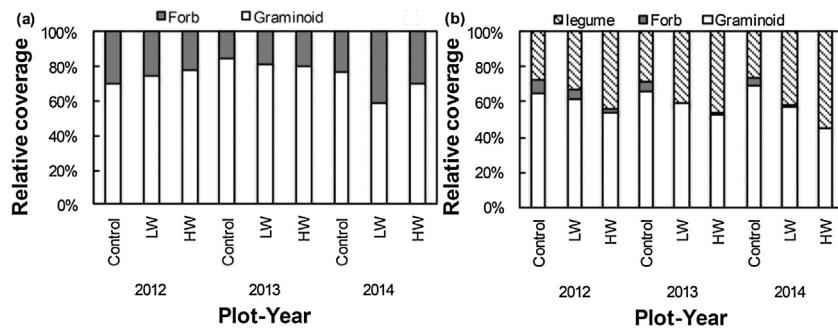


Fig. 5. Relative coverage of functional groups in Control, LW and HW plots in (a) alpine meadow and (b) alpine steppe.

2.4. Data analysis

We calculated the species richness (SR, represented by species number in each plot) and species diversity index to evaluate the treatment effects on plant diversity. Species diversity index (SDI) is represented by Shannon-Wiener diversity index ($H' = -\sum IV \ln IV$). The IV is importance value that characterized by the sum of the mean value of relative cover of each species ($Rci = ci / \sum c$, where ci is the proportion of the ground covered by a vertical projection to the ground from the aerial parts of the species and $\sum c$ is sum of cover for all species) and the relative height of each species ($Rhi = hi / \sum h$, where hi is the height of a given species and $\sum h$ is the sum of the heights for all species).

We use IBM SPSS Statistics version 20.0 software to analyze the data. A GLMANOVA (general linear Model analysis of variance) was used to examine the random effects of treatment, year, and their interactions on aboveground net primary productivity (ANPP), community height (CH), community coverage (CC), species richness (SR) and species diversity index (SDI) at both sites. A PERMANOVA (permutation multi analysis of variance) was used to examine the effects of treatment, year, and their interactions on

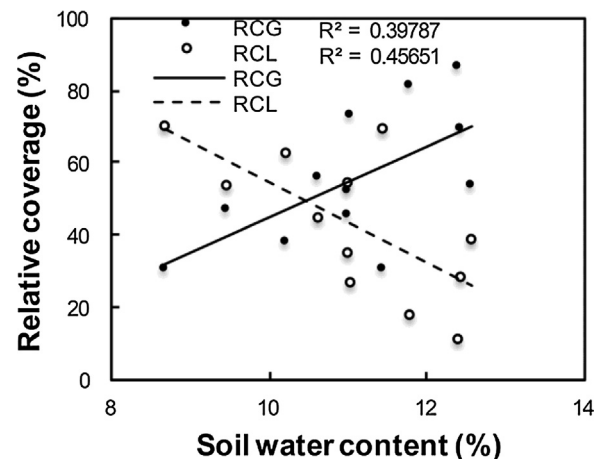


Fig. 6. Correlations between relative coverage of graminoid (RCG)/relative coverage of legume (RCL) and soil water content in the alpine steppe site.

relative coverage of graminoids (RCG), relative coverage of forbs (RCF) and relative coverage of legume (RCL) at both sites.

3. Results

3.1. Soil properties under warming

Over the three years of warming, the shallow soil temperature of treatment plots was significantly higher than control plots during the growing season both in the meadow and the steppe sites (Fig. 1a and b). Average soil temperatures were increased by 1.05 °C and 1.69 °C in low warming (LW) and high warming (HW) plots respectively during the growing season in the meadow site ($P < 0.05$). In steppe site, average soil temperatures were increased by 1.25 °C and 2.55 °C in LW and HW plots, respectively ($P < 0.05$).

Shallow soil moisture of treatment plots was lower in LW and HW plots compared to control plots both in the meadow and the steppe sites (Fig. 1c and d). At the meadow site, average soil moisture decreased by 0.69% and 1.65% in LW and HW plots, respectively ($P < 0.05$). Similarly, at the steppe site, average soil moisture decreased by 0.33% and 0.83% in LW and HW plots, respectively ($P < 0.05$). The baseline soil moisture in steppe ($11.1\% \pm 0.5$) was less than in meadow ($15.5\% \pm 1.0$).

Responses of total organic carbon (TOC) and total nitrogen (TN) to warming were not consistent across the two types of alpine grassland. At the meadow site, both TOC and TN significantly increased under both LW and HW plots ($P < 0.05$). Conversely, both TOC and TN significantly decreased in LW and HW plots in steppe site ($P < 0.05$). Available nitrogen in LW and HW plots was increased significantly in steppe ($P < 0.05$), but did not change in meadow site ($P > 0.05$). The availability of $\text{NH}_4^+ - \text{N}$ and $\text{NO}_3^- - \text{N}$ remained unchanged in LW and HW plots in both sites compared to control plots (Table 1). There were no differences between LW and HW for TOC, TN and available nitrogen in both sites ($P > 0.05$), except for availability of $\text{NO}_3^- - \text{N}$ in alpine meadow site.

3.2. Net primary productivity under warming

After three years of warming, ANPP increased substantially ($P < 0.05$) in treatment plots in meadow site, while the ANPP decreased significantly ($P < 0.05$) in LW (except for 2012) and HW plots in steppe site (Fig. 2a and b, Table 2). We found that ANPP was significantly correlated with soil temperature in meadow site ($r^2 = 0.521$, $P = 0.008$). In the steppe site, ANPP increased with the increase of soil water content ($r^2 = 0.370$, $P = 0.036$, Fig. 3).

3.3. Community characteristics under warming

There was no treatment effect on community coverage in the meadow site except for 2012 ($P < 0.05$, Fig. 4a, Table 2). At the steppe site, community coverage decreased significantly in LW (except for 2012) and HW plots, and the greatest decrease reached 40.1% ($P < 0.05$, Fig. 4b). Our results showed a consistent pattern of increasing plant height with warming at both experimental sites (Fig. 4c and d, Table 2). The meadow community height increased by 134.6% and 106.7% in LW and HW plots, respectively ($P < 0.05$). Similarly, the steppe community height increased significantly ($P < 0.05$) in LW plot (increased by 58.2%) and marginally ($P > 0.05$) in HW plot (increased by 20.2%).

3.4. Community composition under warming

Across the experimental period, coverage of graminoids and forbs was dependent on year, but there have no significant difference among treatments in the meadow site (Fig. 5a, Table 3). At the steppe site, legumes increased significantly ($P < 0.05$) while graminoids decreased substantially ($P < 0.05$) in LW and HW plots compared to control plot from 2012 to 2014 (Fig. 5b, Table 3). After three years of warming, the greatest value of cover of legume reached 41% and 56% in LW and HW plot, respectively. They increased by 15% and 30% in LW and HW plot, respectively, compared to control plots. The soil water content could explain the

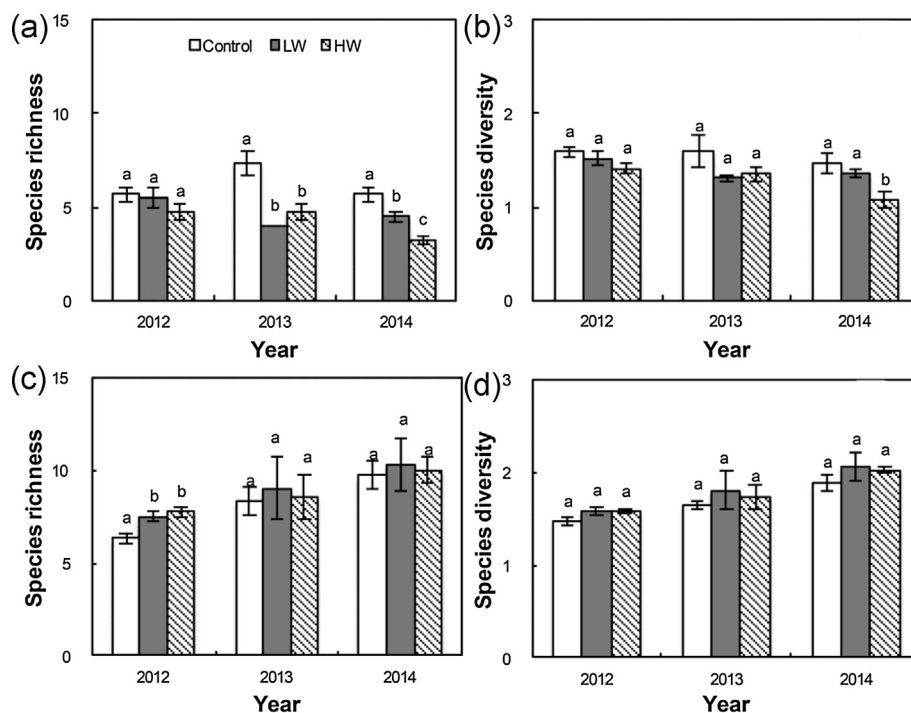


Fig. 7. Average species richness and species diversity index (\pm SE) in Control, LW and HW plots in (a and b) alpine steppe and (c and d) alpine meadow from 2012 to 2014. Different letters indicate significant difference ($P < 0.05$) among treatments.

Table 1
Mean total organic carbon, total nitrogen and available nitrogen (\pm SE) at depth of 0–20 cm and Availability of NH_4^+ -N and NO_3^- -N at depth of 0–5 cm in each treatment in 2014 in alpine meadow and alpine steppe sites.

Factor	System					
	Alpine Meadow			Alpine Steppe		
	Control	LW	HW	Control	LW	HW
Total organic carbon (g kg ⁻¹)	35.43 \pm 1.84a	45.48 \pm 1.53b	51.21 \pm 5.68b	29.10 \pm 0.57a	26.85 \pm 2.86ab	26.52 \pm 0.41b
Total nitrogen (g kg ⁻¹)	4.56 \pm 0.22a	6.10 \pm 0.17b	6.03 \pm 0.72b	4.01 \pm 0.05a	3.72 \pm 0.33ab	3.61 \pm 0.09b
Available nitrogen (mg kg ⁻¹)	147.80 \pm 8.56a	155.85 \pm 19.40a	167.43 \pm 8.30a	63.52 \pm 4.00a	103.62 \pm 3.10b	97.12 \pm 9.26b
Availability of NH_4^+ -N ($\mu\text{g cm}^{-2} \text{ d}^{-1}$)	0.08 \pm 0.02a	0.10 \pm 0.02a	0.08 \pm 0.004a	0.15 \pm 0.03a	0.13 \pm 0.02a	0.10 \pm 0.01a
Availability of NO_3^- -N ($\mu\text{g cm}^{-2} \text{ d}^{-1}$)	0.03 \pm 0.02ab	0.005 \pm 0.003a	0.02 \pm 0.004b	0.04 \pm 0.01a	0.06 \pm 0.01a	0.05 \pm 0.01a

Table 2
Results (P-values) of GLMANOVA on the effects of treatment, year, and their interactions on aboveground net primary productivity (ANPP), community height (CH), community coverage (CC), species richness (SR) and species diversity index (SDI). The bold numbers indicated $P < 0.05$.

Site	Meadow					Steppe				
	ANPP	CH	CC	SR	SDI	ANPP	CH	CC	SR	SDI
Treatment	<0.001	<0.001	0.325	0.636	0.273	<0.001	0.001	<0.001	<0.001	0.002
Year	0.007	0.003	0.001	0.008	<0.001	<0.001	0.492	<0.001	0.022	0.016
Treatment \times Year	0.318	0.775	0.171	0.975	0.998	0.074	0.869	0.074	0.007	0.222

Table 3
Results (F-values and P-values) of PERMANOVA on the effects of treatment, year, and their interactions on relative coverage of graminoids (RCG), relative coverage of forbs (RCF) and relative coverage of legume (RCL). The bold numbers indicated $P < 0.05$.

Factor	Meadow				Steppe					
	RCG		RCF		RCG		RCF		RCL	
	F	P	F	P	F	P	F	P	F	P
Treatment	1.053	0.363	2.755	0.081	7.490	0.003	7.522	0.003	12.806	<0.001
Year	0.450	0.643	7.419	0.003	1.378	0.271	1.709	0.202	2.326	0.119
Treatment \times Year	1.324	0.286	0.776	0.550	1.838	0.154	0.382	0.820	2.313	0.087

45.7% ($r^2 = 0.457$, $P = 0.016$) and 39.8% ($r^2 = 0.398$, $P = 0.028$) cover variations of legume and graminoid, respectively. The soil water content was negatively correlated to cover of legume while positively correlated to cover of graminoid (Fig. 6).

3.5. Plant diversity under warming

Species richness decreased significantly ($P < 0.05$) at the steppe site treatments across the experiment except for 2012 (Fig. 7a). Significant species richness decreases at the steppe site ranged between 20.6% (2014, LW) and 45.4% (2013, LW), with an average decrease of 40.3% and 31.7% by 2013 and 2014, respectively (Fig. 7a). Paralleling species richness, species diversity (SDI) decreased, but this was only significantly ($P < 0.05$) in 2014 at the HW plots relative to LW and control (Fig. 7b). In contrast, there were no significant effects of treatment on species richness (except for 2012) and species diversity at the meadow site (Fig. 7c and d).

4. Discussion and conclusion

Our results provide evidence for the effects of warming on plant community productivity, composition and species diversity in alpine meadow and steppe. Supporting our hypothesis, we found that warming had differential effects on plant productivity in meadow versus steppe. These differences are expressed as increasing plant productivity in meadow but decreasing productivity in steppe. We found that soil moisture was the main difference among the meadow and steppe sites that could regulate plant community productivity and composition. As a consequence, this study

highlights the dominant role of soil moisture for dictating community response to warming in water-limited environments such as Tibetan alpine steppe.

Plant community productivity is an important ecosystem property and a significant indicator of environmental change (Wang et al., 2007). Our results showed that plant community productivity was accelerated in the meadow site at both warming treatment levels. More specifically, increased productivity was correlated with increased soil temperature, but not with increased soil moisture. This pattern indicates that the system is energy/warmth limited rather than water limited. Other results of warming conducted within similar environments (Li et al., 2011; Peng et al., 2014) suggest that this finding is general.

Our data on soil attributes showed that both total organic carbon and total nitrogen increased significantly under warming conditions in alpine meadow site (Table 1). These patterns likely reflect the observed increased productivity in these treatment plots. We also found that an increase of plant community height contributed to plant productivity in alpine meadow site (Fig. 4c), consistent with the findings in arctic tundra (Hudson et al., 2011). In the alpine meadow site, warming did not influence the proportion of each functional group in our experiment. This implies that alpine meadow plant communities have a strong resistance to warming.

Unlike alpine meadow, warming had a negative effect on alpine steppe plant productivity in our study. In addition, the coverage of long-lived graminoids and forbs significantly decreased while a legume (*O. microphylla*) rapidly increased and finally resulted in a rapid species loss under warming (Fig. 5b; Fig. 7). In alpine steppe, warming increased the deep-rooted plant like the unpalat-

able forb *Stellera chamaejasme* (Klein et al., 2007). Also, warming had a negative effect on shallow-rooted species due to water stress (Klein et al., 2008). This implies that warming will have negative effects on plant productivity if the temperature exceeds the ecosystem threshold, which may depend on ecosystem water availability (Welp et al., 2007; Zhao and Running, 2010; Cantarel et al., 2013; Mowll et al., 2015). For example, Mowll et al. (2015) evaluated climate and 67-year ANPP data from semi-arid grasslands in the western US, and found that precipitation and standardized precipitation evaporation were positively related to ANPP. In a recent meta-analysis, Sun et al. (2013) found that on the Qinghai–Tibetan Plateau, aboveground biomass was positively related to precipitation and soil moisture and negatively related to air temperature in the alpine steppe. Their findings supported our hypothesis that soil moisture is the main factor to determine the response of plant productivity to warming in alpine steppe on the Qinghai–Tibetan Plateau.

In the Qinghai–Tibetan Plateau, the cover of alpine steppe (7.5×10^5 sq. km) is approximately three times higher than alpine meadow (2.5×10^5 sq. km) (Ni, 2000). In addition, the projection of future climate change scenarios forecasts that the climate in the central Qinghai–Tibetan Plateau will become warmer and dryer (Gao et al., 2014). Thus, species could be lost in the future in alpine steppe in central Qinghai–Tibetan Plateau, which would be result in extinction risk as documented by Thomas et al. (2004). Moreover, the poisonous plants which cause severe poisoning when eaten by livestock are mainly distributed in alpine steppe (Miehe et al. 2011). Therefore, the poisonous plants would increase which would result in grassland degradation in alpine steppe and perhaps even the whole plateau in the future.

Acknowledgements

We gratefully acknowledge the financial support from the National Natural Science Foundation of China (31570484, 31170460), the National Key Project of Scientific and Technical Supporting Program of China (2012BAC01B02) and the cooperation project with Nagqu Grassland Station and Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agriculture Science. We thank Yawei Li and Zhong Wang for help in field work.

References

- Cantarel, A.A.M., Bloor, J.M.G., Soussana, J., 2013. Four years of simulated climate change reduces aboveground productivity and alters functional diversity in a grassland ecosystem. *J. Veg. Sci.* 24, 113–126.
- Chen, H., Zhu, Q., Peng, C., Wu, N., Wang, Y., Fang, X., Gao, Y., Zhu, D., Yang, G., Tian, J., Kang, X., Piao, S., Ouyang, H., Xiang, W., Luo, Z., Jiang, H., Song, X., Zhang, Y., Yu, G., Zhao, X., Gong, P., Yao, T., Wu, J., 2013. The impacts of climate change and human activities on biogeochemical cycles on the Qinghai–Tibetan Plateau. *Glob. Change Biol.* 19, 2940–2955.
- Frenette-Dussault, C., Shipley, B., Meziane, D., Hingrat, Y., 2013. Trait-based climate change predictions of plant community structure in arid steppes. *J. Ecol.* 101, 484–492.
- Ganjurjav, H., Gao, Q., Zhang, W., Liang, Y., Li, Y., Cao, X., Wan, Y., Li, Y., Danjiu, L., 2015. Effects of warming on CO₂ fluxes in an alpine meadow ecosystem in the central Qinghai–Tibetan Plateau. *PLoS One* 10, e0132044.
- Gao, Q., Ganjurjav Li, Y., Wan, Y., Zhang, W., Borjigidai, A., 2013. Challenges in disentangling the influence of climatic and socio-economic factors on alpine grassland ecosystems in the source area of Asian major rivers. *Quat. Int.* 304, 126–132.
- Gao, Q., Li, Y., Xu, H., Wan, Y., Jiangcun, W., 2014. Adaptation strategies of climate variability impacts on alpine grassland ecosystems in Tibetan Plateau. *Mitig. Adapt. Strateg. Glob.* 19, 199–209.
- Grimm, N.B., Chapin III, F.S., Bierwagen, B., Gonzalez, P., Groffman, P.M., Luo, Y., Melton, F., Nadelhoffer, K., Pairis, A., Raymond, P.A., Schimel, J., Williamson, C.E., 2013. The impacts of climate change on ecosystem structure and function. *Front. Ecol. Environ.* 11, 474–482.
- Hudson, J.M.G., Henry, G.H.R., Cornwell, W.K., 2011. Taller and larger: shifts in Arctic tundra leaf traits after 16 years of experimental warming. *Glob. Change Biol.* 17, 1013–1021.
- IPCC, 2014. Summary for policymakers. In: Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Eds.), *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press Cambridge, United Kingdom and New York, NY, USA, pp. 1–32.
- Klady, R.A., Henry, G.H.R., Lemay, V., 2011. Changes in high arctic tundra plant reproduction in response to long-term experimental warming. *Glob. Change Biol.* 17, 1611–1624.
- Klanderud, K., 2008. Species-specific responses of an alpine plant community under simulated environmental change. *J. Veg. Sci.* 19, 363–372.
- Klein, J.A., Harte, J., Zhao, X.Q., 2007. Experimental warming, not grazing, decreases rangeland quality on the Tibetan Plateau. *Ecol. Appl.* 17, 541–557.
- Klein, J.A., Harte, J., Zhao, X.Q., 2008. Decline in medicinal and forage species with warming is mediated by plant traits on the Tibetan Plateau. *Ecosystems* 11, 775–789.
- Li, N., Wang, G., Yang, Y., Gao, Y., Liu, G., 2011. Plant production, and carbon and nitrogen source pools, are strongly intensified by experimental warming in alpine ecosystems in the Qinghai–Tibet Plateau. *Soil Biol. Biochem.* 43, 942–953.
- McCluney, K.E., Belnap, J., Collins, S.L., González, A.L., Hagen, E.M., Nathaniel Holland, J., Kotler, B.P., Maestre, F.T., Smith, S.D., Wolf, B.O., 2012. Shifting species interactions in terrestrial dryland ecosystems under altered water availability and climate change. *Biol. Rev.* 87, 563–582.
- Miehe, G., Miehe, S., Bach, K., Nölling, J., Hanspach, J., Reudenbach, C., Kaiser, K., Wesche, K., Mosbrugger, V., Yang, Y.P., Ma, Y.M., 2011. Plant communities of central Tibetan pastures in the alpine steppe/*Kobresia pygmaea* ecotone. *J. Arid Environ.* 75, 711–723.
- Mowll, W., Blumenthal, D., Cherwin, K., Smith, A., Symstad, A., Vermeire, L., Collins, S., Smith, M., Knapp, A., 2015. Climatic controls of aboveground net primary production in semi-arid grasslands along a latitudinal gradient portend low sensitivity to warming. *Oecologia* 177, 959–969.
- Ni, J., 2000. A simulation of biomes on the Tibetan Plateau and their responses to global climate change. *Mt. Res. Dev.* 20, 80–89.
- Peñuelas, J., Prieto, P., Beier, C., Cesaraccio, C., De Angelis, P., De Dato, G., Emmett, B.A., Estiarte, M., Garadnai, J., Gorissen, A., Láng, E.K., Kröel-dulay, G., Llorens, L., Pellizzaro, G., Riis-nielsen, T., Schmidt, I.K., Sirca, C., Sowerby, A., Spano, D., Tietema, A., 2007. Response of plant species richness and primary productivity in shrublands along a north–south gradient in Europe to seven years of experimental warming and drought: reductions in primary productivity in the heat and drought year of 2003. *Glob. Change Biol.* 13, 2563–2581.
- Peng, F., You, Q., Xu, M., Guo, J., Wang, T., Xue, X., 2014. Effects of warming and clipping on ecosystem carbon fluxes across two hydrologically contrasting years in an alpine meadow of the Qinghai–Tibet Plateau. *PLoS One* 9, e109319.
- Polley, H.W., Derner, J.D., Jackson, R.B., Wilsey, B.J., Fay, P.A., 2014. Impacts of climate change drivers on C4 grassland productivity: scaling driver effects through the plant community. *J. Exp. Bot.* 65, 3415–3424.
- Qiu, J., 2008. China: the third pole. *Nature* 454, 393–396.
- Saugier, B., Roy, J., Mooney, H.A., 2001. Estimations of global terrestrial productivity: converging toward a single number? In: Roy, J., Saugier, B., Mooney, H.A. (Eds.), *Terrestrial Global Productivity*. Academic Press, San Diego, pp. 543–557.
- Sheldon, K.S., Yang, S., Tewksbury, J.J., 2011. Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure. *Ecol. Lett.* 14, 1191–1200.
- Soon, Y.K., Hendershot, W.H., 2007. Soil chemical analyses. In: Carter, M.R., Gregorich, E.G. (Eds.), *Soil Sampling and Methods of Analysis*. Canadian Society of Soil Science, Boca Raton, FL, pp. 128–332.
- Sun, J., Cheng, G.W., Li, W.P., 2013. Meta-analysis of relationships between environmental factors and aboveground biomass in the alpine grassland on the Tibetan Plateau. *Biogeosciences* 10, 1707–1715.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., De Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. *Nature* 427, 145–148.
- Walker, M.D., Warren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M., Bret-Harte, M.S., Calef, M.P., Callaghan, T.V., Carroll, A.B., Epstein, H.E., Jonsdottir, I.S., Klein, J.A., Magnusson, B., Molau, U., Oberbauer, S.F., Rewa, S.P., Robinson, C.H., Shaver, G.R., Suding, K.N., Thompson, C.C., Tolvanen, A., Totland, O., Turner, P.L., Tweedie, C.E., Webber, P.J., Wookey, P.A., 2006. Plant community responses to experimental warming across the tundra biome. *Proc. Natl. Acad. Sci. U.S.A.* 103, 1342–1346.
- Wang, Y., Yu, S., Wang, J., 2007. Biomass-dependent susceptibility to drought in experimental grassland communities. *Ecol. Lett.* 10, 401–410.
- Wang, X., Dong, S., Gao, Q., Zhou, H., Liu, S., Su, X., 2014. Effects of short-term and long-term warming on soil nutrients, microbial biomass and enzyme activities in an alpine meadow on the Qinghai–Tibet Plateau of China. *Soil Biol. Biochem.* 76, 140–142.
- Welp, L.R., Randerson, J.T., Liu, H.P., 2007. The sensitivity of carbon fluxes to spring warming and summer drought depends on plant functional type in boreal forest ecosystems. *Agric. For. Meteorol.* 147, 172–185.

- Wu, Z., Dijkstra, P., Koch, G.W., Peñuelas, J., Hungate, B.A., 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Glob. Change Biol.* 17, 927–942.
- Xia, J., Niu, S., Wan, S., 2009. Response of ecosystem carbon exchange to warming and nitrogen addition during two hydrologically contrasting growing seasons in a temperate steppe. *Glob. Change Biol.* 15, 1544–1556.
- Xu, Z.F., Hu, T.X., Wang, K.Y., Zhang, Y.B., Xian, J.R., 2009. Short-term responses of phenology, shoot growth and leaf traits of four alpine shrubs in a timberline ecotone to simulated global warming, Eastern Tibetan Plateau, China. *Plant Species Biol.* 24, 27–34.
- Yang, H., Wu, M., Liu, W., Zhang, Z., Zhang, N., Wan, S., 2011. Community structure and composition in response to climate change in a temperate steppe. *Glob. Change Biol.* 17, 452–465.
- Zhao, M., Running, S.W., 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science* 329, 940–943.