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The effects of increased snow depth on plant and microbial biomass and community composition along a precipitation gradient in temperate steppes

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ABSTRACT

Shift in precipitation regime could greatly alter plant and microbial activity, and thus the contemporary and future ecosystem dynamics in grasslands. We investigated how changes in snow depth affect plants, microbes and their relationships after 10 consecutive years of snow treatments in different steppes. We selected 8 snow fences along a mean annual precipitation (MAP) gradient from 225 to 375 mm in Inner Mongolia. For each snow fence, study plots were set up at 7 transects with different levels of snow depth. We found that ecosystem properties, including soil moisture, the biomass and nitrogen (N) pools of microbes and plants, the fungi: bacteria ratio and the grass: forb ratio, increased with increasing snow depth at the drier sites with lower MAP, but not at the wetter sites with higher MAP. At any given site, the sensitivity of these ecosystem properties to changes in snow depth was determined by the slopes of these variables against snow depth. The results showed that the sensitivity of these ecosystem properties to changes in snow depth decreased linearly with increase in MAP levels. In addition, we also found that increased snow depth shifted the relationship between microbial and plant biomass from positive to negative. Our work reveals the importance of snow water in regulating plant and microbial processes in temperate steppes, especially under lower MAP conditions. The greater plant and microbial biomass and the shift of community toward greater fungi: bacteria and grass: forb ratio imply that increased snowmelt input alleviated water limitation in temperate steppes and altered plant and microbial communities. Our study helps to better predict that how changes in winter precipitation could affect the biomass and composition of plants and soil microbes in grasslands.

1. Introduction

Numerous studies have assessed how changes in precipitation regimes influence ecosystem structure and functioning using manipulation experiments (Bachar et al., 2010; Estiarte et al., 2016). Most of these studies focused on the effects of annual or summer precipitation on plant and microbial processes, and often with site-level data (Vicente-Serrano et al., 2013; Estiarte et al., 2016). Climate change is expected to alter the amount of precipitation falling as snow in Northern Hemisphere (Peng et al., 2010; IPCC, 2014). In addition, the changes in wind patterns or vegetation cover will also alter snow redistribution by wind drifting, especially in ecosystems with short-status plants such as grasslands (Ayres et al., 2010). Snow could greatly affect water and nutrient cycles, especially during winter and early growing season (Schimel et al., 2004). However, we know very little about how changes in snow depth or redistribution will affect the productivity and communities of plants and soil microbes, as well as their relationship across the precipitation gradient.

Changes in snow depth can affect soil microbial activity and plant growth through abiotic or biotic mechanisms (Buckeridge et al., 2010; Sorensen et al., 2016). Greater snow accumulation elevates soil temperature by insulating soils from cold winter air (Brooks et al., 2005; Natali et al., 2011), and increases soil moisture (Groffman et al., 2001). Aside from increasing water availability (Groffman et al., 2001), greater snow depth stimulates nitrogen (N) mineralization (Schimel et al., 2004; Freppaz et al., 2007, 2012) and increases N availability during spring, especially in N limited ecosystems (Buckeridge et al., 2010; Leffler and Welker, 2013). Together these mechanisms can increase water and nutrient supply for soil microbes and plants (Groffman et al., 2006; Buckeridge et al., 2010). In addition, greater snow accumulation

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Table 1
Mean annual temperature (MAT), precipitation (MAP), snow depth (measured in 2016), soil properties and the dominant plant species in the 8 sites.

Sites	Coordinates	MAT (°C)	MAP (mm)	Snow depth (cm)	Steppe type	Soil type	Soil C (g kg^{-1})	Soil N (g kg^{-1})	C:N	Soil pH	Dominant plant species
AER Aershan	44.73 N 115.78 E 994 m a.s.l.	1.9	225	10.9 ± 0.76	Typical	Chestnet (China) Kastanozem (FAO)	7.0 ± 0.75	0.8 ± 0.05	8.7 ± 0.5	7.49 ± 0.08	*Aneurotepidimu chinense* *Cleistogenes squarrosa* (Trin.) Keng. *Stipa krylovii* Roshev.
BAY Bayanbaolige	44.05 N 115.94 E 1022 m a.s.l.	2.1	247	6.2 ± 0.58	Typical	Chestnet (China) Kastanozem (FAO)	13.3 ± 0.82	1.5 ± 0.07	9.0 ± 0.5	7.88 ± 0.08	*Aneurotepidimu chinense* *Stipa krylovii* Roshev.
WUL Wulagai	45.68 N 117.46 E 965 m a.s.l.	0.4	280	NA	Typical	Chestnet (China) Haplic Calcisols (FAO)	13.6 ± 0.80	1.3 ± 0.05	10.3 ± 0.5	7.11 ± 0.08	*Aneurotepidimu chinense* *Cleistogenes squarrosa* (Trin.) Keng. *Stipa krylovii* Roshev.
XIL Xilinhot	43.93 N 116.28 E 1230 m a.s.l.	1.5	283	14.7 ± 1.10	Typical	Chestnet (China) Haplic Calcisols (FAO)	15.4 ± 0.68	1.5 ± 0.05	10.0 ± 0.5	7.36 ± 0.08	*Aneurotepidimu chinense* *Carex korshinskyi*
BAI Baiyinxile	43.62 N 116.65 E 1187 m a.s.l.	1.6	301	21.6 ± 0.71	Typical	Chestnet (China) Haplic Calcisols (FAO)	6.6 ± 0.07	0.8 ± 0.07	8.2 ± 0.4	7.15 ± 0.04	*Aneurotepidimu chinense* *Stipa krylovii* Roshev. *Agropyron cristatum* (L.) Gaertn.
DAL Dalinuoer	43.46 N 116.75 E 1257 m a.s.l.	1.5	314	18.8 ± 3.40	Typical	Chestnet (China) Haplic Calcisols (FAO)	7.5 ± 0.06	0.9 ± 0.05	8.6 ± 0.5	7.38 ± 0.08	*Aneurotepidimu chinense* *Artemisia annua* L. *Carex korshinskyi*
HAL Halagaitu	45.83 N 119.43 E 908 m a.s.l.	0.3	368	13.0 ± 0.54	Meadow	Chernozem (China) Chernozem (FAO)	19.2 ± 0.91	1.7 ± 0.05	11.0 ± 0.5	6.86 ± 0.08	*Leymus chinensis* (Trin.) Tzvel. *Carex korshinskyi* *Cleistogenes squarrosa* (Trin.) Keng.
GAN Ganqiaobao	45.69 N 119.52 E 980 m a.s.l.	0.2	375	16.3 ± 0.86	Meadow	Chernozem (China) Chernozem (FAO)	12.9 ± 0.82	1.1 ± 0.09	11.6 ± 0.6	6.95 ± 0.18	*Leymus chinensis* (Trin.) Tzvel. *Agropyron cristatum* (L.) Gaertn. *Cleistogenes squarrosa* (Trin.) Keng.

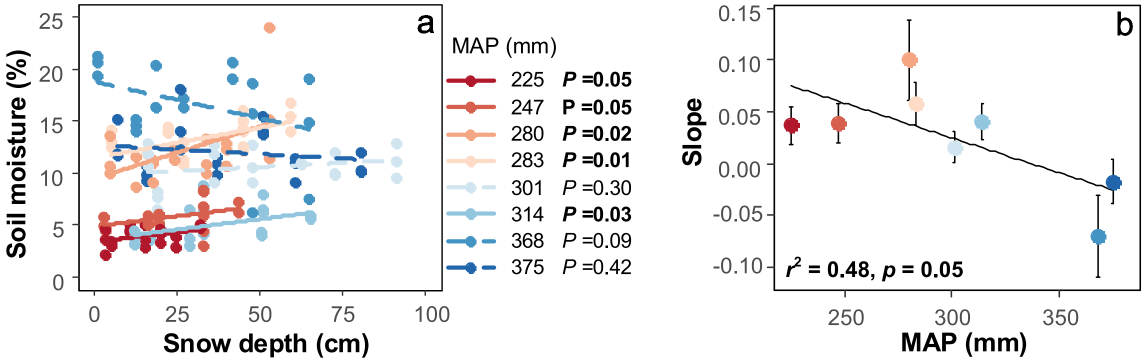

Fig. 1. The relationships between snow depth and soil moisture (0–10 cm) under each MAP level (225 mm, 247 mm, 280 mm, 283 mm, 301 mm, 314 mm, 368 mm, and 375 mm) (a) and the changes in their slopes with increased levels of MAP (b). Solid lines indicate significant relationships ($P \leq 0.05$) and dashed lines indicate non-significant relationships.

could also alter both plant and microbial community compositions (Zinger et al., 2009; Kreyling et al., 2012; Bokhorst et al., 2013; Morgado et al., 2016; Semenova et al., 2016).

The sensitivity of ecosystem productivity to changing precipitation, defined as the slope of the precipitation-productivity relationship, have often found to be related to local precipitation conditions (Knapp et al., 2017). How rainfall changes will affect the sensitivity of plant productivity to precipitation has been studied in various ecosystems using rainfall manipulative experiments (Estiarte et al., 2016; Knapp et al., 2017). However, currently there are limited experimental evidences on how changes in snow depth will affect the productivity and communities of plants and microbes along precipitation gradients, and whether long-term changes in snow amount will modify the patterns of plant-microbe interactions at a landscape scale. Coordinated distributed experiments (CDEs) (Fraser et al., 2013) involving snow gradients offer a tractable approach for addressing these questions. For example, in Inner Mongolia, China, snow fences have been built to reduce snow accumulation on roads during winter. The redistribution of snow by drifting generates a long-term gradient of snow depth on both sides of the snow fences, and eventually alters the amount of snow water input to soils.