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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

47 that how changes in winter precipitation could affect the biomass and composition of
48 plants and soil microbes in grasslands.

49

50 **Keywords:** Microbial biomass; Microbial community; Plant biomass; Plant
51 community; Plant-microbe relationship; Sensitivity.

52

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; Freppaz et al., 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 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; Semanova 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. Those snow fences can be treated as CDEs to test how variation in snow depth affects plant and microbial biomass and communities.

In the current study, we selected 8 snow fences that were built in 2003 across a precipitation gradient from 225 to 375 mm in temperate steppes in Inner Mongolia. We analyzed the biomass and composition of plants and microbes 10 years after the fences were built. Therefore our study includes snow depth variation driven by snow fences within sites and the precipitation gradient across sites. We aimed to test the hypothesis that increased snow depth would increase plant and soil microbial biomass and alter their community compositions. Specifically, increasing snow depth would alleviate water limitation for plants and microbes, and thus increase their biomass. The sensitivity of plant and microbial biomass to increasing snow depth would decrease with the increase in local MAP. In addition, we expected that changes in snow depth will alter plant and microbial community composition, and consequently induce changes in the relationships between plants and microbes.

2. Materials and methods

2.1. Study sites and experimental design

Snow fence sites were located in Inner Mongolia in Northern China (Table 1). Average maximum winter snow depth has ranged from 8.3 to 13 cm over the past 20 years, with an increasing trend over the past 20 years (Peng et al., 2010). Snow fences with a height of 2 m were installed parallel to highways and perpendicular to the prevailing winter wind direction by the Inner Mongolia Department of Transportation. Fences were located 150-200 m from the highways (Figs. S1 and S2).

We selected 8 snow fences built in 2003 along a precipitation gradient (225 to 375 mm/yr) from west to east in Inner Mongolia. These sites included typical and

meadow steppe ecosystems and the details were listed in Table 1. For all fences, there was a consistent pattern of snow accumulation, with early accumulation and deeper snow near the fence to late accumulation and shallower snow away from the fence (Fig. S1). Specifically, we established 6 sampling transects parallel to each of the snow fences, located at 3, 7, and 10 m on either side. We also established another transect 100 m away from the snow fence as an ambient snow treatment. This resulted in 7 snow depth transects in each site. On each transect, we established 3 replicate sampling plots separated by 50 m, resulting in 21 sampling plots total per site (Fig. S2).

Soil samples were collected from all plots during August 1-15, 2013. Sampling was timed to coincide with maximum aboveground biomass in each site. In each plot, four soil cores (5 cm depth and 5 cm diameter) were taken at random and combined into a composite sample. After removing roots and stones by sieving (2 mm mesh), the samples were stored on ice and transferred to the lab for inorganic N concentration and microbial analyses within one week. Subsamples were taken to measure gravimetric water content and soil chemical properties (air-dried, finely ground, and sieved to $< 250\mu\text{m}$).

2.2. Snow depth calculation

During February 15-28, 2016, we measured snow depth using poles to push through the snow to the soil surface at each transect in each site. We measured 3 replicates to get a mean snow depth for each transect.

We used a model based on wind tunnel testing to simulate the maximum snow depths on the windward and leeward sides of each fence for 2013 (Zhao, 2012). The model was validated and calibrated with the snow depth measured in 2016. Snow depth at WUL could not be measured because the access road was temporarily closed to vehicles. For WUL, we used the average of measured snow depth in the two nearby sites (BAY and XIL) to validate modeled snow depth. Prior to calibration, the model was reasonably accurate at predicting the snow depth for most sites, although there was a tendency to overestimate snow depth at AER. To account for any site-level bias, we calibrated the model outputs from 2013 based on a regression of modeled versus measured snow depth in 2016 (Fig. S3). At each site i , we calculated snow depth for 2013 as $D_i^* = (D_i - b_i)/m_i$, where D_i is the modeled 2013 snow depth, and b_i and m_i are the regression intercept and slope for each site in 2016.

Based on the calibrated model outputs, we calculated the cross-site mean snow depth for each of the snow fence transects. Among the 7 transections, there was 1 snow-reduced transect (Snow-R) with 48% reduction in ambient snow depth, 1 ambient snow depth transect (Ambient), and 5 snow-increased transects (Snow-In1, Snow-In2, Snow-In3, Snow-In4 and Snow-In5), which were equivalent to 1.8, 2.3, 3.3, 3.7 and 4.8 mean folds of increase in ambient snow depth, respectively (Table S1).

2.3. Plant and soil properties

Aboveground plant biomass was estimated by clipping live biomass at the same time as soil sampling. All living plant tissues were harvested from a 1×1 m quadrat in

each plot, and plant litter in the same quadrat was also collected. All plant samples were oven-dried at 70 °C for 48 h and weighed to determine biomass.

Soil bulk density was measured by calculating the ratio of the oven-dried mass (105°C) of soil to bulk soil volume. Soil C, soil N, and plant N were determined using elemental analysis (Analysensysteme, Germany).

The biomass and structure of the soil microbial community was assessed by phospholipid fatty acids (PLFA) analysis using the method described by Frostegard & Baath (1996). The resultant fatty acid methyl esters were separated, quantified, and identified using capillary gas chromatography (GC). Qualitative and quantitative fatty acid analyses were performed with an Agilent 6890 gas chromatograph (Agilent Technologies, Palo Alto, CA) and the MIDI Sherlock Microbial Identification System (MIDI, Newark, DE, USA). The concentration of each individual phospholipid fatty acid (PLFA) (among the 25 most abundant PLFAs) was expressed as nmol g⁻¹ dry soil in a given sample based on an internal standard (methyl ester C19:0, Sigma-Aldrich). Using bulk density values, these concentrations were expressed in units of mol m⁻². Total fatty acids were used to represent total soil microbial biomass. The fatty acids i-14:0, i-15:0, a-15:0, i-16:0, 16:1 ω 9, i-17:0, a-17:0, 17:0-cyclo, 18:1 ω 9 and 19:0-cyclo were pooled to represent bacterial PLFA biomass; 18:2 ω 6 was used as an indicator of fungal biomass (representing decomposer fungi, but not arbuscular mycorrhizal fungi) (Frostegard and Baath, 1996), and 16:1 ω 5c was used as an indicator of arbuscular mycorrhizal fungal (AMF) biomass. The ratio of fungal to bacterial PLFA was taken to represent the relative abundance of these two groups.

Soil microbial C and N were estimated using the chloroform fumigation-extraction method (Vance et al., 1987). Briefly, fresh soil samples were transferred to the lab, and field moist samples (15 g dry weight equivalent) were fumigated for 24 h with ethanol-free CHCl_3 . The fumigated and unfumigated samples were then extracted with 60 ml of 0.5M K_2SO_4 for 30 min on a shaker. K_2SO_4 extracts were filtered through 0.45 μm filters and frozen at -20°C prior to analysis for extractable C and N by an elemental analyzer (liquid TOC, Analysensystem, Germany) and Kjeldahl digestion, respectively. Microbial C and N were calculated as the difference between extractable C and N in the fumigated and the unfumigated samples using a conversion factor of 0.45 (Liu et al., 2016). MBC in the BAY and AER sites was not determined due to instrument failure.

2.4. Statistical analysis

We used univariate linear regression to assess how the measurements of ecosystem properties, including soil moisture (0-10 cm), plant aboveground biomass, microbial PLFA biomass, plant and microbial community composition varied along with the snow depth for each site. To assess whether those ecosystem properties were more sensitive to changes in snow depth at the drier sites, we extracted the regression slopes from each sites and used linear model to evaluate whether the slopes decreased along with the increase in MAP across sites. We also used linear model to explore the relationships between soil moisture and soil microbial or aboveground biomass at each site.

To determine how changes in snow depth affect plant-microbe relationship, we conducted linear regressions between total microbial PLFAs and plant biomass across sites for each snow transect. We took the slopes from these regressions as an index of the plant-microbial relationship (i.e. positive slope = positive relationship) and compared the differences in slopes among the 7 snow depth transects by one-way ANOVA. All statistical analyses were performed with R 3.2.2 (R Development Core Team). Significance was accepted at P value <0.05 level of probability.

3. Results

3.1. Soil moisture

Soil moisture increased significantly with increase in snow depth for 5 sites with lower MAP (225, 247, 280, 283, 314 mm), but no significant pattern was observed at the other 3 sites with higher MAP (301, 368 and 375 mm, Fig. 1a). When pooling all sites together, the slopes between soil moisture and snow depth decreased linearly with MAP levels (Fig. 1b).

3.2. Biomass and N pools of soil microbes and plants

Total PLFAs and plant biomass increased with increase in snow depth, although such correlations were significant only at the low MAP sites (Figs. 2a and 3c). The responses of both soil microbial and plant biomass N pools were consistent with the responses of total PLFAs and plant biomass at each site, respectively (Figs. 3a and 3c). Except for soil microbial biomass N pool, the slopes of those variables against snow

depth negatively correlated with MAP levels (Figs. 2b, 2d, 3b and 3d). Changes in snow depth did not affect soil N pool across all sites (Figs. 3e and 3f).

3.3. Community composition of soil microbes and plants

Similarly, fungi:bacteria ratio (Fig 4a), AMF abundance (Fig 4c), grass biomass (Fig 5a) and grass: forb ratio (Fig 5e) tended to increase with increase in snow depth, but the significant correlations were only found at the low MAP sites. When pooling all sites together, the slopes of F:B ratio (Fig 3b), AMF abundance (Fig 3d), grass biomass (Fig 4b) and grass: forb ratio (Fig 4f) against snow depth all declined along with the increase in MAP (Figs. 2b and 2d). No significant pattern was observed for forb biomass (Fig 4c and 4d)

3.4. Plant-microbe correlations

We also pooled data for each snow transect and assessed whether changes in snow depth will alter the relationships between plants and microbes across the precipitation gradient. Microbial PLFA biomass correlated positively with plant biomass at the snow-reduced and the ambient snow transects (Figs. 6a and b). However, the regression slopes declined with increasing snow depth, becoming negative at the transect with deepest snow (Figs. 6c-g). The regression slopes were significantly different among the 7 snow transects (Fig. 6h).

4. Discussion

Our findings indicate that increasing snow depth stimulated plant and soil microbial growth, and altered their community composition in temperate steppes, but

these effects diminished with increasing MAP levels. The stimulation in plant and microbial biomass at the low MAP sites could be due to alleviation of water stress from increased snowmelt (Loik et al., 2013). In Inner Mongolia, plant growth during spring highly relied on snow water, especially in the dry steppes (Peng et al., 2010). The greater sensitivity of plant and microbial productivity to increase in snow depth under lower MAP levels is similar to the more pronounced plant productivity responses to rainfall in the drier regions (Haverd et al., 2017). In addition, we found that soil moisture during summer time was significant higher at transects with deeper snow at five low MAP sites (Fig. 1a), implying that the effects of snow on soil moisture could persist until the summer. This could be due to that increasing winter snow amount enhanced soil water holding capacity by increasing litter layer thickness and root density (Loik et al., 2013). Our findings indicated that the amount of winter snow direct or indirectly regulated soil water availability in temperate steppes, and this effect can even last till summer. How winter snow contributes to ecosystem water use efficiency should be assessed in future studies.

Plant and microbial communities are expected to respond and adapt to environmental changes in the long-term (Walker and Wardle, 2014). Grassland productivity in Inner Mongolia is co-limited by water and N (Bai et al., 2004; Niu et al., 2010). When water limitation is alleviated via greater snowmelt inputs, plants and microbes would require more nutrients to support their growth. Indeed, we found that increasing snow depth increased the size of plant and microbial N pools at the low MAP sites (Figs. 3a and 3c), but soil N pool did not change at any site (Fig. 3e). In

this situation, species with higher capacity to acquire nutrients or with higher nutrients use efficiency could become more dominant (Gong et al., 2011; Yang et al., 2011). Indeed, we found that grass biomass, which have higher C:N ratios (Fig. S4) and denser root systems than forbs, increased with greater snow at the low MAP sites. The high fine root biomass of grasses could reduce nutrient leaching during snow melt (Kreyling et al., 2012). Furthermore, the denser root systems could increase AMF infection as we found AMF increased with snow depth (Fig. 4c), which should facilitate nutrient transfer from soils to plants (Hodge et al., 2000; Phillips et al., 2013).

There is a great interest in exploring how environmental change-induced shift of community will alter the pattern of ecological processes (Estiarte et al., 2016; Knapp et al., 2017). Our study showed that increasing snow amount generally stimulated plant and microbial biomass at the low MAP sites, but did not alter them at the high MAP sites. The differential responses to snow amount could alter the relationship between plants and microbes. Indeed, we found that there were positive relationships across sites between plant and microbial biomass at the two shallow snow transects (Fig. 6), which is consistent with previous predictions that plant productivity positively correlates with microbial biomass because plants and microbes trade C and nutrients with each other (Zak et al., 1994). However, with the increase in snow amount, the plant-microbe relationship shifted from positive to negative. Although our study could not fully reveal the mechanisms that govern the relationship between plants and microbes under increasing snow depth, we demonstrated that the current

relationships of plants and microbes could not be used to predict their relationship in future climate scenario.

Compared to rainfall manipulation studies that have been extensively conducted across biomes, few long-term studies have been done to explore how snow regime changes affect ecosystem processes. Our study, although with a relative narrow range of MAP (225 - 375 mm), provides initial evidence on the importance of snow and rainfall regimes jointly regulating the patterns of plant and microbial processes. Future researches spanning over a wider range of MAP gradient are needed to improve our understanding of the legacy effects of winter snow on ecosystem processes during growing season. In addition, future researches are also needed to improve the techniques to better simulate snow regime changes caused by climate changes. Currently, snow fence is the most widely used method in snow manipulation experiments. However, because snow is redistributed by drifting to create different level of treatments, snow fences could not accurately simulate the changes in the depth and duration of snow cover caused by a real climate change scenario.

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419 **Table 1. Mean annual temperature (MAT), precipitation (MAP), snow depth (measured in 2016), soil properties and the dominant plant**
 420 **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	44.73 N	1.9	225	10.9±0.76	Typical	Chestnet (China)	7.0±0.75	0.8±0.05	8.7±0.5	7.49±0.08	<i>Aneurotepidimu chinense</i>
Aershan	115.78 E 994 m a.s.l.					Kastanozem (FAO)					<i>Cleistogenes squarrosa</i> (Trin.) Keng. <i>Stipa krylovii</i> Roshev.
BAY	44.05 N	2.1	247	6.2±0.58	Typical	Chestnet (China)	13.3±0.82	1.5±0.07	9.0±0.5	7.88±0.08	<i>Aneurotepidimu chinense</i>
Bayanbaolige	115.94 E 1022 m a.s.l.					Kastanozem (FAO)					<i>Stipa krylovii</i> Roshev.
WUL	45.68 N	0.4	280	NA	Typical	Chestnet (China)	13.6±0.80	1.3±0.05	10.3±0.5	7.11±0.08	<i>Aneurotepidimu chinense</i>
Wulagai	117.46 E 965 m a.s.l.					Haplic Calcisols (FAO)					<i>Cleistogenes squarrosa</i> (Trin.) Keng. <i>Stipa krylovii</i> Roshev.
XIL	43.93 N	1.5	283	14.7±1.10	Typical	Chestnet (China)	15.4±0.68	1.5±0.05	10.0±0.5	7.36±0.08	<i>Aneurotepidimu chinense</i>
Xilinhot	116.28 E 1230 m a.s.l.					Haplic Calcisols (FAO)					<i>Carex korshinskyi</i> <i>Cleistogenes squarrosa</i> (Trin.) Keng.
BAI	43.62 N	1.6	301	21.6±0.71	Typical	Chestnet (China)	6.6±0.07	0.8±0.07	8.2±0.4	7.15±0.04	<i>Aneurotepidimu chinense</i>
Baiyinxile	116.65 E 1187 m a.s.l.					Haplic Calcisols (FAO)					<i>Stipa krylovii</i> Roshev. <i>Agropyron cristatum</i> (L.)Gaetrn.
DAL	43.46 N	1.5	314	18.8±3.40	Typical	Chestnet (China)	7.5±0.06	0.9±0.05	8.6±0.5	7.38±0.08	<i>Aneurotepidimu chinense</i>
Dalinuoer	116.75 E 1257 m a.s.l.					Haplic Calcisols (FAO)					<i>Artemisia annua</i> L. <i>Carex korshinskyi</i>
HAL	45.83 N	0.3	368	13.0±0.54	Meadow	Chernozem (China)	19.2±0.91	1.7±0.05	11.0±0.5	6.86±0.08	<i>Leymus chinensis</i> (Trin.) Tzvel.
Halagaitu	119.43 E 908 m a.s.l.					Chernozem (FAO)					<i>Carex korshinskyi</i> <i>Cleistogenes squarrosa</i> (Trin.) Keng.
GAN	45.69 N	0.2	375	16.3±0.86	Meadow	Chernozem (China)	12.9±0.82	1.1±0.09	11.6±0.6	6.95±0.18	<i>Leymus chinensis</i> (Trin.) Tzvel.
Ganqiaobao	119.52 E 980 m a.s.l.					Chernozem (FAO)					<i>Agropyron cristatum</i> (L.)Gaetrn. <i>Cleistogenes squarrosa</i> (Trin.) Keng.

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Figure captions

Figure 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.

Figure 2. The relationships between snow depth and soil microbial biomass as total PLFAs (a), plant biomass (c) under each MAP level (225 mm, 247 mm, 280 mm, 283 mm, 301 mm, 314 mm, 368 mm, and 375 mm), and the changes in their slopes with increased levels of MAP (b and d), respectively. Solid lines indicate significant relationships ($P \leq 0.05$) and dashed lines indicate non-significant relationships.

Figure 3. The relationships between snow depth and the N pools of soil microbial biomass (a), plant biomass (c), and soils (e) under MAP level (225 mm, 247 mm, 280 mm, 283 mm, 301 mm, 314 mm, 368 mm, and 375 mm), and the changes in their slopes with increased levels of MAP (b, d and f), respectively. Solid lines indicate significant relationships ($P \leq 0.05$) and dashed lines indicate non-significant relationships.

Figure 4. The relationships between snow depth and fungi to bacteria ratio (a), and the percentage of arbuscular mycorrhizal fungal (AMF.c) under each MAP level (225

mm,247 mm,280 mm,283 mm, 301 mm, 314 mm, 368 mm, and 375 mm) and the changes in their slopes with increased levels of MAP (b and d), respectively. Solid lines indicate significant relationships ($P \leq 0.05$) and dashed lines indicate non-significant relationships.

Figure 5. The relationships between snow depth and grass biomass (a), forb biomass (c), and grass:forb ratio (e) under each MAP level (225 mm,247 mm,280 mm,283 mm, 301 mm, 314 mm, 368 mm, and 375 mm), and the changes in their slopes with increased levels of MAP (b, d and f), respectively. Solid lines indicate significant relationships ($P \leq 0.05$) and dashed lines indicate non-significant relationships.

Figure 6. The relationship between soil total PLFAs versus plant aboveground biomass across sites for each snow depth transect (a-g), and the comparison of the regression slopes among the 7 snow depth transects (h). Solid lines indicate significant relationships ($P \leq 0.05$) and dashed lines indicate non-significant relationships.

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Supporting Information

Table S1. Cross-site mean snow depth level for each transect across all sites.

Figure S1. Images of snow fences in winter (a) and the growing season (b). Yellow circles represent approximate sampling locations.

Figure S2. Soil sampling design for each site with sampling locations indicated by circles.

Figure S3. The correlations between model-predicted and measured snow depth for sites excluding the site of WUL in Feb 2016. Snow depth at site WUL was not measured due to access road closure. For each site, the snow depth was modeled using empirical functions of fence height and the angle between the snow fence and the prevailing wind direction developed by wind tunnel testing. Snow depth at the windward side of the fence was simulated by a 3rd order polynomial function; the leeward side was simulated by a 2nd order polynomial function. Details of the empirical functions were given by Zhao (2012).

Figure S4. The tissue N concentration and C/N ratio in grasses versus forbs at the regional scale. Differences between forb and grass are statistically significant ($P < 0.05$, t -test).