Interannual variability in responses of belowground net primary productivity (NPP) and NPP partitioning to long-term warming and clipping in a tallgrass prairie

XIA XU*, SHULI NIU*, REBECCA A. SHERRY*, XUHUI ZHOU*†, JIZHONG ZHOU*‡ and YIQI LUO*

*Department of Botany & Microbiology, University of Oklahoma, Norman, OK 73019, USA, †Coastal Ecosystems Research Station of Yangtze River Estuary, Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, The Institute of Biodiversity Science, and Research Institute of the Changing Global Environment, Fudan University, 220 Handan Road, Shanghai, 200433, China, ‡Institute for Environmental Genomics, University of Oklahoma, Norman, OK 73019, USA

Abstract

The dynamics of belowground net primary productivity (BNPP) is of fundamental importance in understanding carbon (C) allocation and storage in grasslands. However, our knowledge of the interannual variability in response of BNPP to ongoing global warming is limited. In this study, we explored temporal responses of BNPP and net primary productivity (NPP) partitioning to warming and clipping in a tallgrass prairie in Oklahoma, USA. Infrared heaters were used to elevate soil temperature by approximately 2 °C since November 1999. Annual clipping was to mimic hay harvest. On average from 2005 to 2009, warming increased BNPP by 41.89% in the unclipped subplots and 66.93% in the clipped subplots, with significant increase observed in wet years. Clipping also had significant positive impact on BNPP, which was mostly found under warming. Overall, f_{BNPP}, the fraction of BNPP to NPP, increased under both warming and clipping treatments, more in dry years. Water availability (either precipitation or soil moisture) was the most limiting factor for both BNPP and f_{BNPP}. It strongly dominated the interannual variability in NPP, f_{BNPP}, and their responses to warming and clipping. Our results suggest that water availability regulates tallgrass prairie's responses to warming and land use change, which may eventually influence the global C cycle. With increasing variability in future precipitation patterns, warming effects on the vegetation in this region may become less predictable.

Keywords: belowground net primary productivity, clipping, NPP partitioning, tallgrass prairie, warming, water availability

Introduction

Net primary productivity (NPP), a key variable of terrestrial ecosystems, is the primary driver of the global carbon (C) cycling (Ni, 2004; Hui & Jackson, 2005). The projected global warming of between 2 and 7 °C by the end of this century (Allison *et al.*, 2009) is anticipated to significantly influence NPP by altering biogeochemical processes such as plant photosynthesis and microbial mineralization of soil organic matter. Therefore, understanding the sensitivity of NPP to projected global warming is of high priority for both empirical studies and future model development. However, how NPP would respond to warmer temperatures is limited by our scarcity of knowledge on belowground NPP (BNPP), which largely inhibits progress in validating global NPP models and projecting future ecosystem function under climate change (Cramer *et al.*, 1999).

Belowground NPP represents more than one-half of NPP in grasslands and is the major input of organic matter into soil (Briggs & Knapp, 1995; McNaughton *et al.*, 1998; Luo *et al.*, 2009). Understanding BNPP dynamics is fundamentally important to improve our knowledge of C allocation and storage in grasslands. However, knowledge of BNPP is still quite limited in comparison to reasonably well-understood aboveground NPP (ANPP), largely due to the methodological difficulties associated with observing and measuring root biomass (Milchunas & Lauenroth, 2001; Wu *et al.*, 2011). Experimental estimates of the magnitude and direction of BNPP change are still few, especially from field manipulative experiments (Long *et al.*, 1989; Scurlock *et al.*, 2002; Wu *et al.*, 2011). The limited available measurements of BNPP in response to projected global warming have resulted in both increases (Piñeiro *et al.*, 2009; Wu *et al.*, 2011) and decreases in BNPP (Lilley *et al.*, 2001). The lack of consistency is not surprising because the responses of BNPP to warming can be regulated by many factors at the site level, such as water availability (Li *et al.*, 2011), and plant species

Correspondence: Xia Xu, 101 David L. Boren Blvd., University of Oklahoma, Norman, OK, 73019, USA, tel. + 405 325 6519, fax + 405 325 7619, e-mail: xia.xu-1@ou.edu

composition (Gao *et al.*, 2008). However, our understanding of temporal patterns of BNPP and its responses to climate change are much weaker comparing with studies on ANPP. Therefore, examining the interannual variability of BNPP and its responses to climate change is critical to understand the driving factors in controlling the BNPP to future global warming.

The partitioning of BNPP with respect to ANPP, commonly defined as f_{BNPP}, is a central issue in plant ecology and evolution, which, however, remains controversial (e.g. Enquist & Niklas, 2002; Shipley & Meziane, 2002). From a physiological perspective, f_{BNPP} may reflect the cumulative responses of plants to environmental changes. Optimal partitioning theory suggests that plants allocate biomass among different organs in response to environmental changes to maximize their growth through efficient capture of resources, such as nutrients and water (Bloom *et al.*, 1985; Chapin *et al.*, 1987). However, how f_{BNPP} would respond to ongoing global warming is still unclear, making quantifying f_{BNPP} important for modeling studies (Hui & Jackson, 2005). In ecosystem C modeling, f_{BNPP} provides important constraints for the calibration and testing of dynamic C-cycling models (Ågren & Franklin, 2003; Hui & Jackson, 2005). However, it is often held constant in majority of global terrestrial models when estimating root C stocks (e.g. Friedlingstein *et al.*, 1999; Wullschleger *et al.*, 2001) due to the lack of reliable f_{BNPP} estimates. Therefore, results from field manipulative experiments which can shed light on the direction and magnitude of f_{BNPP} in response to warming at community level are badly needed.

The responses of BNPP and f_{BNPP} to climate warming may vary strongly with land use practices (McNaughton *et al.*, 1998; Gao *et al.*, 2008). Clipping to mimic hay harvest, for example, a widely practiced land use in the Southern Great Plains of the United States, may further confound warming effects on BNPP and f_{BNPP}. In Oklahoma, hay production occupies 3.25 million acres, nearly as much as wheat (USDA, National Agricultural Statistic Service). Clipping may have considerable effects on BNPP because it directly takes aboveground biomass away from the ecosystem, influencing f_{BNPP} by breaking down inherent allocation rules. Although water availability, temperature, nitrogen (N) availability, and grazing are reported to affect BNPP (e.g. Gower *et al.*, 2001; Ni, 2004; Gao *et al.*, 2011; Li *et al.*, 2011), field-based BNPP data in response to haying or biofuel feedstock harvest are still lacking, making the prediction of potential ecosystem-level responses to future climate change in grasslands difficult.

Grassland ecosystems occupy approximately a quarter of the global land cover and hold 10% of the global C stocks, thus playing an important role in global C cycling (Scurlock *et al.*, 2002). Grasslands with long-term experimental warming and clipping treatments offer an unique opportunity to address potential responses of BNPP to global warming (Hui & Jackson, 2005), because (1) most natural grasslands are potentially sensitive to climate change and land use practices (Mitchell & Csillag, 2001; Luo *et al.*, 2009; Niu *et al.*, 2010) and (2) belowground biomass of grasslands is easier to measure compared with that of forests (Gill *et al.*, 2002). The specific objectives of this study were to (1) explore the effects of warming and clipping on BNPP and f_{BNPP} and (2) examine the driving factors in controlling temporal responses of BNPP and f_{BNPP} to warming and clipping in a tallgrass prairie on the Great Plains of United States.

Materials and methods

Experimental site and design

The experimental site is located on the Kessler Farm Field Laboratory in Oklahoma, USA (34°59′N, 97°31′W). The site has never been cultivated and has not been grazed for the past 40 years. The grassland is dominated by C_4 grasses (*Schizachyrium scoparium* and *Sorghastrum nutans*) and C_3 forbs (*Ambrosia psilostachya, Solidago rigida,* and *Solidago nemoralis*). Mean annual temperature is 16.3 °C and mean annual precipitation is 914 mm (Oklahoma climatological survey, Norman, OK, USA). The soil is part of the Nash-Lucien complex with neutral pH, high available water holding capacity (around 37%), and a moderately penetrable root zone (US Department of Agriculture, 1979).

The experiment uses a paired factorial design with warming as the main factor nested by a clipping factor (Luo *et al.*, 2001; Wan *et al.*, 2005; Niu *et al.*, 2010). Each treatment has six replicates (i.e. six pairs of plots). Each pair has two plots of 2 m × 2 m. One plot has been subjected to continuous warming since 21 November 1999 to the present, whereas the other serves as the control with ambient temperature. Infrared heaters (165 cm × 15 cm; Kalglo Electronics, Bethlehem, PA, USA) having a radiation output of 100 W m^{-2} are suspended 1.5 m above the ground in each warmed plot. The control plot has a 'dummy' heater with same dimensions as the infrared heater suspended at a similar height to mimic the shading effects of the heater. Temperature increments generated by the infrared heaters are relatively even over the entire area of the plots and similar at different soil depths (Wan *et al.*, 2002). For each pair of plots, the distance between warmed and control plots is approximately 5 m from centers to avoid heating of the control plots. The distances between the paired plots vary from 20 to 60 m.

Each 2 m × 2 m plot is divided into four 1 m × 1 m subplots. Plants in two diagonal subplots were clipped at a height of 10 cm above the ground once a year to mimic hay harvesting, while the other two subplots are unclipped. Clipped materials were taken away and not returned back to the plots. Thus, this experiment has four treatments: unclipped and

control (ambient) temperature (UC), unclipped and warming (UW), clipped and control temperature (CC), and clipped and warming (CW).

Temperature, moisture, and precipitation measurements

Air temperature and soil temperature were measured by thermocouples at the height of 25 cm above the ground and at a depth of 2.5 cm in the center of one clipped and one unclipped subplot. Volumetric soil water content (%V) in the top 15 cm was measured twice monthly using portable Time Domain Reflectometry equipment (Soil Moisture Equipment Crop., Santa Barbara, CA, USA). Precipitation data were obtained from an Oklahoma Mesonet Station (Washington Station) located approximately 200 m away from our experimental site. Detailed information of these measurements can be found in Luo *et al.* (2009).

BNPP measurement and f_{BNPP} estimation

From 2005 to 2009, the root ingrowth-core method was applied to estimate BNPP (Derner & Briske, 1999; Gao *et al.*, 2008). Soil cores (5.2 cm in diameter) of 0–45 cm were taken from the same spot in one unclipped and one clipped subplot in each plot every year since 2006. The cores were immediately filled with sieved root-free soil originating from the same depth outside of the plots. Separated soil cores were put into plastic bags, transported in several coolers to the Ecolab at the University of Oklahoma, Norman, and stored at −30 °C before analyzing. Root samples were carefully washed by wet sieving (0.5 mm) under gently flowing water to remove attached soil and dark-brown/black debris, oven-dried at 70 °C for 48 h, and weighted to calculate BNPP. f_{BNPP} is calculated as

f_{BNPP} = BNPP/(ANPP + BNPP) (Hui & Jackson, 2005). ANPP datasets were obtained from Luo *et al.* (2009) in 2005 and from Y. Luo, X. Xu, R. A. Sherry, S. Niu, D. Li, J. Xia (unpublished data) from 2006 to 2009. A detailed description on ANPP estimation is provided by Sherry *et al.* (2008). Rain use efficiency (RUE) is defined as the slope of the relationship between BNPP and precipitation (Le Houerou, 1984).

Statistical analysis

Repeated-measures ANOVA were used to examine the main and interactive effects of experimental warming, clipping, and year on BNPP and f_{BNPP}. Within each year, one-way ANOVA was performed to analyze the differences of the above parameters among the four treatments. Linear regression analyses were used to evaluate the relationships of the above parameters with climatic factors. All statistical analyses were conducted using SPSS 16.0 for windows (SPSS Inc., Chicago, IL, USA).

Results

Microclimate

Annual precipitation varied from 515 mm in 2004 to 1307 mm in 2007 with a mean of 879 mm during the 6 years (Table 1). Air temperature was elevated by experimental warming by an average of 1.38 °C with a twofold variation from 0.99 °C in 2008 to 2.22 °C in 2005. Experimental warming also significantly increased soil temperature by an average of 1.45 °C in unclipped subplots and 2.49 °C in clipped subplots, respectively, from 2005 to 2009. Increase in both air and

Table 1 Precipitation (AP, PPT*), mean air and soil temperature (T_{air}, T_{soil}), and mean soil moisture (W_{soil}) under four treatments

Variable	Treatment	2004	2005	2006	2007	2008	2009	Average
AP (mm)		966	515	744	1307	726	1017	879
PPT* (mm)			741	630	1026	1017	872	857
T_{air} (°C)	C		16.78	17.12	16.58	16.65	16.77	16.78
	W		19.00	18.66	17.61	17.64	17.89	18.16
	W-C		2.22*	1.54*	1.03*	0.99*	1.12*	1.38*
T_{soil} (°C)	UC		16.91	17.31	16.78	16.14	16.74	16.78
	UW		18.95	19.50	18.15	17.22	17.34	18.23
	UW-UC		2.04*	2.19*	1.37*	1.08*	0.60*	1.45*
	CC		17.54	17.86	17.06	16.03	17.04	17.11
	CW		20.23	20.60	19.45	18.19	19.55	19.60
	CW-CC		2.69*	2.74*	2.39*	2.16*	2.51*	2.49*
W_{soil} (%)	UC		24.77	23.50	29.94	26.96	26.55	26.34
	UW		21.7	21.95	28.74	25.21	24.63	24.45
	UW-UC		−3.07*	−1.55ns	−1.20ns	−1.75ns	−1.92*	−1.89ns
	CC		24.10	23.14	29.67	26.05	26.02	25.80
	CW		20.92	20.92	28.58	24.35	23.98	23.75
	CW-CC		−3.18*	−2.22*	−4.09ns	−1.70ns	−2.04*	−2.05*

C, control (ambient) temperature; W, warmed; U, unclipped; C, clipped; AP, annual precipitation; ns, not significant; PPT*, average of precipitation of the current and previous year, for example, PPT*$_{2008}$ = (AP$_{2008}$ + AP$_{2007}$)/2.
*Asterisks indicate significant warming effect at $P < 0.05$.

soil temperature was higher in relatively dry years (2006 and 2007) than in wet years (2008–2010). Over the years, volumetric soil moisture was lowered by an average of 1.89% in the unclipped subplots and 2.05% in the clipped subplots, respectively.

Warming and clipping effects on BNPP

Belowground NPP varied from 255.06 ± 25.57 in 2006 to 335.35 ± 39.85 g m^{-2} in 2007 in UC from 2005 to 2009 (Fig. 1a). The warming effect on BNPP was significant over the years ($P < 0.001$, Table 2) and from 2006 to 2010 (Fig. 1b). On average, it increased BNPP by 41.89% and 66.93% in the unclipped and clipped sub-

plots, respectively (all $P < 0.05$, Fig. 1a, inset). Experimental warming significantly interacted with year in influencing BNPP ($P < 0.05$, Table 2; Fig. 1b), with higher stimulation in wet years than in dry years. No significant relationship was found between the warming effect on BNPP and the warming-induced changes in soil temperature and soil moisture (all $P > 0.05$). Thus, we cannot say that either temperature or soil moisture is more important than the other. Clipping also showed significant impacts on BNPP from 2005 to 2009 ($P = 0.003$, Table 2) and increased BNPP by an average of 7.94% in the unwarmed plots ($P > 0.05$) and 26.99% in the warmed plots ($P < 0.05$, Fig. 1a, inset). The interactive effects of clipping and year had little impact on BNPP ($P = 0.442$, Table 2).

Warming and clipping effects on f_{BNPP}

f_{BNPP} varied from 0.52 ± 0.02 in 2005 to 0.60 ± 0.02 in 2009 in UC across the 2005–2009 growing seasons (Fig. 2a). Both warming and clipping had significant effects on f_{BNPP} (all $P < 0.05$, Table 2). For example, warming increased f_{BNPP} from 0.58 ± 0.02 to 0.60 ± 0.01 ($P = 0.20$) in the unclipped subplots and from 0.64 ± 0.02 to 0.68 ± 0.02 ($P < 0.05$) in the clipped subplots (Fig. 2a, inset). Clipping increased f_{BNPP} from 0.58 ± 0.02 to 0.64 ± 0.02 and from 0.60 ± 0.01 to 0.68 ± 0.02 in unwarmed and warmed subplots, respectively (all $P < 0.05$, Fig. 2a, inset). The interaction of warming and year had little effect on f_{BNPP} ($P = 0.848$, Table 2). Clipping significantly interacted with years in influencing f_{BNPP}, with a higher increase in the dry years. ($P = 0.003$, Table 2; Fig. 2c).

Relationships of BNPP and f_{BNPP} with climatic factors

Belowground NPP significantly correlated with precipitation across the 5 years under each of the four treatments (all $P < 0.05$, Fig. 3a, b). Warming increased the slopes of BNPP vs. precipitation (equivalent to RUE) both with and without clipping (all $P < 0.05$, Fig. 3c). Generally, the effects of precipitation and soil moisture on warming-induced changes in BNPP were positive while that of air temperature were negative (Fig. 4). For clipping-induced changes in f_{BNPP}, negative effects of precipitation and soil moisture and positive effect of air temperature were observed (Fig. 5). Multifactor linear regression showed that water availability, either PPT* (average of precipitation of the current and previous year) or soil moisture, was the dominant climatic factor in controlling interannual variation in warming-induced changes in BNPP ($r^2 = 0.53$, $P = 0.017$) and clipping-induced changes in f_{BNPP} ($r^2 = 0.59$, $P = 0.009$). PPT*, rather than annual precipitation or the previous

Fig. 1 Variation in belowground net primary productivity (BNPP) under four treatments (a) and changes in BNPP induced by warming (b) and clipping (c) from 2005 to 2009. Values are mean ± SE ($n = 6$). Inserted figure in panel a shows the average values of BNPP under four treatments over the years, values are mean ± SE ($n = 30$). Different letters indicate statistically significant difference between treatments at $P < 0.05$. Asterisks (*) represent statistically significant warming or clipping effects on BNPP at $P < 0.05$.

Table 2 Results of repeated-measures ANOVA (*P* values) for responses of belowground net primary productivity (BNPP) and f_{BNPP} to warming (W), clipping (CL), year (Y), and their interactions (*n* = 6)

Factor	Warming	Clipping	Year	W × CL	W × Y	CL × Y	W × CL × Y
BNPP	**<0.001**	**0.003**	**<0.001**	**0.042**	**0.025**	0.442	0.420
f_{BNPP}	**0.038**	**0.001**	*0.076*	0.477	0.848	**0.003**	0.232

P values smaller than 0.05 and 0.08 are bold and italic, respectively.

year's precipitation, significantly correlated with variation in BNPP, warming-induced changes in BNPP, and clipping-induced changes in f_{BNPP} (Figs 3a, b, 4, and 5a), indicating previous year's precipitation had much influence on BNPP and f_{BNPP}.

Fig. 2 Variation in f_{BNPP} under four treatments (a) and changes in f_{BNPP} induced by warming (b) and clipping (c) from 2005 to 2009. Values are mean ± SE (*n* = 6). Inserted figure in panel a shows average values of f_{BNPP} under four treatments over the years, values are mean ± SE (*n* = 30). Different letters indicate statistically significant difference between treatments at *P* < 0.05. Asterisks (*) represent statistically significant warming or clipping effects on BNPP at *P* < 0.05.

Discussion

Warming and clipping effects on BNPP

Temperature is one of the major factors constraining terrestrial plant productivity (Luo *et al.*, 2009; Wu *et al.*, 2011). The significant increase in BNPP under warming (*P* < 0.001, Table 2; Fig. 1a, b) is in line with a meta-analysis which demonstrated that experimental warming which increased soil temperature of 0.1–10.2 °C significantly increased BNPP (Wu *et al.*, 2011). The increase in BNPP in our experiment may result from (1) longer growing season under year-round warming (Wan *et al.*, 2005) and (2) warming-induced increase in nutrient mineralization (Hartley *et al.*, 1999; Rustad *et al.*, 2001) and the consequent increase in plant nutrient uptake (Sardans *et al.*, 2008) and plant productivity (Wan *et al.*, 2005). Another possible reason that may account for the increase in BNPP is higher availability of photosynthates for roots, which originated from increased photosynthetic rates at higher temperatures (Rustad *et al.*, 2001; Luo *et al.*, 2009; Wu *et al.*, 2011). However, a previous study at the same site showed that leaf-level photosynthesis of four dominant species did not change much under warming during the whole growing season (Zhou *et al.*, 2007), suggesting the direct warming effect on photosynthesis is at most only a minor cause of increased BNPP.

Responses of BNPP to warming varied widely by year, with significant warming effects observed in wet years (all *P* < 0.05, Fig. 1a, b) mainly due to water availability being one of the primary controls over plant productivity (Sala *et al.*, 1988; Wu *et al.*, 2011). In clipped subplots in 2007, for example, BNPP was mostly increased by warming probably due to the large amount of precipitation. Our results are similar to other studies investigating interactive effects of warming and drought on plant productivity. For example, Peñuelas *et al.* (2004) found that warming increased biomass in wet northern areas while had no effect in dry southern areas at four shrubland sites. Both Peñuelas *et al.* (2004) and other studies (e.g. Li *et al.*, 2011) indicated that the responses of BNPP to warming were greatly controlled by water availability.

Increased BNPP with clipping may be attributable to at least four causes. First, less standing-litter in the
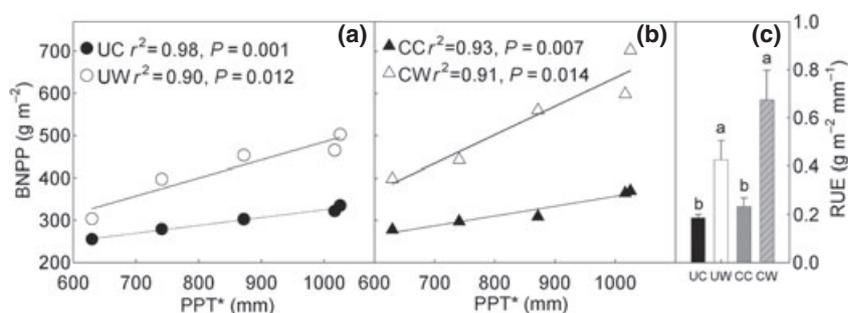
Fig. 3 Relationships of belowground net primary productivity (BNPP) with PPT* under four treatments (a, b) and increased rain use efficiency (RUE) under warming (c). PPT*: average of precipitation of the current year and the previous year.
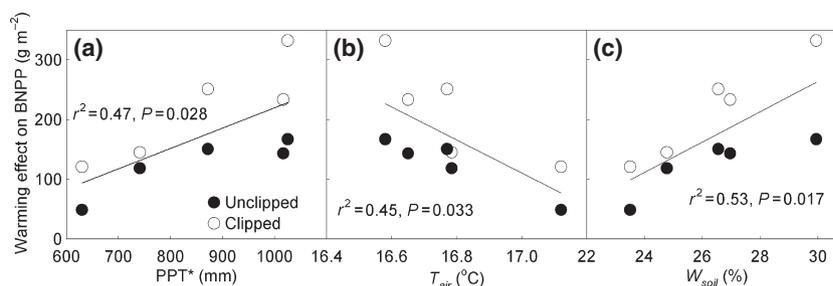
Fig. 4 Relationships of warming-induced changes in belowground net primary productivity (BNPP) with PPT* (a), mean air temperature (T_{air}, b), and mean soil moisture (W_{soil}, c).
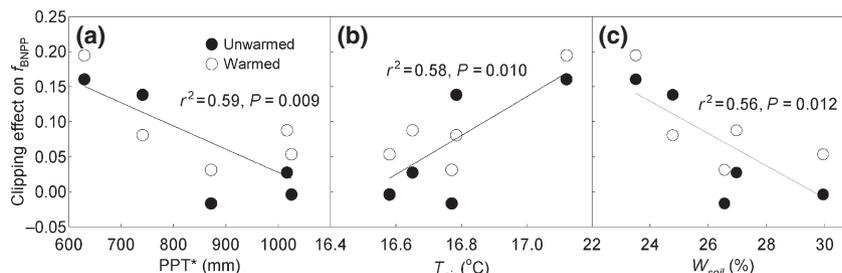
Fig. 5 Relationships of clipping-induced changes in f_{BNPP} with PPT* (a), mean air temperature (T_{air}, b), and mean soil moisture (W_{soil}, c).

clipped than unclipped subplots can improve light conditions for the lower canopy leaves and thus increase leaf photosynthesis and belowground root productivity. Second, there may be positive clipping-induced compensatory growth mechanisms, similar to the grazing optimization hypothesis that increases plant productivity (McNaughton, 1983; McNaughton *et al.*, 1998). Third, if a compensatory growth mechanism exists, belowground plant productivity may be stimulated by a clipping-induced increase in nutrient uptake due to increased sink strength (Wegener & Odasz, 1997). Fourth, clipping may change plant physiological processes and allocation patterns (Oesterheld & McNaughton, 1988), leading to the increase in belowground productivity with decreased soil moisture

(Table 1) based on optimal partitioning theory (Bloom *et al.*, 1985; Chapin *et al.*, 1987) and supported by previous studies (e.g. McConnaughay & Coleman, 1999; McCarthy & Enquist, 2007). Additionally, increased nutrient availability (Rustad *et al.*, 2001) and use efficiency (Sardans *et al.*, 2008; Niu *et al.*, 2010) under warming may explain that the significant clipping effect was mostly observed in warmed subplots (Fig. 1c).

Warming and clipping effects on f_{BNPP}

Our estimates of f_{BNPP} with a mean of 0.61 ± 0.01 under four treatments are comparable with a synthesis of field studies with f_{BNPP} across world's grasslands ranging between 0.40 and 0.86 with a mean of 0.71 (Hui &

Jackson, 2005). Biomass allocation is a specialized survival strategy of plants (Bloom *et al.*, 1985). Allocation patterns among plant organs vary during growth and development (Farrar & Gunn, 1996), and the patterns can reflect the differential investment of photosynthates between the aboveground and belowground organs (Stirling *et al.*, 1998; McConnaughay & Coleman, 1999). Experimental warming significantly increased f_{BNPP} indicating that plants were adjusting their allocation patterns to maximize their relative growth rate. According to optimal partitioning theory (Bloom *et al.*, 1985; Chapin *et al.*, 1987), which is supported by previous studies, such as Hui & Jackson (2005), warming-induced dry conditions increased f_{BNPP} when plants allocate proportionally more biomass to roots in response to low moisture conditions (McConnaughay & Coleman, 1999; McCarthy & Enquist, 2007).

Clipping for hay, similar to grazing in removing aboveground biomass, disturbs the equilibrium between BNPP and ANPP (Gao *et al.*, 2008). We found that clipping significantly increased f_{BNPP} ($P = 0.001$, Table 2). Plants may adjust physiological processes because the demand for water and nutrient supply by aboveground biomass decreased dramatically after clipping, leading to reallocation of more resources to roots (Oesterheld & McNaughton, 1988). Additionally, clipping may increase f_{BNPP} through decreasing soil moisture (Table 1) and stimulating root growth to capture water as supported by previous studies that show plants growing at low water availability exhibited stronger growth in BNPP than those under favorable water conditions (Hui & Jackson, 2005; Gao *et al.*, 2011). Our results also showed that f_{BNPP} was significantly increased by clipping in dry years compared with non-significant changes in wet years (Fig. 2c). With increasing extreme rain events (IPCC, 2007), variation in f_{BNPP} in response to land use change should be considered for incorporation into global C models to accurately predict future climate change.

Interannual variation in BNPP and f_{BNPP} and their responses to warming and clipping

Water availability is one of the most frequent controlling factors over plant productivity (Burke *et al.*, 1997). In our study, the interannual variability in BNPP was dependent on precipitation (Fig. 3a, b). This is in line with the results of a meta-analysis by Wu *et al.* (2011) showing that increased precipitation generally stimulated plant growth, while decreased precipitation had the opposite effect. Moreover, N mineralization increases with increasing precipitation (Burke *et al.*, 1997), resulting in increased N availability to plants, which indirectly stimulated BNPP (Burke *et al.*, 1997;

Wan *et al.*, 2005). Precipitation is especially important among climatic factors in regulating plant productivity as pointed out by Briggs & Knapp (1995). Additionally, RUE of BNPP significantly increased under warming (Fig. 3c) probably due to increased C_4 species dominance (Luo *et al.*, 2009; Niu *et al.*, 2010) because C_4 species have higher RUE compared with that of C_3 species (Niu *et al.*, 2003).

Water availability not only controls the interannual variability in BNPP but also regulates the impacts of warming on BNPP. The multifactor linear regressions showed that soil moisture was the dominant controlling factor on the responses of BNPP to warming across years, leading to the great interannual variability of warming effect on BNPP. Previous field and modeling studies in grasslands both confirmed that changes in plant productivity could be dependent on soil moisture (Knapp & Smith, 2001; Weng & Luo, 2008). Soil moisture, integrating impacts of both precipitation and temperature, can play an important role in regulating variation in BNPP and function as an important index in projecting ecosystems' responses to climate change (Friedlingstein *et al.*, 1999; Sherry *et al.*, 2008).

The clipping effect on f_{BNPP} decreased with increasing water availability (Fig. 5a, c). Multifactor linear regression analyses indicated that precipitation dominated the interannual variation in f_{BNPP}. Very few studies are available that consider clipping effects on the temporal variation in f_{BNPP}. We hypothesized that in comparison to the wet conditions, clipping stimulated BNPP relatively more than ANPP under low water availability conditions. In the unwarmed subplots, for example, clipping increased ANPP and BNPP by -37.74% and 6.68% in 2005 (dry year), respectively, while in 2007 (wet year), clipping increased ANPP by 9.82% and BNPP by 10.42%, resulting in significantly higher clipping effect on f_{BNPP} in 2005 ($P < 0.05$, Fig. 2c). Generally, the correlations of changes in BNPP and f_{BNPP} with climatic factors suggest that water availability (either precipitation or soil moisture) regulates the interannual variation of BNPP and f_{BNPP} in response to warming and clipping. Given the projected increase in extreme rain events under climate change (IPCC, 2007) and fundamental importance of BNPP in understanding C allocation and storage, varied f_{BNPP} should be included in evaluating ecosystem responses to warming from the whole plant perspective.

In our study, lagged effects of precipitation on the temporal variation in BNPP and f_{BNPP} were evidenced by a correlation of BNPP and f_{BNPP} with the average of precipitation of the current and previous year (all $P < 0.05$; Figs 3a, b, 4a, and 5a). The relationships of annual precipitation or previous year's precipitation alone with variation in BNPP and f_{BNPP} were not

statistically significant (all $P > 0.05$). Similar phenomena have been documented in many grassland ecosystems in North America, Europe, and South Africa (e.g. O'Connor *et al.*, 2001; Sherry *et al.*, 2008). For example, an increase in biomass induced by carry-over effects from wet years in grasslands can last one or more years in which higher biomass is usually observed than expected (Oesterheld *et al.*, 2001; Sherry *et al.*, 2008). In general, 1 year is the most commonly reported lag time (e.g. Webb *et al.*, 1978; O'Connor *et al.*, 2001), as observed in our study that previous year's precipitation substantially influenced BNPP and f_{BNPP}. Frequency of extreme weather events, such as unusual wet and dry years, is predicted to increase under global climate change (IPCC, 2007). Therefore, field manipulative experiments with different precipitation quantity, frequency, and intensity are needed to clarify mechanisms that control plant productivity in response to temporal and spatial variation in precipitation.

To conclude, our results from the long-term warming and clipping experiment in the tallgrass prairie in the United States suggest that warming and hay harvest will have substantial and year dependent effects on BNPP and NPP partitioning (f_{BNPP}). Across the years, warming had positive effects on BNPP likely through prolonged growing seasons and higher nutrient availability and nitrogen use efficiency. BNPP also positively responded to clipping, possibly through increased photosynthesis with less shading, compensatory growth, and changed allocation patterns. A relative increase in belowground allocation, f_{BNPP}, was observed as a consequence of the increased BNPP and dry conditions caused by warming and clipping treatments. Practical use of varied f_{BNPP} in global terrestrial models would thus improve C cycle modeling. Multifactor linear regressions showed that water availability regulated the interannual variability in BNPP, warming-induced changes in BNPP, and clipping-induced changes in f_{BNPP}. Global mean temperature and extreme rain events are projected to increase in future. Therefore, to accurately forecast ecosystem feedback to climate change, models may have to simulate responses of BNPP and f_{BNPP} to global warming and land use change as well as their consequences for ecosystem functions.

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