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Net primary productivity and rain-use efficiency as affected by warming, altered precipitation, and clipping in a mixed-grass prairie

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Abstract

Grassland productivity in response to climate change and land use is a global concern. In order to explore the effects of climate change and land use on net primary productivity (NPP), NPP partitioning [f_{BNPP}, defined as the fraction of belowground NPP (BNPP) to NPP], and rain-use efficiency (RUE) of NPP, we conducted a field experiment with warming (+3 °C), altered precipitation (double and half), and annual clipping in a mixed-grass prairie in Oklahoma, USA since July, 2009. Across the years, warming significantly increased BNPP, f_{BNPP}, and RUE_{BNPP} by an average of 11.6%, 2.8%, and 6.6%, respectively. This indicates that BNPP was more sensitive to warming than aboveground NPP (ANPP) since warming did not change ANPP and RUE_{ANPP} much. Double precipitation stimulated ANPP, BNPP, and NPP but suppressed RUE_{ANPP}, RUE_{BNPP}, and RUE_{NPP} while half precipitation decreased ANPP, BNPP, and NPP but increased RUE_{ANPP}, RUE_{BNPP}, and RUE_{NPP}. Clipping interacted with altered precipitation in impacting RUE_{ANPP}, RUE_{BNPP}, and RUE_{NPP}, suggesting land use could confound the effects of precipitation changes on ecosystem processes. Soil moisture was found to be a main factor in regulating variation in ANPP, BNPP, and NPP while soil temperature was the dominant factor influencing f_{BNPP}. These findings suggest that BNPP is critical point to future research. Additionally, results from single-factor manipulative experiments should be treated with caution due to the non-additive interactive effects of warming with altered precipitation and land use (clipping).

Keywords: above- and belowground net primary productivity, climate change, clipping, mixed-grass prairie, net primary productivity partitioning, rain-use efficiency

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Introduction

In response to rising concentrations of atmospheric greenhouse gases, global mean temperature has increased 0.74 °C since 1850 and is predicted to increase another 1.8–4.0 °C by the end of this century (IPCC, 2007). Additionally, precipitation is anticipated to vary greatly under global climate change, with increasing intra- and inter-annual variability (IPCC, 2007). Net primary productivity (NPP), the primary driver of global carbon (C) cycling, is strongly influenced by climatic variables, such as temperature and precipitation (e.g., Rustad *et al.*, 2001; Sherry *et al.*, 2008; Bloor & Bardgett, 2012; Hoeppner & Dukes, 2012). Both empirical and modeling studies have suggested that climatic changes could alter the functioning of terrestrial ecosystems via changes in NPP (e.g., Norby & Luo, 2004; Luo *et al.*, 2009). However, responses of NPP to climate warming, altered precipitation, and their interactions are less clear (Rustad *et al.*, 2001), especially belowground NPP (BNPP). Understanding variation in NPP is critical to discovering the mechanisms of the response of ecosystem functions to ongoing climate change (Ni, 2004; Xu *et al.*, 2012).

Evidence that warming and altered precipitation are influencing ecosystem processes is growing rapidly (e.g., Ni, 2004; Luo *et al.*, 2009; Wu *et al.*, 2011; Polley *et al.*, 2012; Xu *et al.*, 2012). Manipulative experiments in a range of vegetation types have shown that warming may have a variety of impacts on NPP, either stimulating plant productivity (Rustad *et al.*, 2001) or retarding it (Rustad *et al.*, 2001; Wu *et al.*, 2011). Studies examining the effects of altered precipitation on plant productivity have shown that positive correlations typically exist between plant productivity and annual precipitation in grassland ecosystems (Sala *et al.*, 1988; Knapp & Smith, 2001; Dukes *et al.*, 2005; Chimner *et al.*, 2010). However, it is less clear whether the positive relationship holds true under

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extremely altered precipitation, such as double and half precipitation, which has been recognized as a critical manifestation of climate change (Meehl *et al.*, 2007). Moreover, the interactions of warming and altered precipitation may shape the NPP in ways that are hard to predict from measuring responses of an ecosystem to single climate change factors (Dukes *et al.*, 2005; Williams *et al.*, 2007).The variability and unpredictability of NPP under climatic change may also result from our limited understanding of BNPP that represents more than one-half of NPP in grasslands (Hui & Jackson, 2005). In comparison to reasonably well-understood aboveground NPP (ANPP), experimental estimates of BNPP are less and only a few studies have investigated the relation of BNPP with climatic factors (Gill *et al.*, 2002; Ni, 2004; Dukes *et al.*, 2005; Xu *et al.*, 2012). The lack of NPP data, especially the magnitude and direction of its response to current climate change, largely inhibits the progress in validating global NPP models and projecting future climate change (Cramer *et al.*, 1999; Hui & Jackson, 2005).

Net primary productivity partitioning, commonly defined as f_{BNPP} = BNPP/(ANPP + BNPP), is a critical constraint for the calibration and testing of dynamic C-cycling models (Ågren & Franklin, 2003; Hui & Jackson, 2005). From a physiological perspective, f_{BNPP} is sensitive to environmental changes (Bloom *et al.*, 1985; Chapin *et al.*, 1987). For example, drought and warming appear to favor allocation of C from leaves to roots (Poorter & Nagel, 2000; Xu *et al.*, 2012). However, it is generally assumed that f_{BNPP} is constant in a majority of global terrestrial models (e.g., Friedlingstein *et al.*, 1999; Wullschleger *et al.*, 2001). The partitioning of NPP is less well-understood and remains under debate (Enquist & Niklas, 2002; Shipley & Meziane, 2002), especially in relation to climatic changes, leading to tremendous variation for short-term forecasts and long-term projections of global NPP (Friedlingstein *et al.*, 2006; Sitch *et al.*, 2008). Thus, results from field manipulative experiments are fundamentally important to understanding and quantifying f_{BNPP} and its relationships with climatic factors.

Efficient rain use is generally one of the key components of adaptability for natural vegetation (Brueck *et al.*, 2010). Rain-use efficiency (RUE), the ratio of NPP to precipitation, provides us a useful index for evaluating the responses of NPP to precipitation changes (Knapp *et al.*, 2001; Brueck *et al.*, 2010) and is an important constraint for simulating plant productivity in models (Roupsard *et al.*, 2009). However, how RUE will vary under warming and altered precipitation is not clear. In grasslands, RUE either increases (Xu *et al.*, 2012) or decreases (De Boeck *et al.*, 2006) under warming, although it is predicted to decrease in a modeling study (Bell *et al.*, 2010). Similarly, increases (Epstein *et al.*, 1996; Hooper & Johnson, 1999), no changes (Lauenroth *et al.*, 2000), and decreases (Huxman *et al.*, 2004; Bai *et al.*, 2008) in RUE have been reported with increasing precipitation amount. Therefore, greater understanding of how RUE responds to climatic changes is critical to accurately forecast terrestrial C-cycle response and feedback to climate change.

Land-use practices, such as mowing for hay, may further confound the responses of NPP, f_{BNPP}, and RUE of NPP to climate change (McNaughton *et al.*, 1998; Gao *et al.*, 2008) and impact ecosystem C balance (Luo *et al.*, 2009). Hay harvest is a widely practiced land use in the southern Great Plains of the US. Hay production occupies 3.25 million acres in Oklahoma, nearly as much as wheat (USDA, National Agricultural Statistic Service). Clipping to mimic hay harvest has considerable impacts on ANPP because it directly takes aboveground biomass away, lowers the amount of litter on the ground, and indirectly impacts plant growth in the next growing season. On the other hand, clipping influences BNPP and f_{BNPP} by breaking down inherent allocation rules due to lesser demand for water and nutrients from aboveground plant components (Xu *et al.*, 2012). Additionally, clipping may affect NPP and RUE by stimulating evapotranspiration, reducing soil moisture, and exacerbating water stress (Niu *et al.*, 2008; Xu *et al.*, 2012). Although NPP has been reported to be affected by temperature, water availability, nitrogen availability, and grazing (Ni, 2004; Sherry *et al.*, 2008; Gao *et al.*, 2011; Li *et al.*, 2011; Xu *et al.*, 2012), experimental estimates of NPP in response to clipping or haying are still few, making it difficult to predict the potential ecosystem-level responses to land-use practices under climate change in grasslands.

Grassland ecosystems, accounting for ca. 54% of the conterminous US (US Department of Agriculture, 1972), play an essential role in global C cycling. Grasslands are ideal for addressing the potential responses of NPP and its RUE to climate change and land use (Hui & Jackson, 2005; Xu *et al.*, 2012) because of (i) their rapid responses to climate change and land-use practices (Sherry *et al.*, 2008; Luo *et al.*, 2009); and (ii) the relative ease of manipulating temperature, precipitation, and land-use practices, of measuring belowground biomass (Gill *et al.*, 2002). Specifically, we aimed to: (i) examine the effects of warming, altered precipitation, clipping, and their interactions on NPP, f_{BNPP}, and RUE of NPP; and (ii) explore the relationships of NPP and f_{BNPP} with climatic factors and species composition (expressed by the ratio of C_3 contribution to ANPP) in a mixed-grass prairie in the southern Great Plains of the USA.

Materials and methods

Experimental site and design

The experimental site is located on the Kessler Atmospheric and Ecological Field Station (KAEFS) in McClain County, Oklahoma, USA (ca. 34°59′N, 97°31′W), about 40 km southwest of the Norman campus of the University of Oklahoma, USA. KAEFS is located in the Central Redbed Plains of Oklahoma within the mosaic ecotone from tall-grass prairie with woodlands along creeks to mixed-grass prairie in the west (Tarr *et al*., 1980). The site is on an old-field prairie abandoned from field cropping 40 years ago with light grazing until 5 years ago. The mixed-grass prairie is dominated by C_3 forbs (*Ambrosia trifida, Solanum carolinense, and Euphorbia dentata*) and C_4 grasses (*Tridens flavus, Sporobolus compositus, and Sorghum halapense,*). 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 deep (ca. 70 cm), moderately penetrable root zone.

This experiment was established in July of 2009 and manipulates temperature and precipitation, within which is nested a clipping factor. Each treatment is randomly repeated four times for a total 24 plots of 2.5 m × 3.5 m. We utilize infrared heaters to achieve the whole ecosystem warming by ca. 3 °C. In each warmed plot, two infrared heaters (165 cm × 15 cm; Kalglo Electronics, Bethlehem, PA, USA) are suspended ca. 1.5 m above the ground to warm the area of 2.5 m × 1.75 m. The control plot has two 'dummy' heaters with same dimensions as the infrared heaters suspended at a similar height to mimic the shading effects of the heaters. Temperature increments generated by the infrared heaters are found relatively even over the entire area of the plots and similar at different soil depths (Wan *et al*., 2002). The distance between each two adjacent plots is at least 5 m from centers to avoid heating of the control plots.

We use a rainfall-collection-redistribution device as described by Zhou *et al*. (2006) with a same area of the plot to double precipitation and a rainout-shelter as described by Yahdjian & Sala (2002) to halve precipitation. The rainout-shelter design is a fixed-location shelter with a roof consisting of bands of transparent acrylic that block different amounts of rainfall while minimally affecting other environmental variables. To minimize disturbance, we inserted fiberglass sheets into the ground to a depth of 120 cm around each plot as in the Jasper Ridge Global Change Experiment (Zavaleta *et al*., 2003) to cut off lateral movement of soil water. We set the rain shelters above the heaters at an angle of 20° as in the original design by Yahdjian & Sala (2002). The lower side of the rain-out-shelters tilts toward the prevailing upwind direction. In the control plots, we install 'dummy' frames of the rain shelters for consistency of experimental conditions.

Each 2.5 m × 3.5 m plot is divided into two 2.5 m × 1.75 m subplots. Plants in the southern 2.5 m × 1.75 m subplots are clipped at a height of 10 cm above the ground once a year to mimic the land-use practice of mowing for hay while the northern subplots are unclipped. Similar to the hay production, clipped materials are taken away and not returned back to the plots. Thus, this experiment has twelve treatments, six for the unclipped group and the other six for the clipped group. The six treatments are control (ambient) temperature and control precipitation (CC), control temperature and double precipitation (CD), control temperature and half precipitation (CH), warming and control precipitation (WC), warming and double precipitation (WD), and warming and half precipitation (WH).

Soil temperature and moisture, and precipitation measurements

Soil temperature, at the depth of 7.5 cm in the center of one clipped and one unclipped subplot, was measured every 15 min using thermocouples (T-type; Campbell Science Inst., Logan, UT, USA) wired to a Campbell Scientific CR10x datalogger (Campbell Scientific). Volumetric soil water content (%V) in the top 12 cm was measured once or twice a month using portable Time Domain Reflectometry (TDR) equipment (Soil Moisture Equipment Crop., Santa Barbara, CA, USA). Three measurements of soil moisture were made in every subplot each time and the average values were used in analysis. Precipitation data were obtained online from an Oklahoma Mesonet Station (Washington Station) located ca. 50 m away from our experimental site. The amount of actual precipitation received by the plots under different precipitation treatments was measured using surface gauge measurement (Groisman & Legates, 1994; New *et al*., 2001).

NPP measurement and estimation of f_{BNPP} and RUE of NPP

In 2010 and 2011, ANPP, separated into C_3 and C_4 species, was directly measured by annual clipping at peak biomass (usually August) in the southern 2.5 m × 1.75 m clipping subplots and indirectly estimated by pin-contact method (Frank & McNaughton, 1990) in the unclipped subplots. Detailed description of biomass estimation is provided by Sherry *et al*. (2008). The root ingrowth-core method (Gao *et al*., 2008; Xu *et al*., 2012) was applied to estimate BNPP. Soil cores (5.2 cm in diameter, 90 cm in length) were taken once a year in October at an angle of 90° from the same spots in one unclipped and one clipped subplots of each plot every year. Holes were immediately refilled with sieved root-free soils originating from the same depth (4 depths in total: 0–15, 15–30, 30–60, 60–90 cm) outside of the plots. Soil filled into the holes was compressed to a density comparable to the bulk soil. 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 defined as f_{BNPP} = BNPP/(ANPP + BNPP) according to Hui & Jackson (2005). Rain-use efficiency (RUE) of ANPP, BNPP, and NPP is calculated as ANPP, BNPP, and NPP, respectively, divided by the amount of actual precipitation received by specific plots under different treatments. RUE of different components of NPP was estimated to compare the sensitivity between ANPP and BNPP to climate change and land use.

Statistical analysis

Repeated measures split-plot analysis of variance (ANOVA) was used to examine the main and interactive effects of experimental warming (whole-plot factor), altered precipitation (whole-plot factor), clipping (subplot factor), and year on ANPP, BNPP, NPP, f_{BNPP}, RUE_{ANPP}, RUE_{BNPP}, RUE_{NPP}, and soil moisture and temperature. Within each year, one-way ANOVA was performed to analyze the differences in ANPP, BNPP, NPP, f_{BNPP}, RUE_{ANPP}, RUE_{BNPP}, and RUE_{NPP} among the twelve treatments (Duncan's Test) and to test the separate main treatment effects on the parameters mentioned above (Tukey's Test). Linear regression analyses were performed to evaluate the relationships of ANPP, BNPP, NPP, and f_{BNPP} with climatic factors and species composition (expressed by the ratio of C_3 contribution to ANPP). All statistical analyses were conducted using SPSS 16.0 for windows (SPSS Inc., Chicago, IL, USA).

Results

Microclimate

Comparing with the average precipitation of 837 mm from 1994 to 2011, annual precipitation in 2010 and 2011 was 906 mm and 549 mm, respectively (Table 1; Fig. 1). The amount of precipitation received by the control, double, and half precipitation treatment plots differed significantly (all $P < 0.01$). According to our measurements, plots under double and half precipitation treatments received an average of 195.8% and 70.1% of the ambient precipitation, respectively (Fig. 1c). Overall, warming, altered precipitation, and clipping significantly affected both soil moisture and soil temperature (all $P < 0.01$, Table 2). Averaged across years, volumetric soil moisture was lowered by 1.9%, 0.3%, and 0.8% by the treatments of warming, half precipitation, and clipping, respectively, and increased by an average of 1.1% under double precipitation (Table 1). Additionally, warming, double precipitation, half precipitation, and clipping increased soil temperature by an average of 3.1, 0.1, 0.4, and 0.5 °C, respectively, across the years (Table 1).

Treatment effects on NPP and f_{BNPP}

Ecosystem productivity varied greatly from 2010 to 2011. Overall, the productivity in 2011 was much smaller than that in 2010 (Table 2; Fig. 2a–c). ANPP varied from 184.0 ± 23.1 g m^{-2} in 2011 under the treatment of warming plus half precipitation in the clipped subplots to 561.9 ± 39.7 g m^{-2} in 2010 under the control (Fig. 2a). The main effects of warming increased BNPP and NPP by an average of 11.6% ($P < 0.01$) and 9.2%

Table 1 Annual precipitation (PPT), mean soil moisture (W_{soil}), and mean soil temperature (T_{soil}) under 12 treatments in 2010 and 2011

Year	PPT (mm)	Treatment	Unclipped CC	CD	CH	WC	WD	WH	Clipped CC	CD	CH	WC	WD	WH
2010	906	W_{soil} (%)	11.6 ± 0.2	13.0 ± 0.3	11.6 ± 0.6	9.6 ± 0.5	12.1 ± 1.1	8.7 ± 0.6	10.6 ± 0.6	12.3 ± 0.5	11.4 ± 0.3	9.2 ± 0.6	8.8 ± 0.3	7.7 ± 0.6
		T_{soil} (°C)	16.2 ± 0.0	16.3 ± 0.0	16.7 ± 0.1	18.5 ± 0.0	18.9 ± 0.0	18.6 ± 0.0	16.6 ± 0.0	16.7 ± 0.4	16.9 ± 0.0	19.2 ± 0.0	19.6 ± 0.0	20.0 ± 0.4
2011	549	W_{soil} (%)	7.6 ± 0.4	9.1 ± 0.2	7.3 ± 0.5	6.3 ± 0.2	7.2 ± 0.2	5.9 ± 0.1	7.0 ± 0.6	7.9 ± 0.6	6.9 ± 0.4	6.0 ± 0.2	6.5 ± 0.3	5.6 ± 0.2
		T_{soil} (°C)	18.3 ± 0.1	18.1 ± 0.1	18.4 ± 0.1	21.9 ± 0.1	21.7 ± 0.1	21.7 ± 0.1	18.5 ± 0.1	18.1 ± 0.0	18.8 ± 0.1	21.7 ± 0.1	22.0 ± 0.1	22.9 ± 0.1

CC, control temperature plus control PPT; CD, control temperature plus double PPT; CH, control temperature plus half PPT; WC, warmed plus control PPT; WD, warmed plus double PPT; WH, warmed plus half PPT.

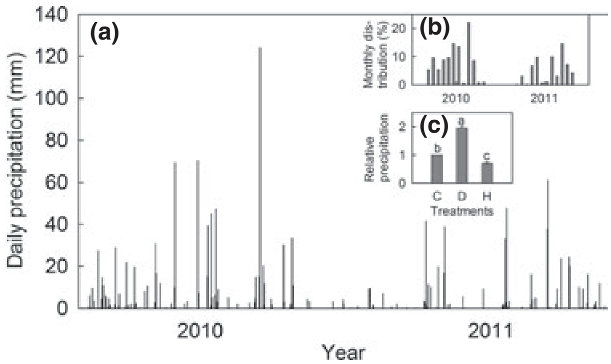

Fig. 1 Daily (a) and monthly (b) distribution of precipitation in 2010 and 2011 and the effectiveness of precipitation treatments (c). Different letters represent statistically significant differences at $P < 0.05$. C, control; D, double precipitation; H, half precipitation.

($P = 0.057$, Table 2; Fig. 3a), respectively. Altered precipitation significantly influenced ecosystem productivity across the years (all $P < 0.05$, Table 2). For example, the main effects of double precipitation increased ANPP, BNPP, and NPP by an average of 3.9%, 3.8%, and 3.9%, respectively (Fig. 3c). In contrast, the main effects of half precipitation decreased ANPP, BNPP, and NPP by an average of 13.5%, 10.9%, and 12.2%, respectively (Fig. 3e). Overall, clipping had no significant impact on ANPP, BNPP, and NPP (all $P > 0.05$, Table 2; Fig. 3g).

f_{BNPP} varied greatly from 0.5 ± 0.0 in 2010 under the control to 0.6 ± 0.0 in 2011 under warming plus clipping in the clipped subplots (Fig. 2d). Warming significantly increased f_{BNPP} across the years ($P < 0.05$, Table 2; Fig. 3b). But neither the main effects of altered precipitation nor the impact of clipping was significant on f_{BNPP} over the years (all $P > 0.05$, Table 2). The main effects of warming and altered precipitation on f_{BNPP} varied between 2010 and 2011 ($P = 0.042$ and 0.057, respectively, Table 2). No interactive effects of warming, altered precipitation, and clipping on f_{BNPP} were found (all $P > 0.05$, Table 2).

Treatment effects on RUE of NPP

The treatments and some of their interactions significantly influenced RUE of NPP across the years (Table 2; Fig. 4). Although warming effects on RUE_{ANPP} and RUE_{NPP} were not significant (all $P > 0.05$), warming increased RUE_{BNPP} by an average of 5.0% across the years ($P < 0.05$, Table 2; Fig. 5a). Generally, altered precipitation greatly affected RUE_{ANPP}, RUE_{BNPP}, and RUE_{NPP} (all $P < 0.01$, Table 2; Fig. 4). Double precipitation on average decreased RUE_{ANPP}, RUE_{BNPP}, and RUE_{NPP} by 24.3%, 26.0%, and 50.4%, respectively, across the years (Fig. 5b). In contrast, the average increases under half precipitation treatment in RUE_{ANPP}, RUE_{BNPP}, and RUE_{NPP} were 11.6%, 14.3%, and 25.9%, respectively (Fig. 5c). Clipping marginally decreased RUE_{ANPP}, RUE_{BNPP}, and RUE_{NPP} by an average of 4.5% ($P = 0.075$), 3.1% ($P = 0.118$), and 7.6% ($P = 0.083$), respectively, across the years (Table 2; Fig. 5d). The main treatment effects on RUE_{ANPP},

Table 2 Results of repeated measures split-plot ANOVA for responses of soil temperature (ST) and moisture (SM), ANPP, BNPP, NPP, f_{BNPP}, and RUE of ANPP, BNPP, and NPP to warming (W), altered precipitation (PPT), clipping (C), year, and their interactions ($n = 4$). P values smaller than 0.05 and 0.10 are in bold and italic, respectively

	ST	SM	ANPP	BNPP	NPP	f_{BNPP}	RUE-$_{ANPP}$	RUE-$_{BNPP}$	RUE-$_{NPP}$
Warming (W)	**0.001**	**<0.001**	0.217	**0.009**	*0.057*	**0.020**	0.454	**0.013**	0.114
PPT	**0.002**	**<0.001**	**0.024**	**0.010**	**0.015**	0.234	**<0.001**	**<0.001**	**<0.001**
Clipping (C)	**0.007**	**<0.001**	0.195	0.157	0.170	0.340	*0.075*	0.118	*0.083*
Year (Y)	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.493	**0.029**
W × PPT	**<0.001**	0.193	0.311	0.211	0.286	0.227	0.435	0.139	0.303
W × C	**<0.001**	0.516	0.451	0.254	0.348	0.634	0.616	0.369	0.487
W × Y	**<0.001**	**<0.001**	0.983	0.422	0.702	**0.042**	0.953	*0.082*	0.355
PPT × C	**<0.001**	0.122	0.247	0.363	0.293	0.211	*0.063*	*0.090*	*0.066*
PPT×Y	0.151	0.326	0.253	0.699	0.447	*0.057*	**0.001**	*0.094*	**0.008**
C × Y	0.200	**0.047**	**0.021**	**0.008**	**0.010**	0.617	**0.048**	**0.012**	**0.017**
W × PPT × C	**<0.001**	0.366	0.793	0.428	0.643	0.449	0.786	0.238	0.510
W × PPT × Y	**<0.001**	*0.057*	*0.069*	*0.068*	*0.056*	0.612	**0.004**	**0.003**	**0.002**
W × C × Y	**<0.001**	**0.021**	0.432	0.449	0.421	0.543	0.478	0.439	0.429
PPT × C × Y	**0.001**	0.447	0.564	0.797	0.654	0.457	0.583	0.781	0.674
W × PPT × C × Y	0.288	**0.041**	0.824	0.879	0.930	0.351	0.826	0.356	0.738

ANPP, aboveground net primary productivity; BNPP, belowground net primary productivity; f_{BNPP}, partitioning of BNPP with respect to ANPP; NPP, net primary productivity; RUE, rain-use efficiency.

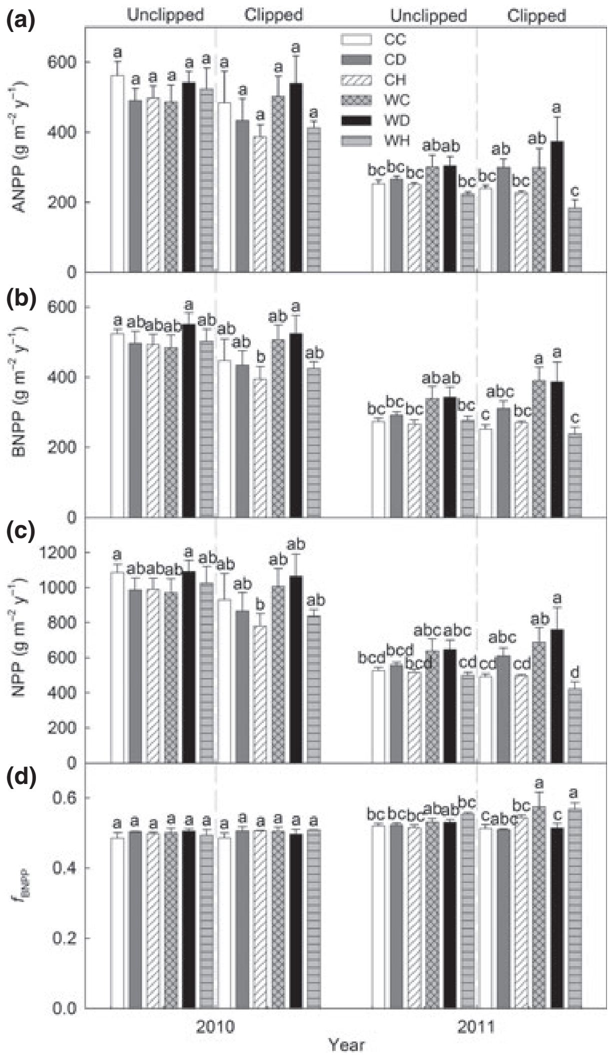

Fig. 2 Variation in aboveground net primary productivity (a), BNPP (b), NPP (c), and f_{BNPP} (d) under 12 treatments in 2010 and 2011. Values are Mean ± SE (n = 6). Different letters represent statistically significant differences at $P < 0.05$. CC, control; CD, double precipitation; CH, half precipitation; WC, warmed; WD, warmed and double precipitation; WH, warmed and half precipitation.

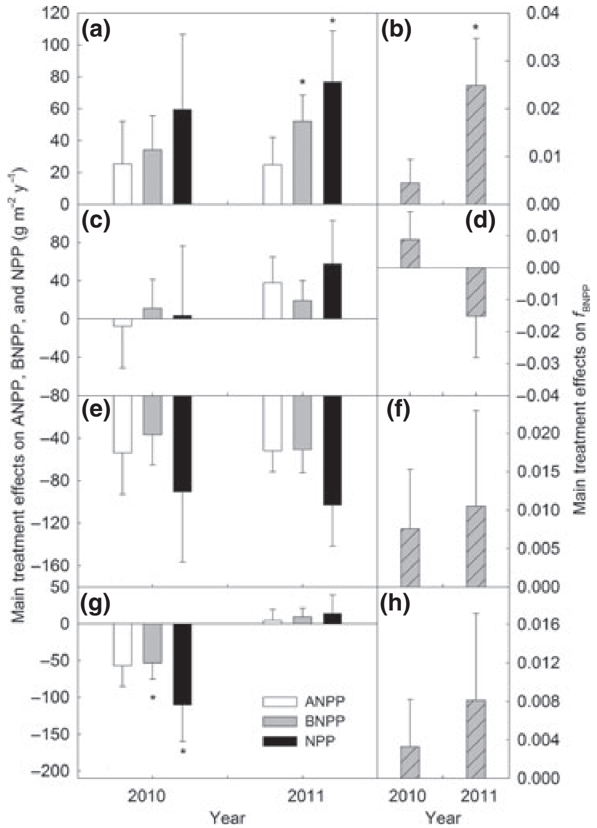

Fig. 3 Main treatment effects of warming (a, b), double precipitation (c, d), half precipitation (e, f), and clipping (g, h) on ANPP, BNPP, NPP, and f_{BNPP} in 2010 and 2011. Values are Mean ± SE. Asterisks indicate statistically significant difference between the control and the specific treatment at $P < 0.05$. ANPP, aboveground net primary productivity; BNPP, belowground net primary productivity; NPP, net primary productivity; PPT, precipitation.

RUE_{BNPP}, and RUE_{NPP} were positively influenced by treatment-induced changes in C_4/C_3 (Fig. 6 and S1). Additionally, the interaction of altered precipitation and clipping marginally influenced RUE_{ANPP}, RUE_{BNPP}, and RUE_{NPP} (all $P < 0.10$, Table 2).

Relationships of NPP and f_{BNPP} with climatic factors and species composition

Generally, variation in ANPP, BNPP, and NPP was positively and negatively regulated by soil moisture (all $P < 0.01$, Fig. 7a–c) and soil temperature (all $P < 0.05$ except for BNPP, $P = 0.056$, Fig. 7e–g), respectively, under different treatments across the years. Multiple regression analysis showed that soil moisture was the dominant climatic factor that controlled the variation in ecosystem productivity. The partitioning of NPP, f_{BNPP}, was negatively correlated with soil moisture and positively correlated with soil temperature (all $P < 0.01$, Fig. 7d and h). Soil temperature was found to be the dominant climatic factor that regulated the variation in f_{BNPP}. Additionally, species composition, expressed as the ratio of C_3 productivity to ANPP, significantly impacted ANPP, BNPP, NPP, and f_{BNPP} across the years (all $P < 0.05$, Fig. 7i–l).

Discussion

Treatment effects on NPP

Our results in general indicated that changes in temperature and precipitation directly and rapidly affected the

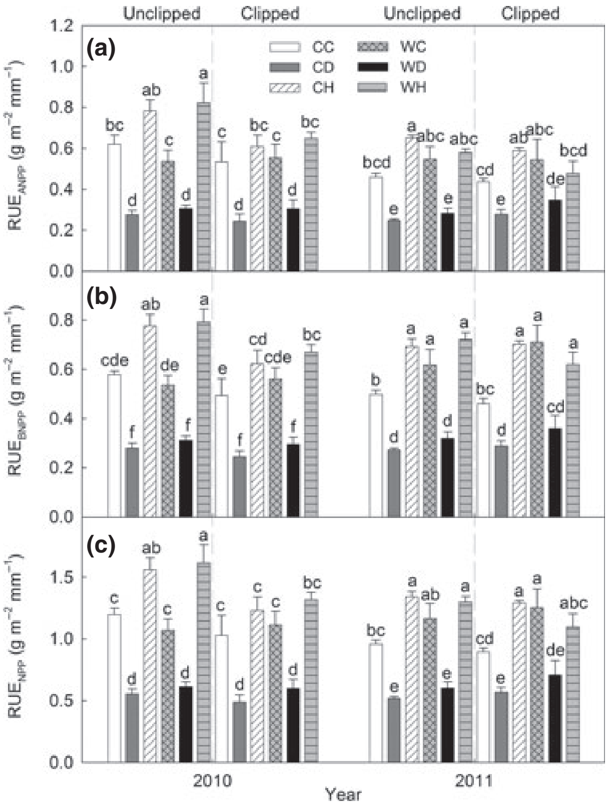

Fig. 4 Variation in the RUE_{ANPP} (a), RUE_{BNPP} (b), and RUE_{NPP} (c) under 12 treatments in 2010 and 2011. Values are Mean ± SE (n = 6). Different letters represent statistically significant differences at $P < 0.05$. CC, control; CD, double precipitation; CH, half precipitation; WC, warmed; WD, warmed and double precipitation; WH, warmed and half precipitation; RUE, rain-use efficiency.

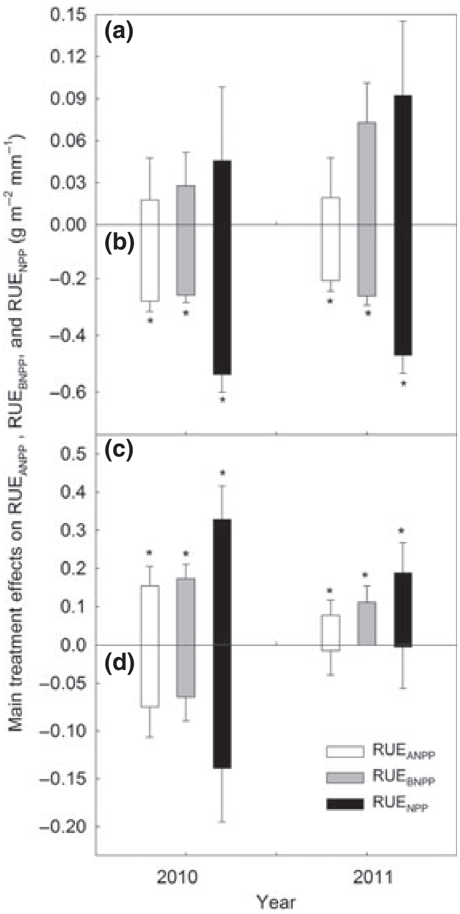

Fig. 5 Main treatment effects of warming (a), double precipitation (b), half precipitation (c), and clipping (d) on RUE_{ANPP}, RUE_{BNPP}, and RUE_{NPP} in 2010 and 2011. Values are Mean ± SE. Asterisks indicate statistically significant difference between the control and the specific treatment at $P < 0.05$. RUE, rain-use efficiency; ANPP, aboveground net primary productivity; BNPP, belowground net primary productivity; NPP, net primary productivity; PPT, precipitation.

production of grasslands. Warming increased BNPP significantly ($P < 0.01$) and NPP marginally ($P = 0.057$) across the years, although its effect on ANPP was not significant ($P > 0.05$, Table 2; Figs 2a–c and 3a). The increases in NPP were consistent with previous studies, which have demonstrated that experimental warming that increased soil temperature ranging from 0.1 to 10.2 °C significantly increased NPP (e.g., Luo *et al.*, 2009; Wu *et al.*, 2011; Xu *et al.*, 2012). The increases in NPP may be attributed to prolonged growing seasons with earlier beginnings and later endings under continuous warming (Wan *et al.*, 2005), increased soil nutrient mineralization and plant nutrient uptake (Rustad *et al.*, 2001; Sardans *et al.*, 2008), and also stimulated photosynthetic rates at higher temperatures (Rustad *et al.*, 2001; Luo *et al.*, 2009; Wu *et al.*, 2011). However, stimulated photosynthesis may be a minor cause of the increase in NPP since warming had no significant effect on photosynthesis according to previous studies (Stirling *et al.*, 1997; Zhou *et al.*, 2007; Rogers *et al.*,

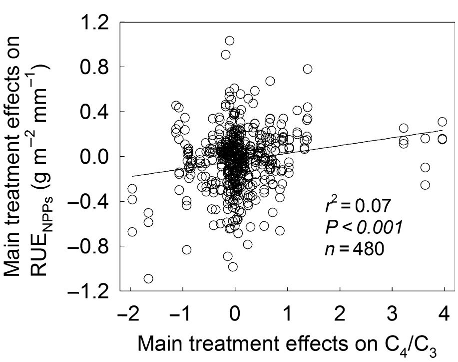

Fig. 6 Relationship of the main treatment-induced changes between C_4/C_3 and RUE_{NPPs} in 2010 and 2011. Treatments include warming, double precipitation, half precipitation, and clipping. RUE_{NPPs} represents RUE_{ANPP}, RUE_{BNPP} and RUE_{NPP}.

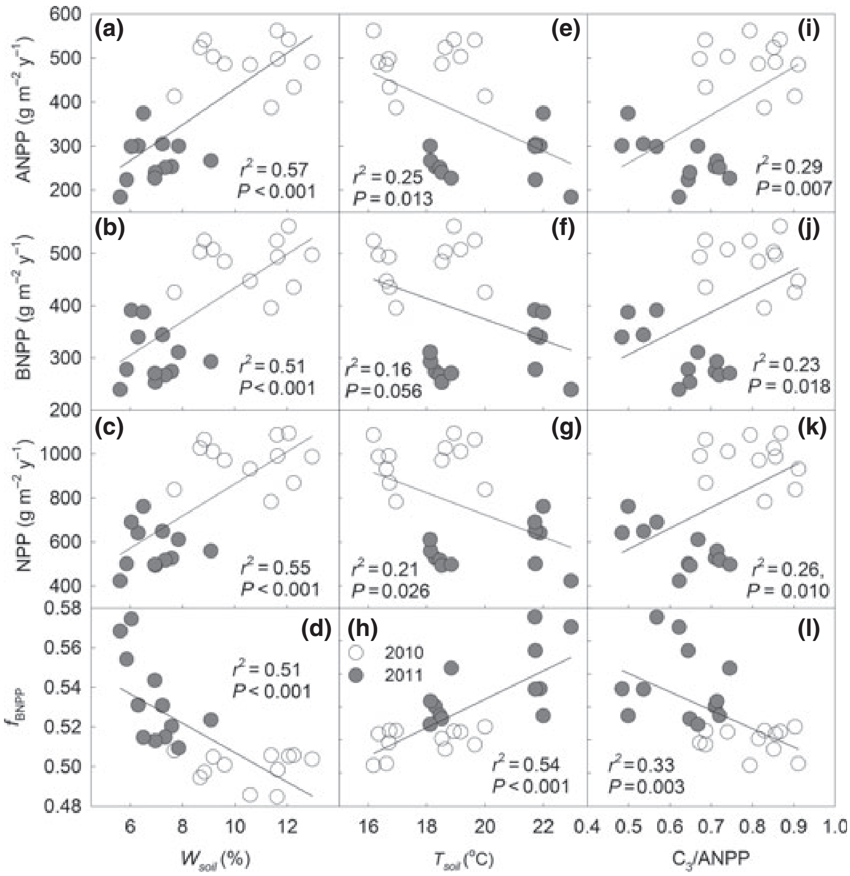

Fig. 7 Relationships of soil moisture (%), soil temperature (°C), and species composition (C_3/ANPP) with aboveground net primary productivity (a, e, i), BNPP (b, f, j), net primary productivity (NPP) (c, g, k), and f_{BNPP} (d, h, c) across the years (n = 24).

2012). The non-significant warming effect on ANPP probably resulted from the translocation of photosynthates from aboveground biomass to roots under warming, which was evidenced by the increased BNPP as well as f_{BNPP} under warming (all $P < 0.05$, Table 2; Figs 2b, d and 3a, b).

In line with previous findings (Sala *et al.*, 1988; Knapp *et al.*, 2001; Bai *et al.*, 2008; Wu *et al.*, 2011), our results showed that altered precipitation significantly influenced ANPP, BNPP, and NPP (all $P < 0.05$, Table 2). Overall, double and half precipitation stimulated and suppressed plant productivity, respectively (Figs 2a–c and 3c, e). Moreover, plant productivity in 2010 was much larger than that in 2011 (all $P < 0.01$, Table 2; Fig. 2a–c), probably due to the precipitation amount that was 1.7 times higher in 2010 than in 2011 (Fig. 2). Water availability is crucial to terrestrial biological activities (Sala *et al.*, 1988; Li *et al.*, 2011). Observed patterns of plant productivity across natural precipitation gradients and years suggest that increases in precipitation positively stimulated plant growth in relatively dry systems (e.g., Sala *et al.*, 1988; Huxman *et al.*, 2004). At least two possible reasons may account for clipping not significantly decreasing NPP across the years (all $P > 0.05$, Table 2). First, decrease in the amount of litter on the ground may increase seed bank stores and thus more germination at the beginning of growing seasons (Ruprecht & Szabo, 2012). Second, during the growing seasons, the photosynthesis of the lower canopy leaves may increase and thus give higher plant productivity due to less standing litter and improved light conditions in the clipped subplots (Xu *et al.*, 2012). Additionally, the responses of NPP to clipping varied widely by year (all $P < 0.05$, Table 2; Fig. 3g), probably related to the difference in precipitation amount, which in turn further confirmed the importance of precipitation in regulating plant productivity. The lack of interactive effects of warming, altered precipitation, and clipping suggest that results from single-factor manipulative experiments should be treated with caution.

Treatment effects on f_{BNPP}

The partitioning of BNPP with respect to ANPP is a critical issue in plant ecology and evolution as well as in C-cycling models (Enquist & Niklas, 2002; Ågren &

Franklin, 2003; Hui & Jackson, 2005). According to optimal partitioning theory, environmental changes may disturb the partitioning between BNPP and ANPP and cause plants to reallocate biomass among different organs to maximize their growth (Bloom *et al.*, 1985; Chapin *et al.*, 1987; Hui & Jackson, 2005). In this study, experimental warming was found to increase f_{BNPP} (P < 0.05, Table 2; Figs 2d and 3b), which has also been demonstrated in another manipulative warming experiment in a tall-grass prairie (Xu *et al.*, 2012). Moreover, in support of optimal partitioning theory, previous studies have shown that plants allocate proportionally more biomass to roots in response to warming-induced dry conditions in order to efficiently capture water (Chapin *et al.*, 1987; McCarthy & Enquist, 2007). Altered precipitation did not significantly impact f_{BNPP} across the years (P > 0.05, Table 2), probably due to the similar magnitude of precipitation-induced changes in both ANPP and BNPP, resulting in no significant net precipitation effect on f_{BNPP} (Fig. 3c–f). Clipping also had no impact on f_{BNPP} across the years (P > 0.05, Table 2) because it did not change ANPP and BNPP much (Table 2; Fig. 3g and h). Additionally, f_{BNPP} on average was smaller in 2010 than in 2011 (0.50 ± 0.003 vs. 0.53 ± 0.005, P < 0.0001, n = 48, Fig. 2d), indicating that low soil moisture conditions may positively impact f_{BNPP}. With global warming and changed precipitation regimes worldwide (IPCC, 2007), variation in f_{BNPP} should be taken into account in projecting climate change-terrestrial C feedback.

Treatment effects on RUE of NPP

Rain-use efficiency, linking the C and water cycles, is an important characteristic of ecosystem productivity and could be used to evaluate the ecosystem productivity in response to water availability (Knapp *et al.*, 2001; Huxman *et al.*, 2004; Bai *et al.*, 2008; Roupsard *et al.*, 2009). In grassland ecosystems, temperature has critical effects on RUE through its impact on evapotranspiration rates, the primary process by which precipitation is returned to the atmosphere (Wilcox *et al.*, 2006). In this study, both above- and belowground processes were examined as they responded to warming, altered precipitation, and clipping. Warming significantly increased RUE_{BNPP} but not RUE_{ANPP} and RUE_{NPP} (Table 2), suggesting that BNPP was more sensitive to warming than ANPP. In contrast to our results, warming has been reported to decrease grassland RUE as a result of reduced plant production (De Boeck *et al.*, 2006). These observations are reasonable because of differences between different grasslands in an array of factors, such as plant species composition, soil texture, and water holding capacity that influence grassland production under warming. For example, compared with a significant warming-induced increase in ANPP in a C_4 dominated grassland (Luo *et al.*, 2009), warming had no significant effect on ANPP in a C_3 dominated grassland (this study).

Rain-use efficiency of NPP in response to altered precipitation was found to be very different between double precipitation and half precipitation treatments. In line with previous studies showing that irrigation decreased RUE (Huxman *et al.*, 2004; Bai *et al.*, 2008; Li *et al.*, 2011), double precipitation reduced and half precipitation increased RUE of NPP, respectively (all P < 0.01, Table 2; Figs 4 and 5b, c), confirming that water is a primary resource limiting plant growth and production (Sala *et al.*, 1988; Bai *et al.*, 2008; Xu *et al.*, 2012). Additionally, clipping marginally decreased RUE_{ANPP} and RUE_{NPP} (all P < 0.05, Table 2; Figs 4 and 5d), probably resulting from stimulated evapotranspiration due to increased soil temperature and decreased soil moisture under clipping treatment (Tables 1 and 2; Wilcox *et al.*, 2006; Xu *et al.*, 2012). Treatment-induced changes in C_4/C_3 positively impacted changes in RUE_{ANPP}, RUE_{BNPP}, and RUE_{NPP} over the years (Fig. 6 and S1), indicating a potentially essential role of plant species composition in regulating RUE and demonstrating C_4 species' higher RUE than C_3 species (Niu *et al.*, 2003). Moreover, the interactions of clipping with altered precipitation marginally impacted RUE of NPP (all P < 0.10, Table 2; Fig. 4), making how ecosystem RUE would change under the interactions of climate change and land use less predictable.

Relationships of NPP and f_{BNPP} with climatic factors and species composition

Water availability, either as precipitation or soil moisture, is an overwhelmingly important controlling factor for grassland production (Sala *et al.*, 1988; Huxman *et al.*, 2004; Xu *et al.*, 2012). In accordance with previous findings that increased water availability always stimulates plant growth (e.g., Sala *et al.*, 1988; Knapp & Smith, 2001; Sherry *et al.*, 2008; Wu *et al.*, 2011), our results showed that variation of ecosystem productivity, including ANPP, BNPP, and NPP, was dominantly regulated by soil moisture across the years according to multiple regression analysis (all P < 0.001, Fig. 5a–c and e–g). Previous modeling studies also confirmed the dependence of plant productivity on soil moisture (e.g., Sherry *et al.*, 2008; Weng & Luo, 2008). Moreover, increases in N mineralization with increasing precipitation may also partly account for the increased plant production as found by Burke *et al.* (1997). The variation in f_{BNPP}, however, was mainly regulated by soil temperature (P < 0.01, Fig. 7h) based on multiple regression analysis, although soil moisture also influenced f_{BNPP} ($P < 0.01$, Fig. 7d), probably because changes in temperature significantly influenced BNPP, as demonstrated by Xu *et al.* (2012).

Soil moisture, co-impacted by an array of factors such as precipitation, temperature, and land-use practices, could serve as an essential index in projecting ecosystems' responses to climatic change (Friedlingstein *et al.*, 1999; Knapp *et al.*, 2001; Sherry *et al.*, 2008). Our results showed that soil moisture increased under double precipitation and decreased under warming, half precipitation, and clipping (all $P < 0.01$, Table 2). The differences in soil moisture between treatments were small (Table 1), which may be due to other factors, such as precipitation distribution and soil infiltration capacity, which may also affect soil moisture (Lee *et al.*, 2007). Increases in the amount of precipitation and precipitation frequency would lead to a decrease in groundwater recharge as soil infiltration capacities are exceeded (Trenberth *et al.*, 2003; IPCC, 2007).

In addition to climatic factors, variation in plant species composition (expressed as C_3 contribution to ANPP) may be another potential factor in influencing ANPP, BNPP, NPP, and f_{BNPP} (all $P < 0.05$, Fig. 7e–h). Our experimental site was dominated by C_3 species (ca. 72% of ANPP), which played a critical role in affecting production. Previous studies have also reported the potential roles of species composition in regulating ecosystem productivity under warming, altered precipitation, and CO_2 enhancement (e.g., Hoeppner & Dukes, 2012; Polley *et al.*, 2012). The negative correlation between species composition and f_{BNPP} (Fig. 7h) suggests that dry conditions favor the growth of C_4 species with an advantage in capturing water by a well-developed root system (Gao *et al.*, 2011; Bloor & Bardgett, 2012; Xu *et al.*, 2012). Moreover, plants invest more in BNPP under low water conditions (Hui & Jackson, 2005; Gao *et al.*, 2011), resulting in an increase in f_{BNPP}. However, we consider species composition to be a potential factor leading to variation in ecosystem productivity, f_{BNPP}, and RUE in this study, but our experimental design could not isolate treatment effects from species composition effects on ecosystem processes.

Our methods may underestimate overall BNPP but the estimation of treatment effects on NPP is reliable because (i) BNPP was measured once a year in this experiment while fine root turnover times could be less than a year (Gill & Jackson, 2000; Luo *et al.*, 2009); (ii) warming and clipping may not affect fine root turnover much (Fitter *et al.*, 1999; Gao *et al.*, 2008; Bai *et al.*, 2010); (iii) root turnover was stimulated by increased precipitation, leading to a further underestimation of BNPP (Bai *et al.*, 2010); and (iv) root turnover was inhibited under potential water stress (decreased precipitation) via prolonging life span for the fine roots to main function (Norby & Jackson, 2000). Additionally, runoff could influence plant water use but it may not have had much impact on the RUE of NPP in this study because runoff is inherently a component of rainfall and our whole experimental site is very flat. In general, to accurately predict the feedback of ecosystems to climate change and land use, we have to understand the responses of ecosystem processes, such as ecosystem productivity, the partitioning of productivity, and RUE, to climate change and land use as well as their consequences for ecosystem functions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Relationships of the main treatment effects on C_4/C_3 with changes in RUE_{ANPP}, RUE_{BNPP}, and RUE_{NPP} under warming (a), double precipitation (b), half precipitation (c), clipping, and all four treatments (e, f). Inserted panels g, h, and i are shown to demonstrate that positive correlations exit with deleting the large values around 3 (*X*-axis).