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GLOBAL CHANGE ECOLOGY - ORIGINAL RESEARCH

Consistent proportional increments in responses of belowground net primary productivity to long-term warming and clipping at various soil depths in a tallgrass prairie

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Abstract Root distribution patterns in soil are critical to understanding the interactions between climate and vegetation. However, it is not clear how climate change and land use practices affect belowground net primary productivity (BNPP) at various soil depths. In order to explore the effects of warming and clipping on root-distribution patterns along soil profile (0–15, 15–30, and 30–45 cm), we conducted a field experiment from 2005 to 2010 in a tallgrass prairie. We used infrared heaters to elevate soil temperature by approximately 2 °C and annual clipping to mimic hay harvest. Results showed that roots were not evenly distributed through the soil profile. On average across treatments and years, 53 and 83 % of the BNPP to 45 cm was distributed in the top 15- and 30-cm soil layers, respectively. Warming- and clipping-induced increases in BNPP were distributed to different soil depths at the proportions similar to those of BNPP. The proportional distribution of BNPP at various soil depths to total BNPP (0–45 cm) was little affected by warming, clipping, and their interactions, resulting in non-significant changes in the distribution of BNPP through the soil profile. These findings suggest that the proportionally vertical distribution of BNPP may remain stable even when the amount of BNPP changes simultaneously in response to climate change and land use practices.

Keywords Belowground net primary productivity · Tallgrass prairie · Soil depth · Warming · Clipping

Introduction

The global mean temperature is projected to increase 2–7 °C by the end of this century (Allison et al. 2009), possibly altering the functioning of terrestrial ecosystems through net primary productivity (NPP)—the primary driver of global C cycling (Norby and Luo 2004; Luo et al. 2009). More than one half of NPP in grasslands occurs belowground in root systems, which subsequently are the major organic matter input to soil (Briggs and Knapp 1995; McNaughton et al. 1998; Xu et al. 2012). In spite of a long history of study, the roots of plants remain the least understood part of the plant and our knowledge of belowground root dynamics is still inadequate (Jackson et al. 1996; Joslin et al. 2006). This is an area in which much remains to be done to better model the interactions between climate and vegetation (Jackson et al. 1996; Yang et al. 2011).

Roots are obscured by soil in the natural environment, leading to considerable difficulties in observing and measuring belowground NPP (BNPP) (Li et al. 2011; Xu et al. 2012). While there is no doubt that our current

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understanding of BNPP response to climate change is far from complete, advances are being made. For example, warming has been found to stimulate BNPP directly through prolonged growing seasons and increased plant nutrient uptake (Sardans et al. 2008; Wu et al. 2011; Xu et al. 2012) and indirectly through warming-induced variation in aboveground plant community structure (Xu et al. 2013), nutrient mineralization and availability (Sardans et al. 2008), and water availability (Li et al. 2011; Xu et al. 2012). Despite the large number of manipulative global change experiments globally (Wu et al. 2011), few studies have yet to include a report and discussion of BNPP distribution patterns in response to warming at various soil depths.

Understanding BNPP distribution at various soil depths is critical to a number of areas of ecology (Hutchings and John 2003). Vertical root distribution patterns have many implications for the hydrological balance and biogeochemical cycling of terrestrial ecosystems (Jackson et al. 1996; Hutchings and John 2003). Roots are pathways for upward water and nutrient transport and for downward carbon and nutrient transport into deeper soil layers (Jobbágy and Jackson 2000, 2001). For example, deep-rooted plants can take in water from deep soil layers and transfer it into upper, drier soil layers, a process known as “hydraulic lift” (Richards and Caldwell 1987; Horton and Hart 1998). Globally, by incorporating the information on root distribution into global models, representations of belowground processes and predictions of ecosystem responses to climate change would be more realistic (Jackson et al. 1996). Root distribution in terms of plant allocation between shallow and deep roots is essential to the relative soil organic C (SOC) distribution with depth and the 95 % rooting depth has been identified as a key variable in quantifying the interactions between plants, soil, and the climate (GCOS/GTOS Terrestrial Observation Panel for Climate 1997). At a local scale, our ability to accurately model plant competition is limited by our poor knowledge of root distribution of individual plants and of root-associated symbionts (Casper and Jackson 1997; Casper et al. 2000). Belowground competition, as a consequence of root distribution patterns, is a ubiquitous phenomenon whose significance has been confirmed by several previous studies (Gerry and Wilson 1995; Cahill 1999; de Kroon et al. 2003). In response to ongoing climate change, root distribution throughout the soil profile may change because BNPP is reported to be sensitive to warming-induced changes in a number of biotic and abiotic factors, such as plant community structure, temperature, soil moisture, and precipitation (e.g. Li et al. 2011; Wu et al. 2011; Xu et al. 2013). To our knowledge, however, no prior studies have examined how BNPP distribution patterns respond to warming at various soil depths in grasslands, reflecting the fact that we know less about BNPP than we would like to.

In grassland ecosystems, how BNPP responds to warming at various soil depths could be confounded by land use practices, such as clipping (Gao et al. 2008; Luo et al. 2009; Xu et al. 2012). In Oklahoma, clipping for hay is a widely practiced land use which occupies 3.25 million acres (USDA, National Agricultural Statistic Service). Possible ways that clipping may influence BNPP are through altering the amount of litter on the ground and seed germination (Ruprecht and Szabo 2012; Xu et al. 2013), aboveground plant community structure (Sherry et al. 2008; Xu et al. 2013), and the allocation patterns between roots and shoots (Farrar and Jones 2000; Xu et al. 2012). However, we know little about the magnitude and temporal patterns of BNPP changes in response to clipping and the interactions between warming and clipping at various soil depths. Given the importance of root distribution patterns in assessing soil C storage (Jackson et al. 1996), results from field manipulative experiments are thus badly needed for predicting ecosystem-level responses to land use practices under climate change.

Globally, 46 % of the fine root biomass is stored in grassland ecosystems, which, translated into C stocks, contains 2.3 % of the C present as atmospheric CO_2 (Jackson et al. 1997; Robinson et al. 2003). Moreover, fine roots are characterized by a short turnover time in grasslands, making them essential components in the study of the interception of nutrients and the regulation of nutrient cycling (Jackson et al. 1996; Gill and Jackson 2000; Luo et al. 2009). The long-term nature of our warming and clipping treatments since November 1999, as well as the special condition that our experimental period covered nearly the full range of annual precipitation (AP) from the previous 110 years (1900–2010; Fig. S1), provide us a unique opportunity to study the potential responses of vertical BNPP distribution to global change. We hypothesized that:

1. Roots decrease exponentially with increasing soil depth under all treatments (control, warming, clipping, and warming plus clipping).
2. The amount of warming- and clipping-induced increases in BNPP (Xu et al. 2012) distribute more to deep soil layers, because both warming and clipping dry the surface soil layer and may stimulate the growth of roots at deep soil layers in order to capture water to support plant growth aboveground.
3. Clipping may confound the root distribution through the soil profile since clipping proportionally decreased C_4 species that have relatively shallow rooting depth in comparison to C_3 species in the community.

Materials and methods

Experimental site and design

The experimental site is located on the Kessler Atmospheric and Ecological Field Station 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 psilostachyia, Solidago rigida,* and *Solidago nemoralis*). Mean annual temperature is 16.3 °C, with monthly air temperature ranging from 3.3 °C in January to 28.1 °C in July. The mean AP is 914 mm (Oklahoma Climatological Survey, Norman, OK). 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 (USDA 1979). This experiment uses a paired factorial design with warming as the main factor, within which is nested a clipping factor. We have six replicates (i.e. six pairs of plots) and each pair has two plots of 2 × 2 m. One plot of each pair has been subjected to continuous warming since 21 November 1999 while the other serves as the control with ambient temperature. Infrared heaters (165 × 15 cm; Kalglo Electronics, Bethlehem, PA) 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 the same dimensions as the infrared heater, suspended at a similar height to mimic the shading effects of the heater. For each pair of plots, the distance between warmed and control plots is approximately 5 m from the centers to avoid heating of the control plots. The distances between the paired plots vary from 20 to 60 m.

Each 2 × 2-m plot is divided into four 1 × 1-m subplots. Plants in two diagonal subplots are clipped at a height of 10 cm above the ground once a year to mimic hay harvest while the other two subplots are unclipped. Clipped materials are taken away and not returned back to the plots. This experiment has four treatments: unclipped and control (ambient) temperature, unclipped and warming, clipped and control temperature, and clipped and warming.

Microclimate and aboveground NPP measurements

Air temperature at the height of 25 cm above the ground was measured by thermocouples at the centers of each plot. Soil temperature was monitored by thermocouples at a depth of 2.5 cm in the centers of one clipped and one unclipped subplots in each plot. Volumetric soil water content in the top 15 cm was measured once or twice a month using portable time domain reflectometry equipment (Soil Moisture Equipment, Santa Barbara, CA). 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). Aboveground NPP (ANPP; separated into C_3 and C_4 species) was directly measured by clipping in clipped subplots and indirectly estimated by pin-contact counts (Frank and McNaughton 1990) in unclipped subplots. Plants were clipped annually at 10 cm height at peak biomass (usually August) in the diagonal clipping subplots (Sherry et al. 2008). Clipped biomass was oven-dried at 65 °C for 48 h.

BNPP measurement

From 2005 to 2009, the root ingrowth-core method was applied to estimate BNPP (Gao et al. 2008; Xu et al. 2012). Soil cores (5.2 cm in diameter) of 0–15, 15–30, and 30–45 cm in depth were taken at an angle of 90° (straight down into the ground) from the same spot in one unclipped and one clipped subplot in each plot every year (sampling once a year would underestimate BNPP due to the fast turnover of the finest roots). The holes were immediately filled with sieved root-free soil originating from the same depth outside of the plots. Soil filled into the holes was compressed to a density comparable to the bulk soil. 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 weighed to calculate BNPP. Vertical BNPP distribution was represented by the contribution of BNPP at soil depths of 0–1 5, 15–30, and 30–45 cm to the total amount of BNPP (0–45 cm).

Statistical analysis

We performed repeated-measures split-plot ANOVA to examine the main and interactive effects of experimental warming, clipping, soil depth (only applicable to BNPP), and year on BNPP and its contributions to total BNPP (0–45 cm) at various soil depths, aboveground productivity [including C_3, C_4, the ratio of C_4/C_3, and C_4 as a proportion of ANPP (C_4 %)], and soil temperature and moisture. Warming effect on air temperature was investigated using repeated-measures ANOVA. All statistical analyses were conducted using SPSS 17.0 for windows (SPSS, Chicago, IL).

Results

Microclimate and ANPP

Across the 6 years, AP varied from 515 mm in 2005 to 1,307 mm in 2007 with a mean of 882 mm (Table 1), which

Table 1 Annual precipitation, air temperature (T_{air}), soil temperature (T_{soil}) and moisture (W_{soil}) under different treatments at the experimental site

Variable	Treatment	2004	2005	2006	2007	2008	2009	2010	Average
AP (mm)		966	515	744	1,307	726	1,017	906	882
T_{air} (°C)	C		16.78 ± 0.39	17.12 ± 0.42	16.58 ± 0.42	16.65 ± 0.43	16.77 ± 0.47	16.67 ± 0.53	16.76
	W		19.00 ± 0.41	18.66 ± 0.42	17.61 ± 0.40	17.64 ± 0.41	17.89 ± 0.45	17.46 ± 0.51	18.06
T_{soil} (°C)	UC		16.91 ± 0.42	17.31 ± 0.41	16.78 ± 0.42	16.14 ± 0.42	16.74 ± 0.42	16.56 ± 0.46	16.74
	UW		18.95 ± 0.42	19.50 ± 0.42	18.15 ± 0.41	17.22 ± 0.40	17.34 ± 0.39	17.93 ± 0.45	18.19
	CC		17.54 ± 0.43	17.86 ± 0.41	17.06 ± 0.42	16.03 ± 0.41	17.04 ± 0.42	16.73 ± 0.44	17.05
	CW		20.23 ± 0.41	20.60 ± 0.42	19.45 ± 0.42	18.19 ± 0.40	19.55 ± 0.42	19.14 ± 0.45	19.54
W_{soil} (%)	UC		24.77 ± 1.11	23.50 ± 0.91	29.94 ± 0.39	26.96 ± 0.79	26.55 ± 2.88	30.34 ± 2.57	27.01
	UW		21.70 ± 0.72	21.95 ± 0.48	28.74 ± 0.50	25.21 ± 0.67	24.63 ± 3.19	28.67 ± 3.08	25.15
	CC		24.10 ± 0.84	23.14 ± 0.73	29.67 ± 0.43	26.05 ± 0.62	26.02 ± 2.78	29.76 ± 2.68	26.46
	CW		20.92 ± 0.83	20.92 ± 0.61	28.58 ± 0.39	24.35 ± 0.62	23.98 ± 2.87	27.99 ± 3.03	24.46

For T_{air}, T_{soil}, and W_{soil} within each year, values are mean ± SE

C Control (ambient) temperature, *W* warmed, *UC* unclipped and control temperature, *UW* unclipped and warming, *CC* clipped and control temperature, *CW* clipped and warming

is comparable with the long-term (1900–2010) mean AP in central Oklahoma of 840 mm (Fig. S1). Warming significantly elevated air temperature by 1.28 °C across the years ($P < 0.05$; Tables 1, 2). In addition, both warming and clipping significantly increased soil temperature and simultaneously decreased soil moisture across the years (all $P < 0.05$; Tables 1, 2). Warming increased soil temperature and decreased moisture by an average of 1.45 °C and 1.86 % in the unclipped subplots and 2.49 °C and 2.00 % in the clipped subplots, respectively. Clipping elevated soil temperature and lowered moisture by an average of 0.31 °C and 0.55 % in the unwarmed subplots and 1.35 °C and 0.69 % in the warmed subplots, respectively. Across the years, warming significantly increased C_4 species' productivity while clipping decreased C_4 species' productivity, the ratio of C_4 to C_3 (C_4/C_3), and the contribution of C_4 to ANPP (C_4 %, all $P < 0.01$, Table 2; Fig. 2). The productivity of C_3 species was not affected by either warming or clipping (all $P > 0.05$, Table 2; Fig. 1).

Treatment effects on BNPP and its vertical distribution

We found that both warming and clipping significantly increased BNPP across soil depths and years (all $P < 0.05$; Tables 2, 3; Fig. 2). BNPP decreased significantly with increasing soil depth ($P < 0.001$, Table 3; Fig. 2a–c). An average of 53 and 83 % of the BNPP to 45 cm was distributed in the top 15- and 30-cm soil layers, respectively, across the treatments and years (Fig. 3a–c). For the distribution of warming- and clipping-increased BNPP, the corresponding values were 61 and 60 % in the 0- to 15-cm layer and 84 and 71 % in the 0- to 30-cm layer, respectively. The proportional distribution of BNPP at various soil depths to total BNPP was little affected by warming, clipping, soil depth, and their interactions (all $P > 0.05$; Tables 2, 3; Fig. 3) except that BNPP distribution decreased significantly with increasing soil depths ($P < 0.001$; Table 3; Fig. 3a–c).

Discussion

BNPP distribution under treatments

Temperature and land use (clipping) are among the major factors affecting the development and growth of the root system (Hutchings and John 2003; Wu et al. 2011; Xu et al. 2012). Our results showed that both warming and clipping persistently increased BNPP at all three soil depths across the years (all $P < 0.05$, Tables 2, 3; Fig. 2), and are consistent with our previous findings (Xu et al. 2012). They indicate the distribution of increased BNPP to the whole root system throughout the soil profile rather than to the roots originating from certain specific soil layers. This distribution pattern may be attributable to the similar temperature increments generated by the infrared heaters and clipping at various soil depths (Wan et al. 2002), which lead to similar edaphic conditions. Roots are not evenly distributed at various soil depths and their distribution patterns are important in regulating the availability of water and nutrients to plants (Jackson et al. 1996; Hutchings and John 2003). In accordance with our first hypothesis, 53 and 83 % of the total BNPP (0–45 cm) was distributed in the top 15 and 30 cm of soil, respectively. The distribution proportions are comparable with a previous global synthesis study, which shows that temperate grasslands have a shallow rooting

Table 2 Results of repeated-measures ANOVA (*P*-values) for responses of mean annual T_{air}, T_{soil} and W_{soil}, belowground net primary productivity (*BNPP*) at various soil depths [0–15 cm (*%BNPP*$_{0-15}$), 15–30 cm (*%BNPP*$_{15-30}$), and 30–45 cm (*%BNPP*$_{30-45}$)], and aboveground productivity [including biomass of C_3 species (*C*$_3$), biomass of C_4 species (*C*$_4$), ratio of C_4/C_3, contribution of C_4 to aboveground net primary productivity (C_4 %)] to warming (*W*), clipping (*CL*), year (*Y*), and their interactions

	Warming	Clipping	Year	W × CL	W × *Y*	CL × *Y*	W × CL × *Y*
T_{air}	0.023*	–	<0.001***	–	<0.001***	–	–
T_{soil}	<0.001***	0.043*	<0.001***	0.202	<0.001***	<0.001***	0.001**
W_{soil}	<0.001***	0.005**	<0.001***	0.689	0.005**	0.809	0.972
BNPP_{0-15}	<0.001***	0.004**	<0.001***	0.046*	0.249	0.592	0.804
BNPP_{15-30}	<0.001***	0.012**	0.002**	0.056†	0.356	0.743	0.953
BNPP_{30-45}	<0.001***	0.005**	0.021	0.025*	0.703	0.981	0.954
$\%\mathrm{BNPP}_{0-15}$	0.189	0.740	0.450	0.629	0.972	0.937	0.979
$\%\mathrm{BNPP}_{15-30}$	0.167	0.969	0.339	0.773	0.981	0.941	0.996
$\%\mathrm{BNPP}_{30-45}$	0.428	0.480	0.893	0.562	0.991	0.955	0.984
C_3	0.105	0.143	<0.001***	0.613	<0.001***	0.068†	0.766
C_4	<0.001***	0.008**	<0.001***	0.875	0.127	<0.001***	0.594
C_4/C_3	0.274	0.007**	0.007**	0.267	0.008	0.056†	0.053
C_4 %	0.538	0.009**	0.003**	0.985	0.048**	0.027**	0.421

For other abbreviations, see Table 1

† $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

profile with approximate 49 and 83 % of root biomass in the top 10 and 30 cm of soil, respectively (Jackson et al. 1996). Interestingly, the distribution patterns of warming- and clipping-induced increases in BNPP at various depths, with 61 and 60 % in the 0–15 cm and 84 and 71 % in the 15–30 cm of soil, respectively, were similar to that of control BNPP. This reflects the surprising results that both warming and clipping did not much affect the contributions of BNPP to total BNPP at various soil depths across the years (all $P > 0.01$, Tables 2, 3; Fig. 3), contrary to the second and third hypotheses that roots would distribute more to deep soil layers.

Consistent proportional increments in BNPP through the soil profile

Plant community structure and environmental factors both influence BNPP distribution (Hutchings and John 2003; Robinson et al. 2003). But our results showed consistent BNPP distribution patterns in response to warming at various soil depths and the patterns persisted from 2005 to 2010. This may be attributed to:

1. In tallgrass prairie, C_4 grasses concentrate total root biomass in the shallow 0- to 10-cm soil layer while C_3 (shrub and forb) species concentrate roots in the surface 0- to 30-cm soil layer (Smith and Knapp 2003; Nippert and Knapp 2007). Warming had no significant impact on either C_4/C_3 or C_4 % (contribution of C_4 biomass to ANPP) across the years (all $P > 0.05$, Table 2; Fig. 1), leading to, partly, few changes in plant rooting patterns at the ecosystem level.
2. Temperature affects root development and growth and the optimal temperatures for maximal root growth typically range from 25 to 35 °C (Gregory 2006). Though warming increased soil temperature by approximately 2 °C (Table 1), it rarely exceeded 35 °C and was always lower than the maximum temperature for root growth which is around 40–45 °C (Fig. S2; Gregory 2006), making soil temperatures actually appropriate for root growth under all treatments. This is supported by the positive interactive effects of warming and clipping on BNPP because soil temperature is usually highest under the treatment of warming plus clipping (Tables 2, 3).
3. Soil moisture strongly governs root growth in grasslands (Hutchings and John 2003; Xu et al. 2013). In spite of a significant warming effect on soil moisture across the years ($P < 0.01$, Table 2), BNPP distribution patterns persisted, possibly due to trivial decrease in soil moisture (Table 2) as well as a potential process of hydraulic lift through which deep-rooted species transfer deep water nocturnally into dry topsoil and benefit neighboring plants (Richards and Caldwell 1987; Horton and Hart 1998).
4. The availability of mineral nutrients, such as N, is a key control over root growth (Hutchings and John 2003). A previous study, however, showed that warming had little impact on either soil or plant N content from 1999 to 2008 at the same experimental site

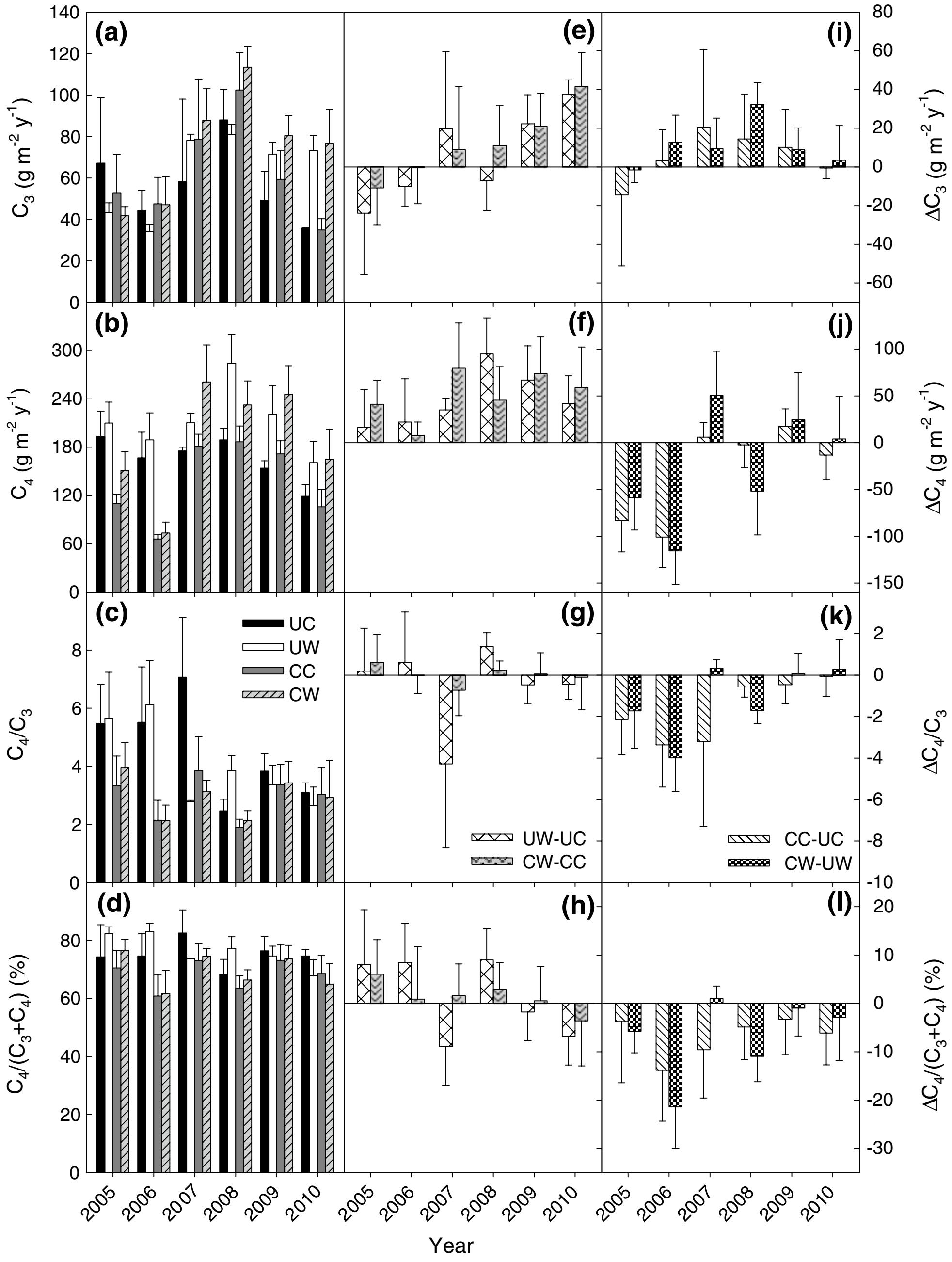

Fig. 1 Variation in the productivity of C_3 (**a**) and C_4 (**b**) species, the ratio of C_4/C_3 (**c**), the contribution of C_4 to aboveground net primary productivity (ANPP) (**d**), and the effects of warming (**e**–**h**) and clipping (**i**–**l**) on these parameters. Values are mean ± SE. $C_3 + C_4 =$ ANPP. *UC* Unclipped and control temperature, *UW* unclipped and warming, *CC* clipped and control temperature, *CW* clipped and warming, *UW-UC* warming effect without clipping, *CW-CC* warming effect with clipping, *CC-UC* clipping effect without warming, *CW-UW* clipping effect with warming, *Y* year

(Niu et al. 2010), probably resulting in little nutrient-induced differences in BNPP distribution patterns under warming. Soil imposes many constraints on the functioning of roots in terms of growth and resource capture (Hutchings and John 2003; Gregory 2006). The mechanism of "compensation for unpredictable resource supplies," by which a plant will adjust the influx and efflux rates of water and nutrients across root cell membranes by specific transport proteins, allows the root system to grown and function with considerable plasticity (Robinson et al. 2003; Glass 2005). Plasticity of plants helps them adapt to climate change and maintain the ecosystem at a relatively stable state (Nicotra et al. 2010).

Undoubtedly, similarity in the effects of clipping and warming on the environmental factors described above (Tables 1, 2; Fig. S2) accounts for, partly, the vertically and temporally persistent BNPP distribution patterns. The difference, however, was that clipping significantly affected plant community structure by lowering C_4/C_3 and C_4 % (all $P < 0.01$) while warming did not (all $P > 0.05$; Table 2; Fig. 1). Since C_3 plants have deeper rooting zones when compared with C_4 species (Smith

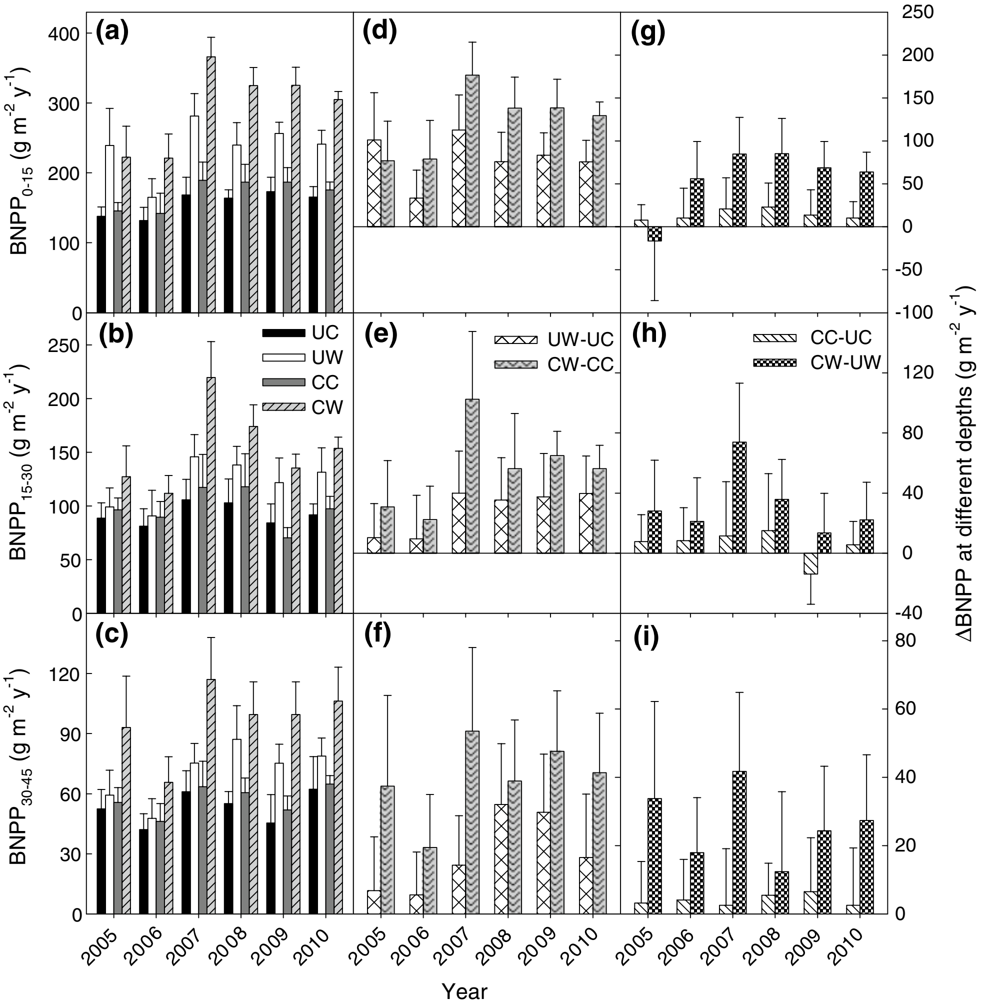

Fig. 2 Variation in the amount of belowground net primary productivity (*BNPP*) (**a**–**c**) and the effects of warming (**d**–**f**) and clipping (**g**–**i**) on BNPP at various soil depths (0–15, 15–30, and 30–45 cm) under the four treatments from 2005 to 2010. For other abbreviations, see Fig. 1

and Knapp 2003; Nippert and Knapp 2007), we hypothesized that the decrease in C_4 % would change the rooting patterns at the ecosystem level by reducing distribution of roots to surface soil layers. Thus, why did BNPP distribution patterns continue to persist at various soil depths? One possible explanation is belowground competition between C_3 and C_4 species, which stimulates the root investment of C_4 by enhancing the asymmetric responses of shoots and roots to clipping (Xu et al. 2012). Wilson and Tilman (1995) found belowground competition increased root:shoot ratios. Under clipping-induced, undesirable conditions, C_4 species may inevitably produce more roots to compete with C_3 species for root territories as well as resources (Gersani et al. 2001; de Kroon et al. 2003). In tallgrass prairie, C_3 and C_4 species competed for soil moisture in the same surface layer when water was not limiting, as demonstrated by Nippert and Knapp (2007). Competition for soil resources is often as intense as, or more intense than, competition for light, yet our understanding of how root-competition mechanisms result in specific rooting patterns is still in its infancy (Wilson 1988; Casper and Jackson 1997; de Kroon et al. 2003).

Potential causes and implications of consistent stimulation of BNPP throughout the soil profile

Increases in BNPP at various soil depths may primarily result from extended growing seasons under continuous warming in conjunction with the enhanced BNPP partitioning with respect to ANPP under warming and clipping. The consistent proportional increments in BNPP at different soil depths may be attributable to plant phenotypic plasticity that helps them adapt to a changing climate (warming and warming-induced environmental changes) and maintain the ecosystem at a relatively

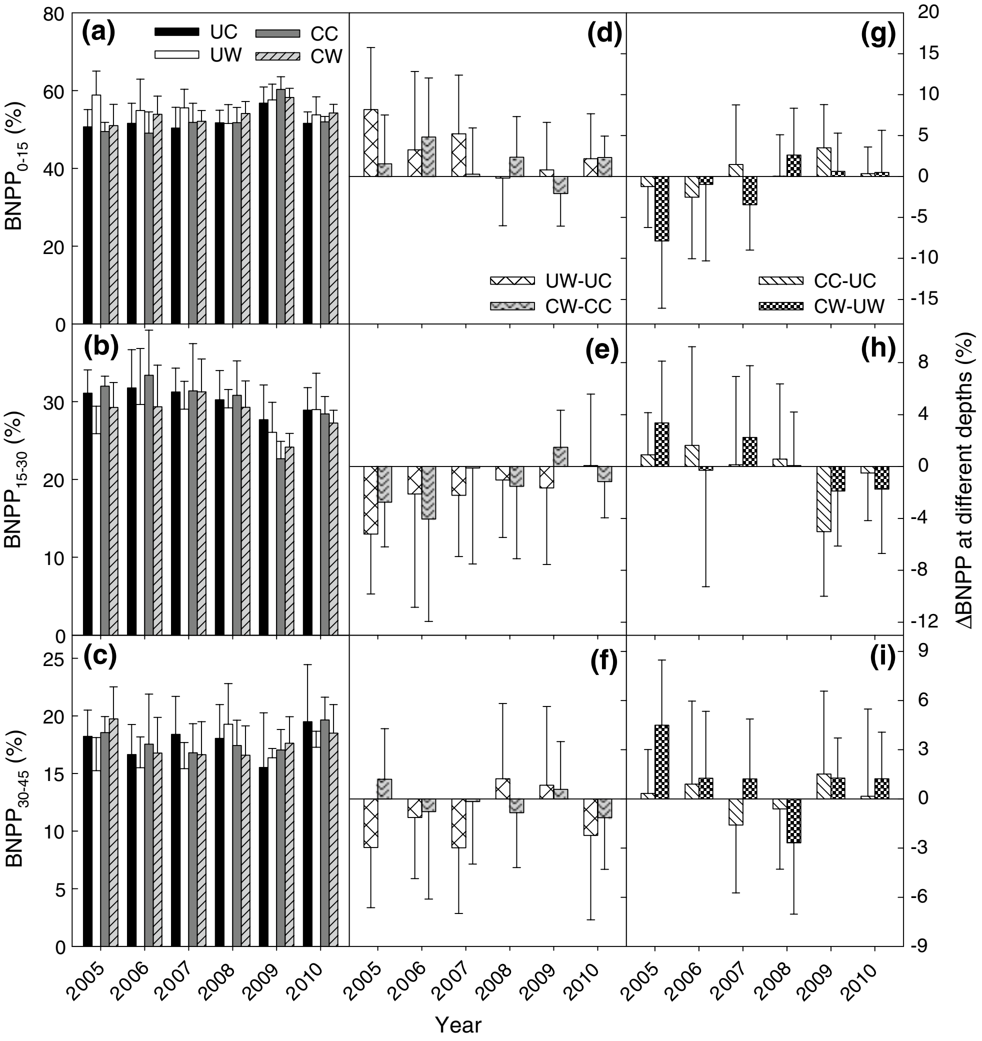

Fig. 3 Variation in vertical BNPP distributions (**a–c**) and the effects of warming (**d–f**) and clipping (**g–i**) on BNPP distributions at various soil depths [0–15 cm (%$BNPP_{0–15}$), 15–30 cm (%$BNPP_{15–30}$), and 30–45 cm (%$BNPP_{30–45}$)] under the four treatments from 2005 to 2010. Vertical BNPP distributions were represented by the contributions of BNPP at soil depths of 0–15, 15–30, and 30–45 cm to the total amount of BNPP (0–45 cm). Values are mean ± SE. For other abbreviations, see Figs. 1 and 2

stable state (Nicotra et al. 2010). Under clipping treatment, belowground competition between C_3 and C_4 species may also play an important role in the stability of BNPP distribution patterns. Accurate modeling of soil water balance and evapotranspiration is affected by belowground properties, such as rooting patterns, which, in turn, affect the terrestrial C budget (Kleidon and Heimann 1998; Hutchings and John 2003). Increased root litter input due to the increases in BNPP may alter soil texture through reshaping the depth profile of labile organic C (Schrumpf et al. 2013), leading to inaccurate prediction of terrestrial C sequestration. Roots in a relatively deep soil layer (30–45 cm) actively responded to climate change and land use, indicating that it is not adequate for typical earth system models to represent the biogeochemistry of soil organic matter with a single-layer (≈30 cm) box-modeling approach. Though most roots occur within the first 50 cm of the soil (Jackson et al. 1996), the small fraction of roots at deep soil layers has a pronounced effect on the hydrological cycle and NPP (Jackson et al. 1996; Kleidon and Heimann 1998), which is poorly understood. To our knowledge, the mechanistic understanding of rooting patterns in response to global change is only at the initial stage. Further research is needed to study the function of deep roots and their contribution to whole-ecosystem processes under climate and land use changes. Our findings, consistent proportional increments of BNPP in response to warming and clipping at various soil depths throughout the study period, may improve our understanding of soil C fluxes. Though our results are far from adequate to improve our ability to predict the consequences of climate and land use changes, they shed light on the direction and magnitude of BNPP to global change at various soil depths.

Table 3 Results of repeated-measures ANOVA (P-values) for responses of vertical BNPP distributions to W, CL, soil depth (D), Y, and their interactions ($n = 6$)

Factor	Warming	Clipping	Depth	Year	$W \times$ CL	$W \times D$	$W \times Y$	CL $\times D$	CL $\times Y$	$D \times Y$	$W \times$ CL $\times D$	$W \times$ CL $\times Y$	$W \times D \times Y$	CL $\times D \times Y$	$W \times$ CL $\times D \times Y$
BNPP	<0.001***	<0.001***	<0.001***	<0.001***	0.001**	<0.001***	0.017*	0.103	0.577	0.034*	0.554	0.818	0.967	0.880	0.980
%BNPP	1.000	1.000	<0.001***	1.000	1.000	0.078	1.000	0.801	1.000	0.202	0.718	1.000	0.994	0.961	0.997

For other abbreviations, see Tables 1 and 2

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

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