Ecosystems (2012) 15: 542–554
DOI: 10.1007/s10021-012-9525-3

ECOSYSTEMS

Root Biomass Dynamics Under Experimental Warming and Doubled Precipitation in a Tallgrass Prairie

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ABSTRACT

Human-induced climate change is expected to increase both the frequency and severity of extreme climate events, but their ecological impacts on root dynamics are poorly understood. We conducted a 1-year pulse warming and precipitation experiment in a tallgrass prairie in Oklahoma, USA to examine responses of root dynamics. We collected data in the pre-treatment year of 2002, imposed four treatments (control, 4°C warming, doubled precipitation, and warming plus doubled precipitation) in 2003, and observed post-treatment effects in 2004. Root biomass dynamics (for example, root growth and death) were measured using sequential coring and ingrowth coring methods. Treatment effects were not significant on standing root biomass in 2003, although root growth rate was significantly higher in the warmed than control plots. However, in the post-treatment year, the warmed plots had significantly lower standing root biomass than the controls, likely resulting from increased root death rate. Root death rate was significantly lower in the doubled precipitation and warmed plus doubled precipitation plots than that in the warmed plots in 2004. The root:shoot ratio showed similar responses to the post-treatments as standing root biomass, whereas aboveground biomass changed relatively little, indicating that roots were more sensitive to lagged effects than aboveground biomass. Our results demonstrate that root growth and death rates are highly sensitive to extreme climate events and lagged effects of extreme climate on root dynamics are important in assessing terrestrial carbon-cycle feedbacks to climate change.

Key words: global change; extreme climate; heat; drought; grassland; root biomass; growth; mortality.

INTRODUCTION

As a consequence of anthropogenic buildup of CO_2 and other greenhouse gases in the atmosphere (IPCC 2007), the surface temperature has risen by about 1°C in the Central Great Plains of the USA since 1950s. Models predict that annual average temperature will increase up to 4.5°C under a low emission scenario and 7.2°C under a high emission scenario by 2090s (Karl and others 2009). With this warming, precipitation regimes may be increasingly altered. The anticipated increase in precipitation is about 0.5–1% per decade in this century globally (IPCC 2007) with more frequent and more severe precipitation events in this region (Knapp and

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Received 21 July 2011; accepted 17 January 2012;

Xuhui Zhou and Shenfeng Fei contributed equally to this study.

Author Contributions: Xuhui Zhou performed research, analyzed data, and wrote the article; Shenfeng Fei performed part of research, analyzed data, and wrote the article; Rebecca Sherry performed part of research; Yiqi Luo conceived of, designed, and oversaw the study.

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others 2008; Karl and others 2009). Predicted changes in climatic extremes are expected to have large and rapid impacts on ecosystem services and socioeconomic systems (Karl and Knight 1998; Kunkel and others 1999).

Our understanding of effects of extreme climate fluctuations is mainly from opportunistic studies with a retrospective examination of ecosystem responses to natural extreme weather conditions. Previous studies found that extreme heat and drought decreased ecosystem primary productivity and respiration (Ciais and others 2005). Extreme climate could directly influence ecosystem carbon dynamics (Knapp and others 2002, 2008; Ciais and others 2005; Arnone and others 2008) but also indirectly impact them through increased ecosystem disturbances such as forest fires (Westerling and others 2006) and insect outbreak (Kurz and others 2008). In addition, extreme climate also induces shifts of species distribution, increases species extinctions (Post and Stenseth 1999; Easterling and others 2000), and changes community structure (Walther and others 2002).

Grassland ecosystems account for 31–43% of the global terrestrial ice-free surface and are a significant component of the global carbon balance (White and others 2000). Root biomass contributes more than half of the total plant biomass in grasslands (Saugier and others 2001; Hui and Jackson 2006), which plays a prominent role in the carbon and nutrient cycling (Ruess and others 2003). However, how extreme climate impacts grassland root dynamics is largely unknown. Soil temperature and moisture are two major environmental factors influencing root biomass, root growth and death, but the results appear to be conflicting from opportunistic studies of extreme weather conditions. Belowground productivity decreases under natural extreme warm conditions in some studies (Beier and others 1995; Asseng and others 1998), but can also remain surprisingly stable (Kreyling and others 2008a, b). Experimental examination of temperature extremes is very rare (Milbau and others 2005; Marchand and others 2006) but necessary. Knowledge from well-controlled, manipulative studies can improve model development under extreme climate conditions.

Experimental warming effects on grassland root dynamics vary largely among different studies. Previous studies have reported that warming caused increases (Edwards and others 2004; Bai and others 2010), no changes (Dukes and others 2005), and seasonally varied responses (Pregitzer and others 2000) in root growth and mortality. Moreover, warming could induce a decrease in soil moisture, causing confounded impacts on root dynamics (Harte and others 1995; Ciais and others 2005; Luo 2007). For example, in a semiarid temperate steppe, warming increased root production, mortality, and standing root biomass under ambient precipitation but decreased these variables under increased precipitation (Bai and others 2010). Increased water availability alleviated plant water stress, which was found to increase root biomass in Great Plains tallgrass prairie (Fay and others 2003), decrease root production in California annual grassland (Dukes and others 2005), or have no or mixed effects on root biomass in forests (Joslin and others 2000; Anderson and others 2003; Brunner and others 2009). Under reduced water availability, it has often been hypothesized and confirmed that plants tend to shift allocations of carbohydrates toward root development to increase water uptake, which leads to an increased root:shoot ratio (Osonubi and Davies 1981; Kramer 1983; Joslin and others 2000). However, water stress often increases fine root mortality, and reduces total root biomass (Green and others 2005; Meier and Leuschner 2008). Despite these efforts, the combined effects of warming and altered precipitation on root dynamics remain unclear, because most manipulative studies focused on single-factor experiments with highly diverse results. Our study is one of the few field experiments to examine the interactive effects of warming and altered precipitation on root dynamics (Gorissen and others 2004; Dukes and others 2005; Bai and others 2010).

Although most of the previous studies focused on root responses to moderate continuous change in climate means, no information is available on how grassland root dynamics respond during and after an extreme climate condition (that is, concurrent and lagged effects). In this study, we applied 1-year pulse warming and doubled precipitation to simulate anomalous high temperature, high precipitation, and both in a tallgrass prairie of central Oklahoma. We investigated how warming and increased precipitation individually and interactively affect root growth, root death, and root biomass during a treatment year, as well as lagged effects after the termination of treatments. We hypothesized that: (1) warming would stimulate root growth, death, and increase standing root biomass due to enhanced metabolism (a set of chemical reactions that happen in a living organism to sustain energetic and material needs, Gillooly and others 2001), (2) doubled precipitation would decrease standing root biomass, decrease root growth and death in the treatment year, due to increased soil moisture, (3) lagged effects would occur after the termination of treatments because altered soil nutrient and moisture conditions in the treatment year would continue to differ among the treatment plots, and (4) warming and doubled precipitation would have interactive impacts on standing root biomass, root growth and death, because doubled precipitation can partly alleviate the higher water stress caused by warming.

MATERIALS AND METHODS

Site Description

This study on root dynamics was carried out as part of a larger project to examine effects of an anomalous year of extreme high temperature and precipitation on community structure and ecosystem processes in a tallgrass prairie ecosystem (Zhou and others 2006; Sherry and others 2007; Bell and others 2010). The experimental site was located at the Kessler Farm Field Laboratory (KFFL, 34° 58′ 54″ N, 97° 31′ W) in McClain County, Oklahoma, USA. The mean annual temperature at the site is 16.3°C. Monthly air temperature ranged from 3.3°C in January to 28.1°C in July. The mean annual precipitation is 915 mm, with monthly precipitation ranging from 30 mm in January to 135 mm in May (average values from 1948 to 1998, data from Oklahoma Climatological Survey). The soil in the top 15 cm is a silt loam with 36% sand, 55% silt, and 10% clay (Subedar and Luo 2003, unpublished data). At deeper soil depths, the proportion of clay in the soils is greater. The soil has high fertility (42.2 kg total N ha^{-1} and 85.6 kg P ha^{-1}), neutral pH (7.05), high available water capacity, and a deep, moderately penetrable root zone (United States Department of Agriculture 1979).

The site was an old-field tallgrass prairie and only lightly grazed for 30 years until large herbivores were excluded in 2002. The dominant plants were perennial C_4 grasses: *Andropogon gerardii*, *Sorghastrum nutans*, *Schizachyrium scoparium*, and *Panicum virgatum*, perennial C_3 forb: *Ambrosia psilostachya*, and the annual C_3 grass: *Bromus japonicus*. Among C_3 plants, the winter annual grass *Bromus japonicus* survived through winter and dominated in spring.

Experimental Design and Treatments

The experiment consisted of twenty 3 × 2-m plots in two rows, with 3 m between the two rows and 1.5 m between plots within a row. There were four treatments of control, +4°C warming, doubled precipitation, and warming plus doubled precipitation with five replicates. Each plot was surrounded by a 1.1-m-deep plastic barrier, which reduces lateral exchange of surface and soil water with the surroundings as well as roots. Warming was achieved by two 165 cm by 15-cm radiant infrared heaters (Kalglo electronics Inc., Bethlehem, Pennsylvania, USA) suspended at a height of 1.5 m above the surface. Previous experimentation determined that, at this height, two heaters, each with a radiation output of 100 W m^2, would warm the soil surface by approximately 4°C (Wan and others 2002). The infrared radiation from the heater does not generate any visible light affecting photosynthesis (Kimball 2005). Two ''dummy'' heaters, made of metal flashing with the same size and shape as the infrared heaters, were suspended in each unwarmed plot at the same height and position as in the warmed plots to exclude the potential effect of shading.

Doubled precipitation was achieved by ''water catchments'' made of an angled sheet of corrugated plastic with the same size as the plots in five of the warmed plots and five of the unwarmed plots. During rainfall events, these catchments directed precipitation onto the plots via three 1.8-cm (inner diameter) polyvinyl chloride (PVC) pipes that distributed water evenly over the plots with many 3.0-mm holes. All the plots were fitted with the PVC pipes whether or not they were attached to water catchments. With this design, extra precipitation was only supplied to the doubled precipitation plots during natural rain without changing the frequency of the rainfall events.

Warming and doubled precipitation treatments were implemented for 1 year from 20 Feb 2003 to 20 Feb 2004 (referred to as the treatment year hereafter). Measurements were made throughout the pre-treatment year (February 2002–February 2003), treatment year, and post-treatment year (February 2004–February 2005). During the experiment, annual ambient precipitation was 824, 698, and 913 mm in 2002, 2003, and 2004, respectively (Oklahoma Climatological Survey). From 1895 to 2009, annual precipitation exceeded 1200 mm in only 5 years, and exceeded 1400 mm in only 1 year (Oklahoma Climatological Survey). Even though the treatment year had lower than average precipitation, the doubled precipitation plots received around 1,400-mm rainfall in that year, well in the range of the extreme precipitation. For mean annual temperature (15.5°C) from 1895 to 2009, only 2 years recorded more than 17.0°C and there is not a single year over 18.0°C. One year pulse 4°C warming and doubled precipitation can thus be considered as an extreme condition.

Temperature was recorded hourly with automated thermocouples (Campbell Science Equipment, Logan, Utah, USA) placed in the middle of each plot at 15 cm above and 7.5, 22.5, 45, 75, and 105 cm below the soil surface. The mean annual air temperature was 15.4, 15.9, and 15.9°C in 2002, 2003, and 2004, respectively. Warming increased air temperature by 4.4°C at the height of 15 cm above the ground. TDR probes (time domain reflectometry, ESI Equipment, Victoria, British Columbia, Canada) were used to monitor volumetric soil water content hourly over 5 depth intervals, 0–15, 15–30, 30–60, 60–90, and 90–120 cm below the soil surface. After each rainfall event, soils dried faster in the warmed than unwarmed plots (Sherry and others 2008). During the treatment year, average soil water content in the layer of 0–15 cm in the controls (C) was 27.6% higher than that in the warmed (W) plots, 7.0% lower than that in the doubled precipitation (DP) plots, and 17.6% higher than that in the warmed plus doubled precipitation (W + DP) plots (Figure 1). After the end of the treatments, it took more than 3 weeks for soil moisture in the layer of 0–15 cm of the W plots to return to the ambient levels of the C plots. In the layer of 60–90 cm, it took about 3 months for soil moisture to return to the ambient levels of the C plots after the treatments terminated.

Measurements

The roots were sampled once a year using two different methods: sequential soil coring and ingrowth coring. One sequential soil core and one ingrowth core were collected in each plot each year (totally 20 soil cores for each method each year) using a metal cylindrical pipe with an inside diameter of 3.71 cm. The soils were separated into four increments: 0–15, 15–30, 30–60, 60–90 cm depths. The sequential soil cores were taken at different spots in each plot to avoid sampling at the same place each year in the fall, whereas the ingrowth soil cores were at the same spot in each plot to estimate root growth rate within 1 year. Samplings took place on 24 Nov 2002, 6 Dec 2003, and 30 Oct 2004. Sampling dates were chosen at around the end of the growing season before winter snow events. After soil cores were taken out every year, we filled the holes immediately with

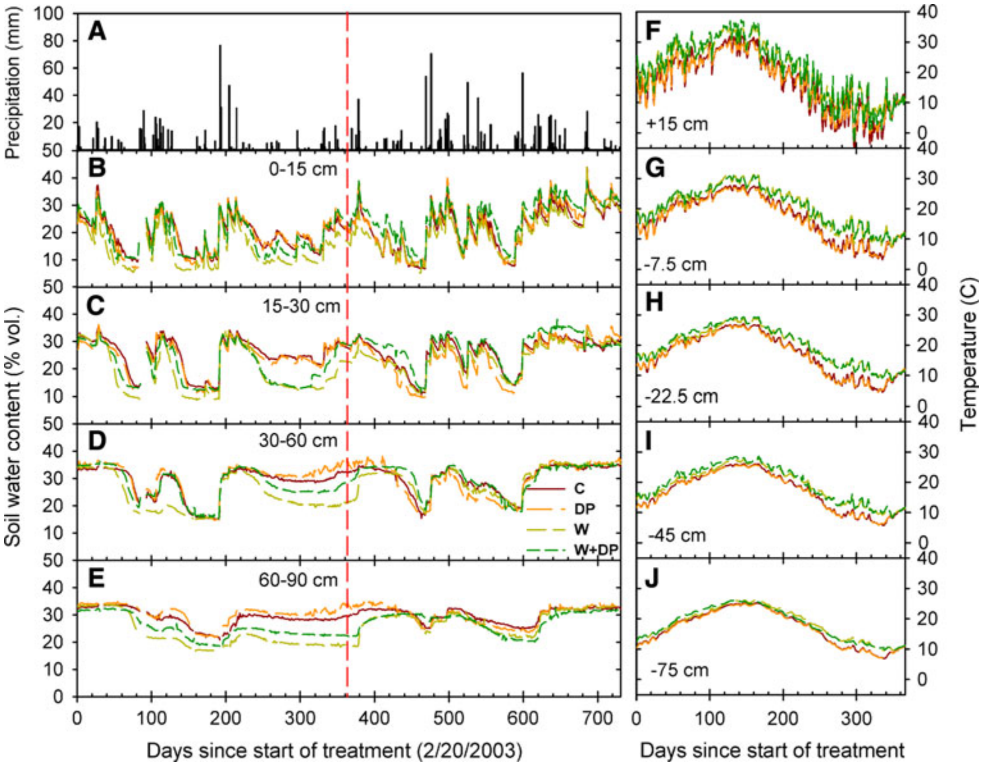

Figure 1. Daily precipitation (**A**) and volumetric soil water content in the soil layers of 0–15 cm (**B**), 15–30 cm (**C**), 30–60 cm (**D**), and 60–90 cm (**E**) under the control (C), warming (W), doubled precipitation (DP), and warming plus doubled precipitation (W + DP) treatments during the treatment (2003) and post-treatment (2004) years as well as air temperature at 15 cm above the soil surface (**F**) and soil temperature at the depth of 7.5 cm (**G**), 22.5 cm (**H**), 45 cm (**I**), and 75 cm (**J**) under the four treatments during the treatment year (2003). Hourly soil moisture and temperature data were averaged from five plots to give daily values for each treatment.

new soil, which was sieved to remove roots, from shallow (0–30 cm) and deep soil layers (30–90 cm) outside of the experimental plots related to the corresponding layers in the holes. The newly filled cores contained similar soil profile properties as the old ones.

Soil samples from the sequential and ingrowth coring were frozen immediately after sampling and stored in a refrigerator at the University of Oklahoma before further processing. Soil samples were soaked in stainless steel sieves containing tap water for the separation of roots and other substances. Only ten randomly chosen ingrowth cores in the pre-treatment of 2002 were processed (2 from the C, 2 from the W, 4 from the DP, and 2 from the W + DP plots). Roots were picked out from each soil sample and placed in the oven at 60°C for 48 h and then weighed to estimate the root biomass. No distinction between live and dead roots was made. Root biomass from the sequential cores represents standing root biomass when we assumed root turnover rates of 1 year in tallgrass prairie, despite large variability of reported turnover rates (Eissenstat and Yanai 1997; Gill and Jackson 2000). Root biomass from the ingrowth cores was considered to be a rough estimation of root growth rate in each measurement year (Higgins and others 2002) because the ingrowth coring would potentially stimulate root growth in the newly filled soil (Neill 1992).

Calculation and Statistical Analysis

Due to high variability among plots in the pre-treatment year, we normalized the standing root biomass values before further statistical analysis. We first calculated the difference between the pre-treatment standing root biomass in each plot and the pre-treatment mean, and then subtracted this difference from standing root biomass values in that plot in the following years. Because only the ten ingrowth cores were sampled from the pre-treatment year, we did not apply normalization on root growth rate.

We estimated the potential root death rate for a particular year from the previous year's standing biomass plus root growth from ingrowth cores of that year minus the standing root biomass of that year based on the steady state of grassland ecosystems. Because root production and mortality could occur simultaneously in grasslands (Higgins and others 2002), our method reflects the lower bound of root death rate. The root:shoot ratio was estimated as normalized standing root biomass divided by normalized aboveground biomass measured at the same time each year. Aboveground biomass in fall was measured directly by clipping half of the plots at 10 cm at each observation time, whereas another half was clipped in the summer. The same half plot was clipped at the same time each year. Clipping each year reduced any effect that number of meristems could have on ensuing biomass by removing all the meristems above 10 cm. Biomass was dried for 3 days in 65°C ovens and weighed. More details of aboveground biomass measurement were described in Sherry and others (2008).

We performed the Kolmogorov–Smirnov test and the Levene's test to ensure data met the assumptions of normality and homogeneity of variances. Three missing data for standing root biomass and two for root growth rate were replaced with the mean annual value for the same year. We used repeated measures ANOVA to examine the effects of warming and doubled precipitation on standing root biomass, root growth, root death, and root: shoot ratio (Table 1). In this analysis, root responses to inter-annual variability in weather were reflected in the within-subject repeated factor (year). Because of the interaction between year and manipulated treatments on root variables, one-way ANOVA with treatment types as between-subject effects was applied to examine the effects of the treatments in each year on different soil layers and the whole section from 0 to 90 cm. Effects were considered significant if $P < 0.05$, and marginally significant if the P values were between 0.05 and 0.10. Multiple comparisons of means were performed with Tukey's test ($P < 0.05$) in repeated measures ANOVA. When the sphericity assumption was violated, the significance level was reported as Greenhouse-Geisser significance. All analyses were conducted using the SPSS statistical package (SPSS, Inc., Chicago, Illinois, 2004).

RESULTS

Standing Root Biomass

Warming and doubled precipitation treatments did not significantly affect standing root biomass in any individual layer or all layers combined or their interaction (Figure 2A; Table 1), which was opposed to our hypothesis. Standing root biomass showed large interannual variability, resulting in significantly year effects (Table 1). Year and doubled precipitation had a significant interactive effect on standing root biomass in the layer of 0–15 cm and all layers combined (Table 1). After the treatments were terminated (that is, the post-treatment year), we observed significantly lower standing

Table 1. *F*-Ratios of the Effects of Warming (W), Doubled Precipitation (DP), and Year on Standing Root Biomass, Root Growth, Root Death, and Root:Shoot Ratio

	Effects	*df*	All layers	0–15 cm	15–30 cm	30–60 cm	60–90 cm
Standing root biomass	W	1	0.14	0.55	0.00	0.63	0.01
	DP	1	0.30	0.04	0.93	0.19	0.31
	Year	2	**11.92****	**4.05***	**7.21****	**9.95****	**8.05****
	Year × W	2	2.06	0.71	0.77	2.62	0.22
	Year × DP	2	**4.75***	**3.69***	2.73	0.03	0.84
	W × DP	1	0.08	0.21	0.40	0.65	0.50
	Year × W × DP	2	0.74	0.54	2.84	0.13	0.10
Root growth	W	1	0.63	0.47	1.35	0.31	0.29
	DP	1	1.31	0.38	2.03	0.96	**5.95***
	Year	2	2.00	1.31	**10.68****	**4.57***	**4.51***
	Year × W	2	0.63	1.47	0.37	0.45	0.37
	Year × DP	2	0.68	1.05	0.18	0.19	0.14
	W × DP	1	0.80	0.04	**4.50***	1.53	3.70
	Year × W × DP	2	1.00	0.19	2.01	2.83	0.78
Root death	W	1	2.01	1.16	0.74	1.75	0.01
	DP	1	2.95	0.76	**7.28***	0.49	4.12
	Year	1	0.40	1.24	0.11	**5.64***	**4.82***
	Year × W	1	0.59	0.01	1.01	2.66	0.35
	Year × DP	1	**6.68***	**13.59****	0.53	0.03	0.02
	W × DP	1	1.93	0.21	**11.99****	1.27	0.60
	Year × W × DP	1	0.05	0.46	0.04	0.33	0.16
Root:shoot ratio	W	1	0.06				
	DP	1	0.23				
	Year	2	**4.29***				
	Year × W	2	2.06				
	Year × DP	2	2.29				
	W × DP	1	0.004				
	Year × W × DP	1	0.498				

Repeated-measure ANOVA was used for each layer and the sum across all layers. The replicate is 5 (N = 5).
Bold values represent the significance of the effects.
*$P < 0.05$.
**$P < 0.01$.

root biomass in the warmed (W) than control (C) plots ($P = 0.048$, Figure 2A). The doubled precipitation (DP) and warmed plus doubled precipitation (W + DP) plots had marginally greater standing root biomass than the W plots ($P = 0.068$, Figure 2A).

Standing root biomass showed an exponentially decreasing distribution pattern with depth (Figure 3). On average of the 20 plots in the pretreatments year of 2002, the root biomass in the soil layers of 0–15, 15–30, 30–60, and 60–90 cm accounted for 64.9, 19.4, 11.2, and 4.5% of the total biomass, respectively (Figure 3A). Warming shifted the vertical distribution of root biomass to the deeper layers in 2003 (Figure 3). Standing root biomass in the W + DP plots was significantly lower than that in the C plots in the treatment year in the layer of 0–15 cm ($P = 0.011$) (Figure 3B). Below 15 cm, standing root biomass in 2003 increased in all treatments compared to that in 2002, by a higher percentage at 30–90 cm than that in shallower layers. In the post-treatment year, standing root biomass in the soil layer of 0–15 cm showed a substantial increase by 74.6% in the DP plots and by 87.45% in the W + DP plots compared to those in the treatment year, whereas they increased by only 18.9% in the C plots and decreased by 31.2% in the W plots. The same pattern also occurred at the soil layer of 15–30 cm, where warming significantly decreased standing root biomass compared to the control ($P = 0.025$, Figure 3C).

Root Growth and Death

Root growth rates in the W plots in the treatment year were significantly higher than that in the C plots when we lumped all samples in the C plots

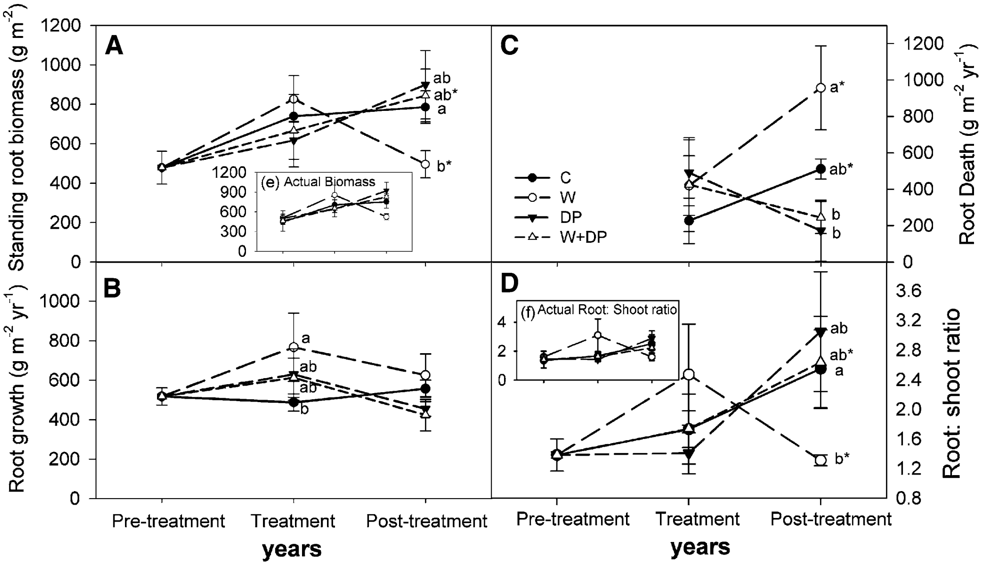

Figure 2. Normalized standing root biomass (**A**), root growth (**B**), root death (**C**), and normalized root:shoot ratio (**D**) under the control (C), warming (W), doubled precipitation (DP), and warming plus doubled precipitation (W + DP) treatments in the pre-treatment, treatment, and post-treatment years. *Inserted panels* show the actual standing root biomass (*e*) and root:shoot ratio (*f*). Root growths from ten sampled plots in the pre-treatment year are combined together to a single mean. Lines between years help visualize the differences between years and do not represent strictly linear increases or decreases during the intervening periods. Data are given as mean ± standard error (SE, g m^{-2}). *Lower case letters* represent statistically significant differences among the treatments in the same year ($P < 0.05$). *Asterisk* represents marginally significant differences between pairs of treatments at $P < 0.10$.

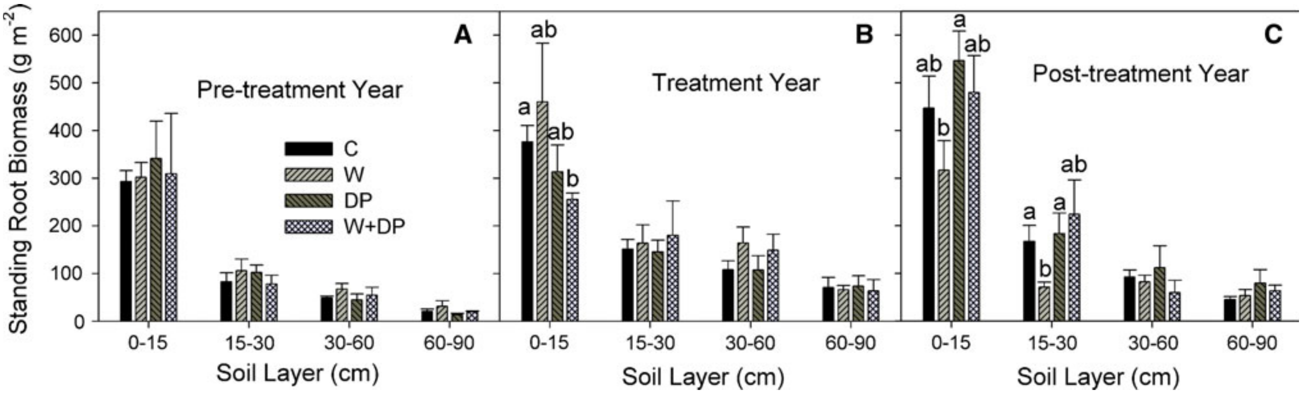

Figure 3. Standing root biomass in the four soil layers (0–15, 15–30, 30–60, and 60–90 cm) under the control (C), warming (W), doubled precipitation (DP), and warming plus doubled precipitation (W + DP) treatments in the pre-treatment (**A**), treatment (**B**), and post-treatment (**C**) years. *Error bars* represent standard error ($n = 5$). *Lower case letters* represent statistically significant differences among the treatments ($P < 0.05$).

from 2002 to 2004 ($P = 0.049$) (Figure 2B). In 2003, the W + DP plots had significantly lower root growth rates than the W plots in the layer of 60–90 cm ($P = 0.013$) (Figure 4B). Root growth rates in the layer of 0–15 cm and all layers combined were not affected by warming, doubled precipitation, year, and their interactions (Table 1). There was an interactive effect of the warming and doubled precipitation treatments in the layer of 15–30 cm ($P < 0.05$, Table 1). Effects of doubled precipitation on root growth rates were significant in the layer of 60–90 cm, although the root biomass in this layer only contributed to a very small fraction of the total biomass (Table 1). In the post-treatment year, root growth rates were significantly higher in the W plots than that in the C plots ($P = 0.049$) and the W + DP plots ($P = 0.044$) in the 15- to 30-cm layer (Figure 4C).

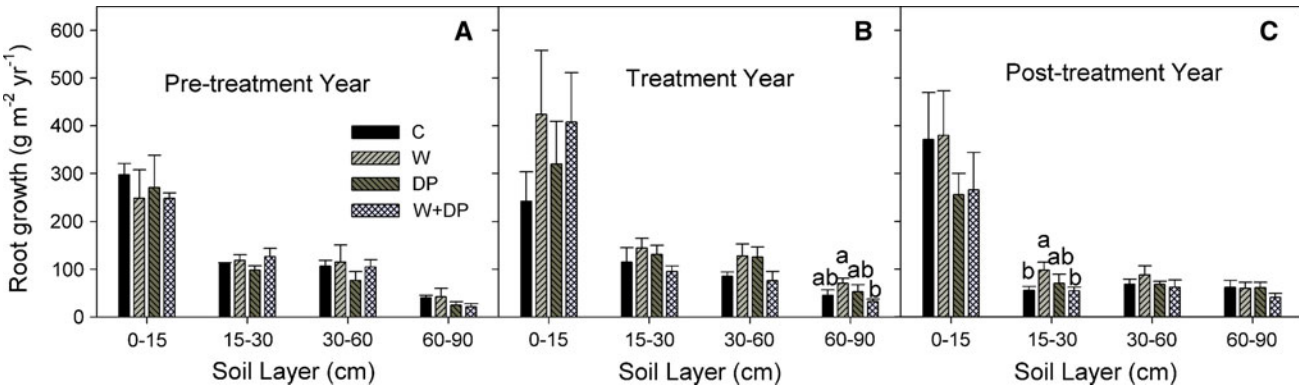

Figure 4. Root growth rate in the four soil layers (0–15, 15–30, 30–60, and 60–90 cm) under the four treatments in the pre-treatment (**A**), treatment (**B**), and post-treatment (**C**) years. *Error bars* represent standard error ($n = 5$). *Lower case letters* represent statistically significant differences among the treatments ($P < 0.05$). See Figure 3 for the notes and abbreviations.

Doubled precipitation significantly affected root death rates in the layer of 15–30 cm and year effects were significant in the layers of 30–90 cm (Table 1). Warming and doubled precipitation showed the significant interactive effects on root death rates in the layer of 15–30 cm as well as the interaction between year and the doubled precipitation in the layer of 0–15 cm and all layers combined (Table 1). Root death rates were lower in the DP and W + DP plots in the post-treatment year than the treatment year, whereas they had opposite trends in the C and W plots (Figure 2C). In the post-treatment year, doubled precipitation significantly decreased root death rates ($P = 0.004$, Figure 2C). The warming-induced stimulation of root death rates in the post-treatment year mainly occurred in the soil layers of 0–30 cm, where the DP and W + DP plots had significantly lower root death rates than the C and W plots in the 0–15 cm layer ($P = 0.007$, Figure 5B).

Root:Shoot Ratio

Warming and doubled precipitation did not significantly affect root:shoot ratio due to large interannual variability (Table 1). During the treatment year, the W plots had the highest root:shoot ratio in the four treatments, although the treatment effects were not significant (Figure 2D). However, the root:shoot ratio in the W plots was significantly lower than that in the C plots in the post-treatment year ($P = 0.048$, Figure 2D).

DISCUSSION

Extreme climate fluctuation is likely to occur more frequently in the future in this region (Karl and others 2009). Although most other studies focused on plant responses to continuous multi-year climate change, our experimental setting simulated anomalous climate conditions for 1 year, which enabled us to study the concurrent and lagged effects of a climatically extreme year on root dynamics of temperate grassland. Although we applied very intense treatments, a more than 4°C increase in temperature and doubled precipitation, their effects were not significant during the treatment year. However, we observed significant lagged effects during the post-treatment year, likely resulting from changes in soil nutrient, moisture conditions, and probably community structure, which are important in assessing terrestrial carbon-cycle feedbacks to climate change.

Approaches of Root Dynamics and Our Limitation

Despite much attention over the past decades, root dynamics remain one of the least understood attributes of terrestrial ecosystems, showing large uncertainty among methods as well as within one approach with high spatial heterogeneity (Lauenroth 2000). Root dynamics have been obtained through conventional biomass assessment (for example, ingrowth and sequential coring) (Gill and Jackson 2000), direct observation in minirhizotrons (Hendrick and Pregitzer 1993), pulse-labeling experiments using ^{14}C isotope (Milchunas and Lauenroth 1992), nitrogen (N) budgeting (Aber and others 1985), and carbon balance (Raich and Nadelhoffer 1989). There is no consensus established yet on which method is the best and can be used as a standard. This situation challenges researchers to overcome the profound methodological and

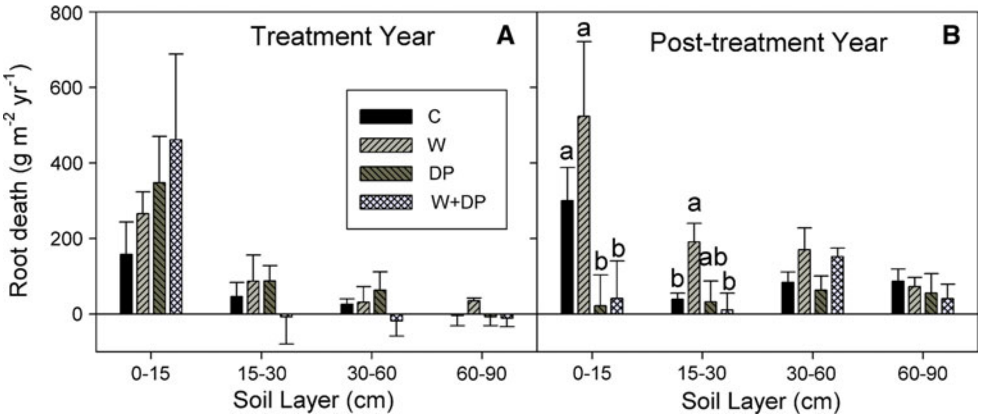

Figure 5. Estimated root death in the four soil layers (0–15, 15–30, 30–60, and 60–90 cm) under the four treatments in the treatment (**A**) and post-treatment (**B**) years. *Error bars* represent one standard error ($n = 5$). *Lower case letters* represent statistically significant differences among the treatments ($P < 0.05$). See Figure 3 for the notes and abbreviations.

analytical problems (Norby and Jackson 2000). Furthermore, global change models have yet to incorporate root dynamics and variability into coupled climate-C cycle feedback, which is important to predict the magnitude and even the direction of terrestrial ecosystem to climate change (Matamala and others 2003).

Our study used ingrowth and sequential coring methods to estimate standing root biomass, root growth rate, and root death rate. The approach is simple, cost effective, and easy to measure. However, this conventional method in this study may have biases in estimating root dynamics in a few sources. First, we measured root biomass only in the fall of each year, which potentially may not be adequate to capture root dynamics between measurements. Among the various means of measuring roots dynamics, minirhizotrons allow for more frequent observations and have the potential to record root dynamics at a high root turnover rate but the cost is high and it is also very time consuming. Second, we only changed precipitation intensity and not its frequency. Although root dynamics might be more responsive to the timing of water dynamics than the amount, both precipitation intensity and frequency should be considered in future research designs (Knapp and others 2002). Third, no distinction between live and dead roots was made due to technical difficulties, which have also been applied in the other studies (Srivastava and Ambasht 1995; Bjork and others 2007). For the ingrowth cores, all the roots in the cores were from the last year, which represented root growth rate. In the sequential soil cores, we assumed root turnover rates of 1 year in tallgrass prairie, despite large variability of reported turnover rates (Eissenstat and Yanai 1997; Gill and Jackson 2000). In addition, dead root biomass changed relatively little over seasons within 1 year (Srivastava and Ambasht 1995). The total root biomass (that is, dead + live roots) thus represented standing root biomass. At last, we assumed a steady state of grassland ecosystems to estimate root death rates, that the extra growth in the treatment year would be matched by mortality. The warming and doubled precipitation treatments may push systems a bit, which may introduce some error but may not change the directions of responses to warming and doubled precipitation.

Effects of Warming and Doubled Precipitation on Root Dynamics

Warming can enhance plant growth directly by stimulating plant photosynthesis and indirectly by extending the growing season (Fitter and others 1998; Majdi and Ohrvik 2004). Decreased soil water availability due to enhanced evapotranspiration under warming could increase the proportional carbon allocation toward roots to facilitate plant water uptake but might also suppress the overall root growth (Rustad and others 2001; Wan and others 2002). The overall impacts of warming on root dynamics depend on the relative positive and negative impacts of warming on ecosystem processes. In our study, experimental warming strongly increased soil temperature during the treatment year (Figure 1). Increased temperature caused significantly lower soil water content in the warmed (W) and warmed plus doubled precipitation (W + DP) plots than that in the control (C) and doubled precipitation (DP) plots, respectively. We expected more water stress in plots receiving the warming treatments, and thus enhanced root production to obtain water.

Although the W plots had the highest standing root biomass among all plots, the difference was not significant (Figure 2A). Two sources likely caused the warming effects to be less prominent than expected. First, the treatment year received 23.7% less rainfall than the long-term average and 15.3% less than the pre-treatment year. Annual average soil water content in the treatment year was 8.1% lower than in the pre-treatment year in the C plots. This drought effect likely enhanced overall standing root biomass in all plots due to increased carbon allocation to roots. In addition, we observed that root biomass distribution shifted toward the deeper soil (Figure 3B), probably because the surface soil layers were more significantly impacted by the drought, and plants grew deeper roots to compensate for lack of water. Second, plots were clipped to measure aboveground biomass (half in summer and another half in fall). Biomass harvesting could also stimulate overall root production (Luo and others 2009).

Our results showed that doubled precipitation did not significantly change standing root biomass, root growth, or root death in the treatment year (Table 1). Similar effects of additional water on root dynamics have been observed in other experiments. For example, no significant changes in standing fine root biomass were observed in a deciduous forest after 5 years of wetting (Joslin and others 2000) and in a Scots pine forest after a 3-year irrigation treatment (Brunner and others 2009). The insignificant response to doubled precipitation may result from the anomalous amount and pattern of ambient precipitation during the treatment year. The long period of drought in June and July (34 days without rain) may negate the effects of doubled precipitation treatment on root dynamics. In addition, a heavy rain of 108.0 mm over two days on 30–31 Aug 2003 resulted in substantial water loss through surface runoff, reducing treatment effects in the DP plots. However, we cannot rule out the possibility that root growth occurred after heavy rain events, and died back after long periods of drought during the treatment year, which then appeared as no change in total root biomass in our annual measurements. Due to limitations of our root sampling methods, we could not observe instantaneous root responses, which have occurred in other studies. For example, in a natural Amazon rainforest, root growth initiates rapidly to exploit transient periods of high soil water availability (Metcalfe and others 2008).

The root:shoot ratio is a good indicator of the allocation of plant production between aboveground and belowground parts, and has been found to have a significantly negative correlation with precipitation across different vegetation types (Mokany and others 2006; Zhou and others 2009). We observed the highest root:shoot ratios in the W plots, followed by the W + DP and C plots, and the lowest in the DP plots. This pattern obeys the optimal allocation theory (Bloom and others 1985). In a warmer and drier environment, increasing relative biomass allocation to roots could be a strategy for plants to cope with water stress and to favor nutrient uptake (Chaves and others 2002).

Lagged Effects on Roots in the Post-Treatment Year

Although warming and doubled precipitation showed very little impact on root dynamics during the treatment year, divergent responses were observed in the post-treatment year, indicating strong lagged effects of the post-treatments (Figure 2). Higher root death rates occurred in the W plots, resulting in significantly lower standing root biomass and then decreased root:shoot ratios (Figure 2). However, aboveground biomass changed relatively little under warming (Sherry and others 2008). This indicated that roots were more sensitive to lagged effects than aboveground biomass in our system, and were thus more important in determining the response of root:shoot ratios in the post-treatment year.

The lagged effects of warming and doubled precipitation may be attributed to several sources in this study. First, increased root death rate in the W plots could result from changed soil nutrient conditions in the treatment and post-treatment years. In our study, the W plots had significantly higher soil inorganic N concentrations throughout the treatment year compared to other plots (Sherry and others 2008), likely due to stimulated microbial activity (Rustad and others 2001). In the following year after warming was terminated, however, soil inorganic N concentration in the W plots decreased to the same level of other plots (Sherry and others 2008). Reduced N availability likely stimulated root death in the W plots in the post-treatment year, which is consistent with other studies (King and others 1999; Burton and others 2004). However, the relationship of root death rate with N dynamics during and after the treatment needs further investigation. Second, experimental warming would stimulate evapotranspiration and then decrease soil water content with the considerably lagged effects, which can reduce the supply of carbohydrates from photosynthates to belowground for root growth (Niu and others 2008), and thus increased root death rate (Bai and others 2010). Third, the lagged effect could be from the changes in community structure. In the treatment year, the warming treatments resulted in a higher proportion of C_4 plants in the W and W + DP plots than the C and DP plots in the fall (Sherry and others 2008). In the following year, the W plots still had higher C_4 plants, but the W + DP plots did not. C_4 plants have higher water use efficiency (Sage and Monson 1999), thus relatively lower root biomass is required for C_4 plants than C_3 plants under the same water stress, which could explain lower root biomass in the W plots in the post-treatment year.

Belowground biomass usually represents much more than a half of total biomass in grasslands. Jackson and others (1996) reported the global average root:shoot ratio to be 3.7. Despite the importance of belowground biomass, few studies have focused on post-treatment lagged effects of an extreme event on plants' belowground parts in manipulative experiments, modeling studies, or observational studies. An experimental study found lagged effects of drought on aboveground processes, such as decreased leaf area, shoot length, and transpiration rates (Löf and Welander 2000). Large-scale observation found lagged effects of temperature, radiation loading, and precipitation on grassland productivity (Potter and others 1999; Löf and Welander 2000; Wiegand and others 2004). The variation of global aboveground net primary productivity can be explained by climate conditions in the previous 1–4 years (Wiegand and others 2004). Andersen and others (1997) studied lagged effects on belowground growth. They showed that ozone exposure decreased root growth and this effect persisted following the removal of ozone in ponderosa pine seedlings. Our results showed that post-treatment responses of root biomass were higher than shoot biomass in the same study reported by Sherry and others (2008), suggesting stronger lagged effects on belowground compartments than aboveground. So, although lagged effects have been considered in models to predict aboveground processes (Wiegand and others 2004), we also need to incorporate lagged effects on belowground processes into these models, especially in assessing terrestrial carbon-cycle feedbacks to climate change.

ACKNOWLEDGEMENTS

The authors thank the two anonymous reviewers for their insightful comments. We would also thank Nancy Zerbach, Jesse Bell, Mike Cyrwus, Dafeng Hui, Delora Mowry, Afzal Subedar, Melissa Talley, Asfaw Tedla, Shiqiang Wan, and Tao Xu for field assistance. Watersheds and other field structures were built with much help from Cody Sheik. Afzal Subedar processed some of the soil cores. We thank Shuli Niu and Yuanhe Yang for their suggestions on the manuscript. We also thank the financial support for this project provided by NSF IRCEB grant # DEB 0078325 and DEB 0444518.

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