



## Response of plant biomass and soil respiration to experimental warming and precipitation manipulation in a Northern Great Plains grassland

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### ABSTRACT

The interacting effects of altered temperature and precipitation are expected to have significant consequences for ecosystem net carbon storage. Here we report the results of an experiment that evaluated the effects of elevated temperature and altered precipitation, alone and in combination, on plant biomass production and soil respiration rates in a northern Great Plains grassland, near Lethbridge, Alberta Canada. Open-top chambers and rain shelters were used to establish an experiment in 2011 with two temperature treatments (warmed and control), each combined with three precipitation treatments (minus 50%, ambient (no manipulation), and plus 50%). A smaller experiment with only the two temperature treatments was conducted in 2012, a year with less rain than 2011. Our objectives were to determine the sensitivity of plant biomass production and soil respiration to temperature and moisture manipulations, and to test for direct and indirect effects of the environmental changes on soil respiration rates. The experimental manipulations resulted primarily in a significant increase in air temperature in the warmed treatment. There were no significant temperature or precipitation treatment effects on soil moisture content. Above-ground biomass was not significantly affected by the experimental manipulations, but the warmed plots of the ambient precipitation treatment showed an increase in root biomass relative to the control plots in 2011. The warmed treatment increased the cumulative loss of carbon in soil respiration (July–September) compared to the control by 497 g C m<sup>-2</sup> during 2011, and by 185 g C m<sup>-2</sup> during 2012. This higher soil respiration rate in both years was not directly caused by significant differences among treatments in soil temperature or soil moisture, but was likely an indirect result of increased carbon substrate availability in the warmed relative to the control treatment.

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### 1. Introduction

Human activities are altering the concentration of atmospheric carbon dioxide with consequences such as warmer air temperatures and variation in precipitation and snow melt patterns (Barnett et al., 2005; Rozenzweig et al., 2008; Weaver, 2008). The interacting effects of altered temperature and precipitation are expected to have significant consequences for ecosystem net carbon storage that depend on their relative influence on CO<sub>2</sub> uptake in photosynthesis and CO<sub>2</sub> release in respiration (Bardgett, 2011; Wu et al., 2011).

In low stature grassland ecosystems, ecosystem respiration rate is primarily influenced by soil processes, the activity of plant roots and soil microbes (bacteria and fungi) (Flanagan and Johnson, 2005; Fontaine et al., 2007; Bardgett, 2011). The areas of highest soil respiration activity are concentrated around plant roots and

their associated microbes, the rhizosphere zone (Fontaine et al., 2007; Bardgett, 2011). Carbohydrate produced in photosynthesis is allocated to plant roots and used as a substrate to support their growth and maintenance metabolism. Roots also release some carbohydrates to the surrounding soil that help to support the metabolic activity of the rhizosphere microorganisms (Bardgett, 2011). This rhizosphere activity contributes to the breakdown of localized soil organic matter and the release of mineral nutrients that are required for both plant and microbial growth. Thus there is a complex and integrated network of interactions that occur between aboveground plant function and belowground ecological processes involving both plants and soil microbes that control soil respiration rate and influence ecosystem carbon budgets (Bardgett, 2011).

Elevated temperatures associated with climate change can influence ecosystem and soil carbon storage in a variety of ways via both direct and indirect mechanisms. For example, some recent studies have shown that soil microbial activity is stimulated directly by relatively small increases in temperature (when carbon availability and enzyme activity were non-limiting), resulting in

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high losses of CO<sub>2</sub> from the ecosystem to the atmosphere (Davidson and Janssens, 2006; Conant et al., 2011). However, there is also the potential for climate change to have strong indirect effects on soil microbe activity and soil carbon storage because of processes acting directly on plants (Bardgett, 2011). Elevated atmospheric CO<sub>2</sub> concentration can directly increase photosynthesis rates, and along with warmer temperatures, may also stimulate plant growth particularly in ecosystems located in cool, northern-latitude climate zones (Ainsworth and Long, 2005; Leaky et al., 2009; Drake et al., 2011; Wu et al., 2011). This can indirectly influence soil respiration because of an increase in the quantity of carbon supplied to soil in the form of root exudates and plant litter (Drake et al., 2011; Phillips et al., 2011). While plants and microbes may acclimate to future environmental changes, there is currently little known about the actual responses of soil organisms to elevated temperatures and the associated consequences for soil carbon storage (Bradford et al., 2008; Hartley et al., 2008). A current consensus suggests that terrestrial ecosystems will have a net loss of CO<sub>2</sub> when exposed to significant climate warming, resulting in a positive feedback to elevated atmospheric CO<sub>2</sub> concentrations and further warming (Heimann and Reichstein, 2008; Weaver, 2008). But the magnitude of the feedback between increasing temperatures and subsequent net release of CO<sub>2</sub> from ecosystems has been suggested to be one of the most important unknowns in global change science (Weaver, 2008).

The influence of elevated temperatures on plant productivity and ecosystem CO<sub>2</sub> exchange depends strongly on temperature–moisture interactions in grassland ecosystems. It is well established that annual variation in grassland primary productivity is strongly correlated with the amount of summer precipitation (Sala et al., 1988; Knapp and Smith, 2001; Weltzin et al., 2003). The size of rain events and the duration of time between rain events can also affect grassland productivity, when the total amount of summer precipitation does not vary (Heisler-White et al., 2008). However, recent analyses of data collected over an 8-year period have indicated a very strong interaction between moisture availability and temperature in controlling grassland productivity and net CO<sub>2</sub> uptake in a northern Great Plains grassland (Flanagan and Adkinson, 2011). For example, in years with only average precipitation and soil moisture content, warmer than normal air temperatures stimulated plant productivity and net carbon sequestration significantly. The temperature sensitivity of ecosystem respiration also varied strongly in association with changes in soil water availability in this Great Plains grassland (Flanagan and Johnson, 2005). Thus, the magnitude of the feedback between climate warming and the subsequent release of CO<sub>2</sub> from grassland ecosystems should depend on the interacting effects between temperature and moisture on plant productivity and ecosystem CO<sub>2</sub> exchange, interactions that are not completely understood. A recently published meta-analysis concluded that, “New experiments with combined temperature and precipitation manipulations are needed to conclusively determine the importance of temperature–precipitation interactions on the C balance of ecosystems under future climate conditions” (Wu et al., 2011).

In this paper we report the results of an experiment conducted in 2011 that evaluated the effects of elevated temperatures and altered precipitation, alone and in combination, on plant biomass production and soil respiration rates in a northern Great Plains grassland. In addition, a smaller experiment with only the two temperature treatments was conducted in 2012, a year with less rain during the growing season (May–October) than 2011. Our objectives were to determine the sensitivity of plant biomass production and soil respiration to temperature and moisture manipulations, and to test for direct and indirect effects of the environmental changes on soil respiration rates.

## 2. Materials and methods

### 2.1. Site description

The study site was located approximately 2 km west of the city limits of Lethbridge, Alberta, Canada (Lat. N: 49.470919; Long. W: 112.94025; 951 m above sea level) in the northwestern short/mixed grassland eco-region of the Great Plains, the second largest ecoregion in North America (Ostlie et al., 1997; Savage, 2004). The region has a semi-arid, continental climate and the mean daily temperatures (1971–2000) for January and July, measured at the Lethbridge airport (14 km from the study site), were  $-7.8^{\circ}\text{C}$  and  $18.0^{\circ}\text{C}$ , respectively (Environment Canada, 2012). Mean annual precipitation (1971–2000) was 386.3 mm, with 30% falling in May and June. The site has very flat terrain and the soil (orthic dark-brown chernozem) was underlain by a thick glacial till with very low permeability and no water table (Flanagan and Adkinson, 2011). The soil A horizon (0.09 m) was clay loam (28.8% sand, 40% silt, 31.2% clay) and the B horizon (0.16 m) had a clay texture (27.4% sand, 29.6% silt, 40% clay; Carlson, 2000). The bulk density of the surface soil horizon (top 10 cm) was  $1.24\text{ g cm}^{-3}$ , and the organic matter content was 5.2%. The site has not been grazed for at least 35 years, so a substantial litter layer has developed on the ground surface ( $288 \pm 13\text{ g m}^{-2}$ , mean  $\pm$  SE,  $n=21$  (carbon content approximately 45%); Flanagan and Johnson, 2005). The plant community at the site was dominated by the grasses *Agropyron dasystachyum* [(Hook.) Scrib.] and *Agropyron smithii* (Rydb.) (Carlson, 2000; Flanagan and Johnson, 2005). Other abundant plant species present included: *Vicia americana* (Nutt.), *Artemisia frigida* (Willd.), *Koeleria cristata* [(L.) Pers.], *Carex filifolia* (Nutt.), *Stipa comata* (Trin. and Rupr.), *Stipa viridula* (Trin.).

### 2.2. Eddy covariance measurements

The study site was associated with the Fluxnet-Canada and Canadian Carbon Program research networks and continuous eddy covariance measurements of net ecosystem CO<sub>2</sub> exchange (NEE) have been made at the site since June 1998 (see Flanagan et al., 2002; Flanagan and Adkinson, 2011). In this paper, net CO<sub>2</sub> exchange data were expressed as net ecosystem productivity (NEP =  $-$ NEE), where positive values of NEP indicate uptake of CO<sub>2</sub> by the ecosystem. The Fluxnet-Canada standard protocol was used for gap-filling CO<sub>2</sub> flux data and partitioning NEP into total ecosystem respiration (TER) and gross ecosystem photosynthesis (GEP) (Barr et al., 2004). Both component fluxes of NEP were considered to be positive, so that GEP was calculated as the sum of NEP and TER (i.e. NEP = GEP  $-$  TER). The half-hourly CO<sub>2</sub> flux data were integrated to determine daily values of NEP, GEP and TER ( $\text{g C m}^{-2}\text{ day}^{-1}$ ). An assessment of random uncertainty in eddy covariance carbon budgets at this site has been recently determined as part of multi-site synthesis study, building on the work of Richardson et al. (2006) and using their daily paired-observation method. For data collected at this site during 2000–2006, the analysis gave 95% confidence interval values (average  $\pm$  SD,  $n=7$ ) of  $12 \pm 3\text{ g C m}^{-2}\text{ year}^{-1}$  for NEP,  $18 \pm 6\text{ g C m}^{-2}\text{ year}^{-1}$  for TER, and  $15 \pm 5\text{ g C m}^{-2}\text{ year}^{-1}$  for GEP (A.G. Barr, D.Y. Hollinger, A.D. Richardson, unpublished data 2012). This translates into a relative uncertainty of  $4.3 \pm 0.4\%$  (average  $\pm$  SD,  $n=7$ ) for the annual TER values calculated from measurements during 2000–2006 (average [ $\pm$ SD,  $n=7$ ] annual TER during 2000–2006 from this analysis was  $411 \pm 125\text{ g C m}^{-2}\text{ year}^{-1}$ ). Graphical presentations of 5-day average NEP, GEP and TER data were used along with NDVI data to illustrate seasonal patterns in biological activity and to identify time periods for aboveground biomass harvests.

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