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Ecosystem respiration responses to experimental manipulations of winter and summer precipitation in a Mixedgrass Prairie, WY, USA

R.A. CHIMNER* and J.M. WELKER
Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, USA;
**Author for correspondence (e-mail: rchimner@nrel.colostate.edu; phone: 970-491-2162)*

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Abstract. Changes in timing or amount of precipitation may be of great consequence for carbon cycling in the Mixedgrass Prairie of N. America, because CO_2 fixation and efflux are tightly coupled to soil water properties. The objective of our project was to quantify how ecosystem respiration (R_e) responds to experimental changes in winter and summer precipitation in a Mixedgrass Prairie using *in situ* field manipulations of snow depth and summer rain. Our study was conducted at the USDA-ARS High Plains Grasslands Research Station, west of Cheyenne, Wyoming. We installed three replicated 50 m snow fences to increase winter snow on the leeward side of the snow fence and experimentally manipulated summer precipitation by either increasing (+50%) or decreasing (−50%) precipitation amounts. We also measured ambient conditions. R_e rates in May were around 2 g C m^{-2} d^{-1} for all treatments and increased to their greatest values in June, up to 10 g C m^{-2} d^{-1}, with the ambient treatment having the largest flux rates. There were no treatment effects during the early summer, but by midsummer, R_e rates were least in the reduced rainfall plots and greatest in the snow plots. Soil moisture and gross photosynthesis had strong influence on the daily R_e rates, but soil temperature had little correlation with daily R_e rates. In summary, the R_e rates in this Mixedgrass Prairie are strongly influenced by changes in precipitation, especially winter snow accumulation. Thus, carbon cycle estimates under future climate change scenarios need to include not only the affects of changes in summer rain, but also, the consequences of deep snow in winter and its' affect on carbon cycling processes in winter and subsequent summers.

Introduction

Summer and winter environmental conditions are changing in terrestrial ecosystems throughout North America, including increased temperatures, and varying degrees of precipitation in the form of both summer rain and winter snowfall (Stefan and Fang 1997; Serreze et al. 2000; Hamilton and Frank 2001). Changes in rainfall or snow regimes may be of great consequence for carbon cycling processes, especially across the western US, because precipitation has a major affect on net primary production (Lauenroth and Sala 1992; Milchunas et al. 1994; Knapp et al. 2001; Fay et al. 2002; Knapp et al. 2002), especially in grasslands. Also, precipitation controls soil water contents, which in turn affect organic matter decomposition and subsequently, ecosystem respiration rates (R_e). Most studies that have addressed how changes in precipitation affect carbon cycling have focused on summer rain responses (e.g., Knapp et al. 2002). However, changes in snow amounts may be just as influential on ecosystem respiration, because deep snow insulates soils in winter leading to greater winter-time CO_2-C losses (Fahnestock et al. 1998, 1999; Schimel et al. 2004). Additionally, snow melt water may percolate to depth and carry over to affect summer soil water contents and summer-time ecosystem respiration (Welker et al. 2000).

Temperate grasslands represent one of the largest biomes where changes in winter and summer climate may have dramatic ecological and social consequences (Follett et al. 2000). These grasslands constitute over 40% of the entire global landscape (Allen-Diaz et al. 1996), they sequester approximately 4.5 Pg C $year^{-1}$ while accumulating the largest amounts of soil carbon per year, 23,600 g C m^2 of all biomes, and they retain the third highest total soil carbon pools (304 Pg) (Amthor et al. 1998). These grasslands are clearly an important constituent in the global carbon cycle (Schimel et al. 1994), and their sensitivity to weather and land management may affect C and N cycling (Schuman et al. 1999, 2000; Povirk et al. 2000). However, today there is no concentrated study of Mixedgrass Prairie responses to simulated changes in climate, even though this is the largest grassland in the Great Plains of North America (142.7×104 km^2 representing 38% of the grassland types in North America, Lauenroth 1979) that supports a diverse flora and fauna and a livestock industry, and additionally supplies a host of recreational and social needs.

Precipitation is a key driver in determining grassland types, productivity and decomposition rates (Lauenroth and Sala 1992). On a regional to continental scale, plant production and decomposition rates both increase with an increase in mean annual precipitation (Epstein et al. 2002). However, using large scale spatial patterns to predict local changes in carbon cycling due to changes in precipitation is not accurate (Lauenroth and Sala 1992). Therefore, experiments are needed at many different locations to actually determine how precipitation changes will alter carbon cycling in grasslands. Thus, the objective of our project was to quantify how ecosystem respiration rates respond to experimental changes in winter and summer precipitation in a Mixedgrass Prairie.

Methods

Study site

Our study was conducted at the USDA-ARS High Plains Grasslands Research Station (HPGRS), west of Cheyenne, Wyoming, located at the southern end of the Mixedgrass Prairie of North America (41°N, 104°W) (Schuman et al. 1999; LeCain et al. 2000). The elevation at the HPGRS averages 1930 m with a mean annual precipitation of 38 cm and an average of 127 frost-free days. In summer, the average temperature is 18 and −2.5 °C on average in winter. The major cool-season (C_3) grasses are western wheatgrass (*Pascopyrum smithii* (Rydb) A. Love) and needle-and-thread grass (*Stipa comata* Trin and Rupr.). The dominant warm season (C_4) grass is blue grama (*Bouteloua gracilis* (H.B.K.). The soils are mixed, mesic, Aridic Argiustolls, with the soil series being an Ascalon sandy loam (Schuman et al. 1999). Our studies were limited to the Ascalon soil type, which is representative of over 50% of the soils in the Mixedgrass Prairie. We noticed no differences in soil properties between the replicated snowfences.

Experimental design

We established a field experiment to address Mixedgrass Prairie responses to coupled changes in winter and summer precipitation. In a lightly grazed pasture, three replicated 50 m snow fences (commercially available lath fences) were installed in the late fall of 2002 to increase winter snow on the leeward side of the snow fence (Jones et al. 1998; Walker et al. 1999). Ambient and summer rainfall treatments were conducted 20 m away from the snow fence on the windward side. We used a 20 m distance away from the fences because personal observation indicated that ambient conditions were present at that distance. The summer rainfall treatment plots (ambient, +50%, and −50%) and snow addition plots were conducted in 2 × 3 m plots for each replicated 50 m snow fence, for a total of three treatments each.

We controlled summer rainfall using a combination of techniques. First we built rain out shelters covering the entire plots (2 × 3 m). The foundation of the rainout shelters were constructed of metal slotted angle and wood beams, and covered with clear PVC sheeting to exclude summer rainfall. The PVC sheets covered two-thirds of the rainout shelter's roof area (with the expectation of excluding about half of the rain). The top of the rainout shelter was angled downward to funnel the rain into gutters, through the downspouts at the lower end, which then ran off the plots. Small plastic rain gauges, placed in front and under the rainout shelter during the early summer, indicated that the shelters were indeed minimizing rainfall by about 50%. To increase summer rainfall, we hand irrigated water once a week at 50% of the 10 year average normal precipitation rates. The plots were hand irrigated using a hand sprinkler system connected to a battery operated pump. Water was hand irrigated every Friday in the late afternoon, and further measurements were not taken until at least the following Tuesday. We added 0.6 cm of water a week to each plot in June, 0.45 cm a week in July, and 0.6 cm a week in August and September. We left one plot unaffected that represented ambient rainfall levels.

We instrumented a single replicate of each treatment type with CS616 soil moisture probes that measures volumetric water content using time-domain reflectometry methods (Campbell Scientific, Logan Utah, USA). We used the standard calibrations to quantify soil moisture between 0 and 30 cm depths. The probes were installed in a random location within each plot. We also installed two type-t thermocouple probes at 3 and 10 cm depths to quantify soil temperatures. The CS616 and thermocouple probes were run by a Campbell CR10X (Campbell Scientific, Logan Utah, USA) datalogger. We also installed a Campbell weather station to quantify the weather conditions, including relative humidity, wind speed, wind direction, irradiance, and a tipping bucket rain gauge.

Ecosystem respiration measurements

Ecosystem respiration (R_e) rates were quantified by taking measurements during the growing season from May to September 2003. Diurnal R_e measurements were taken every 4–6 h biweekly, and mid-day measurements were taken at least weekly between 1000 and 1400 h. CO_2 efflux measurements were taken with an infrared gas analyzer (Licor, LI-6200) connected to a chamber (50 cm × 50 cm × 40 cm) with one small fan continuously mixing air in the chamber during measurements (Vourlitis et al. 1993). Once CO_2 concentrations within the chamber stabilized (typically 30–60 s), net CO_2 exchange determinations were made for each plot. After the net CO_2 exchange measurements the chamber was covered with an opaque cloth to prevent photosynthesis and measurements of R_e rates were determined. Whole ecosystem C assimilation (i.e., gross photosynthesis) was subsequently calculated by subtracting the R_e measurements from the net CO_2 exchange measurements (Walker et al. 1999). Because this paper is about R_e results of net CO_2 exchange and GPP are not presented, except as they relate to explaining patterns of R_e.

Results

Environmental parameters

Spring and early summer were wet and cool with abundant rain though the end of June (Figure 1). Temperatures were hot and conditions dry during July and August. Temperatures were cooler, and late season precipitation occurred by the end of August and early September.

Our precipitation treatments altered soil moisture levels (Figure 2). Soil water contents between May and September were highest where snow had been deep the previous winter, and were also high where summer rain had increased. Rainout shelters resulted in soil water contents that were similar to those under ambient summer rain conditions. Soil temperatures were not affected by the precipitation treatments (Figure 3).

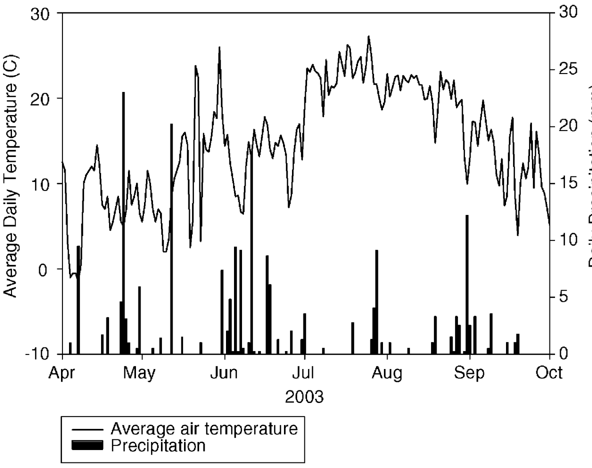

Figure 1. Average summer daily air temperature and precipitation from the High Plain Grassland Research Center, Wyoming.

Ecosystem respiration

Ecosystem respiration rates showed strong daily patterns that varied during the summer (Figure 4). For all sites and dates, ecosystem respiration rates were greatest in the late morning or early afternoon and lowest at night or early morning. Ecosystem respiration rates under ambient precipitation regimes were greatest during mid-June and declined during the remainder of the summer (Figure 4). By mid-August, ecosystem respiration rates were < 1 μmol m^{-2} s^{-1} during the entire day with little diurnal variation. The addition of snow created favorable conditions that facilitated high ecosystem respiration rates throughout the summer. For instance, ecosystem respiration rates under conditions where snow was deep the previous winter were just as high on July 15th as they were in mid-June. Over the course of the summer, R_e rates under conditions where snow was deep the previous winter did not decrease as much as R_e rates did under ambient conditions between July and August. The R_e rates under conditions of added rain followed similar patterns as the added snow treatments with a smaller seasonal decline compared to the ambient conditions (Figure 4). When rain was reduced, R_e rates were similar to rates under ambient conditions (Figure 4). We found an excellent correlation between mid-day and daily ecosystem respiration rates (Figure 5). This correlation allows us to convert all of our mid-day measurements to daily rates, which increases the number of daily values in our analysis.

The magnitude of daily respired CO_2-C showed seasonal patterns as well as treatment differences. Ecosystem respiration rates in May were around 2 g C m^{-2} d^{-1} for all treatments (Figure 6). Ecosystem respiration rates increased to their greatest values in June, up to 10 g C m^{-2} d^{-1}, the largest flux

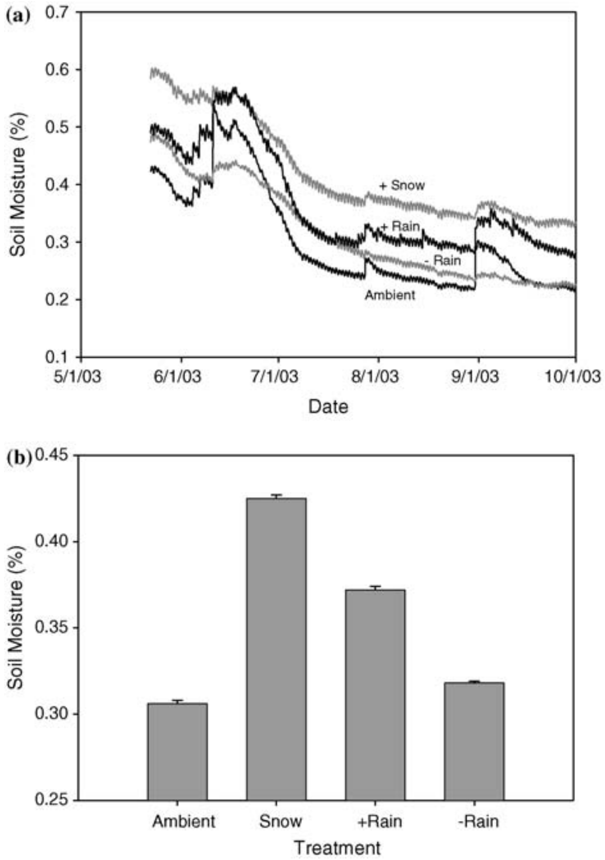

Figure 2. Time series during the summer (a) and average summer soil moisture (b) for the four treatments (ambient, added snow, added rain, and reduced rain).

rates under ambient conditions. Beginning in July, daily ecosystem respiration rates started to decline for the remainder of the summer. Treatment differences were most pronounced and consistent in the second half of the summer. Ecosystem respiration rates were lower in the plots where summer rain was reduced and stayed low for the remainder of the summer. By early August, the daily flux rates of plots under the ambient and rain addition treatments declined to match the daily flux rates of plots where rain had been reduced by 50%. However, R_e rates from plots where snow was deep the preceding winter maintained greater ecosystem respiration rates through August and most September.

Our treatment array created a continuum of temperature and soil moisture values which allow us to investigate how temperature and soil moisture control ecosystem respiration rates in a Mixedgrass Prairie. Ecosystem respiration rates exhibited a linear response to soil water content, but, the highest soil

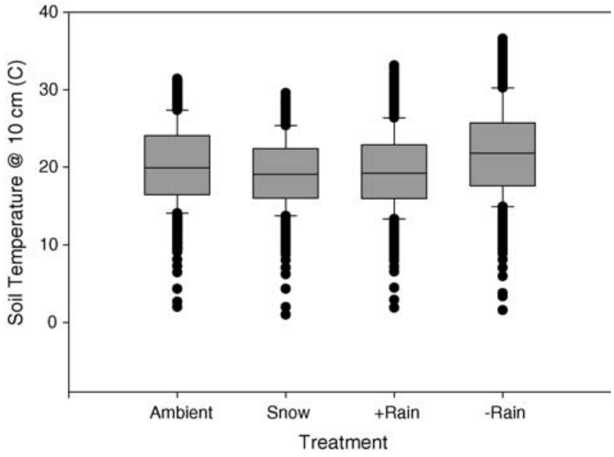

Figure 3. Average soil temperatures during the summer for the four treatments.

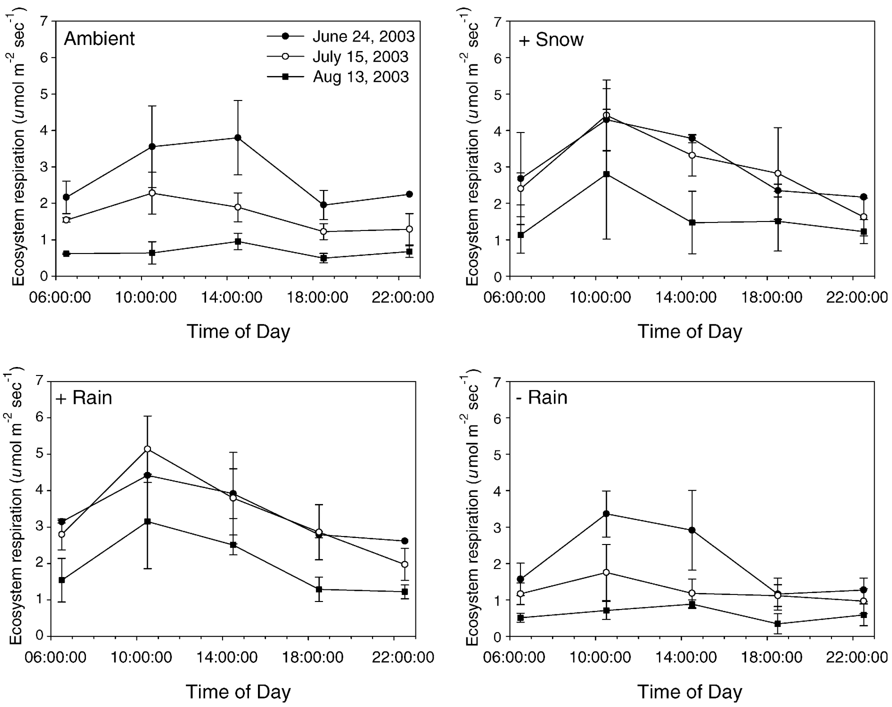

Figure 4. Diurnal patterns of ecosystem respiration for the four treatments on three different days during the early, mid, and late summer.

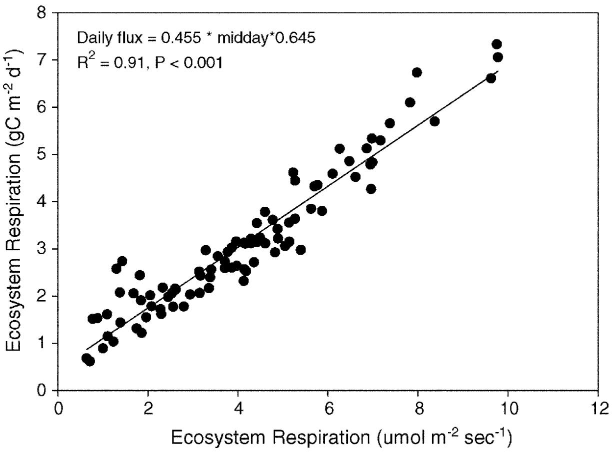

Figure 5. Correlation between mid-day and daily ecosystem respiration rates for all four treatments.

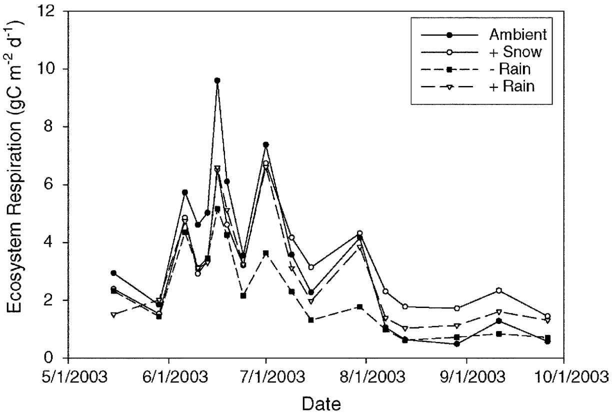

Figure 6. Daily ecosystem respiration rates for the four treatments.

moisture values caused a slight decrease in ecosystem respiration rates (Figure 7a). However, these high soil moisture values were from the earliest part of the summer when soils were cold and plant growth was just starting. Surprisingly, soil temperature had little correlation with ecosystem respiration rates (Figure 7b). The strongest pattern we observed was a strong decrease in ecosystem respiration rates at high temperatures. However, there is little correlation between soil temperature and ecosystem respiration rates between 12 and 22 °C.

The strongest single correlation we found to explain daily R_e rates was daily gross photosynthesis (Figure 8). Daily gross photosynthesis (GPP) explained roughly 80% of the variation in R_e. A multiple regression using GPP, soil

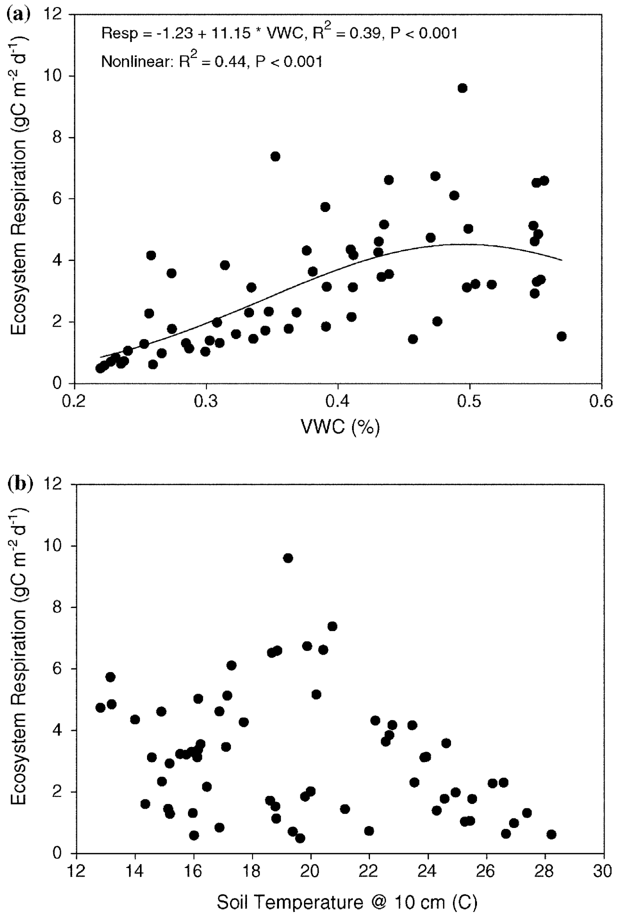

Figure 7. (a) Relationship between volumetric water content in the top 30 cm and daily ecosystem respiration rates; and (b) relationship between average soil temperatures at 10 cm and daily ecosystem respiration rates.

moisture and soil temperature was able to explain 88% of the daily variation in R_e (Table 1).

Discussion

Our measures of carbon cycling in a Mixedgrass Prairie depict that grassland ecosystem respiration will be affected by changes in winter and summer precipitation. These first year responses to coupled changes in winter and summer precipitation are of a magnitude such that over the long-term (10–50 years) soil carbon pools could be significantly changed. The changes in soil carbon could

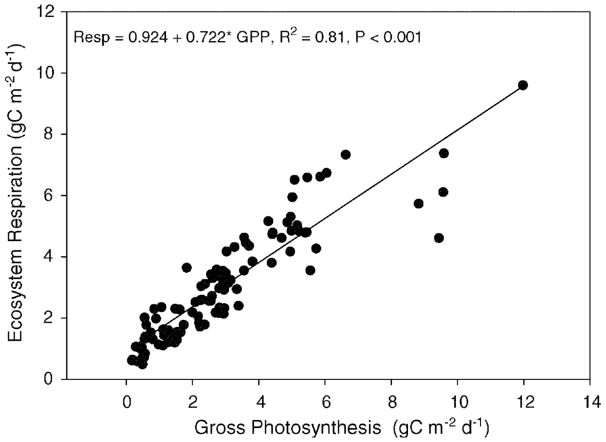

Figure 8. Relationship between ecosystem respiration and gross photosynthesis.

be of regional significance when one considers that the Mixedgrass Prairie covers ~142.7 × 104 km^2 of North America.

Our R_e values are representative of measurements made in other Mixedgrass Prairies and northern grasslands (Lecain et al. 2000; Frank et al. 2002; Kelly et al. 2002; Fahnestock et al. unpublished data; Welker and Chimner unpublished data). Our growing season instantaneous R_e values ranged from a low of near 0.3 $\mu mol\ m^{-2}\ s^{-1}$ to a high of around 10 $\mu mol\ m^{-2}\ s^{-1}$ and our daily values ranged from a low of 0.5 $g\ C\ m^{-2}\ d^{-1}$ to a high of almost 10 $g\ C\ m^{-2}\ d^{-1}$. As we expected, these rates are lower then fluxes measured in tall grass Prairies of the Great Plains (Fay et al. 2000), but greater then those measured in the short-grass Prairies (Del Grosso et al. this issue).

Temperature is a major control of soil and ecosystem respiration rates (Raich and Schlesinger 1992; Lloyd and Taylor 1994; Raich and Potter 1995; Fang and Moncrieff 2001). However, the importance of temperature can vary over spatial and temporal scales. For instance, annual soil respiration rates typically increase as a function of increasing mean annual temperature (Raich and Schlesinger 1992). Temperature is also the dominant control of soil respiration rates over the course of a year with high rates in the summer and low rates in the winter (e.g., see data from Frank et al. 2000). However, within a

Table 1. Results of multiple linear regression relating daily ecosystem respiration to daily gross photosynthesis (GPP), soil moisture (VWC) and soil temperature (SOILTEMP) at 10 cm depth

Effect	Coefficient	*p* (2 tail)
Constant	−2.512	0.001
GPP	0.626	< 0.001
VWC	5.339	< 0.001
SOILTEMP	0.085	0.001

Regression is significant at $p < 0.001$ with an adjusted squared multiple $R = 0.87$.

season (e.g., summer), temperature may be much less a factor, especially if water is limiting. We found a limited relationship between daily R_e rates and average daily temperature during the growing season. Temperature was a significant, but small factor in the multiple regression (Table 1), but had no significant relationship as an independent variable (Figure 6b). However, there is a general trend of increasing maximum values of R_e with an increase in soil temperature up to 20 ° C with decreasing values at higher temperatures (Figure 6b). However, this trend is confounded by the fact that high temperatures (roughly below 22 °C) were correlated with dry soils, while there is no correlation between soil temperature and moisture at lower temperatures (roughly below 22 °C). Therefore, it is difficult to say if R_e is low due to high temperatures, low soil moisture, or a combination of both.

During the growing season, ecosystem respiration rates were more limited by soil moisture than by temperature (Figure 6), especially during the middle of the summer (Figure 5). Decreasing summer precipitation corresponded to lowered ecosystem respiration rates, while increasing summer precipitation slightly increased those rates. This relationship is likely mediated through two processes: (1) greater soil water facilitates microbial decomposition of organic matter and the release of CO_2 (Hobbie et al. 2000); and (2) higher soil water contents may facilitate plant root and shoot growth and associated vegetation respiration (Lauenroth and Sala 1992; Milchunas et al. 1994; Knapp et al. 2001). Under more favorable soil water conditions, greater amounts of plant photosynthates can be allocated to carbon efflux from roots into the rhizosphere, where microbial populations would capitalize on this carbon source and rates of microbial respiration would be greater (Holland et al. 1996). Given the strong correlation between GPP and R_e it seems apparent that increased plant growth had greater control over increased R_e than increased decomposition of soil organic matter.

Manipulating winter snowpacks was found to have a very strong influence on R_e during the entire growing season. In fact, R_e rates in the snowpack treatments were greater in the late summer than all of the other treatments, including increased summer precipitation. We hypothesize that the increased winter snow percolated to deep soil depths and was available for plant growth by deep rooted perennials during the entire growing season, increasing ecosystem respiration. Whereas, increased summer rain only wetted the top of the soil and was quickly absorbed by plants or evaporated, limiting the influence of summer rain. Previous research that used isotopic studies (Dodd et al. 1998), indicated that in grassland settings, C_4 grasses primarily used summer rainfall while deeper rooted shrubs use both summer rain and snow melt water that had percolated into the soil profile in late winter and in early spring.

In summary, we documented that ecosystem respiration rates in a Mixed-grass Prairie are strongly influenced by changes in precipitation, especially winter precipitation. This has implications for forecasting changes to the large pools of carbon stored in temperate grasslands from changes in climate. It also indicates that we must look at projected changes in both winter and summer weather patterns if we are to understand changes to the ecosystem functioning of these systems.

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