

Experimental manipulations of winter snow and summer rain influence ecosystem carbon cycling in a mixed-grass prairie, Wyoming, USA

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ABSTRACT

Water-limited grasslands may be exceedingly vulnerable to changes in the timing or amount of precipitation which may result in shifts in the magnitudes and patterns of carbon cycling. Shifts in CO₂ exchange may lead to alterations in carbon sequestration or net losses and could accentuate the rising CO₂ concentrations in the atmosphere or ameliorate the increases. The objective of our project was to quantify how changes in winter, summer, and combined winter and summer precipitation may alter rates of ecosystem C cycling in the mixed-grass prairie of the United States. Three replicated 50 m snow fences were installed to increase winter snow while summer precipitation was manipulated by either increasing (+50%) or decreasing (−50%) precipitation amounts. Measurements of net ecosystem exchange (NEE), gross ecosystem photosynthesis (GEP), and ecosystem respiration (ER) and plant biomass were conducted throughout the snow-free period. Deeper snow in winter increased summer ER by an average of 27%, GEP by 45%, NEE by 90% and plant biomass by 50% compared to ambient snow conditions. Average plant biomass increased 44% with the addition of summer rain and decreased by 18% where rainfall was excluded under ambient snow conditions. Average NEE was also lower where rain was excluded. Our findings indicate that seasonality changes of precipitation may be important in regulating the future extent of C sequestration and C cycling in one of the most extensive, intact grasslands of North America. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS CO₂; climate change; grasslands; precipitation; production

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INTRODUCTION

Grasslands comprise over 40% of the global landscape (Allen-Diaz *et al.*, 1996), sequester carbon at high rates globally (4.5 Pg C year^{−1} or 23 600 g C m^{−2}), and retain the second highest total soil carbon pools in terrestrial ecosystems (295 Pg) (Amthor *et al.*, 1998). Today and in the future, these large pools of soil C may be volatilized as decomposition increases with warming or changes in precipitation, accelerating the rise in atmospheric CO₂ concentrations. Consequently, it is vital to develop a better understanding of the influence that grasslands have on global carbon cycling and how a changing climate will affect the current processes (Schimel *et al.*, 1994). In particular, there are few studies of mixed-grass prairie responses to climate change, even though this is the largest grassland type in the Great Plains of North America (142.7 × 10⁴ km² representing 38% of the grassland types in North America, Lauenroth, 1979).

Climatic conditions are changing in grasslands with increasing temperatures and altered precipitation amounts and patterns (Stefan and Fang, 1997; Alward *et al.*, 1999;

Serreze *et al.*, 2000; Christensen *et al.*, 2007). Precipitation is one of the most important factors in determining grassland types, productivity and decomposition (Lauenroth and Sala, 1992; Epstein *et al.*, 2002). Precipitation and subsequently soil water content are especially important to the phenology and magnitude of vegetation growth (i.e. deep snow will delay growth); early spring rains will accelerate phenology and stimulate growth of cool-season grasses (C₃-species) (Newbauer *et al.*, 1980), while abundant moisture in the second half of the summer and early fall supports the growth of warm season or C₄-species (Monson *et al.*, 1988). Therefore, changes in precipitation from climate change are predicted to have large influences on ecosystem processes in water-limited grasslands (Lauenroth and Sala, 1992; Milchunas *et al.*, 1994; Knapp *et al.*, 2001; Knapp and Smith, 2001; Fay *et al.*, 2002; McCulley *et al.*, 2005). However, most climate change experiments have examined how changes in summer precipitation amounts or timing affect grassland carbon cycling (Weltzin *et al.*, 2003). No studies exist today that have examined how changes in summer or winter precipitation affect ecosystem C processes in the mixed-grass prairie, though recently we reported that increases in winter snow may greatly enhance the performance of weedy, grassland species (Blumenthal *et al.*, 2008).

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Climate scenarios for the mixed-grass prairies of North America indicate that winters will be wetter and slightly warmer, while summers will become warmer and drier (Christensen *et al.*, 2007). These changes in the amount of winter precipitation may be just as important as summer precipitation on grassland ecosystem processes because winter snow melt water can percolate deep into the soil and provide water to vegetation in the subsequent spring and summer (Walker *et al.*, 1999; Chimner and Welker, 2005; Welker *et al.*, 2005b). In addition, deep snow can insulate soils in winter leading to greater winter-time CO₂ losses from soils (Fahnestock *et al.*, 1998, 1999; Schimel *et al.*, 2004; Welker *et al.*, 2004). Thus, the objective of our project was to quantify how changes in winter, summer and combined winter and summer precipitation altered rates of net ecosystem exchange (NEE), gross ecosystem photosynthesis (GEP) and ecosystem respiration (ER) in a mixed-grass prairie.

METHODS

Study site

Our study was conducted at the USDA–ARS High Plains Grasslands Research Station (HPGRS), west of Cheyenne, Wyoming, USA (41°N, 104°W). The elevation at the HPGRS averages 1930 m with a mean annual precipitation of 38 cm and an average of 127 frost-free days. The average temperature in summer is 18 °C and –2.5 °C in winter. The major cool-season (C₃) grasses are western wheatgrass [*Pascopyrum smithii* (Rydb) A. Love] and needle-and-thread grass (*Stipa comata* Trin and Rupr.). The dominant warm season (C₄) 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 mixed-grass prairie. Basic soil characterization indicated that there were no major differences in gross soil parameters between the fences that would skew results (unpublished data).

Experimental design

We established a field experiment to address mixed-grass prairie responses to combined changes in winter and summer precipitation. In a historically 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; Chimner and Welker, 2005). Grazing was halted during the experiment and was trimmed by hand in the fall to simulate light grazing. Ambient snowfall treatments were conducted 20 m away from the snow fence on the windward side because personal observations indicated that ambient soil water conditions were present at that distance. The summer rainfall treatment plots (ambient, +rain, and –rain) were conducted in both the snow

addition and ambient snow conditions in 2 m × 3 m plots at each of the three 50 m snow fences.

We controlled summer rainfall using a combination of techniques. First, we built rainout shelters covering the entire plots (2 m × 3 m) to reduce rainfall. Measurements were conducted in the centre of the plot to minimize edge effects. The framework of the rainout shelters were constructed of metal slotted angle and wood beams, and covered with clear polyvinyl chloride (PVC) sheeting to exclude summer rainfall (Yahdjian and Sala, 2002). The PVC sheets were arranged in horizontal strips with gaps in between strips, and 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 downwards towards the prevailing winds 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 decreasing rainfall by about 50%. To increase summer rainfall, we irrigated uncovered plots (2 m × 3 m) by hand once a week at 50% of the average long term monthly precipitation rate, converted to weekly rates. 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. 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. One non-irrigated plot served as a control for representing ambient rainfall levels.

We instrumented a single replicate of each treatment type in 2003 and all three replicates in 2004 and 2005 with CS616 soil moisture probes (0–30 cm depth) that measure volumetric water content (VWC) using time-domain reflectometry methods (Campbell Scientific, Logan Utah, USA). We calibrated the CS616 probes with field measurements of VWCs collected over the 3 years. The calibration equation we developed is: $VWC_{corrected} = VWC_{measured} \times 0.261 + 0.046$, $R^2 = 0.74$. 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.

Carbon dioxide exchange measurements

Carbon dioxide exchange patterns were measured using a clear chamber during the growing (snow-free) seasons from May 2002 until September 2005. Manual chamber-based measurements have been used successfully in a variety of short-statured ecosystems (Vourlitis *et al.*, 1993; Angell and Svejcar, 1999; Johnson *et al.*,

2003; Welker *et al.*, 2004; Burrows *et al.*, 2005; Oberbauer *et al.*, 2007, Sullivan *et al.*, 2008). Despite their limitations (e.g. infrequent sampling, alteration of microclimate), manual chamber measurements have been found to be comparable to other carbon flux methods, including eddy flux and Bowen ratio methods (Oechel *et al.*, 1998; Johnson *et al.*, 2003; Zamolodchikov *et al.*, 2003). However, one great advantage of manual chamber measurements is that it allows measuring carbon fluxes in areas with very small footprints; therefore, it has proven to be a good option for either small stunted ecosystems or experiments with multiple treatments in the same ecosystem (Sullivan *et al.*, 2008).

Mid-day measurements of NEE and ER rates were taken at least weekly at each plot. All 18 plots were measured within the same day between 10:00 and 14:00 h. CO₂ exchange rates were determined with an infrared gas analyzer (Licor, LI-6200) connected to a clear chamber (50 cm × 50 cm × 40 cm) with several small fans continuously mixing air in the chamber during measurements (Vourlitis *et al.*, 1993). Flux rates were calculated by measuring the change in CO₂ concentrations within the chamber (Vourlitis *et al.*, 1993). After placement of the chamber, no measurements were taken until a steady mixing occurred. A steady mixing was assumed to occur when the CO₂ concentration in the chamber started increasing or decreasing at a constant rate (typically 20–30 s). After mixing occurred, measurement of NEE commenced and lasted for roughly 1–2 min. The rapid measurements minimized temperature and water vapour increases in the chamber (Vourlitis *et al.*, 1993). The chamber was briefly aired out (20–30 s) after the NEE measurement and then replaced and covered with an opaque cloth to prevent photosynthesis, allowed to mix, and measurements of ER commenced. GEP was then subsequently calculated by subtracting the ER rates from the NEE rates.

Plant biomass and physiological ecology

Vegetation samples for total above-ground plant biomass were collected annually in mid-June and mid-July from ten randomly placed quadrats (1 m²) in each treatment area. All vegetation in each quadrat was harvested to the soil surface and separated by species. Green leaves were separated from dead leaves and stems, all vegetation was oven-dried at 60 °C for 48 h, and total biomass was measured to the nearest 0.1 g.

Statistical analysis

A repeated measures analysis of variance (ANOVA), consisting of a two-factor split-plot design laid out in blocks, was conducted using PROC MIXED to test for experimental differences in ecosystem C efflux (SAS Institute, Inc., 2009). Each plot was an experimental unit, so replicate measurements were averaged by plot for each year of analysis. Individual snow fences were used as replications, snow treatments were treated as whole plots and rainfall treatments were subplots. Snow

and rainfall treatments and all possible interactions were treated as fixed effects, replication and replication * snow were treated as random effects and sample years were treated as repeated measures. We used unstructured covariance structure for repeated measures analysis as determined by looking at the fit statistics and the Kenward and Roger's correction for degrees of freedom (Littell *et al.*, 2006). A two-way, repeated measures ANOVA was also conducted for plant biomass using PROC MIXED (SAS Institute, Inc., 2009). Analysis was conducted by year, using fence as the random variable and harvest date as a repeated measure. Differences between all treatments were conducted using Tukey's *post hoc* test with differences at $P < 0.05$ considered significant.

RESULTS

Environmental parameters

Each of the three study years had distinct precipitation patterns (Figure 1). During the winter of 2002–2003, appreciable amounts of snow did not occur until January when a snow drift developed behind the snow fences. The drifts melted in early May of 2003. A very different snow accumulation pattern occurred in 2003–2004 when snow drifts formed in early December 2003, but melted out by early March 2004, almost 2 months earlier than in 2003. Snowdrifts in 2004–2005 were formed in November and melted out by April 2005. Summer precipitation pattern also differed between the years. The spring of 2003 was wet and cool, while the summer was hot and dry. This contrasted with 2004 which had a hot and dry early spring and summer and a wet late summer. Conditions were more favourable for plant growth in 2005 when conditions were moist for the entire spring and summer.

Our replicated snow fences effectively altered snow accumulation at this mixed-grass prairie site. Snow drifts formed in a zone extending ~5–10 m behind our fences and extended along 90% of our 50 m fences. Ambient winter precipitation averaged 14, 3 and 12 cm in 2002–2003, 2003–2004 and 2004–2005, respectively. Our snow fence treatments had snow water equivalents that averaged 24, 14 and 34 cm in 2002–2003,

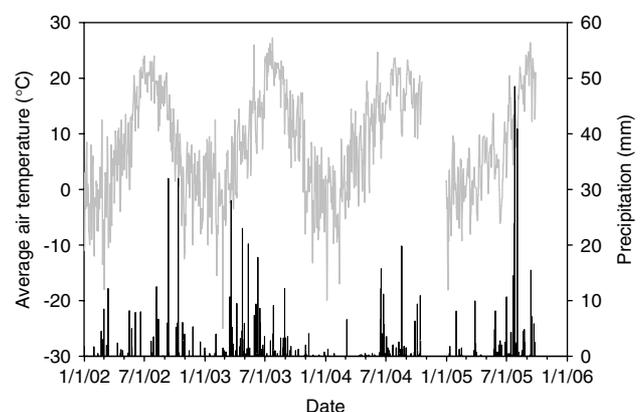


Figure 1. Average daily air temperature (grey line) and precipitation (bar graph) from the High Plain Grassland Research Center, Wyoming.

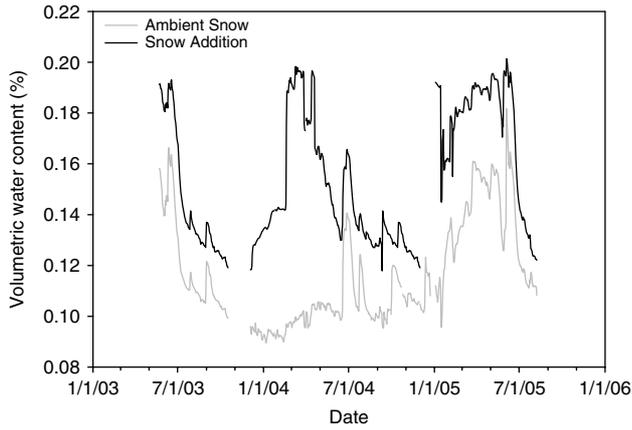


Figure 2. VWC (%) for ambient snow and snow addition treatments from 2003 to 2005 for one snow fence.

2003–2004 and 2004–2005, respectively. Soil moisture was always greater in the snow addition treatments than in the ambient snow treatments (Figure 2 and Table I), an average 3% greater in the snow addition plots during the summer months. Spring soil moisture contents were consistently between 19% and 20% in snow addition plots, whereas spring moisture in ambient snow plots varied from 10% to 16% between years (Figure 2). The greatest difference in soil moisture occurred in the spring of 2004 when the ambient snow plots had very low soil moisture from dry winter and spring, but enough snow accumulated behind the fences to maintain high soil moisture in snow addition plots (Figure 2). The differences in soil moisture between ambient snow and snow addition plots were the least during late 2005 due to a combination of soil drying in the snow addition plots and summer rain increasing the ambient snow plots.

Our summer precipitation treatments also altered soil moisture levels but much less than the added snow treatment (Table I). Under ambient snow conditions, summer rain additions increased the soil VWC by an average 1.5% (Table I). However, summer rain additions did not alter soil water under conditions of added snow. Excluding rain in the summer had a minimal effect on soil water in the ambient snow plots but did slightly lower soil water in the snow addition treatments (Table I). Summer soil temperatures were not greatly affected by the precipitation treatments; however, winter temperatures were higher under the snow addition plots (data not shown). Deeper snow insulated the soil and allowed the soils to maintain temperatures near 0 °C while the soils under ambient winter snow depths had winter temperatures that dropped to a minimum of –3 to –8 °C.

Ecosystem carbon cycling

Ecosystem carbon flux rates exhibited very different patterns for each of the 3 years, closely matching the weather patterns (Figure 3). The spring of 2003 was very wet with modest rates of NEE, GEP and ER under ambient snow conditions. However, a hot and dry mid-summer with little rainfall caused a large reduction in NEE, GEP and ER. In contrast, the spring of 2004

Table I. Average monthly volumetric soil water content (%) and soil temperature (°C) at 3 cm depth by treatment.

	Ambient snow						Plus snow												
	Ambient			+Rain			–Rain			Ambient			+Rain			–Rain			
	VWC (%)	Temperature (C)		VWC (%)	Temperature (C)		VWC (%)	Temperature (C)		VWC (%)	Temperature (C)		VWC (%)	Temperature (C)		VWC (%)	Temperature (C)		
June 03	15.0	17.0		17.7	16.4		15.5	16.5		18.4	17.1		18.4	17.25		16.2	17.0		17.0
July 03	11.6	26.9		13.2	24.9		12.8	25.0		14.4	24.8		14.8	24.3		13.4	25.7		25.7
August 03	10.8	24.8		12.4	22.7		11.2	24.6		13.1	23.6		13.4	24.4		12.2	24.4		24.4
May 04	10.3	13.6		12.2	14.5		10.6	14.35		15.3	12.9		14.3	12.0		15.3	12.7		12.7
June 04	11.4	17.4		12.9	17.6		11.0	18.04		14.4	17.2		13.8	15.5		13.6	16.1		16.1
July 04	11.7	20.3		13.5	21.1		11.5	21.4		14.3	18.8		14.2	18.4		13.2	18.8		18.8
August 04	10.2	19.9		11.6	20.5		10.6	20.7		13.0	18.5		12.6	17.7		12.0	18.2		18.2
May 05	14.8	15.1		16.1	12.7		15.9	13.0		18.9	15.2		17.9	15.2		18.4	16.0		16.0
June 05	15.0	20.0		15.3	19.6		15.1	19.6		17.9	19.0		16.1	19.0		16.4	19.3		19.3
July 05	11.5	25.1		12.4	23.5		11.7	24.6		13.4	22.5		12.7	21.9		12.7	23.3		23.3
Average (std)	12.2 (0.8)	20.0 (0.8)		13.7 (1.2)	19.4 (1.3)		12.6 (1.2)	19.8 (0.9)		15.3 (2.4)	19.0 (0.9)		14.8 (1.1)	18.6 (0.7)		14.3 (0.8)	19.2 (0.8)		19.2 (0.8)

Left side of the table is ambient snow and right side of the table is snow addition (ambient, ambient rain, +rain, rain addition, and –rain, minus rain).

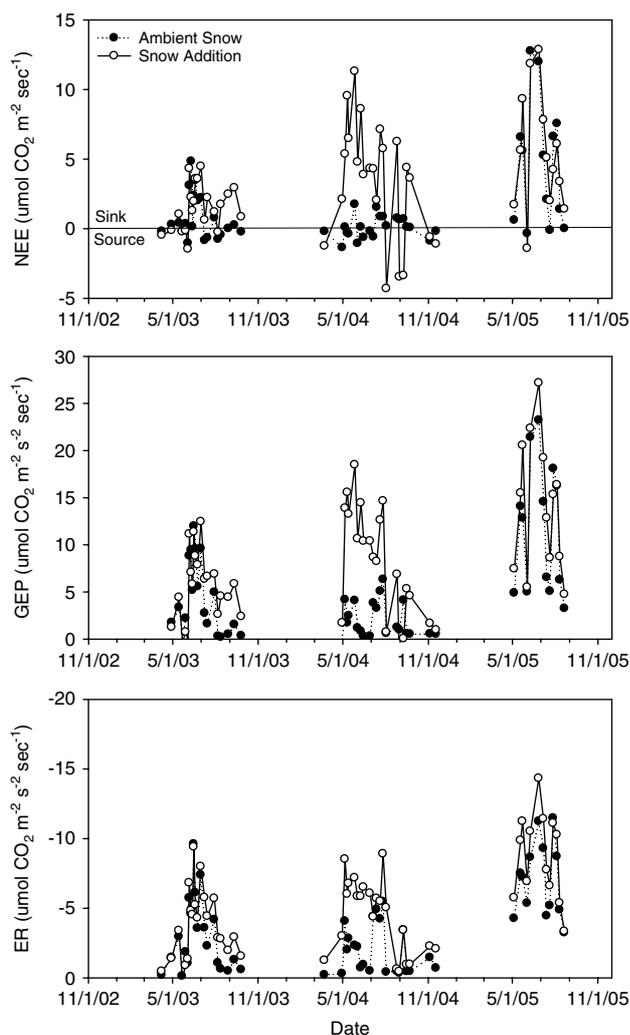


Figure 3. Instantaneous mid-day measurements of NEE, GEP and ER in the mixed-grass prairie under ambient snow and snow addition treatment.

was very hot and dry resulting in very low ambient snow NEE, GEP and ER values (Figure 3). However, abundant rain in the mid to late summer 2004 increased rates of NEE, GEP and ER. The weather in 2005 had no distinctive dry period, which resulted in the highest ambient ecosystem carbon fluxes during the study.

Snow and year were found to be significant factors in the ANOVA model for NEE, GEP and ER (Table II). Mean NEE over the 3 year period was significantly

greater ($P = 0.02$) in the snow addition treatment compared to the ambient snow treatment, averaging 3.4 and 1.8 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively (Figure 4). Average GEP was 6.3 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ under ambient snow conditions increasing to 9.1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ with snow additions ($P = 0.1$). Summer ER was also greater where snow was deeper in the previous winter, averaging 5.7 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ versus 3.4 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the ambient snow conditions ($P = 0.4$).

A significant snow * year interaction was found for NEE and GEP but not for ER (Table II). The effect of snow addition (pooled across rain treatments) was much greater for NEE and GEP during 2004 compared to 2003 or 2005 (Figures 3 and 5). The large differences in NEE and GEP during 2004 in the snow addition plots were due to a combination of wet soils from melting snow and a hot and sunny early summer. Differences between added snow and ambient conditions started to decrease in the late summer of 2004 (Figure 3) due to a combination of heavy rains in July and drying out of the snow pack water (Figure 2).

Altering summer precipitation had much less of an effect on ecosystem carbon fluxes compared to increases in snow (Figure 4). Added rain resulted in C fluxes that were below significant levels ($P < 0.08$) in the ANOVA model for NEE, GEP and ER (Table II). There was no rain * year interaction or rain * snow interaction. Rain exclusion had the greatest influence on the average NEE value (over the 3 years) reducing it by 65% below ambient rainfall ('control') conditions ($P < 0.05$) (Figure 4). Rain addition or exclusion had no significant effects in combination with snow addition on NEE, GEP or ER.

Plant biomass

Above-ground plant biomass showed similar responses to winter and summer precipitation manipulations as the ecosystem carbon flux measurements (Figure 6). Deeper snow in the previous winter significantly increased plant biomass in 2003 ($P < 0.001$) and 2004 ($P < 0.001$) (Table III). Rain additions significantly increased plant biomass in 2004 ($P < 0.001$) where snow depth was at ambient levels in the previous winter. There were no significant differences ($P > 0.05$) in plant biomass

Table II. Results of repeated measures ANOVA designed to test the singular and interactive effect of snow and rain treatments and year on ecosystem C fluxes.

Effect	Num	Den	NEE		GEP		ER	
			DF	DF	F	P	F	P
Rain	2	12	3.10	0.08	3.68	0.06	3.45	0.07
Snow	1	12	66.94	<0.01	28.68	<0.01	9.02	0.01
Rain * snow	2	12	1.55	0.25	0.36	0.70	0.06	0.94
Year	2	11	78.59	<0.01	117.46	<0.01	151.83	<0.01
Year * rain	4	12.4	2.24	0.12	2.37	0.11	2.47	0.01
Year * snow	2	11	27.58	<0.01	9.31	<0.01	2.71	0.11
Snow * rain * year	4	12.4	1.45	0.28	1.09	0.40	0.76	0.57

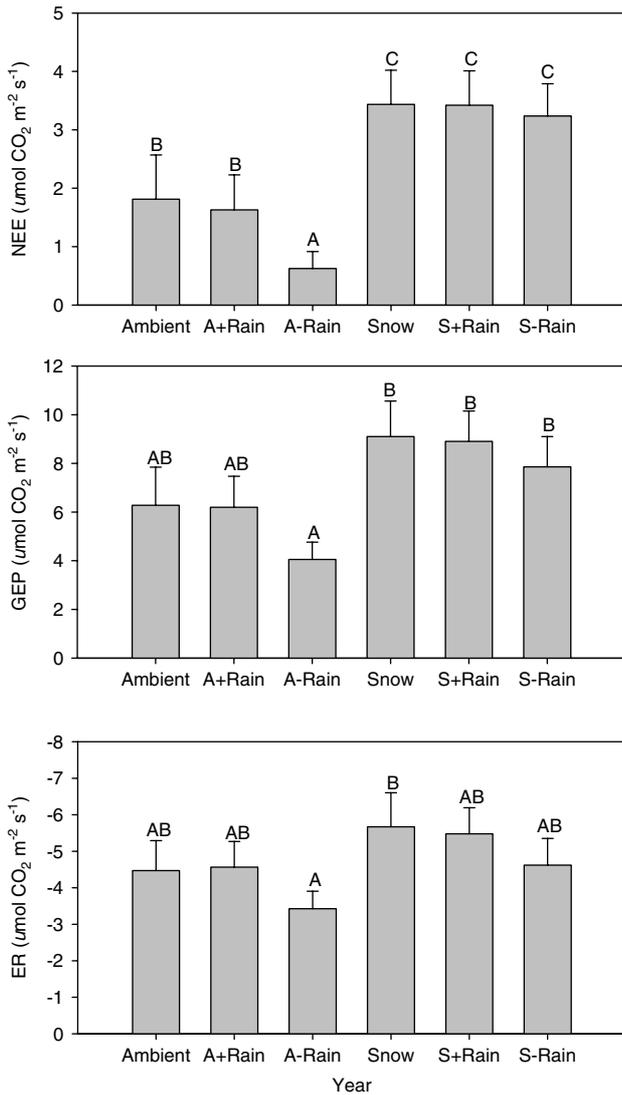


Figure 4. Mean mid-day NEE, GEP and ER by snow and summer precipitation treatments. Different letters denotes significant differences at $P < 0.05$ via Tukey's test. Bars are ± 1.0 SE.

between the different summer precipitation conditions where snow was deep in the previous winter (Figure 6).

There were very few individual plant species that exhibited a strong positive response to winter or summer precipitation changes. The only notable changes occurred in *P. smithii* and *Carex eleocharis* (data not shown). *P. smithii* had significantly greater ($P < 0.05$) biomass in 2004 where snow was deeper in the previous winter and *C. eleocharis* had significantly greater biomass in 2004 and 2005 ($P < 0.05$) where snow was deeper in the previous winter and where summer precipitation was increased, especially in 2004.

DISCUSSION

Our results indicate that changes in winter precipitation have the potential to influence grassland structure and function, especially C fluxes and biomass, in ways not previously appreciated. Changes in winter precipitation

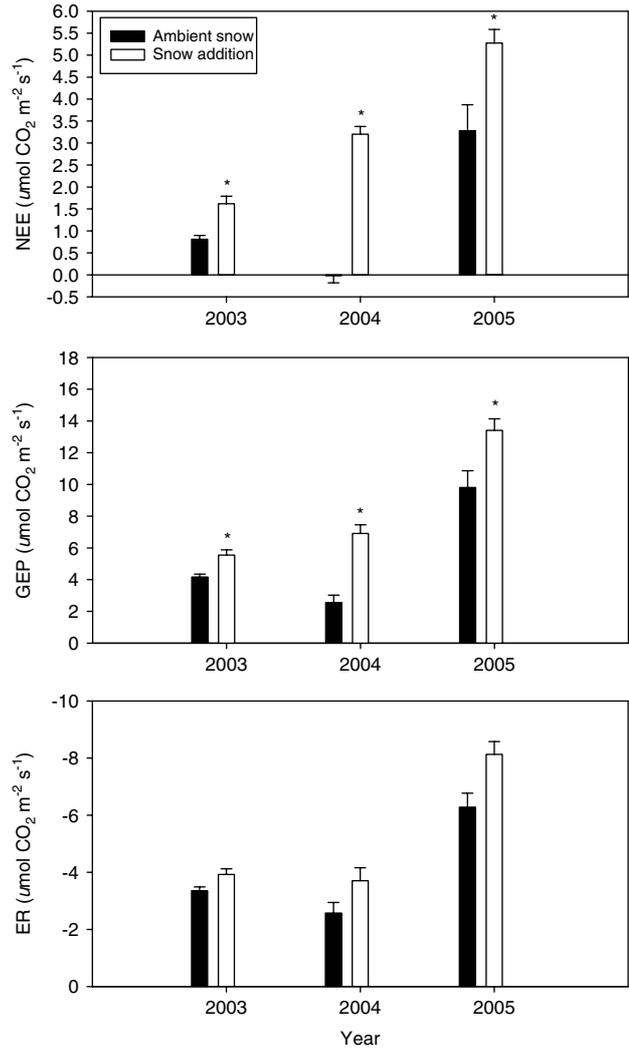


Figure 5. Mean mid-day NEE, GEP and ER by year for ambient and snow addition treatments. Statistical comparisons are pooled across rain treatments and asterisk denotes significant differences at $P < 0.05$ via Tukey's test. Bars are ± 1.0 SE.

may be just as important as: (1) increases or decreases in the amount of rainfall during summer (Fay *et al.*, 2000; Grime *et al.*, 2000; Harper *et al.*, 2005; Harte *et al.*, 2006), (2) the frequency of rainfall (Fay *et al.*, 2000; Knapp *et al.*, 2002; Harper *et al.*, 2005; Heisler-White *et al.*, 2008) and (3) the seasonality of rainfall (Schwinning *et al.*, 2005a) on grasslands. Our observations of a strong effect of winter snow depth on subsequent summer C cycling in these short stature ecosystems are in parallel to those we have observed in the Arctic (Jones *et al.*, 1998; Welker *et al.*, 1999; Schimel *et al.*, 2004; Welker *et al.*, 2005a).

We found that deeper snow in the preceding winter resulted in summer GEP rates that were 45% greater and plant biomass that was 50% higher compared to conditions where snow depth was at ambient levels the previous winter. Our results suggest that when the additional snow melted, it recharged soil moisture throughout the soil profile, providing an extra source of water during the following summer (Welker *et al.*,

Table III. Results of repeated measures ANOVA designed to test the singular and interactive effect of snow and rain treatments by year on plant biomass.

Effect	Num	Den	2003		2004		2005	
			DF	DF	F	P	F	P
Rain	2	12	0.64	0.55	3.77	0.05	2.11	0.17
Snow	1	12	12.33	<0.01	68.44	<0.01	0.71	0.42
Rain * snow	2	12	1.44	0.28	7.04	<0.01	1.62	0.24
Date	1	12	24.07	<0.01	40.85	0.48	0.00	0.10
Date * rain	2	12	0.07	0.93	0.41	0.68	2.28	0.15
Date * snow	1	12	24.98	<0.01	0.78	0.40	1.66	0.22
Snow * rain * date	2	12	0.57	0.58	1.75	0.22	0.70	0.51

2005b). The extra soil water provided more favourable growing conditions for the plants, especially during dry periods in the subsequent summer (see early summer 2004 in Figure 3). This is supported by our soil moisture measurements as we consistently found higher VWC in the upper 30 cm of soils in the snow addition treatments. In addition, we also found up to 20% greater VWC at 1 m depth during the summer under the added snow treatments (data not shown).

Other studies support the importance of winter precipitation, but did not find as strong a response as we observed. Schwinning *et al.* (2005a) reported that plant production on the Colorado Plateau was far more sensitive to winter drought than to summer drought. Morecroft *et al.* (2004) also found that increasing winter rain in England moderated the impact of summer droughts on grassland composition; however, they did not find an increase in plant production. In another study, Bates *et al.* (2006) manipulated winter rain in a sagebrush steppe in the Great Basin but found that plants responded the same as the summer rain treatment. However, this study was on shallow soils (35 cm) which limited the ability for deep percolation. A possible reason why our winter treatment produced stronger treatment effects was that these other manipulation studies altered winter rainfall while we altered winter snow. Snow additions may not be equivalent to season long winter rainfall additions because snowmelt occurs rapidly in the spring providing a large pulse of water that is able to percolate deep into the soil profile with little evaporative loss, especially in loamy or coarse textured soils. Another important factor is that our snow fences captured a lot of snow. We estimate that our snow fences roughly doubled ambient winter precipitation (average of 10 cm ambient winter precipitation vs 24 cm in snow addition treatments).

Besides increasing plant production, augmenting snow also increased ER by an average of 27%. Elevated levels of ER are also likely due to elevated soil moisture levels (Risch and Frank, 2006). Greater soil water can facilitate microbial decomposition of organic matter and the subsequent release of CO₂ (Hobbie *et al.*, 2000). In addition, higher soil water contents increased plant growth and associated respiration (Lauenroth and Sala, 1992; Milchunas *et al.*, 1994; Knapp *et al.*, 2001). Under more favourable soil water conditions, greater amounts

of plant photosynthates can be allocated to carbon efflux from roots into the rhizosphere, providing microbial populations with an additional carbon source and increasing rates of microbial respiration (Holland *et al.*, 1996; Carbone *et al.*, 2008).

Compared to adding winter precipitation, we found much less of an effect of added summer precipitation on ecosystem carbon cycling. In general, decreasing summer rainfall lowered NPP, GEP and ER, whereas increasing summer precipitation had little effect. We found stronger effects on plant biomass when summer rain was either increased or decreased than we did for ecosystem C fluxes. Average plant biomass increased 44% with the addition of summer rain and decreased 18% when rain was lowered. We likely observed greater summer precipitation treatment differences in plant biomass as opposed to ecosystem carbon fluxes because of the integrated nature of plant biomass. Plus, we watered the plots every Friday and did not measure gas fluxes until the following Tuesday. Therefore, we missed some of the episodic fluxes that would have resulted from weekly watering (Lee *et al.*, 2004; Xu *et al.*, 2004). We also feel that our rainout shelters were not perfect at removing rain. The rainout shelters faced downward to the prevailing wind direction, but windy conditions or rain coming from another direction would likely add more rain than designed for. Our rainout shelters were also small, which could allow for horizontal water movement from adjacent soils.

The responses we observed to our summer rain scenarios are in line with findings from several other precipitation experiments. Experimentally increasing summer rain has been found to increase plant biomass and soil CO₂ efflux in several types of grasslands (Grime *et al.*, 2000; Knapp *et al.*, 2001; Shaw *et al.*, 2002; Kochy and Wilson, 2004; Morecroft *et al.*, 2004; Zhou *et al.*, 2006). Decreasing summer rain has been found to decrease plant biomass (Fay *et al.*, 2000; Grime *et al.*, 2000; Kochy and Wilson, 2004; Morecroft *et al.*, 2004; Harper *et al.*, 2005; Zha *et al.*, 2005), fluxes of ER (Harper *et al.*, 2005) and total soil carbon (Harte *et al.*, 2006). It is clear from these experiments that grasslands sequester less carbon during dry periods and more carbon during wet periods. The frequency of precipitation events can also interact with total precipitation amounts to influence carbon cycling (Fay

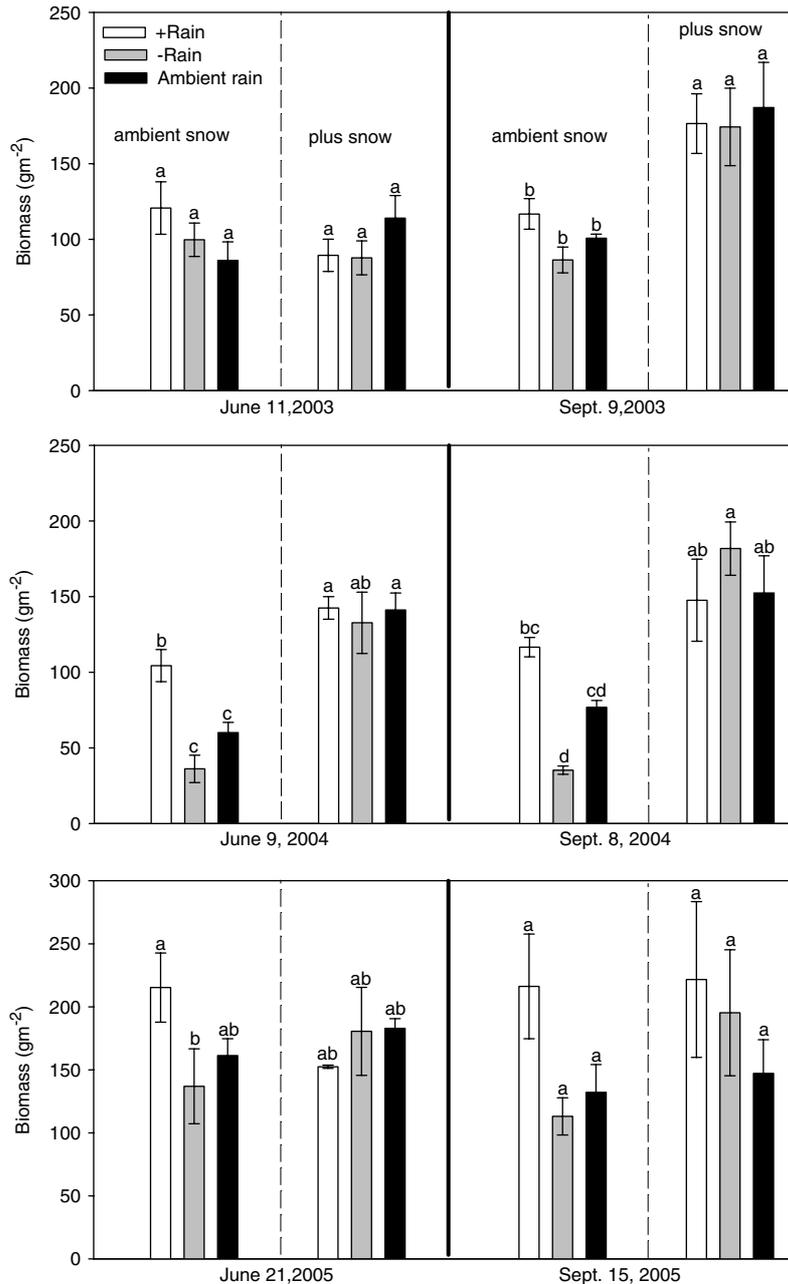


Figure 6. Mean plant dry biomass by year and treatment. Means followed by different letters are significantly different at the $P < 0.05$ via Tukey's test. Bars are ± 1.0 SE.

et al., 2000; Knapp *et al.*, 2002; Nippert *et al.*, 2006). However, there have been few studies that have tried to quantify the interaction between winter and summer precipitation (Schwinning *et al.*, 2005a).

We found a snow * year interaction effect on carbon cycling as the influence of snow addition was greatest during years with dry summers (2004) and least in summers with high precipitation (2005). The interaction between winter and summer precipitation suggests that carbon cycling responds to available soil moisture levels, and not to the form of precipitation (Weltzin *et al.*, 2003; Schwinning *et al.*, 2005b).

Our results suggest that species composition and ecosystem carbon cycling will likely change if more precipitation occurs in the winter as snow. We would expect

to see increases of plants with a deeper root system to take advantage of deeper water from winter snow melt that infiltrated to deeper depths (Carbone *et al.*, 2008). The only plants in our study that increased were *P. smithii* and *C. eleocharis* (data not shown), both of which are deep rooted cool-season plants (LeCain *et al.*, 2006). We also expect that given more time we would likely see increases in the subshrub *Artemisia fridigata* due to its ability to access deeper soil water. Increases in winter precipitation could also increase invasive species in the mixed-grass prairie (Blumenthal *et al.*, 2008). In a companion study, Blumenthal *et al.* (2008) found that without added snow, seeded invasive species were rarely observed. But snow addition greatly increased above-ground biomass of *Centaurea diffusa* (diffuse knapweed), *Gypsophila*

paniculata (babysbreath) and *Linaria dalmatiana* (dalmatian toadflax). Therefore, how climate change will affect carbon cycling in mixed-grass prairies is complicated by changes in species composition and increased invasive species, changes to soil quality, increased CO₂ concentrations in the atmosphere and amount and seasonality of temperature and precipitation changes (Zhou *et al.*, 2008).

In summary, we report that ecosystem carbon cycling rates and species composition in the mixed-grass prairie are influenced by changes in winter, summer or a combination of winter and summer precipitation. This has implications for forecasting changes to the large pools of carbon stored in temperate grasslands as climate change (Christensen *et al.*, 2007). The responses we observed in carbon exchange in responses to 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 altered. Augmenting snow had the net effect of sequestering more carbon during the study as NEE increased an average of 90% over ambient snow conditions. These changes in soil carbon could be of regional significance when one considers that mixed-grass prairies cover $\sim 142.7 \times 10^4$ km² of North America.

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