Impact of precipitation dynamics on net ecosystem productivity

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Abstract

Net ecosystem productivity (NEP) was measured on shortgrass steppe (SGS) vegetation at the USDA Central Plains Experimental Range in northeastern Colorado from 2001 to 2003. Large year-to-year differences were observed in annual NEP, with >95% of the net carbon uptake occurring during May and June. Low precipitation during the 2002 April to June time period greatly reduced annual net carbon uptake. Large precipitation events (>10 mm day^{-1}) promoted carbon uptake, while small precipitation events (<10 mm day^{-1}) enhanced heterotrophic respiration and resulted in a net loss of carbon from the system. Large precipitation event enhanced carbon uptake was attributed to increased soil water content (SWC), which promotes plant photosynthesis. The large precipitation events which occurred from July to October have lower increases in daytime net CO_2 uptake (NEP_d) due to the presence of low live plant biomass compared to earlier in the growing season. Live aboveground plant biomass (AGB), solar radiation, and SWC were the major variables that controlled NEP_d, while AGB, SWC, and relative humidity control nighttime respiration losses (NEP_n). Aboveground plant biomass is the most important variable for controlling both NEP_d and NEP_n dynamics. These results suggest that the major factor controlling growing season NEP_n is the amount of carbon fixed via photosynthesis during the day. Heterotrophic soil respiration is greatly enhanced for one to 2 days following rainfall events with daily rainfall events >5 mm having a similar increase in respiration (>3.00 g m Cm^{-2} day^{-1}). In addition, the size of the heterotrophic respiration pulse is independent of both the amount of time since the last rainfall event and the time of occurrence during the growing season.

Keywords: Bowen ratio, carbon dioxide, CO_2, grassland, NEE, NEP, photosynthesis, precipitation, pulse, respiration, shortgrass steppe

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Introduction

Grasslands play an important role worldwide, comprising over 30% of the Earth's terrestrial surface (Adams *et al.*, 1990). Grasslands tend to exist in dry, continental environments, although some grasslands exist in zones with sufficient precipitation to support woody plants, indicating that fire and herbivory may also be critical to their occurrence (Bond, 2008). These lands are valued for their domestic livestock grazing, but are increasingly being considered for other goods and services, such as the capture and sequestration of atmospheric CO_2 into soil organic matter (Derner & Schuman, 2007). The recent growth of the world's economy and an apparent decline in the Earth's ability to absorb CO_2 (Canadell *et al.*, 2007) have resulted in an increased interest in grassland exchanges of CO_2. Due to their extensive presence worldwide and to the high amounts of C already stored in their soils, grasslands contribute

significantly to terrestrial C fluxes (Scurlock & Hall, 1998; Lal, 2004). Small changes in CO_2 fluxes of grasslands should have significant impacts on biosphere–atmosphere exchanges of CO_2.

Land–atmosphere exchange of CO_2 in grasslands and/or arid and semi-arid systems are determined in large part by soil moisture conditions, with near-normal or abundant precipitation causing C uptake and drought resulting in net C release (Suyker *et al.*, 2003; Hunt *et al.*, 2004; Xu & Baldocchi, 2004; Ivans *et al.*, 2006; Allard *et al.*, 2007; Patrick *et al.*, 2007; Kwon *et al.*, 2008; San José *et al.*, 2008; Wang *et al.*, 2008; Polley *et al.*, 2010; Zhang *et al.*, 2010). However, site- or regional-specific characteristics confound simple relationships between precipitation and net C uptake. For instance, a recent analysis of annual net CO_2 flux measurements conducted on eight North American rangelands found that most rangelands operate as both sinks and sources of CO_2. Nonetheless, native grasslands of the Great Plains and sagebrush steppe ecosystems operated mostly as sinks, while desert grasslands in the southwestern United States tended to be net sources of CO_2

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(Svejcar *et al.*, 2008). The C dynamics in grasslands of the northern Great Plains appear to be near equilibrium, with a trend suggesting drier sites were C sources and wetter sites were C sinks (Wylie *et al.*, 2007; Zhang *et al.*, 2010).

It is also becoming increasingly clear that many aspects of arid and semi-arid ecosystem ecology can be greatly affected by the spatial and temporal variation of soil water availability (Schwinning & Sala, 2004; Heisler-White *et al.*, 2009), including C cycling (Huxman *et al.*, 2004; Xu & Baldocchi, 2004; Xu *et al.*, 2004; Ivans *et al.*, 2006; Swemmer *et al.*, 2007; Zhou *et al.*, 2007; Chou *et al.*, 2008; Kwon *et al.*, 2008). Recent evidence suggests that the effect of precipitation pulses on land–atmosphere exchange of CO_2 depends in large part on the combined responses of the soil microbial community and plants (Austin *et al.*, 2004; Hunt *et al.*, 2004; Huxman *et al.*, 2004; Xu & Baldocchi, 2004; Xu *et al.*, 2004; Chou *et al.*, 2008; Williams *et al.*, 2009). Brief, shallow pulses primarily affect surface or near-surface organisms with fast response times (soil micro-fauna and flora), while more prolonged and intense events impact higher plants (Schwinning & Sala, 2004; Heisler-White *et al.*, 2009). Timing between pulses can be important given it determines the accumulation of respiratory substrates, with longer inter-pulse periods resulting in large flux responses (Xu & Baldocchi, 2004; Sponseller, 2007). Similarly, shallow-rooted plants will be more sensitive to surface fluctuations in soil moisture than deeper-rooted species (Ivans *et al.*, 2006; Kwon *et al.*, 2008; Shim *et al.*, 2009). Further, plants offer substrates for soil respiration so pulses can indirectly influence soil respiration through their effect on plant-derived respiratory substrates (Craine *et al.*, 1999; Flanagan & Johnson, 2005; Bahn *et al.*, 2009).

Finally, different ecosystems can vary tremendously in their temporal responses to precipitation. For instance, while CO_2 uptake of juniper and sagebrush systems was enhanced by fall precipitation events, responses were considerably less for a site planted with crested wheatgrass, especially after a dry summer that resulted in senescence of the grass (Ivans *et al.*, 2006). Similarly, spring drought in a Wyoming sagebrush steppe altered the seasonal CO_2 flux dynamics by essentially eliminating activity of the more shallow-rooted grasses and forbs (Kwon *et al.*, 2008). Such temporal responses that involve changes in plant phenology due to altered soil temperature and water can also have important effects on soil respiration (Del Grosso *et al.*, 2005). As a result, the effect of precipitation events on C balance depends on a complicated interaction of current soil water conditions, timing and magnitude of precipitation, soil type and texture, plant and soil communities, and evaporative demand.

The main objective of this study is to determine the impact of precipitation seasonality and pulses on seasonal and annual patterns in net ecosystem productivity (NEP) for the shortgrass steppe (SGS) in northeastern Colorado. Bowen ratio energy balance (BREB) systems were installed in ungrazed, moderately grazed, and heavily grazed pastures from 2001 to 2003. Diurnal, seasonal, and annual energy balances (soil, sensible, and latent heat fluxes) and NEP were measured for the three grazing treatments, along with soil water and temperature, seasonal patterns in live and dead leaf biomass, and chamber measurements of ecosystem respiration. These data were used to determine: (1) the impact of precipitation seasonality and amount on daily, seasonal, and annual NEP, nighttime respiration (NEP_n), and daytime net carbon uptake (NEP_d); (2) the effect of soil water and temperature and live plant biomass on soil respiration; and (3) the impact of live plant biomass, solar radiation, soil and air temperature and water content (SWC) on growing season NEP_d. Nighttime NEP is negative (C loss) due to both autotrophic respiration from the plants and soil heterotrophic respiration. Daytime NEP is generally positive (C uptake) during the growing season as a result of plant photosynthesis. In a previous report on the same study, seasonal patterns of NEP, plant live biomass, and energy balance were unrelated to grazing treatment (Jamiyansharav *et al.*, 2011). Thus, this article focuses on the seasonal impact and event size of precipitation on NEP. We used the NEP data sets to derive a set of regression equations to evaluate the impact of rainfall, soil water, live plant biomass, relative humidity, soil radiation, and soil and air temperature on growing season NEP_d and NEP_n. This article will speculate on the potential impact of climatic changes in the frequency of small vs. large rainfall events and the timing of rainfall events (early vs. late growing season) on NEP.

Methods

Study site and measurements

Measurements were conducted at the USDA-ARS Central Plains Experimental Range (CPER; 40 50 N, 104 43 W), located at the western edge of the Central Great Plains and the northern limit of the shortgrass steppe ecosystem. The CPER site has a classic continental climate with a mean annual precipitation of 321 mm, a large portion of which occurs from April to June (43%), and mean air temperatures of 15.6 °C in summer, and 0.6 °C in winter. Vegetative basal cover ranges from 23% to 35% (Milchunas *et al.* 1989) and is comprised of a mixture of C_4 and C_3 grasses, a sub-frutescent shrub (*Artemesia frigida*), forbs, and cacti, with the majority of the aboveground plant production coming from *Bouteloua gracilis* (C_4 grass). The CPER site has been extensively grazed by livestock during

the past 120 years, with grazing by American Bison prior to the arrival of the Europeans in the 1850s.

The measurements were conducted in three 65 ha pastures subjected to three different levels of cattle grazing (ungrazed, moderate, and heavy). All three pastures had been moderately grazed (40% removal of current production) for the previous 50 years. Although the responses to grazing are not discussed in this presentation, a brief description of the treatments is given. During the observation period, the ungrazed, moderate, and heavily grazed treatments removed annual forage production of zero, 40%, and 65%, respectively. The grazing treatments were generally stocked by heifers from May to October; however, the animals were removed from all of the grazing treatments on August 9, 2002 due to the low amounts of forage. Precipitation from April to June of 2002 was extremely low, while precipitation from April to June of 2001 and 2003 was near normal for the site.

There are two primary micrometeorological techniques for measuring CO_2 fluxes: (1) the eddy covariance (EC) method, and (2) the BREB method. Both methods have deficiencies under different environmental conditions. The EC technique tends to increase uncertainty and errors during periods of low turbulent mixing, particularly at night (Baldocchi, 2003). The BREB technique is also less effective during conditions of low turbulence, but also suffers from increased numerical errors during transitions between positive and negative net radiation (i.e., sunrise and sunset; Ohmura 1982; Wolf et al., 2008). In general, EC estimates of CO_2 flux tend to be lower than those determined by BREB. Fluxes calculated using the BREB method have been shown to be similar to: (1) daytime and nighttime chamber measurements of ecosystem CO_2 fluxes above sagebrush (Angell et al., 2001); (2) daytime and nighttime fluxes measured using EC instrumentation in tallgrass prairie (Dugas et al., 2001); (3) measurements by several methods above sorghum (Twine et al., 2000); and (4) nighttime fluxes calculated from the sum of measured soil respiration and estimated plant respiration in northern mixed-grass prairie (Frank et al., 2001). We chose to use the BREB system at the time this experiment began because it was the only commercially available micrometeorological system for such measurements.

The BREB systems (Model 023/CO_2 Bowen Ratio System, Campbell Scientific Inc., Logan, UT, USA) were installed in spring 2000 in all three pastures and operated until the end of 2003. Tower locations in each pasture accommodated a fetch of at least 100 m. Humidity, temperature, and CO_2 gradients were measured every 2 min from arms positioned at heights of 1 m and 2 m above the canopy, and were used with observations of net radiation, soil heat fluxes, wind speed, and soil temperature to determine the sensible and latent heat and CO_2 fluxes (Dugas et al., 1999). Canopy height was approximately 15 cm, and was assumed to remain constant, thus sampling arms were not moved throughout the experiment. Standing vegetation included dead vegetation, a small amount of biomass from past growing seasons, and some small subshrubs, so we assume canopy height remains fairly stable through the growing season. Precipitation was measured using a tipping bucket rain gauge (Model TE 525 mm, Texas

Electronics, Dallas, TX, USA). Volumetric SWC was measured using calibrated water content reflectometers (Model CS615, Campbell Scientific Inc., Logan, UT, USA) for the 0–15 cm soil depth. Daily values of soil moisture and temperature, and net carbon exchange for day- and nighttime periods, were calculated from 2001 to 2003 for all three pastures.

Observations from the three BREB systems were processed to provide a continuous time series of meteorological and flux data. An initial screening of the data was performed using thresholds to identify observations that were improbable given regional climatic conditions and observed extremes (see Supporting Information Table S2). Observations that fell outside of the thresholds were removed from the data sets. The total percentage of missing data over all variables (22), sites (3), and years (3), after outliers were removed, was 10.4%, ranging from as little as 0.01% of missing data for the most reliable measurement types (e.g., precipitation in 2003 at the heavily grazed site) to a maximum of 26.7% missing [photosynthetically active radiation (PAR) at the heavily grazed site in 2002].

Gaps in the time series of 1 h or less were filled with linear interpolation. For gaps longer than 1 h, linear regression equations were used. The slope, offset, and r^2 were calculated for each site, and for each variable for each month, against the other sites for the same month so that a variable missing at a particular time at one site could be replaced. These equations were used if there was enough data to derive robust relationships between the sites. Correlations between sites were generally quite high with slopes close to 1.0. Gaps were filled based on the highest calculated r^2 between sites, and the appropriate regression equation for the site, month, and variable was used to estimate the new value. If there were no regressions performed because of lack of data, but observations were available from another site for a particular time, the point was filled by substitution. To fill gaps in wind speed, wind direction, and precipitation, a direct substitution of data from one site to another was used based on the highest calculated r^2 between sites. Even with this procedure, some gaps remained. These gaps were primarily in PAR and Bowen ratios, with a few present in sensible heat and net ecosystem exchange. Substitutions from adjacent days were used for these gaps when no indication of a meteorological event precluded such a substitution (such as for precipitation).

Measurements of the live AGB during the growing season were determined within a 30 m × 30 m sampling area that surrounded each of the BREB towers. One meter squared quadrants were randomly located within each of the nine 10 m × 10 m grids in each sampling area. Aboveground biomass in the quadrants was clipped to the base of the vegetation (crown), oven-dried at 60 °C, and weighed. Biomass samples were classified as green or brown, and we refer to the green biomass in this article as AGB.

Chamber ecosystem respiration was measured with a portable soil respiration chamber (Model EGM-1 with SRC-1, PP Systems, Amesbury, MA, USA). Soil temperature was concurrently measured at a depth of 5 cm, adjacent to the soil collar (Model STP-1, PP Systems). Ecosystem respiration (soil heterotrophic respiration plus root autotrophic respiration) and temperature measurements were collected every 1 to 2 weeks

from five PVC soil collars which were installed monthly adjacent to the BREB. Soil respiration collars were 5 cm tall with a diameter of 10.3 cm and installed to a depth of 3.5 cm. Aboveground phytomass was clipped and removed from the collar prior to sampling (to remove plant C flux). This necessitated relocating the collars which was done every 6 weeks.

Statistical data analysis

We used the Akaike's Information Criterion (AIC) and Akaike weights (W_r) to select regression models that describe the impact of SWC, soil and air temperature, relative humidity, solar radiation, AGB, and rainfall events on NEP_d and NEP_n (CO_2 flux results are expressed in units of C throughout) for the growing season (March to October). We focused our statistical data analysis on the growing season since there was a poor correlation of NEP_d and NEP_n to any of the observed driver variables during the dormant plant growth period (November to February). Potential problems with the estimates of soil water content during the November to February period (with below freezing temperatures) were avoided by focusing on the growing season. Precipitation days were defined as those receiving more than 3 mm; the first day following precipitation events greater than 10 mm was also designated as a precipitation day.

We used AIC to evaluate models on the basis of the supported data found for each model (Burnham & Anderson, 2002). Akaike's Information Criterion account for goodness of fit based on minimizing sum square error, but also includes a penalty for each additional optimized parameter included in the model. The model with the lowest AIC value is considered the best model, and the W_r are the probability that a given model is the best model of the suite of those tested (Burnham & Anderson, 2002). Akaike's Information Criterion has been successfully used to select the best models for biogeochemical model development (Del Grosso *et al.*, 2005).

Results

Results for 2001 (Fig. 1a) show the typical high precipitation during spring pattern for north-central Colorado and SWC from April through June. Subsequent precipitation which mainly occurred during the summer months (July to September 2001) was generally light (daily precipitation <10 mm), and SWC was typically <0.05 cm^3 cm^{-3}. Precipitation and SWC remained low throughout the fall of 2001, winter of 2001/2002, and from spring through the early summer of 2002. Substantive precipitation in late summer of 2002 boosted SWC during the fall and winter. Significant precipitation during the spring of 2003 (Fig. 1c) resulted in high SWC during April, May, and June. Several large precipitation events during the 2003 summer boosted SWC from July through September. Small rainfall events (<5 mm day^{-1}) generally had little impact on SWC during the growing season since daily potential evapotranspiration rates are >5 mm per day (Sala *et al.* 1992).
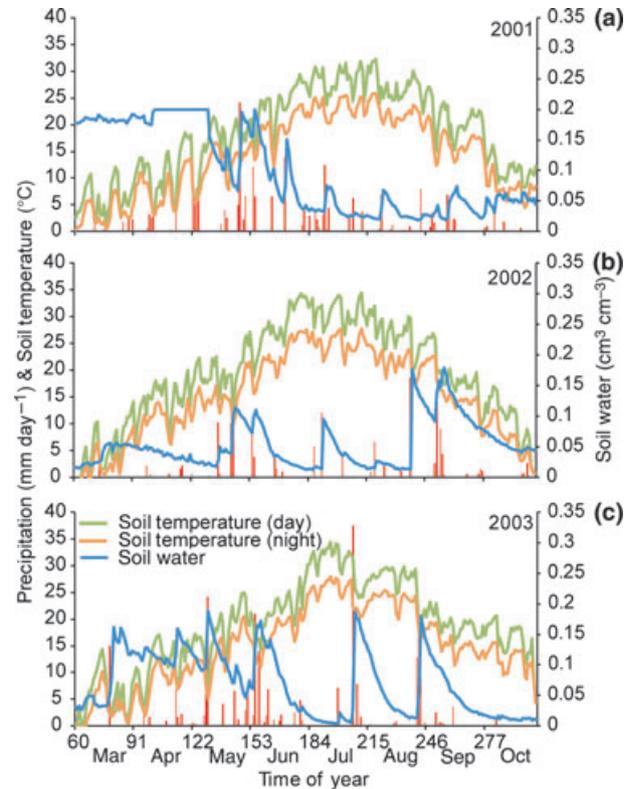

Fig. 1 Growing season patterns in volumetric soil water (SWC) content (0–15 cm), average daytime and nighttime soil temperature (°C at 5 cm depth), and precipitation (mm day^{-1}) for 2001 (a), 2002 (b), and 2003 (c).

Larger rainfall events resulted in clear patterns of partial soil moisture recharge and subsequent dry-down periods. The observed pattern of generally sustained high SWC from March to June, and generally lower SWC from July to October during both 2001 and 2003, represents the typical seasonal pattern in SWC observed at the CPER site (Sala *et al.* 1992).

High SWC from March to June of 2001 (average SWC = 0.17 cm^3 cm^{-3}) resulted in 90 g m^{-2} AGB on June 28, 2001 (Fig. 2). Live aboveground biomass declined from leaf senescence and shedding during the dry summer and remained low for the remainder of the growing season. Low SWC during the ensuing spring and early summer of 2002 (average SWC = 0.05 cm^3 cm^{-3}) resulted in low AGB of only 20 g m^{-2} measured on June 30. High SWC from August to September of 2002 (Fig. 1) had little impact on late-season AGB. Relatively high precipitation and SWC from March to June (average SWC = 0.10 cm^3 cm^{-3}) of 2003 resulted in live biomass of 115 g m^{-2} on June 16 (Fig. 2). Low SWC during the end of June and early July 2003 caused live biomass to decrease rapidly. Substantial precipitation events and increased SWC from late

July through September 2003 had little impact on late-season AGB. In summary: (a) seasonal and apparent peak AGB responded strongly to the March to June SWC; (b) mid-summer dryness, which is fairly typical for the location, caused live biomass to decrease rapidly from apparent peak values in June; and (c) substantial precipitation events and elevated SWC during July and August had no measurable effects on late-season AGB.

Soil respiration increased as SWC increased (Fig. 3a) from 0.02 to 0.08 cm^3 cm^{-3} under conditions of both low (<15.0 °C) and high (>15.0) soil temperatures, increased little for SWC > 0.08 cm^3 cm^{-3}, and as expected, was much greater for high soil temperatures (two to three times higher). Based on the above results, we evaluated the impact of soil temperature on R_s for wet days (SWC > 0.08 cm^3 cm^{-3}) and dry days (SWC < 0.08 cm^3 cm^{-3}), and found that R_s increased exponentially (Q^{10} ranged from 2 to 3 for temperatures > 10 °C) with increased temperatures for wet days (Fig. 3b), while soil temperature had little impact on R_s for the dry days.

In the two typical precipitation years 2001 and 2003, distinct growing season patterns of NEP_d were observed (Fig. 4): (a) consistent negative fluxes of NEP_d during the early growing season (March to April) when plant biomass was low; (b) positive fluxes of NEP_d from May through June, with the highest rates occurring during June; and (c) generally low NEP_d from July through October, interrupted by two periods of moderately high NEP_d in 2003 following two large, late-season precipitation events. During the drought year (2002), NEP_d was much lower during the May to June period due to dry soil conditions, and late-season NEP_d increased slightly following two precipitation events. A comparison of live plant biomass and NEP_d show similar seasonal patterns as NEP_d (Figs 2 and 4). The AIC statistical analysis (see below) indicates that NEP_d has the highest correlation to live plant biomass ($r^2 = 0.47$),

Fig. 3 Response of chamber ecosystem respiration to volumetric soil water content (SWC) when soil temperature (5 cm depth) is >15°C or <15.0 °C (a), and temperature for wet days is SWC > 0.07 cm^3 cm^{-3} and for dry days is SWC <0.07 cm^3 cm^{-3} (b). Regression for temperature on dry days is not significant.

compared to lower correlations for SWC ($r^2 = 0.16$) and solar radiation ($r^2 = 0.07$).

As shown in Fig. 4, NEP_n decreased rapidly following rainfall events, and was generally lower at high SWC. The NEP_n results from both autotrophic and heterotrophic respiration, so lower NEP_n with additional soil moisture indicates, as expected, stimulation of respiration (larger negative fluxes) by increased SWC. The NEP_n also tended to be lower during the May to June time period when maximal values of live biomass were observed, resulting in a reasonably strong negative correlation between AGB and NEP_n ($r^2 = 0.32$). Like NEP_d, the AIC statistical analysis also shows that NEP_n has the highest correlation to AGB ($r^2 = 0.32$) compared to SWC ($r^2 = 0.22$), the next most correlated variable.

A closer examination of soil water and precipitation events (Fig. 5) during the middle (May to June) and late (July to October) growing seasons of 2001 and 2003, respectively, illustrates more clearly how both NEP_n and NEP_d decreased dramatically for 1 to 2 days following rainfall events. Reductions in NEP_d following rainfall events were from high positive rates to near zero during the middle growing season of 2001
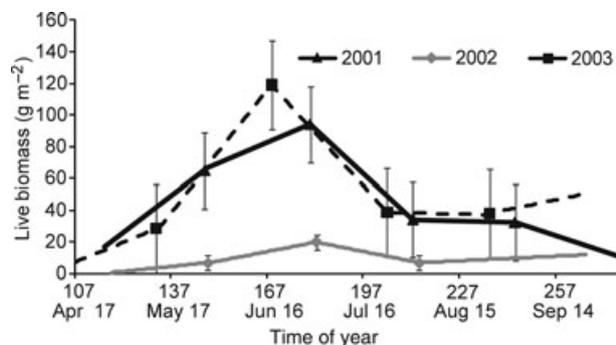

Fig. 2 Mean live aboveground biomass (average biomass for the ungrazed, moderately grazed, and heavily grazed sites) for 2001, 2002, and 2003.
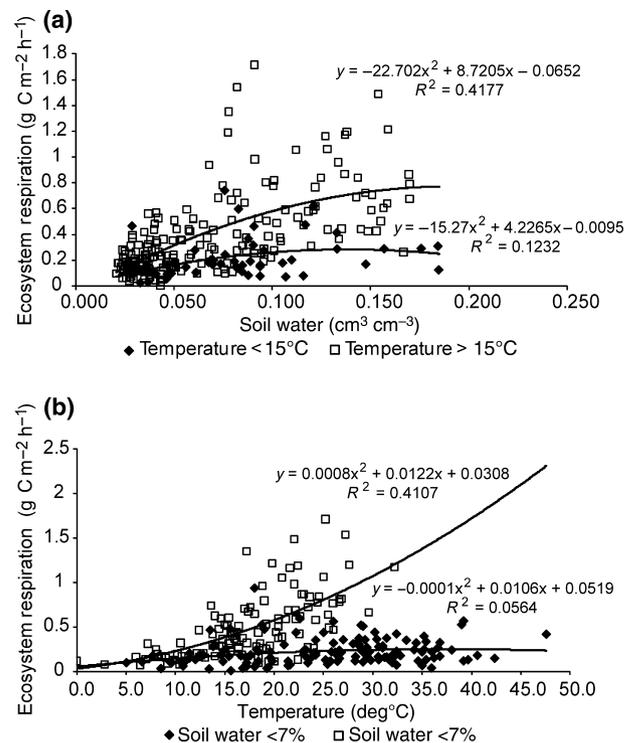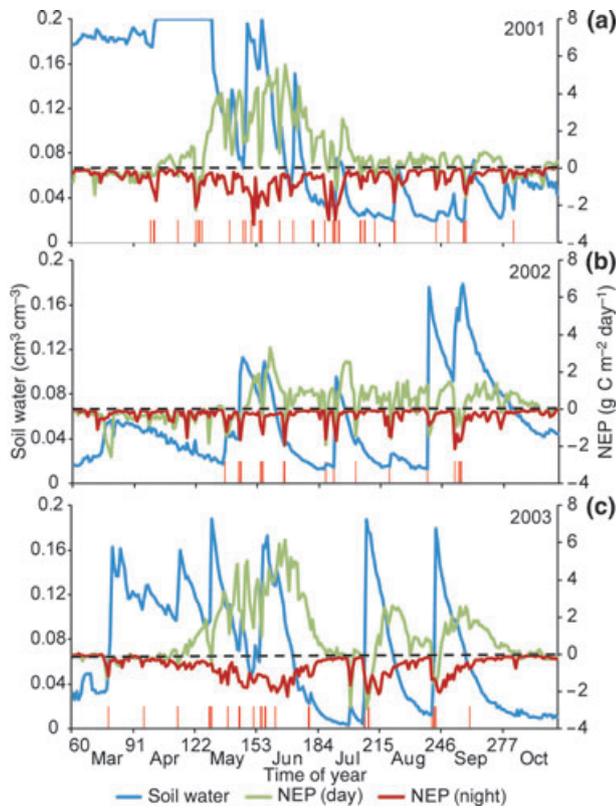
Fig. 4 Seasonal patterns in growing season (March–October) daytime and nighttime net ecosystem productivity (NEP) (averaged across grazing treatments), soil water content (SWC), and daily precipitation events (>3 mm day^{-1}) for 2001 (a), 2002 (b), and 2003 (c).
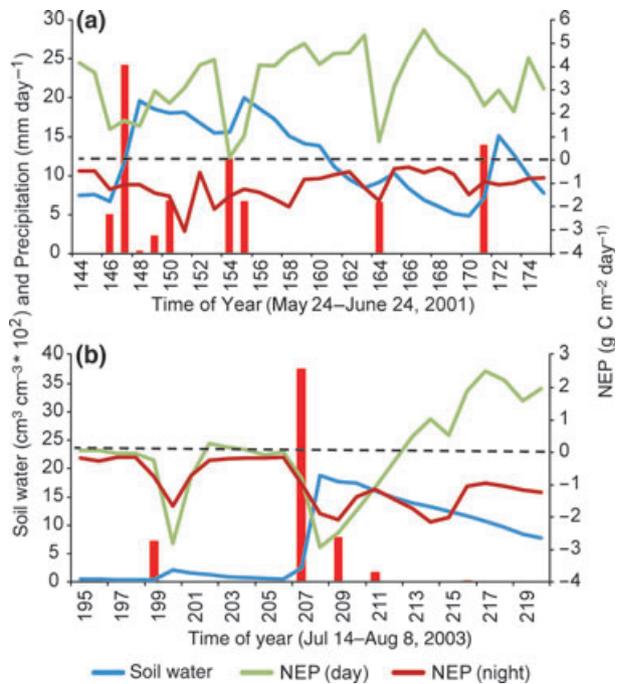

Fig. 5 Changes in daytime and nighttime NEP, soil water, and precipitation for the mid-growing season (May 24 to June 24, 2001) (a), and late growing season (July 14 to August 8, 2003) (b).

(Fig. 5a) when AGB is high (>80 g m^{-2}) (e.g., days 154 and 164), and declined to large negative fluxes in the late growing season of 2003 (Fig. 5b) when AGB is low (<40 g m^{-2}).

The impact of rainfall amounts on NEP$_d$ and NEP$_n$ was nicely illustrated in 2003 (Fig. 5b). A 6 mm rainfall event into dry soil on day of year 199 caused a large decrease in NEP$_d$ and NEP$_n$ (large negative values for both) immediately after the rainfall event, followed by a moderate increase in NEP$_d$ 3 days later. In contrast, a large 37 mm rainfall event on day of year 207, again into dry soil, recharged SWC and caused similar decreases in NEP$_d$ and NEP$_n$ (large negative values) immediately following the rainfall event; but was then followed by a substantive and prolonged increase in NEP$_d$ (along with two additional but small precipitation events). This larger and more sustained response to a significant recharge of SWC was sufficient to switch from net CO$_2$ losses to CO$_2$ uptake.

The impact of rainfall amount on NEP$_d$ and NEP$_n$ is also illustrated by contrasting the results of slightly different precipitation dynamics from July to September

of 2001 and 2003. In 2001, daily rainfall amounts during this time period were <10 mm and SWC was low, while several large (>15 mm) rainfall events over the same period in 2003 temporarily boosted SWC (Fig. 1a and c). This resulted in substantially lower NEP$_d$ fluxes from July to October in 2001 compared to the same time period in 2003 (Fig. 4a and c; cumulative NEP$_d$ fluxes for 2001 were 50% of those for 2003), even though cumulative precipitation at that time was only slightly higher in 2003 than 2001 (100 mm vs. 92 mm). The similarity of cumulative NEP$_n$ was greater between the 2 years (20% higher in 2001 vs. 2003, with fewer negative fluxes) due to the frequent occurrence of small rainfall events during 2001 causing greater short-term pulses in respiration loss (more negative fluxes) with each of the rainfall events. These results suggest that frequent small rainfall events result in elevated respiration losses (larger negative NEP$_n$ values) from the ecosystem, while the larger daily rainfall events (>10 mm) enhance net carbon uptake during the day (>NEP$_d$ values).

We calculated the peak nighttime respiration rates (NEP$_n$) following rainfall events (largest negative value within 2 days of the rainfall event) and evaluated whether the peak respiration flux changed as a function of rainfall amount, time since the last rainfall event, and the time of year. The results for the impact of rainfall
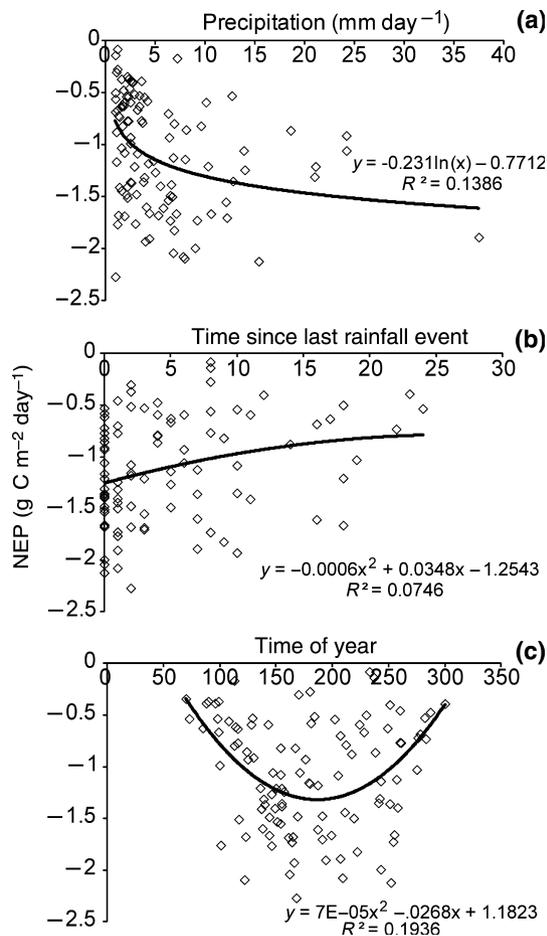
Fig. 6 Peak nighttime respiration rates (NEP_n) following rainfall events (largest negative value within 2 days of the rainfall event) for all growing season rainfall events from 2001 to 2003 as a function of rainfall amount (a), time since the last rainfall event (b), and time of year (c). Rainfall events with less than 1 mm per day were excluded.
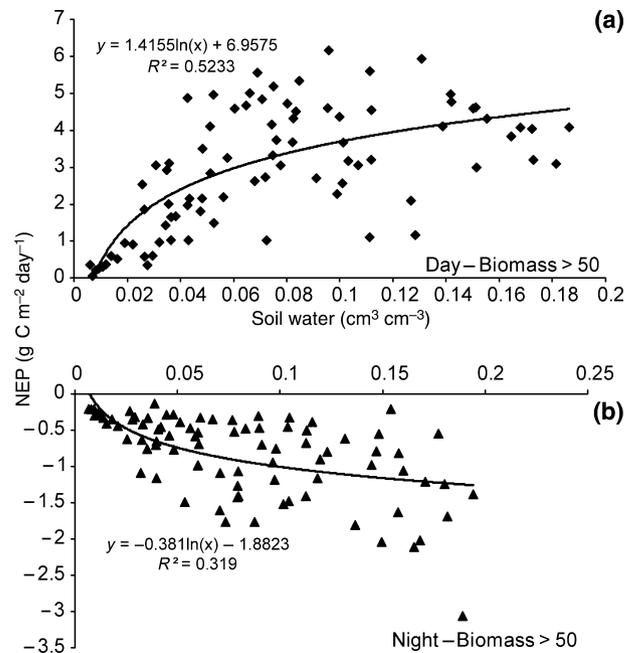

Fig. 7 Net ecosystem productivity (NEP) for daytime (a) and nighttime (b) as a function of volumetric soil water content (SWC) when live aboveground plant biomass was >50 g m^{-2}.

amount on peak respiration fluxes (Fig. 6a) show that peak respiration fluxes (larger negative fluxes) increase as rainfall amount increases to 5 mm day^{-1} with little change for greater rainfall amounts. The impact of time since the last rainfall event on the peak nighttime respiration flux (Fig. 6b) is minimal. Peak respiration flux is similar from May to September (day 120–270); however, peak fluxes are lower during the early and late periods of the growing season (Fig. 6c). These lower peak fluxes occur when soil temperature is less than 10 °C. A statistical analysis of the peak fluxes for soil temperatures >10 °C shows very little correlation to soil temperature ($r^2 = -0.01$).

The combined results from the soil chamber flux and the BREB CO_2 flux measurements suggested that the major factors influencing NEP_d and NEP_n were rainfall events, SWC, soil temperature, and live plant biomass.

To evaluate the impact of SWC on NEP_d and NEP_n without low temperature or the lack of significant plant biomass confounding the analysis (see previous), we plotted NEP_d and NEP_n as a function of SWC for nonrainfall days with high live biomass (>50 g m biomass m^{-2}; values of peak live biomass at the SGS site typically range from 50 to 100 g m biomass m^{-2}) and for soil temperatures >10 °C. The results (Fig. 7a) show that NEP_d increased rapidly as SWC increased from 0.02 to 0.08 cm^3 cm^{-3}, and then increased at a slower rate at SWC > 0.08 cm^3 cm^{-3} (>80% of the change in NEP_d and NEP_n occurred as SWC increased from 0.02 to 0.08 cm^3 cm^{-3}). Similar patterns were observed for NEP_n (Fig. 7b) with rapid decreases as SWC increased from 0.02 to 0.08 cm^3 cm^{-3} and with minimal changes when SWC > 0.08 cm^3 cm^{-3}. These results are similar to those from the ecosystem respiration chambers (Fig. 3a).

The combined impact of rainfall events and live plant biomass during the growing season on NEP_d and NEP_n (Fig. 8a and b) for days with SWC > 0.08 cm^3 cm^{-3} (wet days) shows that NEP_d increased linearly with increasing live biomass (Fig. 8a) for both rain days and nonrain days. In comparisons between rain days vs. wet days (SWC > 0.08 cm^3 cm^{-3}), NEP_d was always 2–3 g C m^{-2} day^{-1} lower on rain days. When live plant biomass was <40 g per m^{-2} for rain days, NEP_d was negative, indicating net carbon loss. Wet day results show that NEP_n decreased linearly with increased AGB
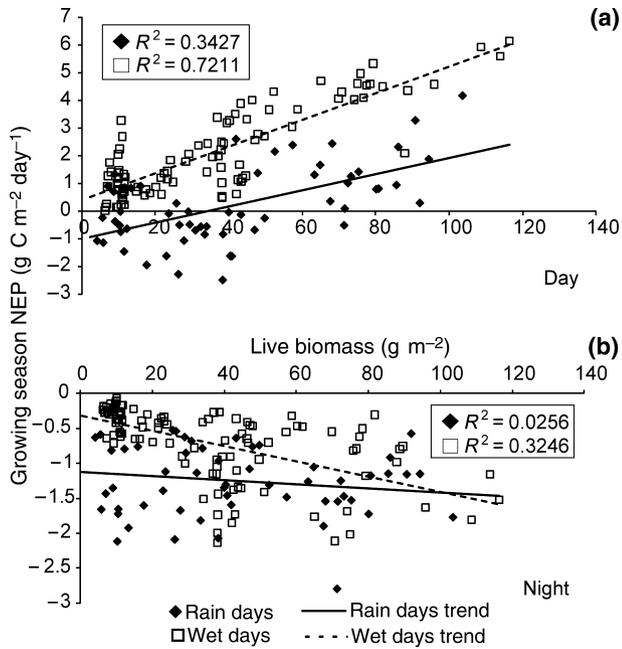
Fig. 8 Comparison of growing season net ecosystem productivity (NEP) for rain days (≥ 3 mm day^{-1}) and nonrainfall wet days (ppt <3 mm day^{-1} and SWC > 0.08 cm^3 cm^{-3}) with live aboveground plant biomass for daytime NEP fluxes (a), and nighttime NEP fluxes (b). Regression for nighttime rain days is not significant.

Table 1 Comparison of cumulative NEP for November to February, March to April, May to June, July to October, and annual time periods for daytime NEP (NEP$_d$), nighttime NEP (NEP$_n$) and net annual NEP for 2001, 2002, and 2003

	2001	2002	2003
Daytime NEP			
Annual	44.71	13.68	58.38
November–February	−5.53	−2.88	−6.07
March–April	−2.11	−8.33	−2.61
May–June	43.64	7.31	48.37
July–October	8.72	17.59	18.70
Nighttime NEP			
Annual	−41.45	−23.61	−47.54
November–February	−5.48	−2.57	−4.51
March–April	−5.76	−4.32	−5.26
May–June	−14.73	−5.64	−18.58
July–October	−15.47	−11.08	−19.20
Annual total	3.27	−9.93	10.84

(Fig. 8b), decreased on rainfall days, and that AGB had little impact on NEP$_n$ during rain days. A summary of results from Figs 7 and 8 indicate that: (1) increased soil moisture during nonrainfall days increased NEP$_d$ and decreased NEP$_n$ (>soil respiration); (2) increased AGB and NEP$_d$, and decreased NEP$_n$ for nonrain days; and (3) rainfall events caused a rapid short-term decrease in NEP$_n$ and NEP$_d$ (>3.0 g C m^{-2} day^{-1} for the combined values of NEP$_d$ and NEP$_n$).

The results suggest that the rapid decrease in NEP$_d$ for rainfall days is a result of increased heterotrophic respiration since average solar radiation on rainfall days is only 20% less than nonrainfall days, which would result in a 20% reduction in NEP$_d$ based on the AIC statistical analysis (presented later in the text). The expected 20% reduction in NEP$_d$ for rainfall days is considerably less than the observed 80% reduction in NEP$_d$ values on rainfall days with AGB > 40 g m^{-2}.

Table 1 shows the cumulative NEP$_d$ and NEP$_n$ for the dormant (November to February), early (March to April), middle (May to June), and late (July to October) growing seasons and annual values for 2001–2003. The results show that NEP$_d$ is negative during the dormant and early growing season, with the largest negative fluxes during the dormant period for 2001 and 2003 and the reverse being true for 2002. Daytime net carbon

losses for the March to April 2002 time period were larger since daytime net carbon uptake started much later during 2002 (May 15 for 2002 vs. April 15 for 2001 and 2003; see Fig. 3). The NEP$_d$ fluxes are positive during the middle and late growing seasons, with >80% of the growing season carbon uptake during the May to June time period for 2001 and 2003, while most of the carbon uptake from 2002 occurred during the July to October time period. The low NEP$_d$ values for the May to June time period in 2002 are a result of low soil water conditions during the spring and early summer (Fig. 1). Annual NEP$_d$ values are positive and highest for 2001 and 2003, and much lower for 2002. The low annual NEP$_d$ value for 2002 is a result of drought conditions which reduced NEP$_d$ during the May to June time period.

Cumulative seasonal NEP$_n$ (Table 1) was negative for all of the time periods with the loss of carbon being similar for dormant and early growing seasons and largest during the middle and late growing seasons. The seasonal patterns of nighttime carbon loss were similar for all 3 years; however, NEP$_n$ carbon losses were lower during the 2002 drought year. The cumulative annual total NEP (NEP$_n$ plus NEP$_d$) were positive for 2001 and 2003 and negative for 2002. The negative annual NEP for 2002 is primarily a result of reduced NEP$_d$ during the May to June time period as a result of drought stress. The results suggest that there were substantial year-to-year differences in the seasonal patterns of NEP$_n$ and NEP$_d$, and annual net carbon exchange which resulted from year-to-year changes in the rainfall patterns and frequency of small and large rainfall events.

Data analysis and model selection

Soil temperature, air temperature, SWC, PAR, relative humidity, and live biomass all potentially affected NEP, but the strength of the correlations between these variables and NEP varied diurnally (day vs. night), and with the timing and amount of precipitation events. Consequently, observations of NEP were regressed separately based on precipitation during the growing season for NEP_d and NEP_n values. The results (Table 2) for NEP_d during the growing season on days without rain show that: (1) AGB was highly correlated to NEP_d; (2) the inclusion of SWC and PAR substantially increased the correlation of NEP_d in the regression equation; and (3) the addition of a soil or air temperature

Table 2 Comparison of the coefficients of determination (r^2), Akaike Information Criteria (AIC), and Akaike weight (W_r) values for the regression models that predict daytime and nighttime daily NEP during the growing season as a function of live aboveground plant biomass, volumetric soil water content (H_2O), soil temperature (Tsoil), air temperature (Tair), photosynthetically active radiation (PAR), relative humidity (RH), and rainfall

	r^2	AIC	W_r (%)
Growing season, no precipitation, daytime			
Biomass	0.47	74	0.0
Biomass, H_2O	0.61	−41	0.0
Biomass, H_2O, Tair	0.62	−47	0.0
Biomass, H_2O, PAR	0.65	−80	40.6
Biomass, H_2O, RH	0.62	−49	0.0
Biomass, H_2O, PAR, Tair	0.65	−77	9.3
Biomass, H_2O, PAR, RH	0.65	−76	7.0
Biomass, H_2O, Tsoil	0.62	−50	0.0
Biomass, H_2O, Tsoil, PAR	0.65	−79	34.9
Biomass, H_2O, Tsoil, RH	0.63	−56	0.0
Biomass, H_2O, Tsoil, PAR, RH	0.65	−76	8.2
Growing season, no precipitation, nighttime			
Biomass	0.32	−702	0.0
Biomass, H_2O	0.50	−805	0.0
Biomass, H_2O, Tair	0.52	−809	0.0
Biomass, H_2O, RH	0.56	−836	0.0
Biomass, H_2O, Tsoil	0.52	−793	0.0
Biomass, H_2O, Tair, RH	0.62	−883	100.0
Biomass, H_2O, Tsoil, RH	0.59	−856	0.0
Growing season, precipitation, daytime			
Biomass linear	0.46	45	0.0
Biomass quad	0.52	16	26.4
Biomass, H_2O	0.55	15	53.1
Biomass, H_2O, PAR	0.56	20	3.6
Biomass, H_2O, Tair	0.59	19	5.9
Biomass, H_2O, Tsoil	0.59	19	5.9
Biomass, H_2O, RH	0.56	21	2.8
Biomass, H_2O, Tair, RH	0.60	21	2.4

function only slightly improved the r^2 of the regression model. The AIC and W_r results suggest that the best model included SWC, PAR, and AGB. The results for NEP_d for rain days (daily precipitation > 3 mm) show that the best model included AGB and SWC, with AGB having the greatest impact on precipitation day NEP_d dynamics. The results for NEP_d precipitation days suggest that PAR had little impact on NEP_d, while soil and air temperature were positively correlated for precipitation days. This contrasts with the results for the no precipitation days where PAR had a much greater impact on NEP_d compared to soil and air temperature.

The AIC model selection for the NEP_n during the growing season on days without rain (Table 2) shows that the model that included AGB, SWC, air temperature, and relative humidity was the best model. No factor or interactions of factors were correlated with NEP_n for rain days, so the model in this case was simply a constant based on the average NEP_n. When the models for NEP_d and NEP_n, precipitation day and precipitation night were combined, the overall fit was good ($r^2 = 0.77$). Regression equations used to fit the NEP data are shown in Table S1 and Fig. S1 (in Supporting Information). The impact of SWC on NEP_d and NEP_n (Fig. S1 in Supporting Information) was similar to the best fit equations shown in Fig. 7. Figure S1 (Supporting Information) also shows that NEP_n decreased (increased respiration) with increasing average nighttime relative humidity, and that NEP_d increased linearly with increasing PAR and AGB.

Discussion

This study shows that precipitation events have a dramatic and predictable impact on NEP patterns. During the March to October growing season, there is a large increase in net carbon loss after precipitation events. For the 2 days after precipitation, NEP decreases, followed by a period of increased NEP for several more days if the precipitation event is of sufficient size. The length of the net carbon uptake period is controlled by the size of the rainfall event (longer period with larger events causing greater increases in SWC). These patterns in NEP are caused by rapid increases in heterotrophic respiration in near-surface soils following rainfall events (Kieft *et al.*, 1987; Franzluebbers *et al.*, 2000; Chou *et al.*, 2008), and subsequent decreased heterotrophic respiration as the upper soil dries out again (Parton *et al.*, 1981; Sala *et al.*, 1981). As a result, maximum NEP occurs several days after rainfall events of sufficient magnitude (>~10 mm) due to the reduction in heterotrophic soil respiration rates with surface soil drying and high photosynthesis rates before the SWC in the 5–20 cm layer decreases to <0.08 cm^3 cm^{-3}. The

response of daily NEP following the rainfall events shown in this article has been observed in dry grasslands in China (Chen *et al.*, 2009) and Africa (Williams *et al.*, 2009). Experimental manipulation of the size of precipitation events in China's arid grasslands (Chen *et al.*, 2009) showed that the period of net carbon uptake following a rainfall event lasts longer for large events. The results presented in this article and in Williams *et al.* (2009) also show that enhanced carbon uptake following large rainfall events is a result of increased SWC which lengthens the period of time when maximum plant photosynthesis occurs (SWC > 0.06).

Our results show that the size of elevated peak in NEP_n (largest negative values of NEP_n) is smaller after rainfall events <5.0 mm but is similar after rainfall events >5.0 mm. Alternatively, these values are independent of the length of time between precipitation events, soil temperatures >10 °C, and time of year during the growing season. These results also show that the nighttime respiration rates decrease by over 50% during the second day following the rainfall event. Elevated heterotrophic soil respiration has been observed in numerous studies following wetting of dry grassland and savanna soils (Fierer & Schimel, 2003) and forest systems (Hanson *et al.*, 2003). A recent study by Castellano *et al.* (2011) shows that peak soil respiration rates occur when the soil water content is near soil saturation following rewetting of the soil and that the soil respiration rate drops rapidly (50–70% drop) during the first 24 h period as the soil dries out to near field capacity. Our results seem to contrast results from other studies which show a greater increase in soil respiration following large rainfall events and an even higher increase if rainfall has not occurred for approximately 2 weeks or more (Aires *et al.*, 2008). These recent studies (Aires *et al.*, 2008; Castellano *et al.*, 2011) suggest the primary mechanisms for causing short-term increases in soil respiration following rainfall events include the above field capacity SWC following the rainfall event and increases in labile carbon generated by desiccation of microbes associated with drying of the soil. The results from our study would suggest that the above field capacity short-term increase in soil water following rainfall events is the major factor controlling the dynamics at the SGS site since we do not see increases in the respiration pulse with increases in the time between rainfall events. We speculate that in this system an important mechanism responsible for increased respiration when soils are wetter than field capacity is that soluble compounds become more available to the microbial community.

For the years of near normal precipitation (2001 and 2003), the vast majority of the net carbon uptake occurred during the period of May to June (>75% for both years). Sala *et al.* (1992) show that precipitation and soil water seasonal patterns observed during 2001 and 2003 (high SWC from April to June and low SWC from July to October) represent the typical pattern observed at the SGS site. However, this was not the case during 2002 due to the extreme spring drought which reduced NEP from May to June by >50% compared to 2001 and 2003. Daily NEP for the July to October period indicated a slight net carbon loss during 2001, minimal net carbon uptake during 2002, and zero net change during 2003. This pattern was primarily driven by lower daytime net carbon uptake during 2001 (50% reduction) compared to 2002 and 2003. The lower July to October NEP_d for 2001 was caused by the high frequency of small rainfall events which increased net carbon losses, while higher July to October NEP_d for 2002 and 2003 was due to large rainfall events. The observed positive correlations of growing season NEP_d to precipitation in May to June are consistent with observations of aboveground plant production (ANPP) at the SGS site (Milchunas *et al.*, 1994; Derner *et al.*, 2008), while the increase in NEP_d from large rainfall events during the July to October time period is consistent with results from other studies (Chen *et al.*, 2009). These observations imply that early in the growing season, substantial NPP is allocated aboveground, but from July to October, the majority of NPP is allocated belowground.

A statistical comparison of the observed growing season daytime and nighttime NEP showed that AGB, SWC, relative humidity, PAR, and soil and air temperature were correlated to NEP (Table 2). Live leaf biomass had the highest correlation to daytime and nighttime NEP with daytime carbon uptake and nighttime respiration (larger negative values) increasing linearly with increasing live leaf biomass. The observed strong seasonal change (high biomass during May to June) and year-to-year changes (low live biomass during 2002) in live biomass are both the primary drivers for the observed seasonal changes in growing season NEP_d, and the positive correlation of NEP_d. As expected, the statistical analysis also showed that NEP_d is positively correlated to PAR, SWC, and AGB. The observed impact of live biomass and PAR on net carbon uptake is consistent with the importance of canopy light interception in driving net primary production in rangeland ecosystems (Polley *et al.*, 2010). Further, the positive influence of leaf biomass on both NEP_d and NEP_n reflects an increasingly common observation that ecosystem-level respiration is often tightly coupled to photosynthetic rate (Craine *et al.*, 1999; Tang *et al.*, 2005; Larsen *et al.*, 2007).

Statistical analysis of the impact of soil water and temperature on growing season daytime and nighttime

NEP showed that soil temperature had little impact on daytime and nighttime respiration, while daytime net carbon uptake and nighttime respiration loss both increase rapidly as the volumetric water content increases from 0.02 to 0.08. These results are similar to those shown by laboratory experiments, field soil respiration observations (Del Grosso et al., 2005), and eddy covariance studies (Williams et al., 2009), with most of the decrease in soil respiration rates occurring as the SWC falls below half of the available water content. The statistical analysis showed a significant correlation of nighttime relative humidity to NEP_n, with NEP_n decreasing (>respiration rates) with increasing relative humidity. The correlation of NEP_n to relative humidity could be a result of higher probabilities of getting dew formation with higher relative humidity and enhanced SWC near the surface (Munn, 1966; Schimel & Parton 1986).

The results from this study show that annual and seasonal patterns in net carbon uptake and aboveground plant production are quite sensitive to seasonal changes in precipitation and thus, could be altered substantially with future potential climatic changes. In the most recent Intergovernmental Panel on Climate Change (IPCC) report, climate change projections for the western and central United States suggest that there will be a slight increase in annual precipitation, but a slight decrease in summer precipitation (Christensen et al., 2007; Meehl et al., 2007). An increase in large precipitation events is also anticipated (Christensen et al., 2007; Meehl et al., 2007). However, analysis of the observed trends in small (<0.5 mm day^{-1}) vs. large (>10.0 mm day^{-1}) rainfall events at the SGS site for the 1960 to 2005 growing season (April to October; data not shown) indicate that there has been a 30% increase in the number of small rainfall events during the last 40 years, while the number of large precipitation events has not changed during that time period (data not shown). The results described in this article suggest two very different outcomes in terms of ecosystem carbon balance depending on which climate trajectory is realized in the future. If the IPCC projections hold true and there are more large precipitation events, the SGS could potentially become a net sink for carbon. However, observed patterns of rainfall suggest a net loss of carbon from the SGS site may have occurred during the last 40 years, and should the trend toward more frequent but smaller events continue, we would expect continued losses of carbon from the system.

We also suggest that changes in the timing of precipitation events could have a major impact on ecosystem NEP, with increased precipitation during the April to June time period greatly increasing NEP and decreased precipitation reducing NEP. The results also suggest that adding large precipitation events during the July to October time period would result in much lower increases in NEP compared to adding rainfall during the April to June time period due to the low AGB during the July to October time period. Thus, the results presented in this article highlight the importance of reducing uncertainties in projections of future changes in precipitation, not only in terms of amount and timing, but also in terms of delivery, as this difference (small vs. large events and early vs. late growing season) could determine the sign of ecosystem carbon response.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Equations for best fitting functions of Net Ecosystem Productivity (NEP) regressions.
Table S1. Best fitting Net Ecosystem Productivity (NEP) models for different weather and diurnal conditions
Table S2. Thresholds for initial data screening. Highlighted variables were screened but not filled.

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