

Biomass, Litter, and Soil Respiration Along a Precipitation Gradient in Southern Great Plains, USA

Xuhui Zhou,* Melissa Talley, and Yiqi Luo

Department of Botany and Microbiology, The University of Oklahoma, Norman, Oklahoma 73019, USA

ABSTRACT

Knowledge of how ecosystem carbon (C) processes respond to variations in precipitation is crucial for assessing impacts of climate change on terrestrial ecosystems. In this study, we examined variations of shoot and root biomass, standing and surface litter, soil respiration, and soil C content along a natural precipitation gradient from 430 to 1200 mm in the southern Great Plains, USA. Our results show that shoot biomass and soil respiration increased linearly with mean annual precipitation (MAP), whereas root biomass and soil C content remained relatively constant along the precipitation gradient. Consequently, the root/shoot ratio linearly decreased with MAP. However, patterns of standing, surface, and total litter mass followed quadratic relationships with MAP along the gradi-

ent, likely resulting from counterbalance between litter production and decomposition. Those linear/quadratic equations describing variations of ecosystem C processes with precipitation could be useful for model development, parameterization, and validation at landscape and regional scales to improve predictions of C dynamics in grasslands in response to climate change. Our results indicated that precipitation is an important driver in shaping ecosystem functioning as reflected in vegetation production, litter mass, and soil respiration in grassland ecosystems.

Key words: biomass; grassland; litter mass; precipitation gradient; soil carbon; soil respiration.

INTRODUCTION

Precipitation is a key environmental factor in determining ecosystem structure and function, especially in grasslands and other water-limited regions (Webb and others 1978; Sala and others 1988; Burke and others 1997; Epstein and others 2002), which account for approximately 45% of the Earth's land surface (Saco and others 2006). The IPCC (2007) has projected more frequent extreme

precipitation and drought events, which may have greater impacts on ecosystem dynamics than the singular or combined effects of rising CO₂ and temperature (Weltzin and others 2003). Previous studies have elucidated that plant species assemblages (Epstein and others 1996), aboveground primary production (Sala and others 1988; Burke and others 1997; Austin and Sala 2002; Epstein and others 2002; Zerihun and others 2006), litter decomposition (Meentemeyer 1984; Austin 2002), and trace gas flux (Matson and Vitousek 1987) all varied with precipitation along regional gradients. Manipulative experiments also have showed strong effects of precipitation on photosynthesis, leaf and soil respiration, plant growth, net primary production (NPP), and litter decomposition (Fay and others

Received 26 January 2009; accepted 5 October 2009;
published online 10 November 2009

Author Contributions: Xuhui Zhou performed research, analyzed data, and wrote the article, Melissa Talley performed part of research, and Yiqi Luo conceived of and oversaw the study.

*Corresponding author; e-mail: zxuhui14@ou.edu

2000, 2003; Knapp and others 2002; Weltzin and others 2003; Yahdjian and others 2006). However, precipitation affects ecosystem structure and functions in complex ways (Burke and others 1998). It not only directly influences ecological processes mentioned above, but also indirectly regulates them by interactions with abiotic attributes such as soil moisture, water recharge, soil temperature, and evaporation (Jenny 1980; Heisler and Weltzin 2006). Complexity in precipitation effects on ecosystem carbon (C) processes remains largely unclear, especially in the changing climate.

One approach to understand precipitation effects is to characterize the patterns of ecosystem processes along natural precipitation gradients. The majority of gradient studies so far have evaluated the control of precipitation on aboveground net primary production (ANPP). It has been shown that ANPP is usually linearly correlated with precipitation along spatial gradients in different continents (Sala and others 1988; Epstein and others 1996, 2002; Paruelo and others 1999; Austin and Sala 2002; Zhou and others 2002; McCulley and others 2005). However, ANPP represents only one-half or less of NPP of grasslands (Sims and Singh 1978; Milchunas and Lauenroth 2001). The belowground compartment of vegetation is also critical for plant production and ecosystem biogeochemical cycles. Few studies have been done to examine responses of both shoot and root biomass growth to variations in precipitation along the spatial gradient.

Another component of ecosystem C and nutrient cycling is litter (Maguire 1994). This layer of undecomposed and decomposed organic material not only protects soils from erosive raindrops and drought (Fowler 1986; Morgan 1986), but also contributes to humus formation and C sequestration (Spain 1984; Matthews 1997). Litter mass is closely related to plant growth, community composition, element fluxes, and environmental variables such as temperature and precipitation (Pedersen and Bille-Hansen 1999; Lawrence and Foster 2002). Total litter mass increased with precipitation along spatial gradients in forests (Simmons and others 1996; Lawrence and Foster 2002). However, in grasslands, much of the dead plant material remains in an aerial standing-dead position for a substantial period (referred to as standing litter) (Newell 1993) before falling to the ground as surface litter. Variations in standing versus surface litter along a precipitation gradient are largely unknown.

Soil is the largest C pool in land ecosystems. At a global scale, soil contains 1500 Pg C (1 Pg = 10^{15} g) in the form of soil organic matter (SOM) in the upper 1 m of soil, an amount considerably larger than that

in plant biomass or the atmosphere (Schlesinger 1977; Amundson and others 2003). Soil respiration releases CO_2 at the soil surface from microbial decomposition of litter and SOM and rhizosphere respiration by live roots and their symbionts (Raich and Schlesinger 1992; Hanson and others 2000). This flux is the largest terrestrial source of CO_2 to the atmosphere ($68\text{--}80 \text{ Pg C y}^{-1}$) in the global C cycle (Raich and others 2002; Luo and Zhou 2006). Previous research has demonstrated that, besides temperature, soil respiration is also greatly affected by moisture and substrate supply (Kirschbaum 1995; Höglberg and others 2001; Liu and others 2002). So far, only a few studies have examined regional patterns of soil respiration and soil C content along precipitation gradients (Simmons and others 1996; McCulley and others 2005).

In this study, we took advantage of a natural precipitation gradient in Oklahoma, USA, that spans from 430 to 1200 mm to examine responses of ecosystem C fluxes and pools to precipitation in grassland ecosystems. Along the precipitation gradient, nine grassland sites were selected with vegetation shifts from short-grass steppe to mixed-grass prairie, and tallgrass prairie. We measured shoot and root biomass, standing and surface litter, soil respiration, and soil C content in three seasons (that is, spring, summer, and winter). Previous transect studies were based on just one variable (usually ANPP or shoot biomass) or on meta-analysis where data were generated in different studies. With the simultaneous collection of data on a set of ecosystem biogeochemical variables, this study was designed to (1) examine patterns of biomass, litter mass, and soil respiration and (2) assess their correlations along a precipitation gradient in southern Great Plains grasslands in Oklahoma, USA.

MATERIALS AND METHODS

Site Description

This transect study was conducted in temperate grasslands of Oklahoma along a precipitation gradient through the southern Great Plains region of the USA (Figure 1). Nine grassland sites were selected to represent three grassland types that differ in physiognomy: short-grass steppe, mixed-grass prairie, and tallgrass prairie (Sims and Singh 1978). The selected sites had a minimum amount of disturbance and land-use impact based on information provided by the site owners or managers of government and conservation organizations, although light grazing occurred on some sites. At those sites with light grazing, grazed areas were excluded from sampling

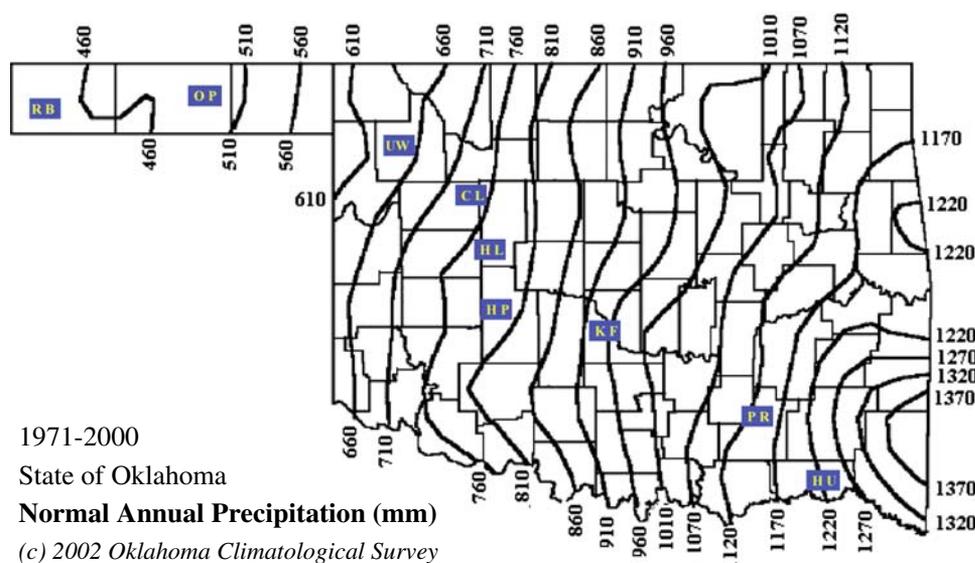


Figure 1. Map showing location of the nine grassland sites and normal annual precipitation (1971–2000) over the state of Oklahoma from Oklahoma Climatological Survey. See Table 1 for abbreviations.

during the study period. Mean annual precipitation (MAP) across these sites varied from 430 mm in northwestern Oklahoma to 1200 mm in southeastern Oklahoma (Table 1). Across this precipitation gradient, mean annual temperature (MAT) changed relatively little, ranging from 13.0 to 16.5°C. Table 1 shows location (latitude and longitude), elevation, MAP, MAT, and soil types of nine grassland sites along the precipitation gradient from northwestern to southeastern Oklahoma.

Sampling Design

Samples along the precipitation gradient were collected in August 2003, February 2004, and May 2005, representing summer, winter, and spring, respectively. Samples were collected within 1 week in August 2003 (summer) and May 2005 (spring) to

minimize effects of temperature variation. In February 2004, sampling was extended to 2 weeks due to low-temperature fluctuation in winter. In summer and winter, seven sites were selected (not including CL and UW in Table 1), and measured variables included shoot biomass, standing litter, surface litter, soil respiration, soil moisture, and soil temperature. In May 2005, we improved our study to sample two more sites and add one more variable (belowground root biomass) and soil characteristics (pH, field capacity, bulk density, and soil C and N content) after we analyzed data from the first two sample periods. At each sampling time for each site, typically five plots with a 0.5×0.5 m² quadrat were randomly selected. Within the selected plot, we first measured soil respiration and soil temperature. Then all vegetation including shoot biomass, standing, and surface litter were harvested. Finally,

Table 1. Location (Latitude and Longitude), Elevation, MAP, MAT, and Soil Type at Nine Grassland Sites from Southeastern to Northwestern Oklahoma, USA

Site	Latitude	Longitude	Elevation (m)	MAP (mm)	MAT (°C)	Soil type
RB	36°31'43" N	102°50'01" W	1263	434	13.0	Fine sandy loam
OL	36°38'45" N	101°13'18" W	913	465	13.8	Loam
UW	36°26'04" N	99°23'58" W	579	660	13.6	Loam fine sand
CL	36°07'30" N	98°37'55" W	485	735	14.4	Fine sandy loam
HL	35°37'50" N	98°30'24" W	493	760	15.4	Fine sandy loam
HP	35°14'53" N	98°51'41" W	480	806	15.3	Clay loam
KF	34°58'54" N	97°31'14" W	340	915	16.3	Silt loam
PR	34°30'05" N	96°36'59" W	309	1048	16.2	Silt loam
HU	34°01'50" N	95°25'24" W	174	1203	16.5	Fine sandy loam

Note: Elevation, MAP, and MAT are NOAA monthly normals of the nearest weather station from each site (<http://cdo.ncdc.noaa.gov/climatenormals/clim81/OKnorm.pdf>). Soil type is from Soil Conservation Services (SCS), State Soil Geographic Database (STATSGO) http://www.xdc.arm.gov/data_viewers/sqp_surfchar/Oklasoil_new.html. HU, Hugo Lake; PR, Pontotoc Ridge Preserve; KF, Kessler's Farm Field Laboratory; HP, Hulsey's private land; HL, American Horse Lake; CL, Canton Lake; OL, Optima Lake; RB, Rita Blanca National Grassland; UW, USDA Southern Plains Range Research Station in Woodward, Oklahoma.

we collected one soil core with two increments (0–15 and 15–30 cm) for root biomass and another core (0–5 cm) for field capacity at each plot. Soil moisture, soil C and N content, and pH were measured in the 0–15 cm soil core. We stored soil samples in an ice chest until they were brought back to the laboratory and stored in a freezer (–4°C) for analysis.

Measurements of Biomass, Litter Mass, and Soil Respiration

Shoot biomass and standing litter were determined by the harvest method. All live and standing-dead materials within a $0.5 \times 0.5 \text{ m}^2$ quadrat were clipped above the soil surface at each plot. Once returned to the laboratory, samples were oven dried at 60°C for 48 h, and then separated into categories of live shoot biomass and dead-standing litter and weighed.

Surface litter was removed with a hand rake in a $0.5 \times 0.5 \text{ m}^2$ quadrat prior to soil sampling at each plot. The litter samples were cleaned, oven dried at 60°C for 48 h, and weighed.

Root biomass: one soil core sample was collected in the middle of plant stubble and the center of interspace using a 4-cm-diameter steel corer at each plot. The soil was separated into two increments: 0–15 and 15–30 cm depths. After washing soil through a 0.25-mm mesh sieve, roots were oven dried at 60°C for 48 h and weighed. We chose this place for root biomass based on our preliminary experiment under plant stubble, between plant stubble (that is, the center of interspace), and in the middle of plant stubble and the center of interspace at Kessler Farm Field Laboratory. We found that samples in the middle of plant stubble and the center of interspace better represented the average root biomass.

Soil respiration was measured in the interspace between plants using a LI-COR 6400 portable photosynthesis system attached to a soil CO₂ flux chamber (LI-COR Inc., Lincoln, Nebraska, USA) at each quadrat. A measurement consisted of placing the chamber on soil including surface litter, scrubbing the CO₂ to sub-ambient levels, and determining soil CO₂ efflux over several 5-s periods. Data were recorded at 5-s intervals by the datalogger in the LI-COR 6400 console. Each measurement usually took 1–3 min after placing the chamber on the ground.

Measurements of Other Variables

Soil temperature at the depth of 5 cm was monitored using a thermocouple probe (LI-COR 6000-09TC)

connected to the LI-COR 6400 at the same time as when soil respiration was measured.

Soil moisture was measured gravimetrically from soil cores for root biomass at the top of 15 cm at each plot. Soil samples were oven dried at 105°C for 48 h and weighed. Gravimetric soil moisture was expressed as a percent of dry soil on a mass basis.

Soil pH was measured as a 1:10 soil-to-water ratio with a pH electrode (Model 9165BN Thermo Orion, Beverly, Massachusetts, USA) connected to a pH meter (Model 420A+ Thermo Orion). Samples were first mixed end-over-end for 1 h.

Field capacity was measured by soaking the soil with water for 12 h in a plastic cylinder (diameter = 3.5 cm, height = 5 cm) with a 0.3-mm nylon mesh at the bottom. After the soil drained for 1 h, the soil was emptied into a container, and field capacity was determined as gravimetric soil moisture.

Soil total C and N content: soil samples were taken from the top 15 cm of the soil cores for below-ground biomass. Prior analysis found that the soil contains carbonates. To avoid misinterpretation of soil C and N data, soils were acid-treated to remove the carbonates based on a procedure used by Subedar (2005) that was recommended by the Colorado Stable Isotope Laboratory. In brief, 5 ml of 6N H₂SO₃ was added to 0.5 g of soil in clean glass vials. The samples were agitated for a few seconds to suspend the soil in the solution. The presence of carbonates was indicated by a formation of bubbles. The samples were incubated at room temperature for approximately 6 h and then dried overnight at 60°C. Analyses of soil samples for total C and N content were done using a Finnigan DELTA plus Advantage gas isotope-ratio mass spectrometer (Thermo Finnigan MAT GmbH, Barkhausenstr, Germany), which was configured through the CONFLO III for automated continuous-flow analysis of solid inorganic/organic samples using a Costech ECS 4010 elemental analyzer (Costech Analytical Technologies Inc., Valencia, California, USA) in Colorado Stable Isotope Laboratory, Arizona, USA.

Data Analysis

Regression analysis was conducted on relationships of biomass, litter mass, soil respiration, soil C and N content, pH values, soil moisture and temperature with MAP. Differences in those measured variables among sites were tested using a Kruskal–Wallis ANOVA median test with seven (2003 and 2004) or nine (2005) groups and six or eight degrees of freedom. Pearson product-moment correlations were performed to test correlations among all measured

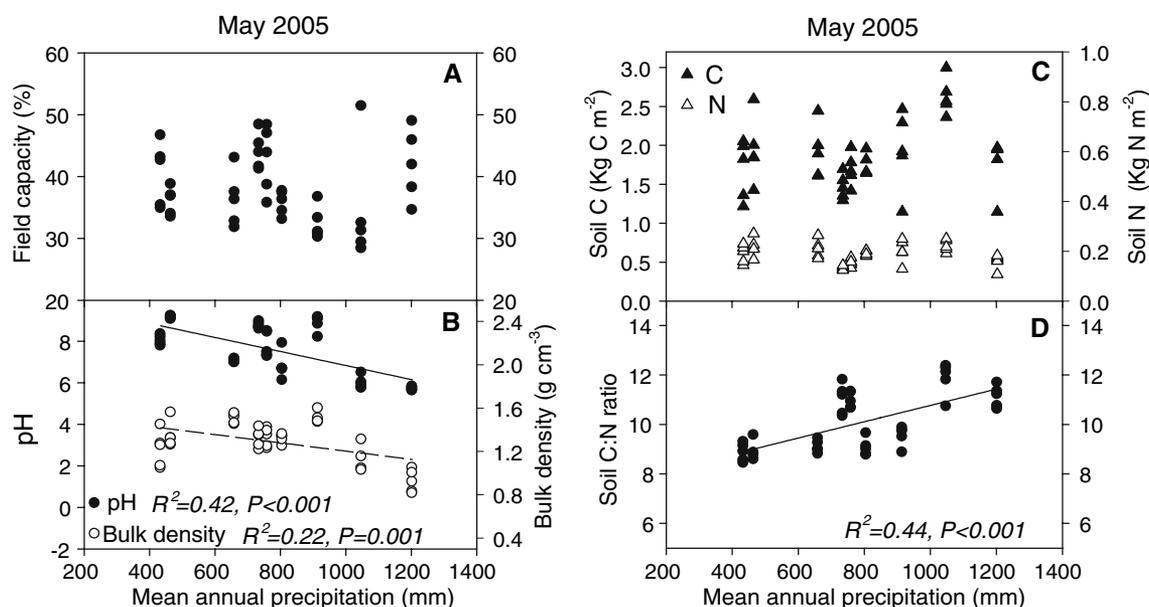


Figure 2. Soil characteristics along a precipitation gradient from dry to wet sites: field capacity (%), pH and bulk density (B), soil C and N content at the depth of 0–15 cm (kg m^{-2}), and soil C:N ratio (D).

variables including biomass, litter mass, soil respiration, and environmental factors. Stepwise multiple regression analysis was also applied to examine effects of other factors (for example, elevation, soil temperature and moisture, soil C and N, pH, and field capacity) on biomass, litter mass, and soil respiration. In addition to examining the effects of precipitation on ecosystem C fluxes and pools, we also studied seasonal variability in spring, summer, and winter and site effects using a two-way ANOVA. Although we conducted the samplings for the three seasons in different years and interannual variability may affect seasonal variability, we did not find significant differences between the years in microclimate data. Also seasonal variability in ecosystem C fluxes and pools is usually much larger (sometimes orders of magnitude larger) than interannual variability (Hui and others 2003). Nevertheless, it is a caveat to interpret the data collected in different years, given the magnitude, and direction of our results in the transect study. All statistical analyses were performed using SPSS 13.0 for Windows (SPSS Inc., Chicago, Illinois, USA, 2004).

RESULTS

Soil Characteristics Along the Precipitation Gradient

Along the precipitation gradient from dry to wet sites, pH values and bulk density decreased significantly, whereas soil C:N ratios increased with MAP

(Figure 2B, D). Surprisingly, soil C and N content remained relatively constant with MAP along the precipitation gradient, and, on average, ranged from 1.47 to 2.63 kg C m^{-2} and from 0.13 to 0.22 kg N m^{-2} , respectively, at a depth of 0–15 cm (Figure 2C). Field capacity also did not significantly vary with increasing precipitation (Figure 2A).

Plant Biomass Along the Precipitation Gradient

Green shoot biomass, on average, increased linearly from 86 to 350 g m^{-2} in August 2003 and from 68 to 160 g m^{-2} in May 2005 with MAP (Figure 3). Interestingly, root biomass at the depth intervals of 0–15, 15–30, and 0–30 cm remained relatively constant along the precipitation gradient in May 2005 (Figure 4A, B). Similarly, total plant biomass (shoot + root) varied little due to higher root (that is, about 400 g m^{-2}) than shoot biomass (Figures 3B and 4B, C) in May 2005. The root/shoot ratio decreased linearly with MAP along the gradient (Figure 4D).

Litter Mass and Soil Respiration Along the Precipitation Gradient

Total litter mass was separated into standing litter and surface litter. Their relationships with MAP were best described by quadratic curves in all three seasons along the precipitation gradient (Figure 5A–I). The results showed that litter mass generally

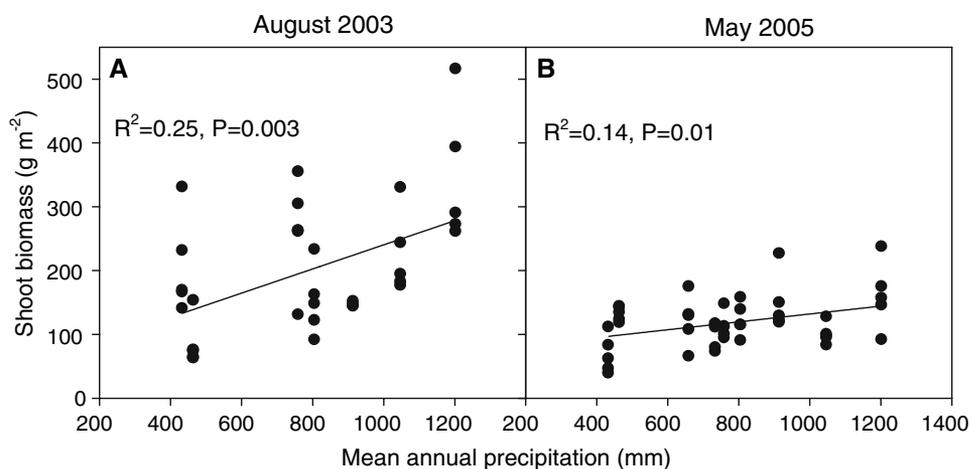


Figure 3. Shoot biomass in Aug 2003 (A) and May 2005 (B) as a function of MAP along a precipitation gradient.

attained maximums between 750 and 1000 mm of MAP (Figure 5) except that surface litter in February 2004 reached the maximum around 600 mm (Figure 5E).

Soil respiration rates in May 2005 were significantly higher compared to those in August 2003 (drought) and February 2004 (low temperature) (Figure 6A–C). Along the precipitation gradient, soil respiration increased linearly with MAP in all three seasons. Soil moisture also linearly increased with MAP along the gradient (Figure 6D–F), although field capacity did not significantly vary (Figure 2A). As expected, soil temperature did not show a large change with MAP along the precipitation gradient in all three seasons (Figure 6D–F), although MAT increased from 13.0 to 16.5°C along the gradient (Table 1).

Relationships Among Measured Variables

Table 2 shows Pearson correlation coefficients among environmental factors, soil characteristics, biomass, litter mass, and soil respiration in May 2005. Along the precipitation gradient, MAP was linearly correlated with elevation, MAT, pH, and bulk density, indicating that these variables may affect responses of biomass, litter, and soil respiration to precipitation to some degree along the gradient. For example, soil respiration rates were linearly correlated not only with MAP but also with elevation and MAT (Table 2). In addition, soil respiration rates were also linearly correlated with shoot biomass in May 2005 (Table 2) and with litter mass in August 2003 and February 2004 (data not shown) along the precipitation gradient. Shoot biomass showed significant relationships with MAP, MAT, elevation, and soil moisture, but not with root biomass and litter mass (Table 2).

Stepwise multiple regression analysis with all measured variables including MAP, elevation, MAT, soil temperature and moisture, and soil characteristics showed that MAP and/or elevation were the only variables included in the model for shoot biomass, litter mass, and soil respiration (data not shown).

DISCUSSION

Biomass Along the Precipitation Gradient

Vegetation dynamics are tightly coupled with hydrologic processes (Saco and others 2006). Our results show that shoot biomass increased linearly with MAP along the precipitation gradient from xeric to mesic sites (Figure 3). Although the simple regression analysis suggested a significant correlation of shoot biomass with MAT (13–16°C; Table 1) among our study sites (Table 2), our stepwise multiple regression analysis did not show that MAT was an important variable for shoot biomass. The positive relationship of shoot biomass or ANPP with MAP has been observed in grasslands (Sala and others 1988; Lauenroth and others 2000; Epstein and others 2002; McCulley and others 2005), forests (Austin 2002), and regions with diverse biomes (Austin and Sala 2002; Zhou and others 2002). Our results, together with those from previous studies, suggest that water limitation imposes a common constraint on aboveground plant production or biomass across diverse biomes (Huxman and others 2004). In contrast, root biomass and total plant biomass remained relatively constant along the precipitation gradient (Figure 4). Similar patterns were observed by Santantonio and Hermann (1985) and Pietikäinen and others (1999). The lack of response of root biomass to precipitation was probably due to a decrease in the proportion of C

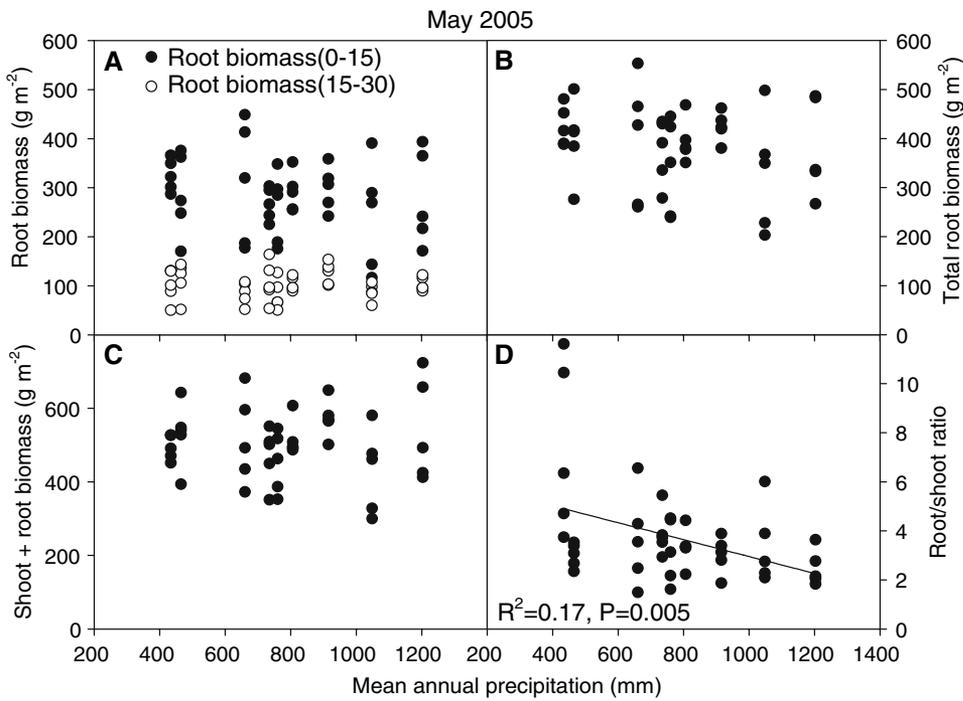


Figure 4. Patterns of belowground root biomass at the depth of 0–15 and 15–30 cm (A), total measured root biomass at the depth of 0–30 cm (B), total biomass including shoot and root biomass (C), and root/shoot ratio along a precipitation gradient (D).

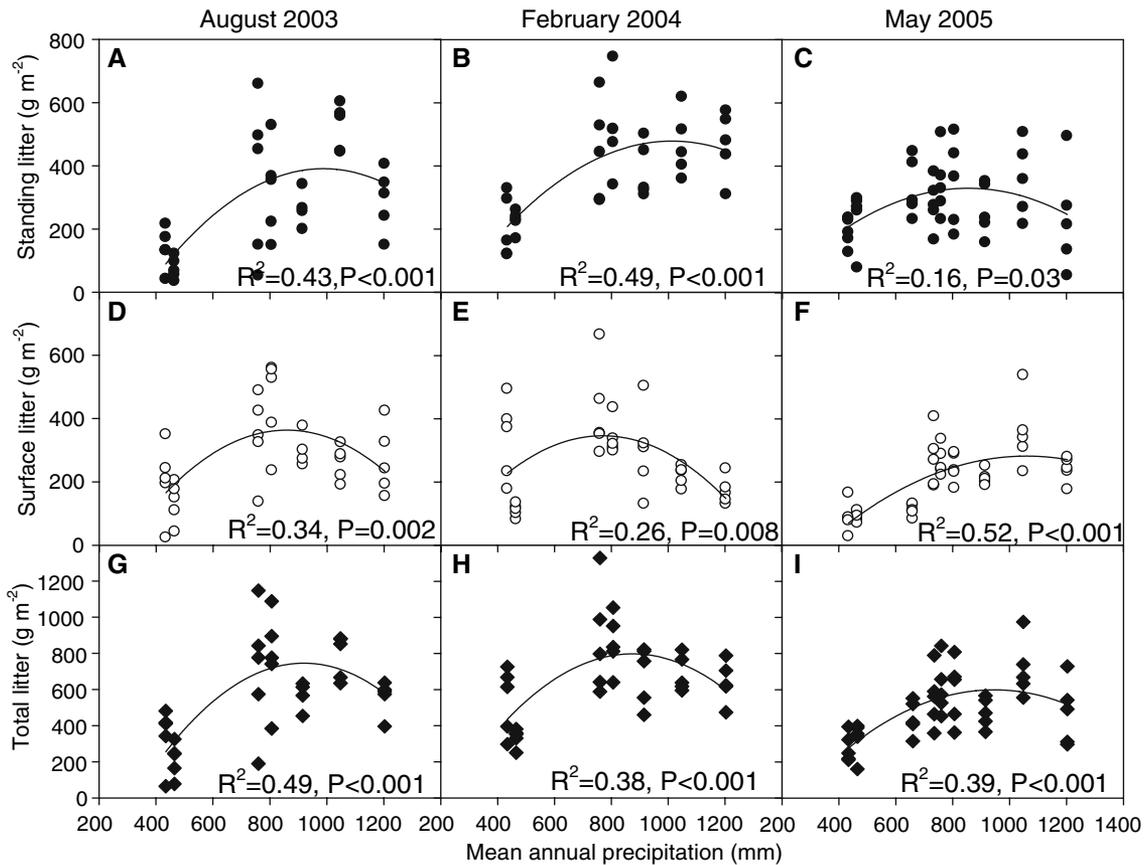


Figure 5. Standing litter, surface litter, and total litter mass in August 2003 (A, D, G), February 2004 (B, E, H), and May 2005 (C, F, I) as a function of MAP along a precipitation gradient.

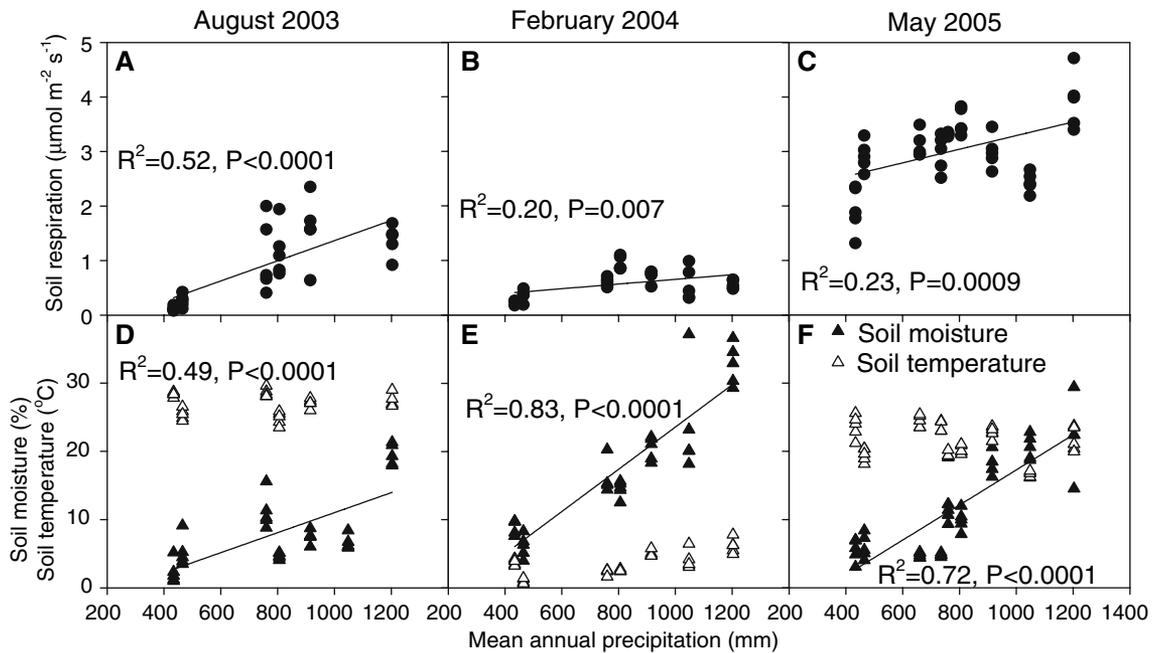


Figure 6. Patterns of soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$), soil moisture (%), and soil temperature ($^{\circ}\text{C}$) in August 2003 (A, D), February 2004 (B, E), and May 2005 (C, F) along a precipitation gradient.

allocation to roots and an increase in turnover of roots with increasing precipitation (Comeau and Kimmins 1989; Pietikäinen and others 1999).

Indeed, root/shoot ratio, an indicator of plant C allocation, decreased with precipitation (Figure 4D), which was consistent with other studies (Comeau and Kimmins 1989; Schulze and others 1996; Zerihun and others 2006) and predictions of the resource balance/optimality theory (Bloom and others 1985; Friedlingstein and others 1999). The decreasing trend in the root/shoot ratio likely resulted from changes in the relative importance of limiting resources (that is, water, light, and nutrients) along the precipitation gradient (Tilman 1988; Vinton and Burke 1997). In the Great Plains, for example, water is a primary limiting factor for plant growth in semi-arid short-grass steppe (Lauenroth and others 1978). Plants increase the root/shoot ratio to optimize growth under the dry environment. Conversely, production is limited more by light and nutrients than water in tallgrass prairie with high precipitation, resulting in a low root/shoot ratio (Knapp and Seastedt 1986; Schimel and others 1991; Lane and others 2000). Although we did not separate dead from live roots due to technical difficulties, the inclusion of dead roots may have not altered the overall pattern of root/shoot ratio along the precipitation gradient. Dead roots have been shown to persist longer and decompose slower at cool than warm sites (Sala and others 1996) but they were not

significantly affected by precipitation (Pietikäinen and others 1999). In addition, temperature may confound the root/shoot ratio to some degree with a MAT range of 13.0 to 16.5 $^{\circ}\text{C}$ along the precipitation gradient due to the inclusion of dead roots for root biomass. However, from the stepwise multiple regression analysis, MAT was not an important variable affecting the root/shoot ratio and other measured variables. The effects of temperature on the root/shoot ratio are thus probably minor as well as in other ecosystem C processes.

Litter Mass Along the Precipitation Gradient

Litter mass represents an essential C pool linking plant production to soil C dynamics. Our results showed that standing litter, surface litter, and total litter mass followed quadratic curves with MAP, which increased at first, reached a maximum, and then decreased along the precipitation gradient in all three seasons (Figure 5). The trends were consistent with regional and global patterns of detritus for different ecosystems in diverse precipitation regimes (Schlesinger 1977; Simmons and others 1996; Austin 2002). The quadratic relationships between litter mass and MAP suggest counteracting mechanisms of litter production and decomposition that regulate litter dynamics along the precipitation gradient. At low rainfall sites, low input of litter

Table 2. Correlation Analysis of Environmental and/or Ecological Variables with Each Other in May 2005

		Pearson correlation coefficients																
		MAP	Elev	MAT	SoilM	SoilT	pH	FC	BD	Soil C	Soil N	C:N	Rs	Shoot	Root	StanL	SurfL	TotalL
P values	MAP	-0.913	0.630	0.851	-0.290	-0.652	-0.038	-0.465	0.247	-0.123	0.664	0.480	0.377	-0.165	0.155	0.648	0.468	
of the	Elev	0.000	-0.432	-0.680	0.253	0.475	0.061	0.188	-0.180	0.154	-0.618	-0.602	-0.432	0.184	-0.264	-0.655	-0.540	
correlations	MAT	0.003	0.000	0.537	0.055	-0.537	0.219	-0.662	-0.082	-0.249	0.322	0.521	0.387	-0.015	-0.168	0.107	-0.044	
	SoilM	0.000	0.000	0.000	-0.424	-0.497	-0.148	-0.476	0.345	0.067	0.481	0.284	0.311	-0.169	0.127	0.541	0.378	
	SoilT	0.056	0.098	0.723	0.004	0.293	0.176	0.332	-0.428	-0.192	-0.399	-0.024	0.046	0.225	-0.364	-0.505	-0.518	
	pH	0.000	0.001	0.000	0.054	-0.031	0.564	-0.303	-0.066	-0.414	-0.278	-0.083	0.155	-0.290	-0.394	-0.407		
	FC	0.803	0.691	0.149	0.333	0.841	-0.267	-0.169	-0.236	0.179	0.211	-0.097	-0.128	-0.056	0.179	-0.067		
	BD	0.001	0.216	0.000	0.028	0.000	0.076	-0.060	0.192	-0.427	-0.152	0.068	0.035	0.089	-0.335	-0.136		
	Soil C	0.102	0.238	0.594	0.020	0.043	0.268	0.694	0.853	0.333	-0.127	-0.032	-0.087	0.150	0.179	0.197		
	Soil N	0.421	0.311	0.099	0.663	0.211	0.668	0.119	0.206	0.000	-0.199	-0.186	-0.051	0.036	0.062	-0.184	-0.066	
	C:N	0.000	0.000	0.031	0.001	0.005	0.239	0.003	0.025	0.189	0.153	0.032	-0.233	0.188	0.632	0.479		
	Rs	0.001	0.000	0.003	0.058	0.878	0.164	0.319	0.405	0.222	0.316	0.447	-0.027	0.090	0.218	0.181		
	Shoot	0.011	0.003	0.009	0.038	0.765	0.524	0.656	0.837	0.740	0.936	0.002	0.042	-0.136	0.025	-0.071		
	Root	0.280	0.225	0.922	0.267	0.142	0.308	0.402	0.818	0.570	0.862	0.862	0.784	-0.158	-0.384	-0.381		
	StanL	0.310	0.080	0.270	0.405	0.015	0.053	0.713	0.560	0.324	0.686	0.217	0.555	0.374	0.300	0.391	0.850	
	SurfL	0.000	0.000	0.485	0.000	0.007	0.240	0.024	0.240	0.227	0.000	0.150	0.872	0.009	0.008	0.000	0.817	
	TotalL	0.001	0.000	0.774	0.010	0.006	0.662	0.373	0.196	0.664	0.001	0.233	0.643	0.033	0.000	0.000		

The environmental/ecological variables are MAP, elevation (Elev), MAT, soil moisture and temperature (SoilM and SoilT), pH, field capacity (FC), bulk density (BD), soil C and N content (Soil C and Soil N), soil C:N ratio (C:N), soil respiration (Rs), shoot and root biomass (Shoot and Root), standing litter (StanL), surface litter (SurfL), and total litter (TotalL). The values on the upper-right side of the diagonal are Pearson correlation coefficients. The values on the lower-left side of the diagonal are P values to indicate statistical significance of the correlation coefficients. The bold values represent significant relationships between those two variables.

from biomass production may result in low accumulation of detritus, although litter decomposition is also slow (Fyles and others 1985; Austin 2002). As precipitation increases, litterfall input may increase at a higher rate than mass loss, leading to a larger accumulation of standing litter as well as surface litter (Austin 2002). At very high rainfall sites, a decline in standing and surface detritus probably stems from increased decomposition due to favorable temperature and rainfall conditions compared to litterfall input (Schlesinger 1977; Austin 2002; Lawrence 2005).

Along the precipitation gradient in the southern Great Plains of the USA, the maximum litter mass occurred between 750 and 1000 mm of MAP (Figure 5). In the literature, there was no consistent range of precipitation for the occurrence of maximum litter mass. For example, in Hawaii's forests, the maximum detritus (including leaf and woody) appeared between 1500 and 2000 mm of MAP (Austin 2002). In the Pacific Northwest of the USA, precipitation from 2000 to 3000 mm was most favorable for detritus accumulation (Sun and others 2004). The diverse ranges of precipitation for maximum litter mass may result from different ecosystem types, litter quality, environmental variables, and other confounding factors such as soil texture. Surface litter in February 2004 reached the maximum around 600 mm of precipitation (Figure 5E). This likely resulted from enhanced decomposition of surface litter with anomalously high precipitation between September 2003 and February 2004 in comparison to that during the same period of the other years.

Soil Respiration, C and N Content, and Characteristics

Precipitation generally has greater effects than temperature on soil respiration in xeric ecosystems and in dry seasons of mesic ecosystems (Luo and Zhou 2006). Our results show that measured soil respiration rates in grassland ecosystems increased linearly with MAP along the gradient in all three seasons (Figure 6). This trend has also been demonstrated on the global scale (Raich and Schlesinger 1992) and in other gradient studies (Simmons and others 1996; Gårdenäs 2000; McCulley and others 2005). For example, soil respiration and decomposition rates both increased with MAP across the Great Plains of North America (McCulley and others 2005). CO₂ effluxes from litter decomposition were positively correlated with MAP in northern hardwood ecosystems in Maine, USA (Simmons and others 1996). Precipitation is

thus a key factor in regulating regional variability in soil respiration (Luo and Zhou 2006).

Soil C content is the result of the net balance between inputs from plant production and outputs from decomposition and from relatively low leaching and/or volatile losses (Jenny 1980; Jobbágy and Jackson 2000). Both production and decomposition are strongly regulated by precipitation. The N cycle is closely linked to C, usually expressed by the C:N ratio (Figure 2D). Many studies have observed that soil C and N increased with MAP (Jenny 1980; Burke and others 1989; Zhou and others 2002). Surprisingly, our results showed that soil C and N content remained relatively constant along the precipitation gradient (Figure 3C), due to at least two causes. First, the relatively unchanged pattern of root biomass probably contributed to part of this trend because belowground allocation may leave more distinct imprints on soil C and N pools than aboveground production and litter mass (Jobbágy and Jackson 2000). Second, increases in litter inputs were roughly balanced by litter decomposition, resulting in little changes in soil C content along the precipitation gradient (Figure 2).

For soil characteristics, the increasing trend of pH values along the gradient may be due to a decrease in soil calcium carbonate (CaCO₃), which is strongly influenced by precipitation (Jenny 1980; Gunal and Ransom 2006). This trend was also confirmed by our observation that acid treatments with H₂SO₃ before soil C and N analysis produced more bubbles in soil samples from dry than wet sites (see "Materials and Methods" section). A decrease in bulk density probably resulted from combined effects of changes in soil texture and organic matter, which affect porosity volume, size, and shape. Increased litter mass would alleviate the effect of rainsplash on soil compaction with increasing precipitation along the gradient (Regüés and Gallart 2004).

CONCLUSION

This transect study examined patterns of shoot and belowground root biomass, litter mass (including standing and surface litter), soil respiration, and soil C and N content in the southern Great Plains grasslands along a precipitation gradient. The results showed that shoot biomass and soil respiration were positively, linearly related to MAP and a quadratic curve best described the relationship of litter mass with MAP. However, root biomass and soil C and N content remained relatively constant. The root/shoot ratio thus decreased linearly with MAP probably due to decreased plant allocation to

root growth and increased nutrients or light constraints along the gradient. Nevertheless, the linear/quadratic equations describing variation of ecosystem C processes with precipitation could be useful for model development, parameterization, and validation at landscape and regional scales to improve predictions of C dynamics in grasslands in response to climate change.

ACKNOWLEDGEMENTS

The authors thank the three anonymous reviewers for their insightful comments. The authors would also like to thank Drs. Kessler and Hulsey as well as seven other government and conservation organizations (Oklahoma State Parks, the Nature Conservancy, Rita Blanca National Grassland, and USDA-ARS southern plains range research station) for providing access to the sites used in this study. The authors also thank Michael Cyrwus, Rebecca A. Sherry, Jesse Bell, Afzal Subedar, Carlos Recinos, Tao Xu, Haihe Liang, Bo Su, Yuan An, and Shiliang Gu for assistance with field sampling. This research was financially supported by US National Science Foundation (NSF) under DEB 0078325 and DEB 0444518, and by the Terrestrial Carbon Program at the Office of Science, US Department of Energy, Grant No.: DE-FG02-006ER64317.

REFERENCES

- Amundson R, Austin AT, Schuur EAG, Yoo K, Matzek V, Kendall C, Uebersax A, Brenner D, Baisden WT. 2003. Global patterns of the isotopic composition of soil and plant nitrogen. *Global Biogeochem Cycles* 17, 1031. doi:10.1029/2002GB001903.
- Austin AT. 2002. Differential effects of precipitation on production and decomposition along a rainfall gradient in Hawaii. *Ecology* 83:328–38.
- Austin AT, Sala OE. 2002. Carbon and nitrogen dynamics across a natural precipitation gradient in Patagonia, Argentina. *J Veg Sci* 13:351–60.
- Bloom AJ, Chapin FS, Mooney HA. 1985. Resource limitation in plants—an economic analogy. *Annu Rev Ecol Syst* 16:363–92.
- Burke IC, Lauenroth WK, Parton WJ. 1997. Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. *Ecology* 78:1330–40.
- Burke IC, Lauenroth WK, Vinton MA, Hook PB, Kelly RH, Epstein HE, Aguiar MR, Robles MD, Aguilera MO, Murphy KL, Gill RA. 1998. Plant-soil interactions in temperate grasslands. *Biogeochemistry* 42:121–43.
- Burke IC, Yonker CM, Parton WJ, Cole CV, Flach K, Schimel DS. 1989. Texture, climate, and cultivation effects on soil organic matter content in US grassland soils. *Soil Sci Soc Am J* 53:800–5.
- Comeau PG, Kimmins JP. 1989. Above-ground and below-ground biomass and production of lodgepole pine on sites with differing soil-moisture regimes. *Can J For Res* 19:447–54.
- Epstein HE, Burke IC, Lauenroth WK. 2002. Regional patterns of decomposition and primary production rates in the US Great Plains. *Ecology* 83:320–7.
- Epstein HE, Lauenroth WK, Burke IC, Coffin DP. 1996. Ecological responses of dominant grasses along two climatic gradients in the great plains of the United States. *J Veg Sci* 7:777–88.
- Fay PA, Carlisle JD, Knapp AK, Blair JM, Collins SL. 2000. Altering rainfall timing and quantity in a mesic grassland ecosystem: design and performance of rainfall manipulation shelters. *Ecosystems* 3:308–19.
- Fay PA, Carlisle JD, Knapp AK, Blair JM, Collins SL. 2003. Productivity responses to altered rainfall patterns in a C-4-dominated grassland. *Oecologia* 137:245–51.
- Fowler NL. 1986. Microsite requirements for germination and establishment of 3 grass species. *Am Midland Nat* 115:131–45.
- Friedlingstein P, Joel G, Field CB, Fung IY. 1999. Toward an allocation scheme for global terrestrial carbon models. *Glob Change Biol* 5:755–70.
- Fyles JW, Fyles IH, Bell MAM. 1985. Vegetation and soil development on coal-mine spoil at high elevation in the Canadian Rockies. *J Appl Ecol* 22:239–48.
- Gårdenäs AI. 2000. Soil respiration fluxes measured along a hydrological gradient in a Norway spruce stand in south Sweden (Skogaby). *Plant Soil* 221:273–80.
- Gunal H, Ransom MD. 2006. Clay illuviation and calcium carbonate accumulation along a precipitation gradient in Kansas. *Catena* 68:59–69.
- Hanson PJ, Edwards NT, Garten CT, Andrews JA. 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* 48:115–46.
- Heisler JL, Weltzin JF. 2006. Variability matters: towards a perspective on the influence of precipitation on terrestrial ecosystems. *New Phytol* 172:189–92.
- Högberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Hogberg MN, Nyberg G, Ottosson-Lofvenius M, Read DJ. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411:789–92.
- Hui DF, Luo YQ, Katul G. 2003. Partitioning interannual variability in net ecosystem exchange between climatic variability and functional change. *Tree Physiol* 23:433–42.
- Huxman TE, Smith MD, Fay PA, Knapp AK, Shaw MR, Loik ME, Smith SD, Tissue DT, Zak JC, Weltzin JF, Pockman WT, Sala OE, Haddad BM, Harte J, Koch GW, Schwinning S, Small EE, Williams DG. 2004. Convergence across biomes to a common rain-use efficiency. *Nature* 429:651–4.
- Jenny H. 1980. *The soil resource: origin and behavior*. New York, NY: Springer-Verlag.
- Jobbágy EG, Jackson RB. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol Appl* 10:423–36.
- Kirschbaum MUF. 1995. The temperature-dependence of soil organic-matter decomposition, and the effect of global warming on soil organic-C storage. *Soil Biol Biochem* 27:753–60.
- Knapp AK, Fay PA, Blair JM, Collins SL, Smith MD, Carlisle JD, Harper CW, Danner BT, Lett MS, McCarron JK. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* 298:2202–5.
- Knapp AK, Seastedt TR. 1986. Detritus accumulation limits productivity of tallgrass prairie. *Bioscience* 36:662–8.
- Lane DR, Coffin DP, Lauenroth WK. 2000. Changes in grassland canopy structure across a precipitation gradient. *J Veg Sci* 11:359–68.
- Lauenroth WK, Burke IC, Paruelo JM. 2000. Patterns of production and precipitation-use efficiency of winter wheat and

- native grasslands in the central Great Plains of the United States. *Ecosystems* 3:344–51.
- Lauenroth WK, Dodd JL, Sims PL. 1978. Effects of water-induced and nitrogen-induced stresses on plant community structure in a semi-arid grassland. *Oecologia* 36:211–22.
- Lawrence D. 2005. Regional-scale variation in litter production and seasonality in tropical dry forests of southern Mexico. *Biotropica* 37:561–70.
- Lawrence D, Foster D. 2002. Changes in forest biomass, litter dynamics and soils following shifting cultivation in southern Mexico: an overview. *Interciencia* 27:400–8.
- Liu XZ, Wan SQ, Su B, Hui DF, Luo YQ. 2002. Response of soil CO₂ efflux to water manipulation in a tallgrass prairie ecosystem. *Plant Soil* 240:213–23.
- Luo Y, Zhou XH. 2006. Soil respiration and the environment. San Diego, CA: Academic Press/Elsevier.
- Maguire DA. 1994. Branch mortality and potential litterfall from Douglas-fir trees in stands of varying density. *For Ecol Manage* 70:41–53.
- Matson PA, Vitousek PM. 1987. Cross-system comparisons of soil nitrogen transformations and nitrous oxide flux in tropical forest ecosystems. *Global Biogeochem Cycles* 1:163–70.
- Matthews E. 1997. Global litter production, pools, and turnover times: Estimates from measurement data and regression models. *J Geophys Res* 102:18771–800.
- McCulley RL, Burke IC, Nelson JA, Lauenroth WK, Knapp AK, Kelly EF. 2005. Regional patterns in carbon cycling across the Great Plains of North America. *Ecosystems* 8:106–21.
- Meentemeyer V. 1984. The geography of organic decomposition rates. *Ann Assoc Am Geogr* 74:551–60.
- Milchunas DG, Lauenroth WK. 2001. Belowground primary production by carbon isotope decay and longterm root biomass dynamics. *Ecosystems* 4:139–50.
- Morgan RPC. 1986. Soil erosion and soil conservation. New York, NY: Longman Sci. & Tech.
- Newell SY. 1993. Decomposition of shoots of a saltmarsh grass: methodology and dynamics of microbial assemblages. *Adv Microb Ecol* 13:301–26.
- Paruelo JM, Lauenroth WK, Burke IC, Sala OE. 1999. Grassland precipitation-use efficiency varies across a resource gradient. *Ecosystems* 2:64–8.
- Pedersen LB, Bille-Hansen J. 1999. A comparison of litterfall and element fluxes in even aged Norway spruce, Sitka spruce and beech stands in Denmark. *For Ecol Manage* 114:55–70.
- Pietikäinen J, Vaijarvi E, Ilvesniemi H, Fritze H, Westman CJ. 1999. Carbon storage of microbes and roots and the flux of CO₂ across a moisture gradient. *Can J For Res* 29:1197–203.
- Raich JW, Potter CS, Bhagawati D. 2002. Interannual variability in global soil respiration, 1980–94. *Glob Change Biol* 8:800–12.
- Raich JW, Schlesinger WH. 1992. The global carbon-dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus B Chem Phys Meteorol* 44:81–99.
- Regüés D, Gallart F. 2004. Seasonal patterns of runoff and erosion responses to simulated rainfall in a badland area in Mediterranean mountain conditions (Vallcebre, southeastern Pyrenees). *Earth Surf Process Landforms* 29:755–67.
- Saco PM, Willgoose GR, Hancock GR. 2006. Eco-geomorphology and vegetation patterns in arid and semi-arid regions. *Hydrol Earth Syst Sci Discuss* 3:2559–93.
- Sala OE, Lauenroth WK, Burke IC. 1996. Global change: effects on coniferous forests and grasslands. In: Melillo JM, Ågren GI, Breymeyer A, Eds. *SCOPE 56: global change: effects on coniferous forests and grasslands*. New York: Wiley.
- Sala OE, Parton WJ, Joyce LA, Lauenroth WK. 1988. Primary production of the central grassland region of the United States. *Ecology* 69:40–5.
- Santantonio D, Hermann RK. 1985. Standing crop, production, and turnover of fine roots on dry, moderate, and wet sites of mature Douglas-fir in Western Oregon. *Annales Des Sciences Forestieres* 42:113–42.
- Schimel DS, Kittel TGF, Knapp AK, Seastedt TR, Parton WJ, Brown VB. 1991. Physiological interactions along resource gradients in a tallgrass prairie. *Ecology* 72:672–84.
- Schlesinger WH. 1977. Carbon balance in terrestrial detritus. *Annu Rev Ecol Syst* 8:51–81.
- Schulze ED, Mooney HA, Sala OE, Jobbagy E, Buchmann N, Bauer G, Canadell J, Jackson RB, Loreti J, Oesterheld M, Ehleringer JR. 1996. Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. *Oecologia* 108:503–11.
- Simmons JA, Fernandez IJ, Briggs RD, Delaney MT. 1996. Forest floor carbon pools and fluxes along a regional climate gradient in Maine, USA. *For Ecol Manage* 84:81–95.
- Sims PL, Singh JS. 1978. Structure and function of 10 western north-american grasslands. 3. Net primary production, turnover and efficiencies of energy capture and water-use. *J Ecol* 66:573–97.
- Spain AV. 1984. Litterfall and the standing crop of litter in 3 tropical Australian rainforests. *J Ecol* 72:947–61.
- Subedar AA. 2005. Effects of warming and clipping on carbon and nitrogen content and their isotope ratios in soil organic matter aggregates in a tall grass prairie ecosystem. M.S. Thesis, University of Oklahoma.
- Sun OJ, Campbell J, Law BE, Wolf V. 2004. Dynamics of carbon stocks in soils and detritus across chronosequences of different forest types in the Pacific Northwest, USA. *Glob Change Biol* 10:1470–81.
- Tilman D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton, NJ: Princeton University Press.
- Vinton MA, Burke IC. 1997. Contingent effects of plant species on soils along a regional moisture gradient in the Great Plains. *Oecologia* 110:393–402.
- Webb W, Szarek S, Lauenroth W, Kinerson R, Smith M. 1978. Primary productivity and water-use in native forest, grassland, and desert ecosystems. *Ecology* 59:1239–47.
- Weltzin JF, Loik ME, Schwinning S, Williams DG, Fay PA, Haddad BM, Harte J, Huxman TE, Knapp AK, Lin GH, Pockman WT, Shaw MR, Small EE, Smith MD, Smith SD, Tissue DT, Zak JC. 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience* 53:941–52.
- Yahdjian L, Sala O, Austin A. 2006. Differential controls of water input on litter decomposition and nitrogen dynamics in the Patagonian steppe. *Ecosystems* 9:128–41.
- Zerihun A, Montagu KD, Hoffmann MB, Bray SG. 2006. Patterns of below- and aboveground biomass in *Eucalyptus populnea* woodland communities of northeast Australia along a rainfall gradient. *Ecosystems* 9:501–15.
- Zhou G, Wang Y, Wang S. 2002. Responses of grassland ecosystems to precipitation and land use along the Northeast China Transect. *J Veg Sci* 13:361–8.