

Precipitation Regulates the Response of Net Ecosystem CO₂ Exchange to Environmental Variation on United States Rangelands

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Abstract

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Rangelands occupy 50% of Earth's land surface and thus are important in the terrestrial carbon (C) cycle. For rangelands and other terrestrial ecosystems, the balance between photosynthetic uptake of carbon dioxide (CO₂) and CO₂ loss to respiration varies among years in response to interannual variation in the environment. Variability in CO₂ exchange results from interannual differences in 1) environmental variables at a given point in the annual cycle (direct effects of the environment) and in 2) the response of fluxes to a given change in the environment because of interannual changes in biological factors that regulate photosynthesis and respiration (functional change). Functional change is calculated as the contribution of among-year differences in slopes of flux-environment relationships to the total variance in fluxes explained by the environment. Functional change complicates environmental-based predictions of CO₂ exchange, yet its causes and contribution to flux variability remain poorly defined. We determine contributions of functional change and direct effects of the environment to interannual variation in net ecosystem exchange of CO₂ (NEE) of eight rangeland ecosystems in the western USA (58 site-years of data). We predicted that 1) functional change is correlated with interannual change in precipitation on each rangeland and 2) the contribution of functional change to variance in NEE increases among rangelands as mean precipitation increases. Functional change explained 10–40% of the variance in NEE and accounted for more than twice the variance in fluxes of direct effects of environmental variability for six of the eight ecosystems. Functional change was associated with interannual variation in precipitation on most rangelands but, contrary to prediction, contributed proportionally more to variance in NEE on arid than more mesic ecosystems. Results indicate that we must account for the influence of precipitation on flux-environment relationships if we are to distinguish environmental from management effects on rangeland C balance.

Resumen

Los pastizales ocupan 50% de la superficie del planeta y por lo tanto son importantes en el ciclo de Carbono (C) terrestre. Para los pastizales y otros ecosistemas terrestres, el balance entre el consumo fotosintético del dióxido de carbono (CO₂) y la pérdida de CO₂ debido a la respiración varía de un año a otro en respuesta a la variación del medio ambiente en el transcurso del año. La variabilidad en el intercambio del CO₂ resulta de las diferencias que se dan durante el año en 1) variables ambientales en un momento dado en el ciclo anual (efectos directos del medio ambiente) y en 2) la respuesta de los flujos hacia un determinado cambio en el medioambiente debido a los cambios en el transcurso del año en los factores biológicos que regulan la fotosíntesis y la respiración (cambio funcional). El cambio funcional se calcula como la contribución de las diferencias entre los años en la pendiente de las relaciones del flujo y el medio ambiente a la varianza total en los flujos explicada por el medio ambiente. El cambio funcional complica las predicciones basadas en el medio ambiente del intercambio del CO₂. Sin embargo, sus causas y la contribución a la variabilidad de los flujos no se han definido satisfactoriamente. Determinamos las contribuciones del cambio funcional y los efectos directos del medio ambiente a la variación entre años en el intercambio neto del ecosistema de CO₂ (NEE) de ocho ecosistemas de pastizales en la parte oeste de los Estados Unidos (58-sitios-años de datos). Pronosticamos que 1) el cambio funcional esta correlacionado con los cambios entre años de la precipitación en cada tipo de pastizal y 2) la contribución del cambio funcional a la variación en NEE aumenta entre los pastizales a medida que la precipitación se incrementa. El cambio funcional explicó 10–40% de la variación en NEE y representaron más del doble de la variación en los flujos de los efectos directos de la variabilidad ambiental para seis de ocho ecosistemas. Los cambios funcionales estuvieron

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asociados con la variación entre años en la precipitación de la mayoría de los pastizales, pero contrariamente a la predicción contribuyó proporcionalmente más a variación en NEE en ecosistemas áridos que los mésicos. Estos resultados indican que debemos de tomar en cuenta la influencia de la precipitación en la relación del flujo y medio ambiente para poder distinguir los efectos que ejerce el medio ambiente de los que tiene el manejo del balance de C en los pastizales.

Key Words: climatic variability, deserts, functional change, grasslands, shrublands, variability in carbon flux

INTRODUCTION

In the absence of disturbances that remove carbon (C), the C budget of terrestrial ecosystems is determined largely by the balance between net uptake of CO₂ via photosynthesis and CO₂ loss to respiration. For most ecosystems studied, this balance (net ecosystem exchange of CO₂; NEE) is highly dynamic even at the annual time scale (Barford et al. 2001; Sims and Bradford 2001; Dunn et al. 2007). Interannual variation in NEE can be particularly large for ecosystems known collectively as rangelands, which occupy about 50% of the Earth's land surface (Sims and Risser 1999). On these ecosystems, the annual C balance often varies between net uptake (sink) and net release (source) in response to among-year variation in precipitation and other environmental variables (Sims and Bradford 2001; Flanagan et al. 2002; Frank 2002).

Most efforts to model flux variation have been less than fully successful, partly because of the difficulty of mathematically capturing the temporal dynamics of biological processes that regulate photosynthesis and respiration (Hanson et al. 2004). If we are to predict CO₂ fluxes at scales relevant to the terrestrial C cycle, we must determine how controls on C balance vary temporally and across geographic gradients in climate.

In relatively undisturbed ecosystems, interannual differences in NEE usually are attributed to variation in environmental variables such as precipitation, temperature, and net radiation that regulate CO₂ exchange. We refer to short-term (days to months) changes in environmental variables as variation in the environment. Longer-term changes in these variables, including interannual differences in the timing and amount of precipitation, are considered as variation in weather. A given change in the environment can have a similar effect on CO₂ exchange among years. Hui et al. (2003) regarded these repeatable effects of environmental variation as indicative of "direct effects of the environment" on CO₂ exchange, a term used here. Alternatively, the response of CO₂ fluxes to a given change in the environment can differ among years because of interannual changes in biological processes that regulate photosynthesis and respiration (change in biological functioning). Interannual variation in biological functioning is termed "functional change" and can be assessed by calculating the contribution of interannual differences in slopes of flux-environment regressions to the total variance in CO₂ fluxes explained by environmental variability (Hui et al. 2003). Many of the biological processes that regulate flux responses to the environment, including canopy development and N mineralization rates, are affected by interannual differences either in seasonal means of environmental variables or within-season patterns of weather. Consequently, functional change can result from year-to-year differences in factors such as the annual amount or seasonal timing of precipitation.

Partitioning interannual variation in NEE between direct effects of environmental variation and functional change is a first step toward improving the prediction of ecosystem C balance. If interannual variability in CO₂ exchange results largely from direct effects of environmental variation, C balance might be predicted using flux-environment relationships measured during a single year. If flux responses to the environment vary among years, however, C balance can be predicted only by accounting for changes in the biological functioning of ecosystems.

Rangelands exhibit among the largest variability in above-ground net primary productivity (ANPP) of biomes in North America in response to variability in precipitation (Knapp and Smith 2001). Most of the biological processes that regulate ANPP responses to precipitation in these ecosystems also affect flux responses to short-term change in the environment. For example, seasonal or annual precipitation amounts regulate the timing and duration of canopy development which, in turn, influences the sensitivity of CO₂ exchange to variation in light, temperature, and current rainfall on northern mixed-grass prairie (Polley et al. 2008). Flux responses to the environment thus would be expected to vary among years on rangelands in response to interannual changes in precipitation patterns.

Plant productivity varies more among years on grasslands and other ecosystems dominated by herbaceous plants than on more arid rangelands despite the greater inherent variability in precipitation on the latter (Knapp and Smith 2001). The herbaceous vegetation of grasslands responds quickly and grows rapidly following precipitation events. On arid ecosystems, by contrast, low plant densities limit the response of vegetation to changes in precipitation. Ecosystem CO₂ exchange, like productivity, can vary more among years on grasslands than deserts in response to changes in precipitation. We thus predicted that functional change would contribute more to interannual variability in NEE on relatively mesic than more arid rangelands.

We used CO₂ flux measurements collected by participants in the Rangeland Carbon Flux network (United States Department of Agriculture, Agricultural Research Service) to determine how interannual variation in environmental variables affects growing-season values of NEE for eight native rangeland ecosystems in the western United States, including Great Plains grasslands, desert shrubland, desert grasslands, and sagebrush steppe (Table 1). We used the homogeneity-of-slopes (HOS) regression model developed by Hui et al. (2003) to distinguish effects of among-year (interannual) from within-year (seasonal) variability in the environment on growing season values of rangeland NEE and to partition effects of interannual variability into two components, functional change and direct effects of among-year variation in the environment. We predicted that 1) functional change on each rangeland results from variation among years in seasonal or annual

Table 1. Location, vegetation type, site characteristics, and the years and growing season period considered for flux measurements for rangeland ecosystems in this study.

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Location	Vegetation type	Mean annual precip. (mm)	Elev. (m)	Lat. (°N)/Long. (°W)	Years	Max./Min. precip. (mm)	Growing season (doy)
Las Cruces, New Mexico (NM)	Desert grassland	227	1230	32°60′/106°75′	1996–2001	327/175	71–301
Tucson, Arizona (AZ; Lucky Hills)	Desert shrubland	356	1372	31°44′/110°03′	1997–2002	457/207	1–365
Tucson, Arizona (AZ; Kendall)	Desert grassland	356	1526	31°44′/109°56′	1996–2003	490/198	1–365
Burns, Oregon (OR)	Sagebrush steppe	298	1380	43°29′/119°43′	1995–2000, 2003	339/107	106–266
Nunn, Colorado (CO)	Shortgrass steppe	321	1660	40°41′/104°45′	1996, 1998–2001	420/233	120–294
Dubois, Idaho (ID)	Sagebrush steppe	340	1700	44°16′/112°08′	1996–2003	389/188	99–280
Mandan, North Dakota (ND)	Northern mixed-grass prairie	482	518	46°46′/100°55′	1995–2001	601/322	106–301
Woodward, Oklahoma (OK)	Southern mixed-grass prairie	728	219	36°36′/99°35′	1995–2005	802/454	92–315

precipitation patterns and 2) the contribution of functional change to variance in NEE increases among rangelands as mean precipitation increases.

MATERIALS AND METHODS

Site Description

The rangelands studied were considered to be in good ecological condition based on species composition and were not grazed by livestock, burned, or fertilized during the period of measurements. Svejcar et al. (2008) provided a description of land-use history, soils, and dominant plant species for each rangeland site. Annual precipitation differs by as much as a factor of three among these rangelands (Table 1). The timing of peak precipitation also differs among these sites. Precipitation usually peaks during the summer months of June through August on desert rangelands and during the May through August period for grasslands in the Great Plains of the United States. By contrast, the growing season months of July and August are among the driest during the year for sagebrush steppe ecosystems in the northwestern United States.

CO₂ Fluxes and Climatic Variables

Fluxes on each rangeland were measured using Bowen ratio/energy balance (BREB) instrumentation (Model 023/CO₂ Bowen ratio system; Campbell Scientific, Inc., Logan, UT). Fluxes were calculated using methods described by Dugas (1993) and Dugas et al. (1999). Bowen ratios were calculated using air temperature and water vapor gradients measured every 2 s at 1 m and 2 m above the plant canopy. Gradients in water vapor and CO₂ were measured with Model 6262 infrared gas analyzers (Li-Cor, Inc., Lincoln, NE) that were calibrated weekly. Sensible heat flux was calculated using the Bowen ratio, average net radiation (Rn) measured with Model Q*7.0 and 7.1 net radiometers (REBS, Seattle, WA), and soil heat flux measured using two Model HFT soil heat flux plates (REBS) and soil temperature (ST) (see Table 2 for a listing of abbreviations used for environmental variables). The turbulent diffusivity (assumed equal for heat, water vapor, and CO₂) was calculated using the temperature gradient, sensible heat flux, and air density. Carbon dioxide fluxes were derived by multiplying turbulent diffusivity

by the change in the density of CO₂ measured between 1 m and 2 m above the canopy and correcting for differences in water vapor density (Webb et al. 1980). Latent heat was determined as the energy remaining after subtracting soil heat flux and sensible heat flux from net radiation. Actual evapotranspiration (AET) was calculated by dividing the latent heat of evaporation by the latent heat of vaporization. Flux toward the surface was considered to be negative in sign.

Two aerodynamic methods are widely used to measure CO₂ fluxes, the BREB technique used here and the eddy covariance technique. Both methods can be unreliable during periods of stable atmospheric conditions as sometimes occur at night. Results from the two approaches are similar, however, when data are processed appropriately (Dugas et al. 2001; Wolf et al. 2008). When turbulent diffusivity estimated by the BREB approach failed, as evidenced by differences in signs of the sensible/latent heat flux calculations and the temperature/water vapor gradient, we calculated turbulent diffusivity using wind speed, atmospheric stability, and canopy height (Dugas et al. 1999). This alternative method of estimating diffusivity was used in about 10% of calculations, mostly at night. Frank et al. (2000) showed that CO₂ fluxes measured at night on grasslands using the BREB method were only slightly smaller than the sum of estimated nighttime plant and soil respiratory losses. Fluxes calculated using the BREB method also have been shown to be

Table 2. Environmental variables that influenced net ecosystem exchange of CO₂ on rangelands.

Variable	Symbol
Actual evapotranspiration	AET
Air temperature	AT
Potential evapotranspiration	PET
Evaporative deficit	Deficit (= PET – AET)
Mean precipitation per week (1–8 wk)	ppt1–ppt8
Net radiation	Rn
Relative humidity	RH
Soil temperature	ST
Vapor pressure	e
Wind speed	WS

similar to those estimated from biomass production (Dugas et al. 1999) and canopy chambers (Angell et al. 2001).

Svejcar et al. (2008) describe measurements of additional environmental variables, including ST, wind speed (WS), relative humidity (RH), vapor pressure (e), and temperature of air (AT). Following Stephenson (1990), we define the parameter “evaporative deficit” as evaporative demand not met by available water. A value of evaporative deficit for each day was calculated as the difference between daily values of potential evapotranspiration (PET) and AET. Daily values of PET were calculated with the Penman–Monteith equation using measurements of Rn, WS, AT, and e. Daily values of NEE and of climatic variables were calculated from measurements every 20 min. We did not attempt to gap-fill missing data. Missing flux values typically are estimated using the associated environmental conditions. Gap-filling would have introduced autocorrelation between fluxes and the environment.

In order to reduce fluctuations inherent in daily values, we calculated weekly means of CO₂ fluxes and climatic variables. For each week during each growing season, we also calculated the weekly sum of precipitation (ppt1), the mean of precipitation per week for the current week and the previous 1 to 7 wk (denoted as ppt2–ppt8).

We considered only data collected during the growing season for each rangeland. The beginning date of the growing season was considered the first of three or more consecutive weeks with negative values of NEE during daylight hours (net CO₂ uptake). The ending date of the growing season was identified as the final week with negative values of daytime NEE prior to three or more consecutive weeks with positive daytime NEE. Beginning and ending dates from each year were averaged for each rangeland to define the growing season for each site. The first and final week of net CO₂ uptake during daylight varied greatly among years for the two desert sites in Arizona (Lucky Hills, Kendall), so we considered the entire year as the growing season for these sites.

Partitioning of Variance in NEE

We used the HOS regression model (Hui et al. 2003) to statistically partition variation in NEE into seasonal and interannual components. Interannual variation in NEE was defined as among-year differences in NEE measured at daily to annual time scales. We first tested for linearity of relationships between fluxes and each of eight environmental variables for each rangeland using simple linear regression analysis and data from all years of record. Environmental variables used in regressions included AT, ST, evaporative deficit, Rn, PET, RH, WS, and various indices of time-lagged precipitation (e.g., ppt5). For each rangeland, we then used stepwise multiple linear regression (forward selection of variables) analysis to determine relationships between weekly means of CO₂ fluxes and the weekly averages of environmental variables that were significantly linearly correlated with fluxes in simple regression (single-slopes model). Variables retained in multiple regression models with fluxes when data from all years were considered then were entered into a HOS analysis (separate-slopes model). Interannual differences in the response of NEE to the environment or functional change were detected when the slope of one or more of the NEE-environment relationships

differed significantly among years. Finally, we statistically partitioned total variance in NEE among functional change, the direct effects of interannual variation in the environment, the effects of seasonal variability in climatic variables, and random error by partitioning the total sum of squares (SS_t) among these components.

The SS for functional change for each rangeland was calculated by summing across years the squared difference between CO₂ exchange estimated using a separate-slopes regression model and NEE calculated with a single-slope multiple regression model. The SS for direct effects of interannual variability in the environment was calculated by summing across years the squared difference between NEE estimated for each week with a single-slope regression model and the average of modeled estimates of NEE for the given week. Differences between means of modeled NEE across all years for a given week and the mean of NEE estimates for all weeks result from week-to-week changes in the environment. The squared sum of these differences equaled the effect of seasonal variability in the environment on fluxes. The SS attributable to random error was calculated by summing across years the squared difference between NEE measured on a given week and NEE estimated for that week with the separate-slopes regression model.

In order to determine how functional change affected CO₂ exchange at each site, we calculated NEE each year using the separate-slopes model. NEE was calculated using the multiyear average of each environmental variable included in the regression model. The proportion of variance in NEE explained by regression models differed among rangelands. In order to standardize for these differences in comparing functional change, we calculated the relative contribution of functional change to variance in NEE explained by regression models at each location ($SS_{\text{functional change}}/SS_{\text{model}}$).

Flux data contain random measurement errors, often called uncertainty. Uncertainty can include errors associated with the measurement system and with changes in turbulence (Hollinger and Richardson 2005). Uncertainty is perhaps best estimated by simultaneously measuring fluxes on the same ecosystem with two or more flux systems, an option for which we lack data. Hollinger and Richardson (2005) showed that the uncertainty in flux measurements rises as the magnitude of fluxes increases. Uncertainty in flux data thus might have increased each season as values of environmental drivers of CO₂ exchange increased. It is unlikely that random measurement errors altered major conclusions of this study, however. Values of environmental drivers of CO₂ exchange spanned similar ranges each year at a given site, hence any uncertainty associated with the magnitude of fluxes should not have differed greatly among years.

RESULTS

Environmental Correlates of NEE

NEE varied seasonally and interannually on all rangelands (Fig. 1). NEE increased (net CO₂ uptake is considered to be negative in sign) during spring then declined during late summer and autumn during most growing seasons on Great Plains grasslands (Nunn, Mandan, Woodward) and sagebrush steppe at Dubois (panels on the right of Fig. 1). Within-season changes in NEE generally were smaller on desert rangelands

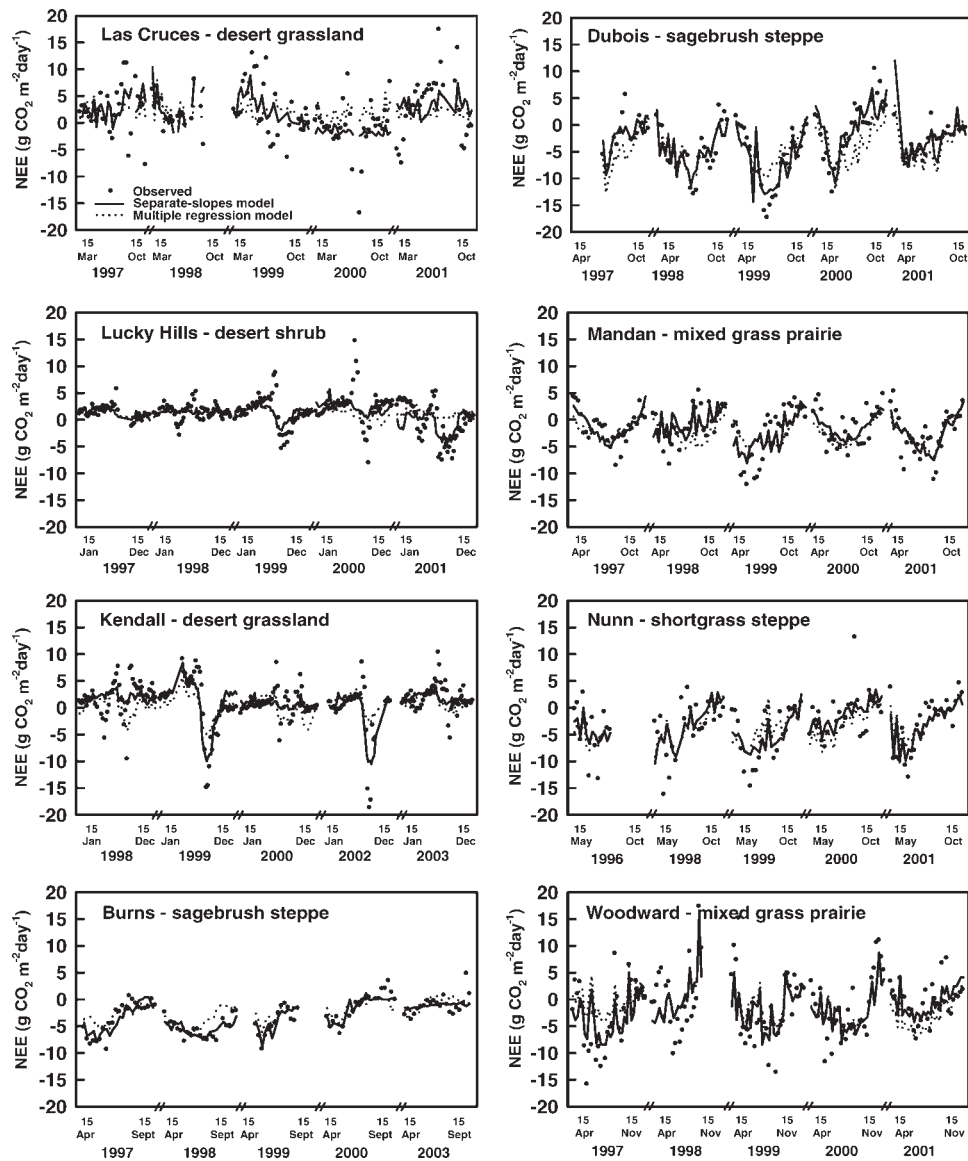


Figure 1. Weekly means of net ecosystem exchange of CO₂ (NEE) for rangeland ecosystems at eight locations in the western United States. Illustrated are data from five growing seasons at each location, including seasons with the greatest and smallest annual total of precipitation. Note that growing season years differ among panels. Dashed lines indicate flux estimates derived from a multiple regression model fit to weekly values of NEE from all years combined. The solid line indicates NEE estimates derived using a regression model in which slopes of significant NEE-environment relationships were allowed to vary among years rather than remain invariant.

(Las Cruces, Lucky Hills, Kendall) and sagebrush steppe at Burns.

Stepwise multiple regression analyses were used to relate weekly means of NEE at each site to means of environmental variables such as temperature, net radiation, and evaporative demand that were significantly correlated with NEE in simple regression. The r^2 values of these single-slope multiple regression models varied between 0.05 for desert grassland at Las Cruces and 0.40 for sagebrush steppe at Dubois ($P < 0.01$ for all models). Each of the two to three variables identified using multiple regression analysis for each site was retained in a separate-slopes model in which slopes of NEE-environment relationships were allowed to vary among years rather than remain invariant (Table 3).

Variation in weekly values of NEE was correlated mainly with time-lagged indices of precipitation and water-related environmental variables, such as RH, evaporative deficit, and PET, for desert sites and sagebrush steppe at Burns, and with Rn for grasslands and sagebrush steppe at Dubois (Table 3). When retained in regressions, time-lagged indices of precipitation including mean precipitation per week for 5–7 wk preceding flux measurements (pp5t–ppt7), were negatively correlated with NEE. These negative correlations indicate that net CO₂ uptake increased as recent precipitation increased. Greater precipitation during the week of flux measurements (ppt1) reduced net CO₂ uptake at Woodward. Rn was negatively correlated with NEE at Nunn, Dubois, Mandan, and Woodward, meaning that CO₂

Table 3. An analysis of variance of a separate-slopes regression model of net ecosystem CO₂ exchange (NEE; g CO₂ · m⁻² · d⁻¹) for each of eight rangeland ecosystems. Signs of relationships between weekly means of NEE and environmental variables for each rangeland are shown in parentheses (see Table 2 for a listing of abbreviations used for environmental variables). ****P* < 0.0001, ***P* < 0.001, **P* < 0.01, ++*P* < 0.05, +*P* < 0.10.

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Source (sign)	df	SS	F
Las Cruces			
RH (+)	1	236.3	7.35*
WS (+)	1	106.4	3.31 ⁺
RH × Year	5	641.4	3.99*
WS × Year	5	302.0	1.88 ⁺
Error	136	4372.9	—
Total	148	5659.0	—
Lucky Hills			
WS (+)	1	130.0	18.66***
ppt5 (-)	1	66.8	9.59*
WS × Year	5	264.4	7.59***
ppt5 × Year	5	126.6	3.63*
Error	276	1922.9	—
Total	288	2510.7	—
Kendall			
WS (+)	1	535.4	60.59***
deficit (+)	1	275.4	31.16***
ppt7 (-)	1	249.0	28.18***
WS × Year	7	803.1	12.98***
deficit × Year	7	253.7	4.10**
ppt7 × Year	7	656.6	10.66***
Error	296	2615.6	—
Total	320	5388.8	—
Burns			
AT (+)	1	57.6	20.12***
deficit (+)	1	254.4	88.88***
PET (-)	1	91.3	31.89***
AT × Year	6	343.1	19.98***
deficit × Year	6	36.3	2.12 ⁺⁺
PET × Year	6	94.0	5.47***
Error	108	309.1	—
Total	129	1185.8	—
Nunn			
AT (+)	1	125.4	9.21*
Rn (-)	1	825.9	60.25***
AT × Year	4	135.2	2.48 ⁺⁺
Rn × Year	4	111.1	2.04 ⁺
Error	97	1320.9	—
Total	107	2518.5	—
Dubois			
WS (-)	1	340.7	31.33***
Rn (-)	1	2200.7	202.34***
ppt5 (-)	1	90.7	8.34*
WS × Year	7	1421.5	18.67***
Rn × Year	7	366.1	4.81***
ppt5 × Year	7	289.2	3.80**

Table 3. Continued.

Source (sign)	df	SS	F
Error	168	1827.2	—
Total	192	6536.1	—
Mandan			
ST (-)	1	676.3	75.02***
Rn (-)	1	225.7	25.03***
ppt5 (-)	1	86.9	9.64*
ST × Year	6	305.2	5.64***
Rn × Year	6	266.3	4.92***
Error	165	1487.6	—
Total	180	3048.0	—
Woodward			
Rn (-)	1	2614.6	164.69***
ppt1 (+)	1	675.3	42.54***
Rn × Year	10	1579.1	9.95***
Error	320	5080.2	—
Total	332	9949.2	—

uptake on these rangelands increased as Rn increased. Increased AT was associated with reduced NEE at Burns and Nunn, whereas greater ST increased CO₂ uptake at Mandan.

Slopes of regression relationships between NEE and most of the variables retained in multiple regression models differed significantly among years (Table 3), indicating that interannual variability in NEE at each site resulted partly from functional change. Functional change explained between 9.8% (Nunn) and 39.9% (Burns) of variance in NEE among sites (Table 4). Functional change explained more than twice the variance in NEE of direct effects of interannual variation in the environment on desert rangelands at Las Cruces, Lucky Hills, and Kendall, sagebrush steppe at Burns and Dubois, and northern mixed-grass prairie at Mandan. Functional change and direct effects of the environment accounted for similar fractions of variance in NEE on shortgrass steppe at Nunn and southern mixed-grass prairie at Woodward. The variance in NEE explained by functional change and direct effects of the environment together (total effect of interannual variability in climate) was greater than 1.4 times the variance in NEE explained by seasonal change in the environment for the desert and sagebrush steppe ecosystems and mixed-grass prairie at Woodward. Seasonal and interannual variability in the environment explained similar proportions of variance in NEE on northern mixed-grass prairie at Mandan and short-grass steppe at Nunn.

Relationship Between Functional Change and Interannual Variation in Precipitation for Each Rangeland

Interannual variation in precipitation contributed to functional change on most rangelands. In order to assess the impact of functional change on NEE for each site, we calculated a single value of NEE for each year using the separate-slopes regression model and the multiyear average of each environmental variable included in the model. For five of

Table 4. Results from a homogeneity-of-slopes model for each of eight rangeland ecosystems ($P < 0.0001$). Variance in weekly values of NEE for each rangeland was partitioned into three modeled components (direct effects of interannual variation in the environment [direct], effects of seasonal variation in the environment [seasonal], and functional change) plus random error. Proportion represents the portion of total variance in NEE explained by the model and attributed to error and each of the three components of the model.

Source	SS	Proportion	SS	Proportion
	Las Cruces		Lucky Hills	
Model	1286.1	0.227	587.8	0.234
Direct	263.4	0.046	76.44	0.030
Seasonal	79.3	0.014	120.4	0.048
Functional change	943.4	0.167	391.0	0.156
Error	4372.9	0.773	1922.9	0.766
Total	5659.0	-	2510.7	-
	Kendall		Burns	
Model	2773.2	0.515	876.7	0.739
Direct	376.0	0.070	200.6	0.169
Seasonal	683.8	0.127	202.7	0.171
Functional change	1713.4	0.318	473.4	0.399
Error	2615.6	0.485	309.1	0.261
Total	5388.8	-	1185.8	-
	Nunn		Dubois	
Model	1197.6	0.476	4708.9	0.720
Direct	235.4	0.094	808.3	0.123
Seasonal	715.9	0.284	1823.8	0.279
Functional change	246.3	0.098	2076.8	0.318
Error	1320.9	0.524	1827.2	0.280
Total	2518.5	-	6536.1	-
	Mandan		Woodward	
Model	1560.4	0.512	4869.0	0.489
Direct	203.8	0.067	1747.9	0.176
Seasonal	785.1	0.257	1542.0	0.155
Functional change	571.5	0.188	1579.1	0.159
Error	1487.6	0.488	5080.2	0.511
Total	3048.0	-	9949.2	-

the eight rangelands, interannual differences in calculated values of NEE correlated with interannual differences in precipitation (Table 5). That is, precipitation patterns apparently indirectly affected NEE by altering processes that regulate the sensitivity of CO₂ exchange to environmental variation. Calculated NEE increased as precipitation increased on rangelands at Woodward, Mandan, Lucky Hills, and Las Cruces, but decreased linearly as a function of rainfall summed for day 176 through 203 of the current season on sagebrush steppe at Dubois. For sagebrush steppe at Burns and desert grassland at Kendall, interannual differences in slopes of flux-environment relationships correlated linearly with rainfall variability (Table 5). Increasing the average size of precipitation events reduced effects of week-to-week variation in evaporative deficit and PET on NEE on sagebrush steppe at Burns. The greater was week-to-week variation in rainfall on desert grassland at Kendall, the greater was the detrimental effect of a given level of deficit on net CO₂ uptake and the smaller was the stimulating effect of a given input of precipitation on NEE. Only for shortgrass steppe at Nunn where growing season rainfall varied relatively little among years (range of 207.52–288.45 mm during four of five

seasons), did NEE not correlate with precipitation or precipitation variability.

Precipitation and Among-Location Differences in Functional Change

Precipitation patterns also explained differences in the contribution of functional change to regression estimates of NEE among the eight rangelands. The contribution of functional change to the variance in NEE explained by a separate-slopes regression model ($SS_{\text{functional change}}/SS_{\text{model}}$) increased among sites as the coefficient of variation (CV; standard deviation/mean) in precipitation increased (Fig. 2). Precipitation was summed each year through the day on which Rn reached its maximum value (doy 161 at Lucky Hills to doy 210 at Mandan). The CV of precipitation varied inversely with precipitation amount among sites ($r^2 = 0.60$, $P = 0.01$; not shown), as is commonly observed (Knapp and Smith 2001). Consequently, the contribution of functional change to modeled NEE also declined linearly among seven of the eight rangelands as precipitation increased. Functional change contributed relatively little to NEE for shortgrass steppe at Nunn where the CV of precipitation was the smallest among the eight rangelands.

Table 5. Results of regression analyses relating either net ecosystem exchange of CO₂ (NEE; g CO₂ · m⁻² · d⁻¹) or slopes of NEE-environment relationships (Kendall, Burns) calculated for each growing season using a separate-slopes regression model to precipitation and growing season means of temperature (air temperature, AT; soil temperature, ST; definition; EC). A single value of NEE was calculated for each season at each location (*n* = 5–11 seasons) using the multiyear average of each environmental variable included in the separate-slopes model. Environmental variables include deficit (mm · day⁻¹), potential evapotranspiration (PET; mm · day⁻¹), and the average of precipitation per week over seven wk (ppt7; mm). NEE was fit with a multiple regression for Woodward. Other relationships are linear. 5

Location (dependent variable)	Independent variable	Intercept	Slope	r ²	P value
Las Cruces					
NEE	Precipitation: day 120–180 (mm)	4.90	-0.051	0.87	0.004
Lucky Hills					
NEE	Precipitation: day 1–180 (mm)	3.77	-0.03	0.47	0.08
Kendall					
NEE-deficit	Mean of among-week differences in precipitation (mm)	80.96	30.54	0.56	0.02
NEE-ppt7		-0.74	0.10	0.23	0.13
Burns					
NEE-PET	Mean size of precipitation events (mm)	-5.81 × 10 ³	509.61	0.67	0.01
NEE-deficit		5.03 × 10 ³	-437.07	0.69	0.01
Dubois					
NEE	Precipitation: day 176–203 (mm)	-6.92	0.21	0.35	0.07
Mandan					
NEE	Precipitation before season (mm)	1.17	-0.03	0.90	0.0007
Nunn					
NEE	ST (growing season; °C)	-27.27	1.20	0.65	0.06
Woodward					
NEE	AT (growing season; °C)/Precipitation previous season (mm)	-30.88	1.23/-7.63 × 10 ⁻³	0.47	0.08

DISCUSSION

Interannual variability in slopes of flux-environment relationships (functional change) alone explained 10–40% of variance in NEE on ungrazed native rangelands in the western United States and accounted for more than twice the variance in fluxes of direct effects of interannual variation in environmental variables for six of eight of these ecosystems. Functional change was associated with interannual differences in precipitation on most rangelands, implying that changes in precipitation altered ecological processes that determine the sensitivity of NEE to seasonal trends in the environment. Greater precipitation during or prior to the growing season increased the stimulating effect of recent rainfall or greater Rn on CO₂ uptake of desert shrubland at Lucky Hills, northern mixed-grass prairie at Mandan, and southern mixed-grass prairie at Woodward. Increasing week-to-week variation in rainfall or increasing the average size of precipitation events during the season reduced the amount by which a given input of rainfall increased NEE on desert grassland at Kendall and sagebrush steppe at Burns, respectively. Significantly, functional change contributed proportionally more to variance in NEE on rangelands on which precipitation during the first one-half of the year was lowest and varied the most. Results indicate that as mean precipitation decreases and precipitation variability increases across geographic gradients in the western United States, so too does our

capacity to predict NEE simply from interannual variation in environmental variables.

Functional change accounted for most of interannual variability in NEE on rangeland ecosystems. Hui et al. (2003) found that functional change explained slightly more of variance in NEE for loblolly pine forest than did direct effects of interannual variation in the environment. Similarly, Richardson et al. (2007) attributed slightly more variance in NEE for spruce forest to among-year change in biotic responses to environmental drivers than to direct effects of environmental variation. Several have noted that NEE-environment relationships can vary through time (e.g., Barford et al. 2001; Luyssaert et al. 2007). Studies by Hui et al. (2003) and Richardson et al. (2007) were among the first to quantify how temporal changes in biotic responses influence CO₂ exchange. The greater the differences in biotic responses among years, the more difficult it is to predict C balance from measurements of environmental variation alone.

For most of the rangelands we studied, the response of NEE to a given change in Rn, evaporative demand, or other environmental variable differed among years because the response of canopy-level photosynthetic parameters to environmental drivers differed among years (Polley et al. 2009). Functional change in NEE was associated with among-year differences in relationships between apparent light-use efficiency, calculated as the initial slope of the ecosystem light-

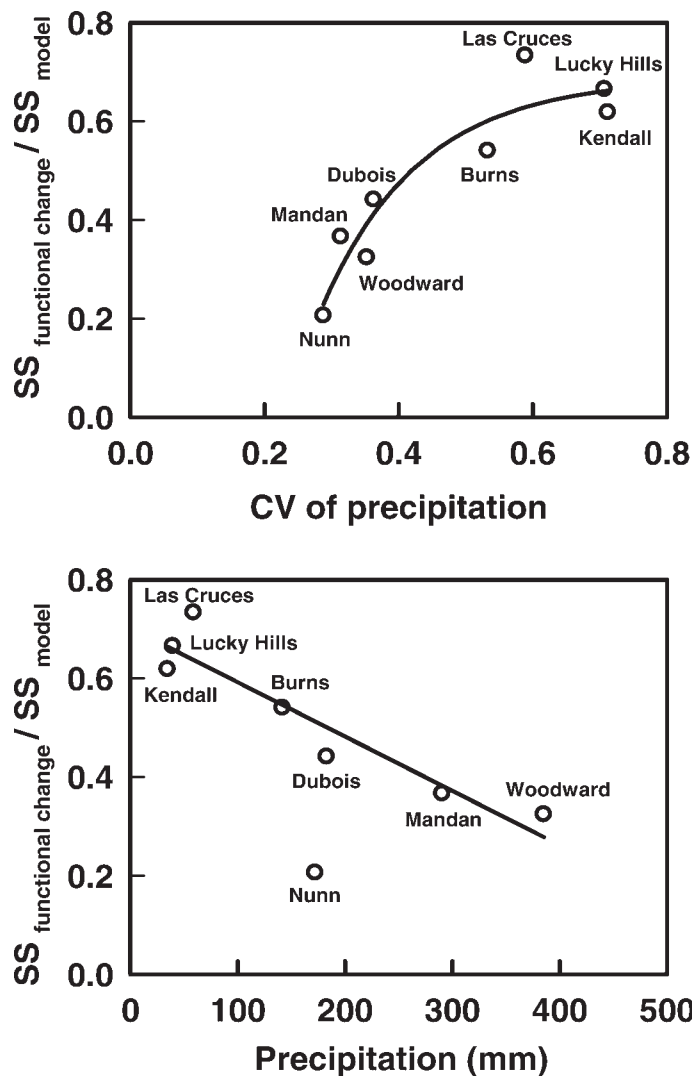


Figure 2. Relationships between the contribution of functional change to the variance in net ecosystem exchange of CO₂ (NEE) explained by a separate-slopes regression model ($SS_{\text{functional change}}/SS_{\text{model}}$) for rangeland ecosystems at each of eight locations and the coefficient of variation (CV) and mean of precipitation, each calculated using precipitation summed through the first one-half of each calendar year of NEE measurements. Lines are exponential and linear regression fits to observations ($r^2 = 0.84$, $P = 0.004$ and $r^2 = 0.86$, $P = 0.002$, respectively). Net radiation increases to its maximum value on each rangeland during the first one-half of each year. Physiological activity presumably increases simultaneously. Among-site differences in the variability and amount of precipitation during this period contributed to differences in biotic response functions (functional change) among rangelands.

response curve, and the environment for three ecosystems. These included sagebrush steppe at Dubois and northern and southern mixed-grass prairies at Mandan and Woodward, respectively. Among-year differences in relationships between the maximum rate of ecosystem gross photosynthesis and the environment explained functional change in NEE on desert rangelands at Kendall and Lucky Hills. Net CO₂ uptake was greatest during years when apparent light-use efficiency and the rate of gross photosynthesis were greatest. Similarly, temporal variability in NEE was controlled mainly by seasonal fluctua-

tions in daytime net CO₂ uptake in a Mojave Desert shrubland (Jasoni et al. 2005).

Interannual variability in precipitation contributed to functional change on all rangelands, probably by altering canopy development, N mineralization rates, or other ecological processes that regulate CO₂ exchange. Change in precipitation predated change in NEE-environment responses by several months on mixed grass prairies (Mandan, Woodward) and desert shrubland (Lucky Hills), suggesting that rainfall patterns affected subsequent canopy development. Grassland fluxes are highly responsive to live biomass and leaf area index (LAI; Sims and Bradford 2001; Flanagan et al. 2002; Li et al. 2005; Phillips and Beerli 2008) which, in turn, are highly responsive to rainfall (Knapp and Smith 2001; Knapp et al. 2002). Indeed, year-to-year differences in the maximum value of LAI contributed to functional change in NEE on the three rangelands for which we have repeated measurements of LAI (Nunn, Mandan, Woodward; Polley et al. 2009). The response of CO₂ exchange to environmental drivers was not explained by variation in LAI alone, however. Variation in photosynthetic capacity of the canopy likely also was involved. Drought or excessive evaporative demand and low N availability all can reduce C uptake per unit of leaf area (Nouvellon et al. 2000; Flanagan et al. 2002; Barr et al. 2007). Numerous studies, including several of rangelands, have shown that variability in the timing and amount of precipitation contributes to variability in NEE (Frank and Dugas 2001; Emmerich 2003; Xu and Baldocchi 2004; Gilmanov et al. 2006; Aires et al. 2008). Our results imply that interannual variability in precipitation or in seasonal patterns of precipitation contributed to change in NEE at each site largely by altering biotic responses to environmental drivers.

The variance in NEE explained by functional change increased among rangelands as the mean of precipitation for the first one-half of the year declined and precipitation variability increased. This implies that NEE responded less predictably to environmental variation on relatively arid compared to more mesic rangelands. Variability in NEE often has been attributed to variability in precipitation (Frank and Dugas 2001; Flanagan et al. 2002; Emmerich 2003; Aires et al. 2008). Our data show that NEE responded not only to precipitation variability but, increasingly as mean rainfall declined, to variability in the response of CO₂ exchange to a given amount of precipitation or change in temperature, light, or evaporative demand. Water usually was available on Great Plains grasslands and sagebrush steppe at Dubois while Rn was increasing each year. Consequently, the response of CO₂ exchange to weekly variation in Rn and other environmental variables was more reliable among years on these relatively mesic than the drier rangelands. By contrast, little precipitation fell during winter and early spring on desert rangelands and sagebrush steppe at Burns. Low rainfall likely limited canopy development, as evidenced by the absence of a correlation between NEE and Rn on desert rangelands, and resulted in more variable NEE-environment relationships. Precipitation variability causes greater interannual variability in ANPP on grasslands than drier ecosystems, including deserts (Paruelo et al. 1999; Knapp and Smith 2001), but our results indicate that NEE might respond more predictably to recent rainfall and other environmental variables on grasslands than deserts.

Annual precipitation is a good predictor of mean ANPP across sites in the central grassland region of the United States (Sala et al. 1988) and of interannual variability in ANPP within rangeland sites (Huxman et al. 2004), but is a poor predictor of the net C balance of rangeland ecosystems. Annual NEE was not significantly correlated with annual precipitation across the rangelands we studied (Svejcar et al. 2008) and was weakly correlated with annual precipitation at sagebrush steppe sites alone (Gilmanov et al. 2006). Similarly, Law et al. (2002) found that the annual water balance, calculated by subtracting precipitation from evapotranspiration, explained just 29% the variation in gross photosynthesis among forests and grasslands. The correlation between water balance and NEE, which includes respiration in addition to gross photosynthesis, probably would have been smaller. Annual precipitation might fail to explain net C balance if NEE is more sensitive to precipitation patterns than to precipitation amount (Zhao et al. 2006; Kwon et al. 2008). The NEE of alpine shrubland in China depended more on the timing of precipitation events than the total amount of precipitation, for example (Zhao et al. 2006). Precipitation also might fail to explain ecosystem C balance if, as demonstrated here, precipitation affects the sensitivity of CO₂ exchange to other environmental drivers. For example, Kwon et al. (2008) found that growing season NEE for a sagebrush-steppe ecosystem was regulated mainly by soil water availability during a drought period, but by the vapor pressure deficit of air when water availability was greater.

IMPLICATIONS

There is substantial interest in increasing and quantifying C sequestration by terrestrial ecosystems because of potential negative impacts of rising atmospheric CO₂ concentration. Rates of net CO₂ uptake are regulated partly by environmental factors. Respiration by plants and soil microorganisms depends on temperature, whereas photosynthesis varies as a function of “light” availability, for example. At the ecosystem level, the magnitude of CO₂ fluxes and response of fluxes to the environment also depend on the sizes and activity levels of respiring and photosynthesizing organisms. Photosynthesis responds more to a change in light when leaf area and leaf N content are large than small, for example. Similarly, respiration increases as the availability of C substrates increase. Factors that change the sizes or activity levels of respiring and photosynthesizing organisms will change the sensitivity of ecosystem-level CO₂ exchange to environmental variation, with potential impacts on C sequestration. Flux-environment relationships depended mainly on precipitation patterns on the ungrazed grasslands we studied, partly because the LAI of plant canopies varied with precipitation (Polley et al. 2009). Periodic disturbances, such as grazing, can cause large changes in both leaf area and photosynthetic activity per unit of leaf area (e.g., Owensby et al. 2006) and thus can alter flux-environment relationships (Polley et al. 2008). Our results indicate that interannual variation in net CO₂ exchange on rangelands resulted more from interannual differences in relationships between NEE and the environment than from short-term changes in the environment alone. It is critical, therefore that we identify the biological factors most responsible for inter-

annual variation in biotic responses and determine how these factors are affected by weather patterns (precipitation, temperature) and disturbances (grazing, fire) if we are to predict changes in rangeland C balance.

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