Global Change Biology

Global Change Biology (2010) **16**, 990–1002, doi: 10.1111/j.1365-2486.2009.01966.x

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Physiological and environmental regulation of interannual variability in CO_2 exchange on rangelands in the western United States

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Abstract

For most ecosystems, net ecosystem exchange of CO_2 (NEE) varies within and among years in response to environmental change. We analyzed measurements of CO_2 exchange from eight native rangeland ecosystems in the western United States (58 site-years of data) in order to determine the contributions of photosynthetic and respiratory (physiological) components of CO_2 exchange to environmentally caused variation in NEE. Rangelands included Great Plains grasslands, desert shrubland, desert grasslands, and sagebrush steppe. We predicted that (1) week-to-week change in NEE and among-year variation in the response of NEE to temperature, net radiation, and other environmental drivers would be better explained by change in maximum rates of ecosystem photosynthesis (A_{max}) than by change in apparent light-use efficiency (α) or ecosystem respiration at 10 °C (R_{10}) and (2) among-year variation in the responses of NEE, A_{max}, and α to environmental drivers would be explained by changes in leaf area index (LAI). As predicted, NEE was better correlated with A_{max} than α or R_{10} for six of the eight rangelands. Week-to-week variation in NEE and physiological parameters correlated mainly with time-lagged indices of precipitation and water-related environmental variables, like potential evapotranspiration, for desert sites and with net radiation and temperature for Great Plains grasslands. For most rangelands, the response of NEE to a given change in temperature, net radiation, or evaporative demand differed among years because the response of photosynthetic parameters (A_{max}, α) to environmental drivers differed among years. Differences in photosynthetic responses were not explained by variation in LAI alone. A better understanding of controls on canopy photosynthesis will be required to predict variation in NEE of rangeland ecosystems.

Keywords: climatic variability, desert, functional change, grassland, leaf area, light-use efficiency, net ecosystem exchange of CO_2, precipitation, respiration, shrubland

Received 13 March 2009 and accepted 27 April 2009

Introduction

Micrometeorological measurements of CO_2 fluxes have been initiated in a number of ecosystems to determine mechanisms regulating terrestrial carbon (C) balance (Baldocchi *et al.*, 2001; Svejcar *et al.*, 2008). A specific goal

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of these measurements is to determine how environmental drivers of C accumulation vary among ecosystems and to assess the sensitivity of net ecosystem exchange of CO_2 (NEE) to interannual variability in climate. Ultimately, it is hoped that these measurements can be used to develop CO_2 exchange–climate relationships relevant to the terrestrial C cycle (i.e., Friend *et al*., 2007).

The response of CO_2 exchange to climate has been found to vary through time, however, thus limiting our ability to predict NEE from change in climatic variables alone (Barford *et al*., 2001; Hui *et al*., 2003; Richardson *et al*., 2007; H. W. Polley, W. Emmerich, and J. A. Bradford, unpublished data). If climatic variation is to be useful as a predictor of ecosystem CO_2 exchange, we must understand why and how flux–climate relationships change through time. We refer to short-term (days to months) changes in climatic variables as variation in the environment. Longer-term changes in these variables are taken as climatic variation. A given change in the environment may have a similar effect on CO_2 fluxes among years. Following Hui *et al*. (2003), we regard these repeatable effects of environmental variation as 'direct effects of the environment' on CO_2 exchange. Alternately, a given change in the environment may affect CO_2 fluxes differently among years because of year-to-year variation in the biological processes that regulate CO_2 uptake and release. Variation in biological functioning is termed 'functional change,' and may be quantified by calculating the contribution of year-to-year differences in slopes of flux–environment relationships to the total variance in CO_2 fluxes explained by environmental variation (Hui *et al*., 2003). Many of the biological processes that regulate flux responses to the environment are affected by longer-term climatic patterns, and so functional change often results from climatic variation. Richardson *et al*. (2007) attributed a slightly greater proportion of the variance in NEE for spruce forest to interannual differences in the response of CO_2 exchange to environmental drivers than to direct effects of environmental variation on fluxes. H. W. Polley, W. Emmerich, and J. A. Bradford (unpublished data) found that functional change accounted for more than twice the variance in NEE of direct effects of environmental variability for six of eight rangeland ecosystems. Functional change in NEE on rangelands was associated with interannual variation in precipitation.

NEE represents the relatively small difference between the larger fluxes of photosynthesis and the sum of autotrophic and heterotrophic respiration (Valentini *et al*., 2000). Photosynthesis and respiration may respond to different environmental and other variables or to climatic variability at different rates (Luyssaert *et al*., 2007; Polley *et al*., 2008). It is likely, therefore, that environmental effects on NEE cannot be predicted accurately without understanding how NEE is regulated by its component processes.

It is also likely that we must identify the biological processes that explain functional change in NEE and its physiological components in order to calculate C balance. Several biological processes regulate flux responses to environmental drivers, but canopy development is among the most important in the arid and semiarid ecosystems known collectively as rangelands. Grassland fluxes are highly responsive to seasonal and among-year variation in live biomass and leaf area index (LAI; Sims & Bradford, 2001; Flanagan *et al*., 2002; Li *et al*., 2005; Phillips & Beeri, 2008), for example. Canopy development and other biological processes that regulate photosynthesis and respiration, in turn, are affected by seasonal or annual amounts of precipitation (Knapp & Smith, 2001; Knapp *et al*., 2002).

We used CO_2 flux measurements collected by participants in the Rangeland Carbon Flux network (United States Department of Agriculture, Agricultural Research Service) to assess the contributions of photosynthetic and respiratory components of NEE to variation in growing season values of CO_2 exchange for eight native rangeland ecosystems in the western United States. Rangelands included Great Plains grasslands, desert shrubland, desert grasslands, and sagebrush steppe. Functional change explained 10–40% of the variance in NEE for these eight rangelands (Polley *et al*., submitted); hence, a primary objective was to identify the physiological component of flux most responsible for among-year variation in NEE–environment relationships. We also sought to determine the extent to which flux responses to environmental drivers were regulated by interannual variation in LAI. We hypothesized that (1) week-to-week variation in NEE would be better explained by variation in maximum rates of ecosystem photosynthesis ($A_{\max}$) than by change in apparent light-use efficiency (α) or basal rates of ecosystem respiration (R_{10}), consistent with the finding that variability in NEE depended mainly on variation in daytime net CO_2 uptake in a desert shrubland (Jasoni *et al*., 2005); (2) functional change in NEE would correlate more highly with among-year variation in the response of $A_{\max}$ to the environment than with variation in responses of α or R_{10} to the environment; and (3) variation in LAI would explain functional change in NEE, $A_{\max}$, and α on grasslands, as implied by the strong correlation between grassland fluxes and leaf area reported by Flanagan *et al*. (2002) and others.

Materials and methods

Site description

We measured CO_2 exchange on eight native rangeland ecosystems in the central and western United States

(Table 1). Rangelands 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. Before measurements, the rangelands studied either had not been grazed for 10 or more years or had been lightly to moderately grazed by livestock. Svejcar *et al.* (2008) provide a description of soils and dominant plant species for each rangeland.

CO_2 *fluxes and climatic variables*

Fluxes on each rangeland were measured using Bowen ratio/energy balance (BREB) instrumentation (Model 023/CO_2 Bowen ratio system, Campbell Scientific Inc., Logan, UT, USA). Flux rates 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 and 2 m above the plant canopy. Gradients in water vapor and CO_2 were measured with Model 6262 infrared gas analyzers (Li-Cor Inc., Lincoln, NE, USA) 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, USA), and soil heat flux measured using two Model HFT soil heat flux plates (REBS). The turbulent diffusivity (assumed equal for heat, water vapor, and CO_2) was calculated using the temperature gradient, sensible heat flux, and air density. Carbon dioxide fluxes ($\mathrm{mg\,m^{-2}\,s^{-1}}$) were derived by multiplying turbulent diffusivity by the change in the density of CO_2 measured between 1 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 CO_2 fluxes: the BREB technique used here and the eddy covariance technique. Both methods depend on calculated values of diffusivity, which may be unreliable for 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 CO_2 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 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 climatic variables, including soil temperature (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.

Leaf area was measured at four positions surrounding Bowen ratio equipment on each of the three Great Plains grasslands at approximately 2-week (Mandan) or 4-week intervals (Nunn, Woodward). On each sampling date, one quadrat ($0.25\,\mathrm{m}^2$) was randomly placed within each of four permanently located plots (each $30\,\mathrm{m} \times 30\,\mathrm{m}$) on each grassland. Vegetation in each quadrat was clipped to ground level, and the surface area of green tissues (leaf area) was measured with a photoelectric meter. Leaf area was not measured repeatedly during each growing season on other rangelands.

Daily values of NEE and of climatic variables were calculated from measurements every 20 min. We did not attempt to gap fill missing data, which accounted for $<1\%$ of data points during daylight hours and 2% of data points at night (Svejcar *et al.*, 2008). Missing flux values typically are estimated using the associated environmental conditions. Gap filling would have introduced autocorrelation between fluxes and climate.

In order to reduce fluctuations inherent in daily values, we calculated weekly means of CO_2 fluxes and climatic variables. For each week during each growing season, we also calculated the weekly sum of precipitation (ppt1) and the mean of precipitation per week for the current week and the previous 1–7 weeks (denoted as ppt2–ppt8).

We were concerned primarily with environmental and biological regulation of CO_2 uptake, and so we only considered data collected during the growing season for each rangeland. The beginning date of the growing season was considered the first of 3 or more consecutive weeks with negative values of NEE during daylight hours (net CO_2 uptake). The ending date of the growing season was identified as the final week with negative values of daytime NEE before 3 or more consecutive weeks with positive daytime NEE. Beginning and

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

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

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 CO$_2$ uptake during daylight varied greatly among years for the two desert sites in Arizona (Lucky Hills, Kendall); hence, we considered the entire year as the growing season for these sites.

Ecosystem physiological parameters

Mean diurnal trends in NEE, Rn, and ST were derived by averaging observations for each 20-min period during the day over each week. Physiological components of NEE were then calculated for each week by fitting a simple physiological model to diurnal trends, where

$$\mathrm{NEE} = ((A_{\max}\alpha\,\mathrm{PPFD})/(A_{\max} + \alpha\,\mathrm{PPFD})) + R_{10}Q_{10}{}^{((\mathrm{ST}-10)/10)}, \qquad (1)$$

and $A_{\max}$ is the maximum rate of ecosystem gross photosynthesis (GPP, $\mu\mathrm{mol\,CO_2\,m^{-2}\,s^{-1}}$) at infinite photosynthetic photon flux density (PPFD; $\mu\mathrm{mol\,photons\,m^{-2}\,s^{-1}}$), α is the initial slope of the ecosystem light-response curve or the apparent light-use efficiency ($\mathrm{mol\,CO_2\,mol^{-1}}$ photons), R_{10} is ecosystem respiration rate at 10 °C ($\mu\mathrm{mol\,CO_2\,m^{-2}\,s^{-1}}$), Q_{10} is the temperature sensitivity of ecosystem respiration for a 10 °C change in ST, and PPFD equals Rn × 3.002, as determined from year-long measurements at the Lucky Hills site (PPFD was not measured at each site). Physiological components of NEE ($A_{\max}$, α, R_{10}, Q_{10}) were estimated by fitting nonlinear, least-squares regressions to diurnal trends using the Gauss–Newton method. Parameter values were restricted during regression to the following ranges: $A_{\max}$ (0.1–60), α (0.001–0.08), R_{10} (0.1–8.0), and Q_{10} (1.0–3.0). Respiration depends on soil water content and the availability of C substrates to plants and microbes as well as on temperature (Davidson *et al.*, 2006; Polley *et al.*, 2006). Estimates of the apparent temperature sensitivity of respiration (Q_{10}) may be confounded if photosynthetic activity and soil water content covary with temperature, as often occurs over periods of several days. In order to reduce the influence of these confounding variables on Q_{10}, we calculated a mean value of Q_{10} for each year following methods of Reichstein *et al.* (2005). For each site and year, we fit Eqn (1) to data from 3-week periods created by shifting the initial week of the period by 1 week before each regression was fit. A value of Q_{10} for each season at each site was then derived by averaging the Q_{10} values estimated for each 3-week period using the inverse of the standard error of estimate as the weighting factor. We set the Q_{10} parameter in Eqn (1) to this average value for the growing season, then refit the physiological model to derive $A_{\max}$, α, and R_{10} for each week.

Calculation of function change in NEE and physiological parameters

We used the homogeneity-of-slopes (HOS) regression model (Hui et al., 2003) to determine the contribution of interannual variation in flux–environment relationships or functional change to variance in NEE, $A_{\max}$, α, and R_{10}. We first tested for linearity of flux–environment relationships for each rangeland using simple linear regression analysis and data from all years of record. For each rangeland, we then used stepwise multiple linear regression (forward selection of variables) analysis to determine relationships between weekly values of NEE, $A_{\max}$, α, and R_{10}, and weekly averages of environmental variables that were significantly linearly correlated with NEE in simple regression (single-slopes model). Environmental variables retained in multiple regression models when data from all years were considered were then entered into a HOS analysis (separate-slopes model). Functional change was detected when the slope of one or more of the flux–environment relationships differed significantly among years. The sum of squares for functional change for each flux (NEE, $A_{\max}$, α, or R_{10}) and each rangeland was calculated by summing across years the squared difference between fluxes estimated using a separate-slopes regression model and fluxes calculated with a single-slope multiple regression model.

In order to determine how functional change affected NEE and it physiological components at each site, we calculated NEE, $A_{\max}$, α, and R_{10} each year using the separate-slopes model. Each flux variable was calculated using the multiyear average of each environmental variable included in the regression model.

Results

Seasonal trends in CO_2 exchange and climate

The seasonal trend in NEE for each rangeland became evident when CO_2 flux for each week was averaged among years and plotted against day of the year. These multiyear averages of NEE for each week increased (became more negative) from the winter low to a maximum during summer then declined during late summer and autumn on Great Plains grasslands at Nunn, Mandan, and Woodward and on sagebrush steppe at Dubois and Burns (Fig. 1). On average, these ecosystems functioned as CO_2 sinks during most of the growing season. By contrast, desert rangelands at Las Cruces, Lucky Hills, and Kendall functioned as CO_2 sinks only for brief periods during the season.

Multiyear averages of $A_{\max}$, α, and R_{10} followed seasonal patterns similar to those of NEE (Fig. 2). Like NEE, $A_{\max}$ increased from winter to summer, and then declined during late summer and autumn for grasslands at Nunn, Mandan, and Woodward and sagebrush steppe at Dubois and Burns. Peak values of mean $A_{\max}$ were smallest for sagebrush steppe ecosystems (Dubois, Burns) and greatest for southern mixed-grass prairie (Woodward). Means of R_{10} increased in summer to maximum values coincident with the seasonal maxima of $A_{\max}$ on most rangelands.

Averages of NEE for each week were highly linearly correlated with averages of $A_{\max}$ on all rangelands (not shown; $r^2 = 0.45$–0.89; $P < 0.0001$ for all regressions), except desert grassland at Las Cruces ($P = 0.88$). Mean values of $A_{\max}$, in turn, were positively correlated with precipitation on each rangeland (Fig. 3). $A_{\max}$ was best fit with a power function of precipitation per week averaged over the 5 and 8 weeks before flux measurements for desert ecosystems at Lucky Hills and Kendall, respectively ($P < 0.001$). $A_{\max}$–precipitation relationships for remaining rangelands were linear. Means per week of $A_{\max}$ increased by 0.72–0.99 μmol m^{-2} s^{-1} for each 1 mm week^{-1} increase in precipitation over the 5–7 weeks before flux measurements. Mean values of $A_{\max}$ were also positively corrected with AT on all rangelands (not shown; $r^2 = 0.23$–0.74; $P < 0.001$ for all regressions), except sagebrush steppe at Dubois ($P = 0.78$). Air temperature explained a smaller fraction of the variation in $A_{\max}$ than precipitation on all rangelands except mixed-grass prairie at Mandan and Woodward.

Weekly values of NEE were also more highly correlated with $A_{\max}$ than α or R_{10} for six of the eight rangelands (Table 2). As estimated from linear regression equations, NEE increased by 0.1–1.0 g CO_2 m^{-2} day^{-1} for each 1 μmol m^{-2} s^{-1} increase in $A_{\max}$. The increase in NEE per unit increase in $A_{\max}$ was greater for sagebrush steppe ecosystems at Dubois and Burns than for other rangelands. Weekly NEE values correlated most strongly with R_{10} on desert grassland at Las Cruces ($r^2 = 0.10$, $P < 0.0001$, $n = 145$) and with α on mixed-grass prairie at Woodward ($r^2 = 0.17$, $P < 0.0001$, $n = 296$). The slope of the NEE–R_{10} regression for Las Cruces was positive (1.76 g CO_2 m^{-2} day^{-1} per 1 μmol m^{-2} s^{-1} increase in R_{10}), indicating that net CO_2 uptake decreased as the rate of respiration at 10 °C increased on this desert grassland.

Relationships of physiological components of NEE to the environment and LAI

Single-slopes regression models were used to relate weekly values of NEE and of physiological parameters at each site to environmental variables that were significantly correlated with NEE in simple regression (Table 3). Environmental variables explained between 5% and 40% of the variation in weekly observations of

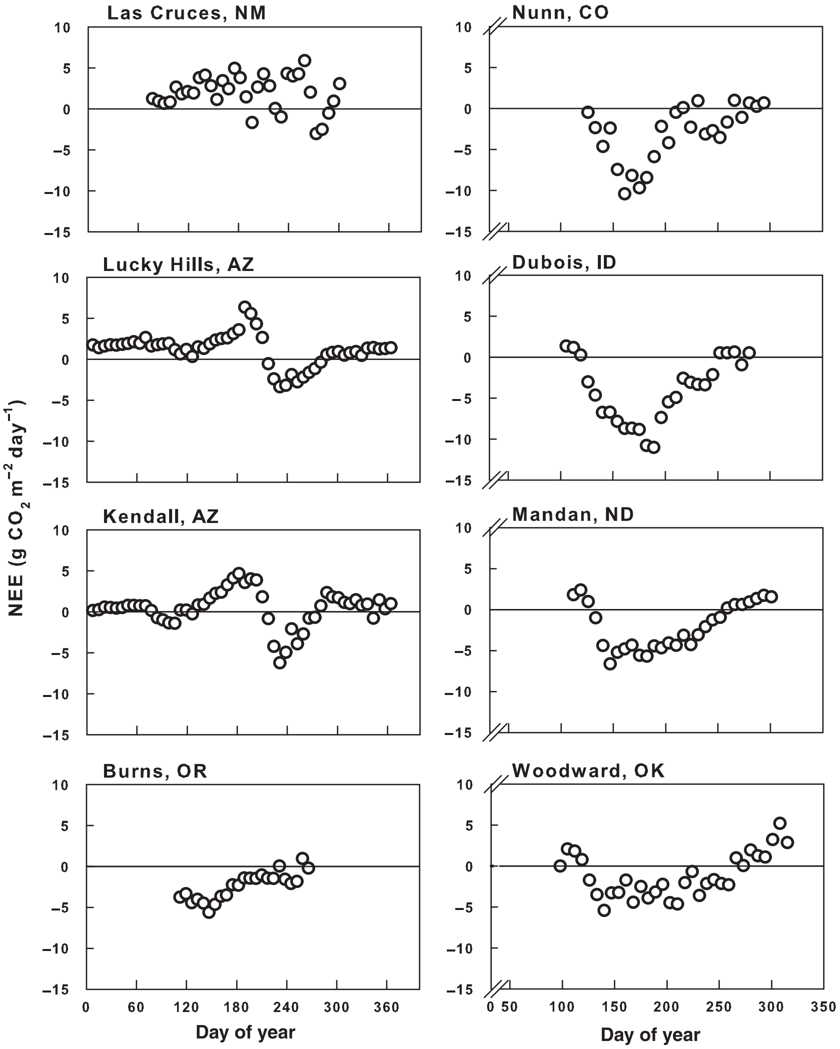

Fig. 1 Seasonal variation in net ecosystem exchange of CO_2 (NEE) for rangeland ecosystems at eight locations in the western United States. Measurements for a given week during the growing season were averaged for all years of observations ($n = 5$–11 years).

NEE ($P < 0.01$ for all models) and between 16% and 63% of the variance in $A_{\max}$ ($P < 0.0001$ for all models). Environmental variables explained $>24\%$ of the variance in R_{10} on all rangelands except the three Great Plains grasslands and $>13\%$ of the variance in α on all rangelands except the three desert ecosystems. Weekly values of NEE and of derived physiological parameters were 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 net radiation (Rn) and temperature (AT, ST) for grasslands at Nunn, Mandan, and Woodward and sagebrush steppe at Dubois. Time-lagged indices of precipitation, including mean precipitation per week for 5–7 weeks preceding flux measurements (ppt5–ppt7), and Rn were negatively correlated with NEE and positively correlated with physiological parameters. The implication is that both greater Rn and greater precipitation increased net CO_2 uptake by increasing $A_{\max}$ and α. Interestingly, the observation that R_{10} also increased with greater Rn and precipitation indicates that increases in CO_2 uptake were associated with increases in respiration rate at 10 °C. Both $A_{\max}$ and R_{10} responded positively to increased precipitation during the week of flux measurements (ppt1) at Woodward. The positive effect of ppt1 on respiration apparently more than offsets benefits of greater $A_{\max}$ for net CO_2 uptake, for greater ppt1 reduced net CO_2 uptake (positive association with NEE) on this mixed-grass prairie.

Canopy development may change seasonally as Rn, temperature, and precipitation change; hence, the flux–environment correlations we observed ultimately may result from environmental effects on leaf area or other properties of the plant canopy. Indeed, $A_{\max}$ was positively and linearly correlated with LAI for each of the three rangelands for which leaf area data are available

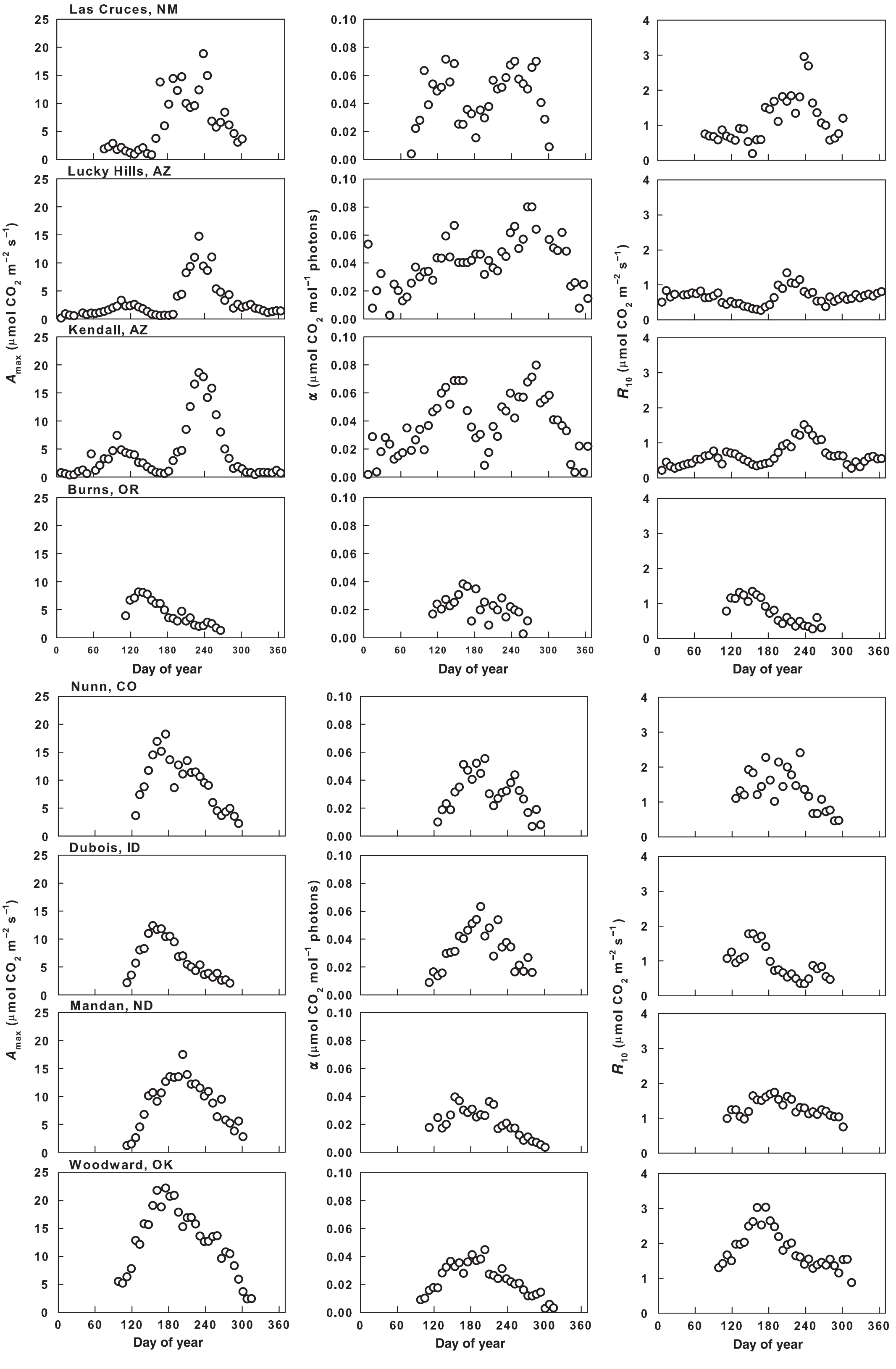

Fig. 2 Seasonal variation in the maximum rate of ecosystem gross photosynthesis (A_{max}), apparent light-use efficiency (α), and ecosystem respiration rate at 10 °C (R_{10}) for rangeland ecosystems at eight locations in the western United States. Measurements for a given week during the growing season were averaged for all years of observations ($n = 5$–11 years).

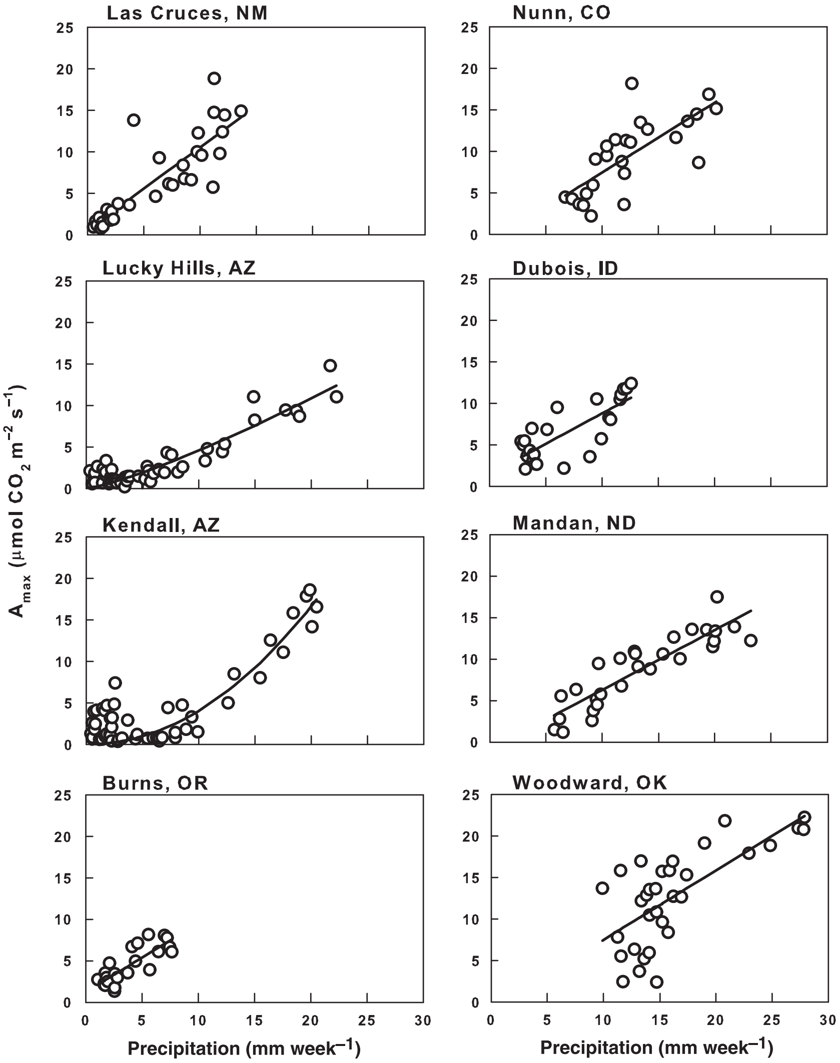

Fig. 3 Relationships between means of the rate of ecosystem gross photosynthesis (A_{max}) for each week during the growing season and weekly means of precipitation for rangelands at eight locations in the western United States. A_{max} is plotted as a function of precipitation per week averaged for the week A_{max} was measured and the previous 6 weeks (ppt7; Nunn), 7 weeks (ppt8; Kendall), or 4 weeks (ppt5; remaining rangelands). A_{max} for Lucky Hills and Kendall was fit with a power function of precipitation ($P < 0.001$). Lines shown for other rangelands are linear regression fits to data ($P < 0.0001$ for all regressions).

(not shown), including northern and southern mixed-grass prairie at Mandan and Woodward, respectively, and short-grass steppe at Nunn ($r^2 = 0.43$, 0.31, and 0.58, and $n = 69$, 44, and 30, respectively; $P < 0.0001$ for all regressions). Slopes of A_{max}–LAI regressions differed significantly among years at Mandan ($P < 0.0001$), but not at Nunn or Woodward ($P = 0.51$ and 0.30, respectively). Environmental effects on canopy photosynthesis were apparently mediated largely through changes in leaf area at the latter two sites.

Functional change

Slopes of regression relationships among A_{max}, α, and R_{10} and most of the environmental variables that explained variation in NEE differed significantly among years (Table 3). Interannual variability in physiological parameters, like variability in NEE, thus resulted partly from change in functional properties of these ecosystems or from functional change. Functional change explained between 10.4% (Woodward) and 32.0% (Nunn) of variance in A_{max} among the seven sites with significant A_{max}–environment relationships. Functional change accounted for 14.2% (Woodward) to 45.0% (Burns) of the variance in α and between 9.0% (Woodward) and 42.0% (Mandan) of variance in R_{10} values.

Functional change in net CO_2 uptake was highly correlated with functional change in at least one physiological component of NEE on six of the eight rangelands (Table 4). Functional change in NEE was associated with among-year differences in slopes of relationships between α and the environment for sagebrush steppe at Dubois and both northern and southern mixed-grass prairies at Mandan and Woodward, respectively. Among-year variation in A_{max}–environment relationships largely explained functional change in NEE on desert rangelands at Kendall and Lucky Hills, whereas year-to-year variation in R_{10}–environment relationships explained functional change in NEE on sagebrush steppe at Burns. Slopes of linear regressions linking differences in NEE caused by functional change with among-year differences in A_{max} and α caused by functional change were negative, indicating that CO_2 uptake was greatest during years when A_{max} and α were greatest. By contrast, CO_2 uptake on sagebrush steppe at Burns was greatest during years when R_{10} values were smallest. Functional change in NEE was not correlated with change in physiological components of CO_2 flux on either desert grassland at Las Cruces or shortgrass steppe at Nunn.

Functional change in NEE was explained partly by among-year differences in the maximum value of LAI for shortgrass steppe and mixed-grass prairie at Mandan and Woodward and partly by variation in the length of growing seasons for grasslands at Nunn and Woodward and for sagebrush steppe at Dubois. The greater was LAI during a given year, the greater was net CO_2 uptake. Among-year variation in $\mathrm{LAI}_{\mathrm{max}}$ was not correlated with among-year differences in α–environment relationships at Mandan and Woodward ($P = 0.99$), however, indicating that functional change in α and ultimately in NEE depended on factors other than leaf area. Net CO_2 uptake was also greater during years in which the growing season was longer (Dubois; $r^2 = 0.84$, $P < 0.0008$), began earlier (Nunn; $r^2 = 0.56$, $P = 0.09$), or ended later (Woodward; $r^2 = 0.30$, $P = 0.05$).

Table 2 Linear regression analyses for relationships between weekly values of net ecosystem CO_2 exchange (NEE; $\mathrm{g\,CO_2\,m^{-2}\,day^{-1}}$) and weekly values of A_{max} ($\mu\mathrm{mol\,m^{-2}\,s^{-1}}$; independent variable) for each of eight rangeland ecosystems

Location	Intercept	Slope	*n*	r^2	*P*-value
Las Cruces, NM	2.72	−0.12	145	0.03	0.01
Tucson, AZ (Lucky Hills)	2.30	−0.37	273	0.30	< 0.0001
Tucson, AZ (Kendall)	2.51	−0.46	298	0.62	< 0.0001
Burns, OR	0.63	−0.66	134	0.40	< 0.0001
Nunn, CO	−0.08	−0.33	105	0.21	< 0.0001
Dubois, ID	1.83	−0.97	185	0.57	< 0.0001
Mandan, ND	1.96	−0.46	178	0.48	< 0.0001
Woodward, OK	1.71	−0.24	309	0.16	< 0.0001

Discussion

Variation in NEE was better correlated with change in A_{max} than with variation in α or R_{10} for six of eight ungrazed native rangeland ecosystems in the western United States. Week-to-week variation in NEE and in derived physiological parameters, A_{max}, α, and R_{10}, correlated mainly with time-lagged indices of precipitation and water-related environmental variables, like PET, for desert sites and with net radiation and temperature for Great Plains grasslands. For most rangelands, the response of NEE to a given change in temperature, net radiation, or evaporative demand differed among years because the photosynthetic parameters A_{max} and α responded differently to environmental drivers among years. Differences in photosynthetic responses were not explained by differences in LAI alone, however. We obviously must better understand how CO_2 uptake is regulated to predict NEE of these ecosystems.

Seasonal patterns

When averaged among years, weekly values of photosynthetic and respiratory parameters displayed a strong seasonal pattern that was correlated with seasonal trends in NEE. Seasonal patterns of NEE correlated most strongly with trends in A_{max}. Canopy photosynthetic capacity, in turn, was positively correlated with time-lagged indices of precipitation at each site, underscoring the critical role of water availability in the functioning of rangeland ecosystems. Hollinger *et al.* (1999) and Syed *et al.* (2006) observed large seasonal variation in A_{max} and R_{10} in boreal forest and treed fen, respectively. In these relatively mesic ecosystems, seasonal variation in A_{max} was associated with variation in temperature.

Environmental and physiological regulation of interannual variation in NEE

Week-to-week change in NEE was associated primarily with change in canopy photosynthetic capacity rather than with variation in apparent light-use efficiency or in the basal respiration rate. The strong correlation between NEE and A_{max} may partly be a consequence of the temporal scale at which data were analyzed. Photosynthesis should respond quickly to changes in Rn and evaporative deficit. By contrast, respiration rates are sensitive to factors like soil water content and the availability of C substrates that may change more slowly or exert effects that are lagged in time (Davidson *et al.*, 2006). Ultimately, however, photosynthetic capacity may affect both respiration and apparent light-use

Table 3 Sums of squares (SS) associated with effects of environmental variation on net ecosystem CO_2 exchange (NEE; $g\,m^{-2}\,day^{-1}$), A_{max} ($\mu mol\,m^{-2}\,s^{-1}$), α ($mol\,CO_2\,mol^{-1}$ photons), and R_{10} ($\mu mol\,m^{-2}\,s^{-1}$) for each of eight rangeland ecosystems

Source	df	NEE	A_{max}	α ($\times 10^{-3}$)	R_{10}
Las Cruces					
RH	1	236.3** (+)	–	6.0** (–)	49.4** (+)
WS	1	106.4^{+} (+)	–	1.5 (–)	0.9 (–)
RH × Year	5	641.4**	–	15.0**	21.5**
WS × Year	5	302.0^{+}	–	36.3**	20.5**
Error	136	4372.9		98.9	94.6
Total	148	5659.0		158.0	186.9
Lucky Hills					
WS	1	130.0** (+)	1020.3** (–)	–	4.7** (+)
ppt5	1	66.8** (–)	1574.7** (+)	–	12.4** (+)
WS × Year	5	264.4**	714.8**	–	22.6**
ppt5 × Year	5	126.6**	177.4**	–	–
Error	276	1927.9	1881.7		31.7
Total	288	2510.7	5368.9		71.4
Kendall					
WS	1	535.4** (+)	1945.5** (+)	1.6** (–)	1.4(+)
Deficit	1	275.4** (+)	964.3** (+)	34.8** (+)	9.4**(–)
ppt7	1	249.0** (–)	3704.4** (+)	4.7** (+)	11.6**(+)
WS × Year	7	803.1**	1468.1**	42.4	25.0**
Deficit × Year	7	253.7**	863.3**	31.0**	–
ppt7 × Year	7	656.6**	1626.1**	–	5.8
Error	296	2615.6	5207.5	230	31.7
Total	320	5388.8	15 779.3	340	85.0
Burns					
AT	1	57.6** (+)	311.2** (–)	0.4^{+} (+)	10.9** (+)
Deficit	1	254.4** (+)	296.9** (–)	0.4^{+} (+)	2.2** (–)
PET	1	91.3** (–)	127.9** (+)	3.4** (–)	7.8** (+)
AT × Year	6	343.1**	104.6**	5.9**	9.6**
Deficit × Year	6	36.3*	12.7	1.7^{+}	1.3*
PET × Year	6	94.0**	33.6*	5.0**	5.4**
Error	108	309.1	273.8	11.2	10.6
Total	129	1185.8	1160.6	28.0	47.7
Nunn					
AT	1	125.4**(+)	205.1** (–)	14.6** (+)	2.0** (–)
Rn	1	825.9** (–)	1032.1** (+)	–	4.8* (+)
AT × Year	4	135.2*	1092.3**	15.1**	23.7**
Rn × Year	4	111.1^{+}	431.4**	–	–
Error	97	1320.9	1939.4	33.0	82.7
Total	107	2518.5	4700.3	62.0	113.2
Dubois					
WS	1	340.7** (–)	7.7 (+)	1.0** (+)	2.14** (–)
Rn	1	2200.7** (–)	986.6** (+)	20.0** (+)	–
ppt5	1	90.7** (–)	837.5** (+)	–	42.57** (+)
WS × Year	7	1421.5**	358.4**	28.0**	11.60**
Rn × Year	7	366.1**	102.0^{+}	5.0^{+}	–
ppt5 × Year	7	289.2**	224.7**	–	2.70^{+}
Error	168	1827.2	1195.6	67.0	32.97
Total	192	6536.1	3732.4	123.0	91.97
Mandan					
ST	1	676.3** (–)	2196.0** (+)	5.7** (–)	4.8** (+)
Rn	1	225.7** (–)	–	1.4** (+)	–
ppt5	1	86.9**(–)	–	–	–
ST × Year	6	305.2**	965.4**	5.5**	20.4**

Continued

Table 3. (*Contd.*)

Source	df	NEE	A_{max}	α ($\times 10^{-3}$)	R_{10}
Rn × Year	6	266.3**	–	2.0**	–
Error	165	1487.6	3343.2	14.9	23.4
Total	180	3048.0	6604.6	25.0	48.6
Woodward					
Rn	1	2614.6** (–)	2806.1** (+)	21.0** (+)	12.73** (+)
ppt1	1	675.3** (+)	1302.6** (+)	–	43.62** (+)
Rn × Year	10	1579.1**	2606.4**	12.6**	30.30**
Error	320	5080.2	18 336.2	54.8	267.77
Total	332	9949.2	25 051.3	88.5	344.42

NEE and its component processes were analyzed using a separate-slopes regression model. Shown are the degrees of freedom (df) for the model for NEE. Signs (+, –) of relationships between weekly values of NEE, A_{max}, α, and R_{10} and environmental variables for each rangeland are shown in parentheses. Environmental variables include air and soil temperature (AT, ST), evaporative deficit (deficit), net radiation (Rn), potential evapotranspiration (PET), relative humidity (RH), wind speed (WS), and various indices of time-lagged precipitation (e.g., ppt5; mean of precipitation per week over the 5 weeks preceding flux measurements).

$^{**}P<0.01$, $^{*}P<0.05$, $^{+}P<0.10$. The r^2 for a single-slopes regression model for each rangeland may be calculated by dividing the SS associated with the main effects of environmental variables by the total SS. The proportion of the variance in each flux component explained by functional change is calculated by dividing the SS associated with environment × year interaction terms by the total SS.

efficiency. Soil and ecosystem-level respiration rates are often highly correlated with rates of CO_2 uptake (Polley *et al.*, 2006), for example. For many of the rangelands we studied, A_{max}, α, and R_{10} all were positively correlated with Rn and precipitation.

Functional change

Functional change in NEE was associated with functional change in one or more of the physiological components of CO_2 flux on most rangelands. NEE–environment relationships thus differed among years partly because A_{max}, α, or R_{10} responded differently to environmental drivers among years. For most rangelands, functional change in NEE resulted from among-year variation in the response of photosynthetic parameters, A_{max} and α, to environmental drivers. Temporal variability in NEE was controlled mainly by variability in GPP in a boreal and two temperate pine forest (Luyssaert *et al.*, 2007) and by seasonal fluctuations in daytime net CO_2 uptake in a Mojave Desert shrubland (Jasoni *et al.*, 2005). By contrast, variability in NEE was explained by fluctuations in ecosystem respiration in European forests (Valentini *et al.*, 2000) and was stabilized by offsetting variation in GPP and respiration in a spruce-dominated forest (Richardson *et al.*, 2007).

The physiological component that best explained functional change in NEE was not necessarily the component that best explained variation in weekly values of NEE. Week-to-week change in A_{max} accounted for most of variation in weekly values of NEE on six of the eight rangelands, but among-year differences in A_{max}–environment relationships explained functional change in NEE only on desert rangelands at Kendall and Lucky Hills. Functional change in NEE was better predicted by year-to-year differences in the response of α to the environment, by among-year variation in maximum values of LAI, or by the combination of differences in α–environment slopes and LAI_{max} than by variation in A_{max}–environment relationships for sagebrush steppe at Dubois and the three Great Plains grasslands. Importantly, these four ecosystems are also those for which NEE correlated strongly with Rn rather than with precipitation or water-related parameters alone. Net CO_2 uptake on sagebrush steppe at Dubois and Great Plains grasslands was apparently regulated by the availability of light (Rn) and efficiency with which light was used in CO_2 capture during a least portion of most growing seasons.

Apparent light-use efficiency, measured as the rate of increase in GPP per unit of increase in PPFD, will be relatively small when little light is absorbed by the plant canopy, as when LAI is reduced, or when GPP per unit of absorbed light is small, as when photosynthesis is constrained. Drought (Nouvellon *et al.*, 2000) or excessive evaporative demand and low N availability (Turner *et al.*, 2003) all may reduce α and alter α–environment response functions either by reducing CO_2 fixation directly or by limiting canopy development.

Rangeland CO_2 fluxes are very sensitive to changes in canopy development (Sims & Bradford, 2001; Flanagan *et al.*, 2002; Li *et al.*, 2005; Phillips & Beeri, 2008; Polley *et al.*, 2008) and to factors like precipitation that affect biomass and LAI (Knapp & Smith, 2001; Flanagan *et al.*,

Table 4 Results of regression analyses relating net ecosystem exchange of CO_2 (NEE; $g\,m^{-2}\,day^{-1}$) calculated for each growing season using a separate-slopes regression model (effect of functional change) to maximum values of LAI (LAI_{max}) each season and to values of A_{max} ($\mu mol\,m^{-2}\,s^{-1}$), α ($mol\,CO_2\,mol^{-1}$ photons), and R_{10} ($\mu mol\,m^{-2}\,s^{-1}$) calculated for each season using separate-slopes models developed independently for each physiological parameter (independent variables)

Location	Independent variables	Intercept	Slope	r^2	P-value
Lucky Hills	A_{max}	3.68	−0.48	0.66	0.05
Kendall	A_{max}	2.32	−0.46	0.47	0.04
Burns	R_{10}	−1.51	3.60	0.90	0.0007
Dubois	α	3.68	−249.81	0.81	0.002
	A_{max}	5.66	−1.54	0.80	0.002
Mandan	α	-7.0×10^5	3.26	0.61	0.024
	R_{10}	−0.80	3.27	0.60	0.025
	R_{10}/LAI_{max}	5.54	−4.04/−5.16	0.84	0.012
Nunn	LAI_{max}	−0.61	−6.23	0.63	0.07
Woodward	α	−4.74	−190.76	0.29	0.05
	α/LAI_{max}	2.46	−182.27/−5.61	0.82	0.001

Shown are significant correlations with the greatest r^2 values for each rangeland. A single value of NEE, A_{max}, α, and R_{10} 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 for each flux. NEE for Mandan was fit to α and R_{10} values with a power function. Other relationships were fit with simple linear or multiple regression analysis.

2002; Knapp *et al*., 2002). Functional change in NEE thus may have resulted partly because changes in leaf area influenced the response of α or other components of CO_2 flux to environmental drivers. On northern mixed-grass prairie, for example, net CO_2 uptake increased more per unit increase in ST when LAI peaked late rather than early in the season (Polley *et al*., 2008). Not surprisingly, we found that weekly values of net CO_2 uptake correlated positively with LAI for each of the three grasslands for which we have repeated measurements of leaf area (Nunn, Mandan, Woodward). Year-to-year differences in the maximum value of LAI also provided the best single explanation for functional change in NEE at Nunn and were correlated with functional change at Mandan and Woodward. For mixed-grass prairies at Mandan and Woodward, however, functional change in NEE was explained partly by among-year differences in the response of α to environmental drivers that was not correlated with differences in LAI_{max}.

Functional change complicates climate-based predictions of CO_2 exchange and requires that we account for changes in the biological functioning of ecosystems in order to predict ecosystem C balance. Functional change in NEE of most rangelands resulted from change in the response of photosynthetic parameters to environmental drivers. The question of why environmental effects on A_{max} and α differed among years remains to be determined. Differences were not explained by change in LAI alone. Canopy photosynthetic capacity has been shown to track seasonal changes in the N content of grassland vegetation (Flanagan *et al*., 2002), indicating that year-to-year differences in the N concentration of vegetation could account for change in responses of A_{max} or α to temperature, Rn, and other environmental variables. Indeed, among-year variation in the C : N ratio of aboveground biomass partially explained interannual variation in NEE on the Northern Great Plains of the United States (Phillips & Beeri, 2008). But, canopy characteristics like live biomass and C : N ratio together explained relatively little of variability in grassland NEE. Phillips & Beeri (2008) used multiple regression analysis to model variability in growing season values of NEE as a function of canopy characteristics, annual precipitation, and year. Most of the variability in NEE was attributed to year. Clearly, a better understanding of environmental and other controls on CO_2 exchange will be required to accurately predict among-year variation in NEE of rangeland ecosystems.

Acknowledgements

Patricia Mielnick and Bill Dugas screened and compiled data. Stuart Hardegree and Howard Skinner provided insightful reviews.

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