

Long-Term Dynamics of Production, Respiration, and Net CO₂ Exchange in Two Sagebrush-Steppe Ecosystems

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Abstract

We present a synthesis of long-term measurements of CO₂ exchange in 2 US Intermountain West sagebrush-steppe ecosystems. The locations near Burns, Oregon (1995–2001), and Dubois, Idaho (1996–2001), are part of the AgriFlux Network of the Agricultural Research Service, United States Department of Agriculture. Measurements of net ecosystem CO₂ exchange (F_c) during the growing season were continuously recorded at flux towers using the Bowen ratio-energy balance technique. Data were partitioned into gross primary productivity (P_g) and ecosystem respiration (R_e) using the light-response function method. Wintertime fluxes were measured during 1999/2000 and 2000/2001 and used to model fluxes in other winters. Comparison of daytime respiration derived from light-response analysis with nighttime tower measurements showed close correlation, with daytime respiration being on the average higher than nighttime respiration. Maxima of P_g and R_e at Burns were both 20 g CO₂·m⁻²·d⁻¹ in 1998. Maxima of P_g and R_e at Dubois were 37 and 35 g CO₂·m⁻²·d⁻¹, respectively, in 1997. Mean annual gross primary production at Burns was 1 111 (range 475–1 715) g CO₂·m⁻²·y⁻¹ or about 30% lower than that at Dubois (1 602, range 963–2 162 g CO₂·m⁻²·y⁻¹). Across the years, both ecosystems were net sinks for atmospheric CO₂ with a mean net ecosystem CO₂ exchange of 82 g CO₂·m⁻²·y⁻¹ at Burns and 253 g CO₂·m⁻²·y⁻¹ at Dubois, but on a yearly basis either site could be a C sink or source, mostly depending on precipitation timing and amount. Total annual precipitation is not a good predictor of carbon sequestration across sites. Our results suggest that F_c should be partitioned into P_g and R_e components to allow prediction of seasonal and yearly dynamics of CO₂ fluxes.

Resumen

Presentamos una síntesis de mediciones de largo plazo del intercambio de CO₂ de 2 ecosistemas intermontanos de estepas de "Sagebrush" del oeste del Estados Unidos. Las localidades cercanas a Burns, Oregon (1995–2001) y Dubois, Idaho (1996–2001) son parte de la red AgriFlux del Servicio de Investigación Agrícola del Departamento de Agricultura del los Estados Unidos. Durante la estación de crecimiento se registraron en forma continua mediciones del intercambio neto de CO₂ del ecosistema (F_c) en torres de flujo usando la técnica de Bowen de la relación de balance de energía. Los datos se dividieron en productividad primaria bruta (P_g) y respiración del ecosistema (R_e) usando el método de función de respuesta a la luz. Los flujos invernales se midieron durante los periodos de 1999/2000 y 2000/2001 y se usaron para modelar los flujos en otros inviernos. La comparación de la respiración diurna, derivada del análisis de respuesta a la luz, con las mediciones nocturnas de la torre mostró una correlación estrecha siendo la respiración diurna en promedio mayor a la respiración nocturna. En 1998, los valores máximos a P_g y R_e en Burns fueron ambos de 20 g CO₂·m⁻²·d⁻¹. En Dubois, en 1997, los valores máximos de P_g y R_e fueron 37 y 35 g CO₂·m⁻²·d⁻¹, respectivamente. La media anual de la producción primaria bruta en Burns fue de 1 111 (rango 475–1 715) g CO₂·m⁻²·año⁻¹ o aproximadamente 30% menor que en Dubois (1 602, rango 963–2 162 g CO₂·m⁻²·año⁻¹). A través de los años, ambos ecosistemas fueron depósitos netos de CO₂ atmosférico con una media de intercambio neto de CO₂ del ecosistema de 82 g CO₂·m⁻²·año⁻¹ en Burns y 253 g CO₂·m⁻²·año⁻¹ en Dubois, pero en base anual, cualquier sitio pudo ser un depósito o fuente de C, dependiendo de la cantidad de precipitación y época en que esta ocurre. Los valores medios y rangos de P_g y R_e de los ecosistemas de "Sagebrush" de nuestro estudio fueron similares a los valores de los ecosistemas de zacates cortos y praderas mixtas del norte.

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Nuestros resultados sugieren que F_c debe ser dividida en los componentes de P_g y R_e para permitir la predicción de las dinámicas estacional y anual de los flujos de CO_2 .

Key Words: CO_2 flux tower measurements, gross primary production, ecosystem respiration, flux partitioning, daytime respiration, nighttime respiration, light-response function method, US Intermountain West.

INTRODUCTION

Sagebrush-steppe (*Artemisia-Pseudoroegneria*) ecosystems cover more than half (36 million ha) of the shrub-steppe subzone of the US Intermountain West and represent about 14% of the total US rangeland area (Yorks 1980; West 1983). Sagebrush rangelands are used as a forage resource for livestock production and have important wildlife and biogeochemical functions (Rickard et al. 1988). Since the mid-1990s, continuous measurements of CO_2 exchange were obtained at 2 sagebrush-steppe sites in the US Department of Agriculture-Agricultural Research Service (USDA-ARS) AgriFlux Network (Svejcar et al. 1997; Angell et al. 2001; Gilmanov et al. 2003a). These long-term measurements covered a wide range of environmental conditions (cold and warm, wet and dry years) that make them valuable for modeling CO_2 fluxes across large areas of the Intermountain West occupied by this ecosystem. Information concerning the magnitudes of these fluxes and their relationships to major environmental factors is essential for understanding the role of sagebrush-steppe ecosystems in regional and continental carbon budgets under various climate change and management scenarios.

MATERIALS AND METHODS

Tower CO_2 flux data analyzed in this study were obtained at 2 sagebrush-steppe sites located in Oregon and Idaho, United States. The Oregon site was established in 1995 on the Northern Great Basin Experimental Range (43°29'N, 119°43'W, 1 380 m elevation), located 64 km west of Burns, Oregon. The site is a 65-ha ungrazed Wyoming big sagebrush (*Artemisia tridentata* Nutt., subspecies *wyomingensis*) community with shrub canopy cover of about 10%. Vegetation includes Thurber's needlegrass (*Stipa thurberiana* Piper), bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), Sandberg's bluegrass (*Poa sandbergii* Vasey), bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) Smith), prairie lupine (*Lupinus lepidus* Dougl.), hawkbeard (*Crepis occidentalis* Nutt.), and longleaf phlox (*Phlox longifolia* Nutt.). Maximum leaf area index (LAI) is estimated as $0.56 \text{ m}^2 \cdot \text{m}^{-2}$. Soil at the site is described as aridic duric haploxerolls and orthidic duricerolls, with coarse-to-fine sandy loam texture in the Holte-Milcan complex with 0%–2% slopes. Grazing at the site has been excluded since 1995.

The Idaho site is located at the US Sheep Experiment Station (44°16'N, 112°08'W, 1 700 m elevation), about 10 km north of Dubois, Idaho. Shrubs at the site include three-tip sagebrush (*Artemisia tripartita* Rydb. spp. *rupicola* Beetle), green rabbitbrush (*Chrysothamnus viscidifloris* [Hook] Nutt.), and gray horsebrush (*Tetradymia canescens* DC.); shrub canopy cover is about 40%. Herbaceous vegetation is dominated by bluebunch wheatgrass and arrowleaf balsamroot (*Balsamorhiza sagittata* [Pursh] Nutt.). Other common understory species include needle-and-thread grass (*Stipa comata* Trin. and Rupr.), Sand-

berg's bluegrass, junegrass (*Koeleria cristata* L. Pers.), yarrow (*Achillea millefolium* L.), tapertip hawkbeard (*Crepis acuminata* Nutt.), longleaf phlox, and milkvetches (*Astragalus* spp.). Maximum measured LAI for Dubois was $1.03 \text{ m}^2 \cdot \text{m}^{-2}$. Soils are classified as a complex of typical calcixerolls, pachic haploxerolls, and pachic argixerolls of loamy texture with slopes of 0%–12%.

Climatic characteristics of the 2 sites (Fig. 1) are quite similar (mean temperature 7.6°C and 6.2°C, and precipitation 283 mm and 302 mm at the Burns and Dubois sites, respectively), but seasonal characterizations of the 2 sites are different, which affect their productivity. This agrees with growing season duration (determined from the tower-flux data as a period when gross photosynthetic assimilation is continuously positive), where the Dubois growing season (202, range 190–220 d) is 45 days shorter than that at the Burns site (247, range 218–273 d). Precipitation distribution at the Dubois site has a pronounced May–June maximum, which makes the Dubois site more favorable for biomass production than the Burns site. Drought is typical at Burns from mid-June to September.

Measurements of net CO_2 exchange, F_c , $\text{mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (see Table 1 for the list of symbols and units), were conducted at both sites using Bowen ratio-energy balance (BREB) instrumentation (Model 023/ CO_2 Bowen ratio system, Campbell Scientific, Logan, UT). Methodology and operation of the BREB system were described in detail by Dugas (1993), Campbell Scientific (1995), and Dugas et al. (1999). At the data postprocessing stage, fluxes were corrected 1) for the effects of vapor density and temperature differences at the 2 sampling heights (Webb et al. 1980) and 2) for the conditions when the direction of the heat or water flux was opposite to the sign of the temperature or moisture gradient, respectively, or when the Bowen ratio was close to -1.0 (Ohmura 1982). In the latter case, estimation of the turbulent transfer coefficient K_b could not be made with the BREB algorithm but was obtained using the empirical relationship between K_b and wind speed (W. A. Dugas, personal communication, 2004) or estimated using wind speed and the stability function for heat transfer (Monteith and Unsworth 1990).

Measurements at the Burns site began in 1995 and at the Dubois site in 1996 and were limited to April–October through 2000. During the winters of 1999/2000 and 2000/2001, systematic measurements of winter fluxes were made, which required thermal insulation and heating of the field equipment. CO_2 flux measurements during the winters of 1999/2000 and 2000/2001 were used to identify phenomenological models relating wintertime fluxes to environmental factors (Gilmanov et al. 2004b) that could be used to gap-fill winter fluxes for years without cold-season measurements.

CO_2 flux data generated by the BREB algorithm (including corrections) were postprocessed for outliers by visual inspection of diurnal fluxes (time domain graphs) and physiological light-response functions. These missing points were gap-filled using appropriate algorithms at the later stages of analysis. Gap-filling techniques consisted of either interpolation of time series or

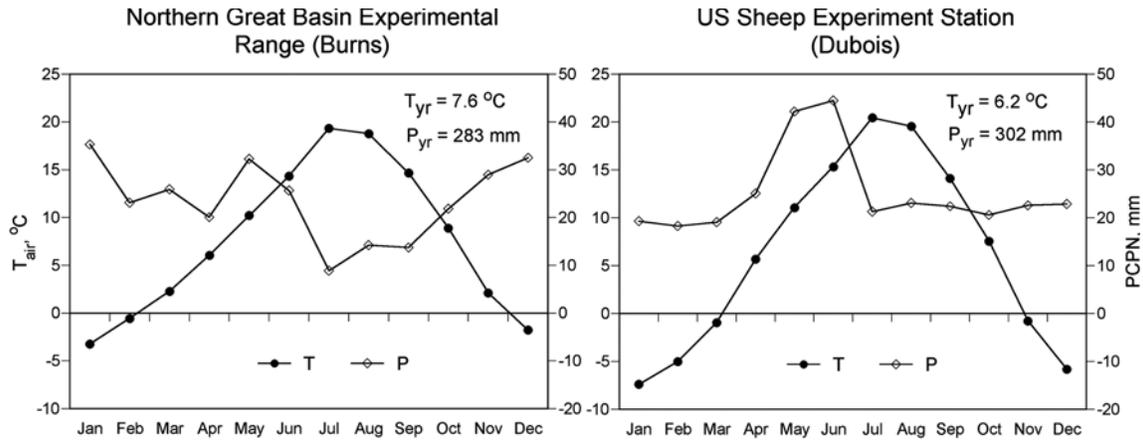


Figure 1. Climate diagrams of the Burns and Dubois sites (monthly temperature and monthly precipitation plotted on the scale $5^{\circ}\text{C} = 10\text{ mm H}_2\text{O}$). Periods with the temperature curve above the precipitation curve indicate drought.

physiologically based regressions of fluxes on radiation, temperature, and other factors (see Table 2 for percentage gap-filled data).

To describe CO_2 exchange during daytime, we introduced the variable $P(t)$, which was defined as $P(t) = F_c(t)$ for daytime (photon flux density $Q > 0$) and as $P(t) = 0$ during night ($Q = 0$). Analysis of hundreds of diurnal flux measurement data sets in the sagebrush-steppe ecosystem demonstrated (Gilmanov et al. 2003a) that for days without precipitation and for some days with precipitation, dynamics of $P(t)$ were mostly determined by $Q(t)$. For days without moisture or temperature stress, the relationship between Q and P can be expressed as

$$P(t) = f(Q[t], \alpha, A_{max}, r_d, \theta) + e_p, \quad [1]$$

where α , A_{max} , r_d , θ are empirical parameters and e_p is random error. Among many forms for the light-response function (1), the nonrectangular hyperbolic equation (Rabinowitch 1951) is the most flexible tool that allows physiological interpretation of its parameters:

$$f(Q, \alpha, A_{max}, \theta, r_d) = \frac{\alpha Q + A_{max} - \sqrt{(\alpha Q + A_{max})^2 - 4\alpha A_{max} \theta Q}}{2\theta} - r_d, \quad [2]$$

where α is the initial slope of the light-response curve, A_{max} is light-saturated gross photosynthesis, r_d is average daytime ecosystem respiration, and θ is the curvature parameter ranging from $\theta = 0$ for classical rectangular hyperbolic model to $\theta = 1$ for the Blackman-type saturated linear response.

During certain days, especially under moisture stress, the light-response function shows a hysteresis when the morning branch of the $P(Q)$ graph is higher than that in the afternoon. Taking into account that respiratory processes are more sensitive to temperature than photosynthesis, we described hysteresis by the light-temperature-response function

$$P(t) = g(Q[t], T_s[t], \alpha, A_{max}, r_d, \theta, r_0, k_T) + e_p, \quad [3]$$

where e_p is random error and the function $g(Q, T_s, \alpha, A_{max}, r_d, \theta, r_0, k_T)$ is a generalization of equation 2 obtained by the introduction of the soil temperature-dependent term $r_d(T_s) = r_0 \exp(k_T T_s)$:

$$g(Q, T_s, \alpha, A_{max}, \theta, r_0, k_T) = \frac{\alpha Q + A_{max} - \sqrt{(\alpha Q + A_{max})^2 - 4\alpha A_{max} \theta Q}}{2\theta} - r_0 \exp(k_T T_s). \quad [4]$$

Estimation of parameters α , A_{max} , r_d , θ , r_0 , and k_T that best fit the data was achieved using iterative nonlinear identification procedures from the ‘‘Global Optimization’’ package by Loehle Enterprises (2006) working under the Mathematica® system.

Description of daytime respiration by the term $r_0 \exp(k_T T_s)$ in equation 4 has the potential to overestimate respiration, because decreases in $P(t)$ during daytime may be caused not only by increasing respiration, but also by decreasing photosynthesis (e.g., due to stomatal regulation). Therefore, estimates of daytime respiration (and, therefore, gross primary productivity) based on equation 4 are considered upper estimates. One way to assess the magnitude of this overestimation is to compare r_d with measured r_n . Total daytime net production (P_d) and total daytime ecosystem respiration (R_d) were calculated as integrals of corresponding rates from sunrise (t_r) to sunset (t_s):

$$P_d = \int_{t_r}^{t_s} P(t) dt, \quad [5]$$

$$R_d = r_0 \int_{t_r}^{t_s} \exp(k_T T_s[t]) dt, \quad [6]$$

where $P(t)$ is directly provided by flux measurements, while r_0 and k_T are obtained from light-response analysis. Then, daily gross primary productivity (P_g) was calculated as the sum of these 2 values:

$$P_g = P_d + R_d. \quad [7]$$

Analysis of wintertime fluxes demonstrated that it was possible to find relatively stable regression relationships for winter flux for particular periods (late fall, winter, early spring) and soil temperature intervals ($T_s < -1^{\circ}\text{C}$; $-1^{\circ}\text{C} < T_s < +1^{\circ}\text{C}$; $T_s > +1^{\circ}\text{C}$) to factors such as soil temperature, wind speed,

Table 1. Table of symbols.

Latin symbols	
A	Intercept of the regression line
A_{max}	Light-saturated gross photosynthesis, $\text{mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$
$A_{max, wk}$	Mean weekly light-saturated gross photosynthesis, $\text{mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$
b	Slope of the regression line
e_x	Error term for variable x in regression equation
$f(\dots)$	Function of given arguments
F_c	Net ecosystem CO_2 exchange, $\text{mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$
F_d	24-h integral of net ecosystem CO_2 exchange, $\text{g CO}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$
$g(\dots)$	Function of given arguments
GPP	Annual gross primary production, $\text{g CO}_2 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$
K_h	Turbulent transfer coefficient, $\text{m}^2 \cdot \text{s}^{-1}$
k_T	Coefficient of the exponential relationship of respiration on temperature ($^{\circ}\text{C}$) $^{-1}$
n	Sample size
NEE	Annual net ecosystem CO_2 exchange, $\text{g CO}_2 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$
NEE_{cum}	Cumulative NEE , $\text{g CO}_2 \cdot \text{m}^{-2}$
p	Probability level, dimensionless
P	Daytime CO_2 flux, $\text{mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$
PAR	Photosynthetically active radiation, $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$
P_d	Daytime net CO_2 flux integral, $\text{g CO}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$
P_g	Gross primary productivity, $\text{mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ or $\text{g CO}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$
$PCPN$	Atmospheric precipitation, $\text{mm} \cdot \text{day}^{-1}$ or $\text{mm} \cdot \text{y}^{-1}$
$PCPN_{hyd}$	Hydrologic year precipitation, $\text{mm} \cdot \text{y}^{-1}$
P_{yr}	Mean annual precipitation, $\text{mm} \cdot \text{y}^{-1}$
Q	Photon flux density, $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ or daily PAR total, $\text{mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$
r	Correlation coefficient
r_0	Mean daytime ecosystem respiration at reference temperature $T_s = 0$, $\text{mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$
r_d	Mean daytime ecosystem respiration, $\text{mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$
$r_{d, wk}$	Mean weekly daytime ecosystem respiration, $\text{mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$
R_d	Daytime integral of ecosystem respiration, $\text{g CO}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$
R_e	Total ecosystem respiration, $\text{mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ or $\text{g CO}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$
RE	Annual ecosystem respiration, $\text{g CO}_2 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$
r_n	Nighttime ecosystem respiration, $\text{mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$
$r_{n, wk}$	Mean weekly nighttime ecosystem respiration, $\text{mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$
SE	Standard error
S_x	Standard error of parameter x
t	Time or Student's t statistic (depending on context)
t_r	Time of sunrise
t_s	Time of sunset
T_s	Soil temperature, $^{\circ}\text{C}$
T_{yr}	Mean annual air temperature, $^{\circ}\text{C}$
Greek symbols	
α	Apparent quantum efficiency, $\text{mg CO}_2 \cdot \mu\text{mol}^{-1}$, $\text{g CO}_2 \cdot \text{mol}^{-1}$, or $\text{mmol CO}_2 \cdot \text{mol}^{-1}$
α_{wk}	Mean weekly apparent quantum efficiency, $\text{mg CO}_2 \cdot \mu\text{mol}^{-1}$, $\text{g CO}_2 \cdot \text{mol}^{-1}$, or $\text{mmol CO}_2 \cdot \text{mol}^{-1}$
θ	Curvature of the light-response curve, dimensionless

and snow depth (Gilmanov et al. 2004b). These empirical relationships were used to gap-fill winter fluxes for years when winter flux measurements were not available.

Annual totals of gross primary production (GPP) and ecosystem respiration (RE) were calculated as the sums of

measured or estimated daily values, while net ecosystem CO_2 exchange, $NEE = GPP - RE$. Both the daily estimates of P_g , R_e , and F_c , as well as their annual totals, GPP, RE, and NEE, based on tower flux measurements, have errors characterized by a number of systematic and random components (Moncrieff et al. 1996; Baldocchi 2003; Foken et al. 2004). A formal procedure for uncertainty analysis and error propagation calculation for tower flux measurements and postprocessing is not yet available, although several research teams have come up with error approximations for annual flux totals, with SE_{NEE} in the $90\text{--}250 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ range for grassland, wetland, crop, and forest ecosystems on relatively level terrain (Goulden et al. 1996; Lee et al. 1999; Yang et al. 1999; Lafleur et al. 2001; Lohila et al. 2004; Hagen et al. 2006).

RESULTS

At both the Burns and Dubois sites, meteorological conditions during the years of study were different from long-term averages (Table 2). At Burns, the weather was warmer and wetter than normal, whereas at Dubois, the weather was colder and drier than normal. Observations at both sites included years with contrasting weather, with 1998 being the wettest and 2001 being the driest, resulting in considerable deviations from long-term precipitation averages. Particular weather events occurred that were important for interpretation of weather–productivity relationships at the Burns site. At the peak of the 1996 growing season at the Burns site, a sudden drop of temperature occurred on 18 and 19 June with daily minima of -7.2°C and -5.9°C , respectively. This apparently resulted in severe frost damage of photosynthetic tissues, as demonstrated by a nearly 2-week-long drop of gross primary productivity from $P_g > 10 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ during the first 2 weeks of June to values less than $1 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ during the third and fourth weeks of June 1996. Although photosynthetic capacity of the vegetation was somewhat restored during July and August, total annual gross primary production (GPP) for 1996 was substantially lower than expected from the temperature and amount of precipitation received that year.

Light-Response Functions

Light-response functions for days when CO_2 exchange was driven by photosynthetically active radiation (PAR) are shown in Figure 2, which describes the nonrectangular hyperbolic fit (equation 2) to the data for day 166 at Burns in 1998 and for day 142 at Dubois in 2000, which exemplify cases of close $P(Q)$ relationships.

More commonly, temperature or moisture conditions also can affect CO_2 exchange in addition to radiation. This results in a hysteresis effect on light response. Those cases are illustrated in Figure 3, which shows typical light-temperature-response surfaces $P(Q, T_s)$ for day 155 at Burns 1996 and day 183 at Dubois 1998.

Examination of the time-domain plots of light-response parameters demonstrated that patterns existed for seasonal and year-to-year dynamics. These patterns reflected both the phenological dynamics of production and respiration during the year (regular uni- or bimodal patterns) and the fluctuations during particular years (Figs. 4, 5; Table 3). For example,

Table 2. Climatic characteristics and percent gap-filled flux data for the Burns and Dubois sites.

Year	Mean air temperature, °C	Hydrologic year ¹ precipitation, mm	Photosynthetically active radiation, mol·m ⁻² ·y ⁻¹	Percent gap-filled data during measurement period	Percent gap-filled data for the whole year
Burns, Oregon					
1995	8.2	360	11 590	12	71
1996	8.0	336	11 209	13	55
1997	7.6	334	12 079	5	44
1998	7.8	569	11 435	10	43
1999	8.2	394	12 152	37	62
2000	7.7	268	12 029	31	31
2001	7.9	205	12 000	26	64
Mean for the period	7.9	352	11 785	21	53
Long-term mean	7.6	283	Not available	Not available	Not available
Dubois, Idaho					
1996	5.2	244	11 408	28	63
1997	5.1	361	11 209	30	56
1998	5.4	396	10 644	19	42
1999	5.1	307	11 118	12	35
2000	5.4	210	11 333	3	6
2001	5.8	181	11 055	12	12
Mean for the period	5.3	283	11 128	16	36
Long-term mean	6.2	302	Not available	Not available	Not available

¹Hydrologic year is defined as the period from 1 October of the previous year to 30 September of the current year.

parametric depictions of data from the Burns and Dubois sites during 1998 (a year with high precipitation) showed that photosynthetic (α , A_{max}) and respiratory (r_d) activity at Burns was concentrated mostly in May–June, while at Dubois, relatively high CO₂ exchange was maintained during the whole summer with a decline in October. During 2001 (a drought year, especially at Burns), both photosynthesis and respiration were substantially lower than in 1998. At Burns, after the mid-May maximum of photosynthesis, an abrupt reduction in both apparent quantum yield (α) and maximum photosynthesis (A_{max}) occurred at the end of May, resulting in reduced primary production during the following months. At Dubois, water-stress conditions of 2001 resulted in a more gradual decrease of light-response parameters from mid-June to the end of August (Fig. 5).

With the interpolation of parameters $\alpha(t)$, $A_{max}(t)$, and $r_d(t)$ for the periods with missing measurements and using these estimates in light-response functions, equations 2 and 4 provide an option to gap-fill fluxes for days when meteorological drivers $Q(t)$ and $T_s(t)$ are available. The advantage of this gap-filling method compared to using only the time series $\{F_c(t)\}$ itself is that it uses information about $Q(t)$ and $T_s(t)$ during the period of missing measurements, which are often crucial in determining daytime fluxes.

Besides seasonal dynamics, light-response parameters at both sites exhibit yearly variation, as shown in Table 3. While average annual maxima of mean weekly quantum efficiency (α_{wk}) are similar at Burns and Dubois (27 and 28 mmol CO₂·mol photons⁻¹, respectively), the plateau of gross photosynthesis ($A_{max,wk}$) and daytime respiration ($r_{d,wk}$) at the Burns

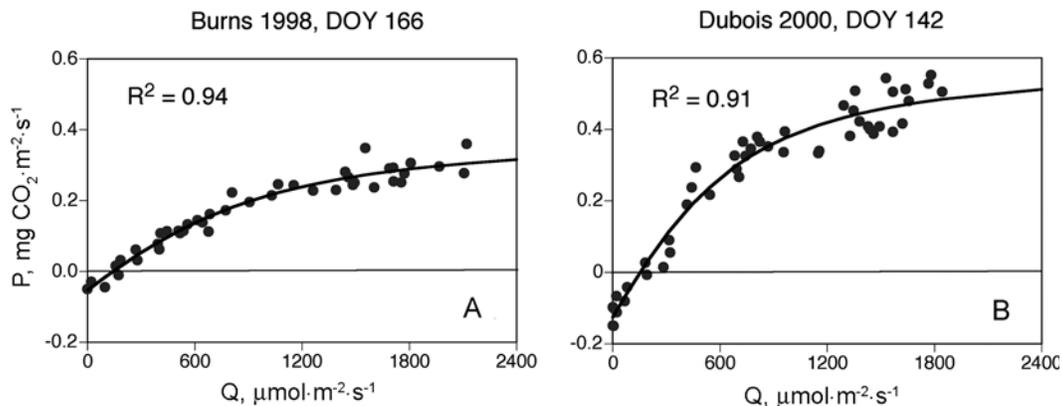


Figure 2. Nonrectangular hyperbolae (equation 2) fitted to the light-response data for **A**, day 166 at Burns 1998 ($\alpha = 0.0004$ mg CO₂·μmol⁻¹; $A_{max} = 0.44$ mg CO₂·m⁻²·s⁻¹; $\theta = 0.69$; $r_d = 0.053$ mg CO₂·m⁻²·s⁻¹; $R^2 = 0.94$), and **B**, day 142 at Dubois 2000 ($\alpha = 0.0009$ mg CO₂·μmol⁻¹; $A_{max} = 0.72$ mg CO₂·m⁻²·s⁻¹; $\theta = 0.71$; $r_d = 0.126$ mg CO₂·m⁻²·s⁻¹; $R^2 = 0.91$).

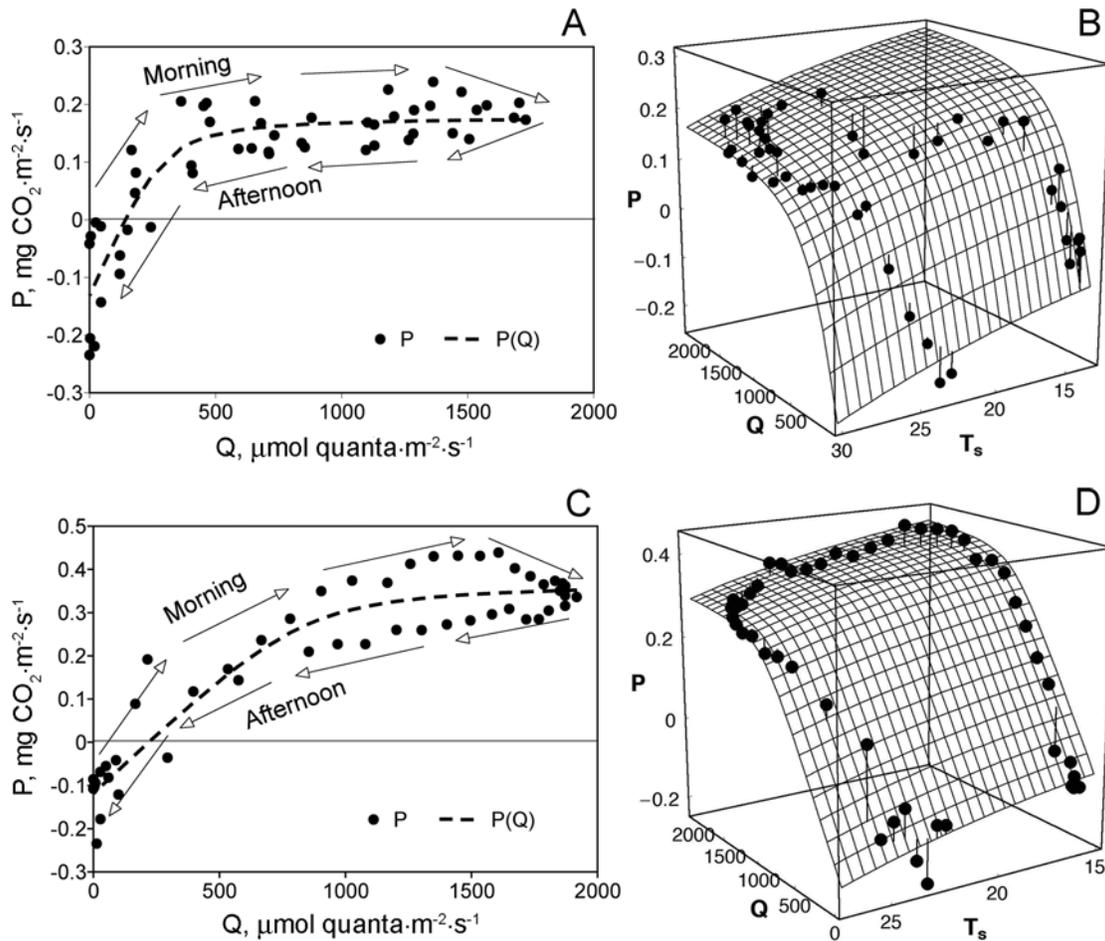


Figure 3. Hysteresis of light-response in sagebrush-steppe ecosystems shown for day 155 at Burns 1996: **A**, P - Q diagram and light-response curve fitted by equation 2 (dashed line); **B**, light-temperature-response surface described by equation 4 ($\alpha = 0.0011 \text{ mg CO}_2 \cdot \mu\text{mol}^{-1}$; $A_{max} = 0.43 \text{ mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; $\theta = 0.71$; $r_0 = 0.052 \text{ mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; $k_T = 0.051 \text{ (}^\circ\text{C)}^{-1}$; $R^2 = 0.88$), and day 183 at Dubois 1998; **C**, P - Q diagram and light-response curve fitted by equation 2 (dashed line); and **D**, light-temperature-response surface described by equation 4 ($\alpha = 0.0005 \text{ mg CO}_2 \cdot \mu\text{mol}^{-1}$; $A_{max} = 0.47 \text{ mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; $\theta = 0.98$; $r_0 = 0.020 \text{ mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; $k_T = 0.084 \text{ (}^\circ\text{C)}^{-1}$; $R^2 = 0.96$).

site are substantially lower than those at Dubois (0.46 and $0.10 \text{ mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ compared to 0.59 and $0.14 \text{ mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, respectively).

Daytime vs. Nighttime Respiration

Comparison of daytime (r_d) and nighttime (r_n) respiration for various sites and years reveals that CO_2 evolution during light and dark periods of the same day may be different (e.g., due to precipitation events), though the trend is toward a 1:1 relationship. The regression model for individual days at the Burns site in 1998 ($n = 227$ and $R^2 = 0.63$) was

$$r_d = (0.0084 \pm 0.0027) + (1.029 \pm 0.053)r_n. \quad [9]$$

The intercept was significantly greater than 0, while the slope was not significantly different from 1 ($p = 0.05$). For Dubois 2000 ($n = 348$ days, $R^2 = 0.74$) the regression model,

$$r_d = (0.0064 \pm 0.0018) + (0.961 \pm 0.031)r_n \quad [10]$$

had an intercept that was significantly greater than 0, and a slope that was not significantly different from 1 ($p = 0.05$).

The relationship becomes clearer if we group day- and nighttime respiration data into weekly blocks. For Burns 1998, the relationship between weekly averaged daytime and nighttime respiration was given by

$$r_{d,wk} = (0.0041 \pm 0.0017) + (1.02 \pm 0.11)r_{n,wk}. \quad [11]$$

This showed that the regression lies above the 1:1 line, though nearly parallel to it.

The regression equation for the weekly grouped Dubois 2000 data was

$$r_{d,wk} = (-0.031 \pm 0.001) + (1.140 \pm 0.078)r_{n,wk}. \quad [12]$$

Compared to the daily data where outliers tended to distort the overall relationship, regression of the weekly grouped data, calculated taking into account errors in both variables (we used the LinearFit program by Harrison 1996), showed that both the intercept and slope were significantly greater than the 1:1 relationship. This means that for Dubois 2000 data, daytime respiration on average was higher than nighttime respiration.

Table 4 summarizes regression parameters for weekly daytime vs. nighttime respiration for all years of study. Out of all

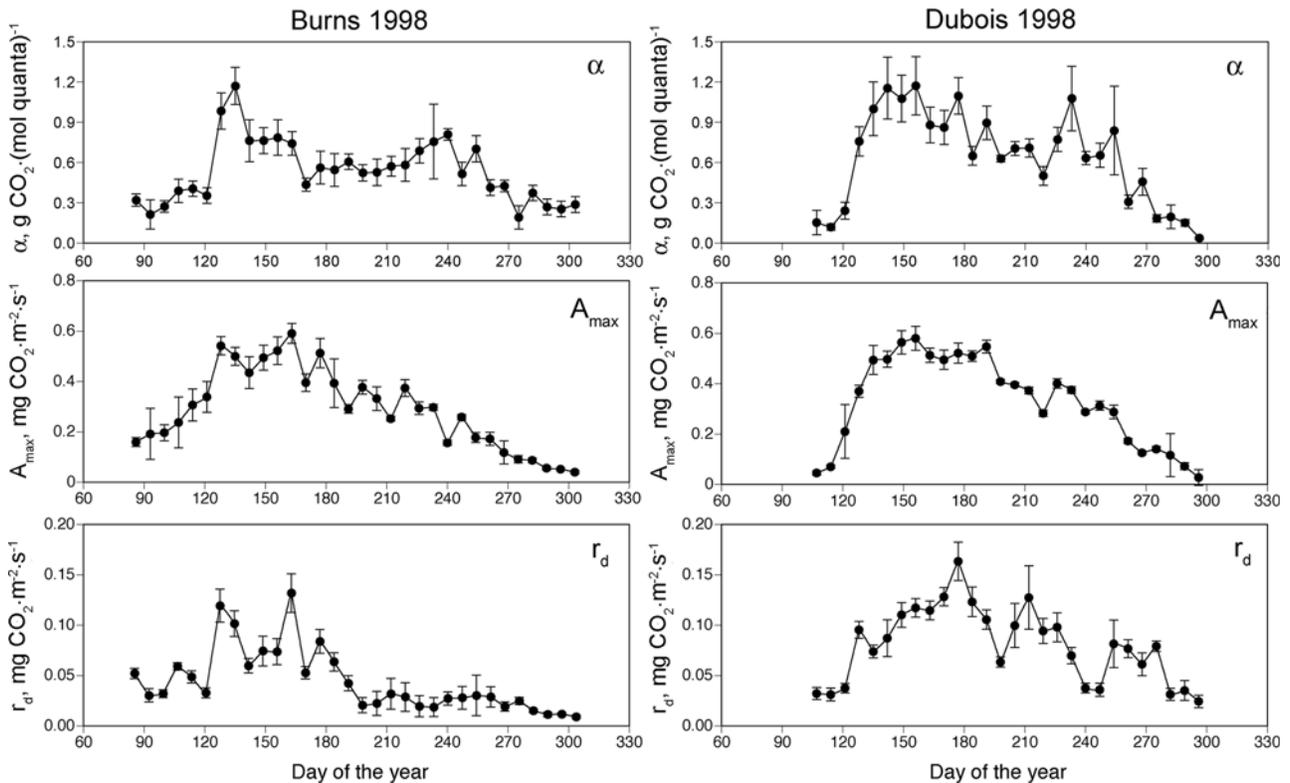


Figure 4. Dynamics of light-response parameters for the Burns and Dubois sites during 1998 (a year with high precipitation). Data include weekly means (dots) and their standard errors (bars) for quantum yield (α panels), maximum photosynthesis (A_{max} panels), and average daytime respiration (r_d panels).

13 years, only in 1 year (Dubois, 1999) the slope b of the regression $r_{d,wk} = a + br_{n,wk}$ was less than 1. Nevertheless, because of high data variability and resulting high standard errors (s_b) of the b estimates for individual years, only in 3 years out of 13 were the regression slopes significantly greater than 1 ($p < 0.05$) (Burns, 1999, 2000; Dubois, 2000).

Combining data across all years for both sites into a single scatter diagram and calculating the corresponding regressions (Fig. 6) indicated that slopes of the linear regression of $r_{d,wk}$ vs. $r_{n,wk}$ were greater than 1 ($p = 0.001$) (Table 4).

Seasonal and Yearly Dynamics of CO₂ Exchange Components

Estimates of daytime respiration (R_d) from light-response analysis were combined with daytime flux integrals (P_d) to obtain daily gross primary productivity (P_g) (Figs. 7A, 8A). The estimated daytime (R_d) and measured nighttime (R_n) respiration values were summed to obtain 24-hour respiration ($R_e = R_d + R_n$, Figs. 7B, 8B). Gap-filling during daytime was performed using light-response equations 2 and 4 with parameters interpolated according to their seasonal patterns (Figs. 4, 5). Nighttime fluxes were gap-filled using several methods, including 1) linear interpolation in cases with few missing 20-minute values, 2) use of diurnal patterns of respiration curves (Falge et al. 2001), 3) applying regressions of nighttime fluxes to environmental drivers (e.g., soil temperature and moisture), or 4) extrapolation of light-response functions for the corresponding day to PAR values of 0 ($Q = 0$). During

winter, gap-filling was performed using regressions of F_c with soil temperature, wind speed, and snow depth established for periods with available flux measurements (Gilmanov et al. 2004b).

Maximum P_g at Burns occurred in late May–early June and reached $20 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ (1998). Maximum R_e was also nearly $20 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ for several years, especially 1996. During 7 years of measurements, various combinations of production and respiration processes occurred, resulting in substantial changes of annual carbon budget. Considerable variation was evident in particular years with a source of CO₂ in 1996 and 2000 and a sink in 1997 and 1998. Across the 7-year period, the sagebrush-steppe site at Burns accumulated $573 \text{ g CO}_2 \cdot \text{m}^{-2}$ (Fig. 7D). This is equivalent to about 4 times the mean aboveground biomass at this site ($767 \text{ kg} \cdot \text{DM} \cdot \text{ha}^{-1}$). Thus, for our study years, the Burns site may be characterized as a weak sink for atmospheric carbon.

The carbon cycle at the Dubois site was distinguished by significantly higher assimilation (P_g of $37 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ was observed in 1997) and respiration fluxes (maximum R_e of $35 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ occurred the same year) than that at Burns. While the seasonal pattern of $P_g(t)$ reached a single peak in May–June, the seasonal curve of $R_e(t)$ typically was bimodal with a first peak during the growing season and a smaller second maximum in the fall (Fig. 8B). The curve of accumulated net ecosystem exchange (NEE_{cum}) (Fig. 8D) indicates that production and respiration in this ecosystem were in balance during 1996–1997. The ecosystem accumulated significant

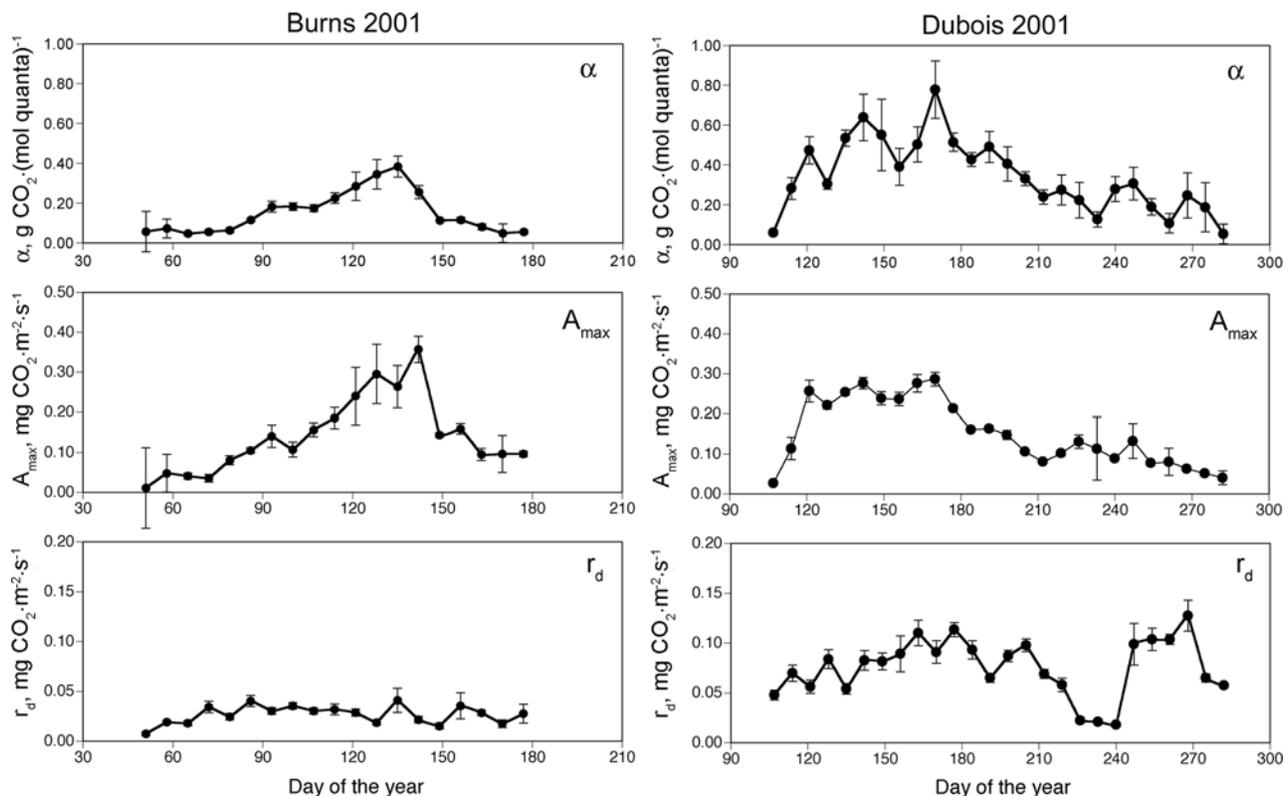


Figure 5. Dynamics of light-response parameters for Burns and Dubois sites during 2001 (drought year). Data include weekly means (dots) and their standard errors (bars) for quantum yield (α panels), maximum photosynthesis (A_{max} panels), and average daytime respiration (r_d panels).

Table 3. Long-term dynamics of maximum values of mean weekly ecosystem scale, light-response parameters, where α_{wk} is apparent quantum yield ($\text{mmol CO}_2 \cdot \text{mol photons}^{-1}$), $A_{max,wk}$ is the saturated gross photosynthesis ($\text{mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), and $r_{d,wk}$ is daytime ecosystem respiration ($\text{mg CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$).

Year	α_{wk}	$A_{max,wk}$	$r_{d,wk}$
Burns, Oregon			
1995	27	0.35	0.12
1996	35	0.51	0.14
1997	39	0.39	0.08
1998	37	0.59	0.13
1999	18	0.65	0.11
2000	25	0.36	0.08
2001	9	0.36	0.04
Mean	27	0.46	0.10
Dubois, Idaho			
1996	19	0.42	0.11
1997	33	0.78	0.20
1998	27	0.58	0.16
1999	44	0.76	0.15
2000	27	0.69	0.12
2001	18	0.29	0.10
Mean	28	0.59	0.14

amounts of carbon in 1998–1999. This accumulated carbon was retained during the last 2 drier years (2000–2001). As a result, during the 6 years of our study, the sagebrush steppe at Dubois accumulated $1\,520 \text{ g CO}_2 \cdot \text{m}^{-2}$.

Annual CO₂ Budget

Comparison of annual totals of GPP, RE, and NEE (Table 5) confirmed differences in the carbon cycling intensity and capacity at the 2 sites in relation to their biomass production (shrub cover and population density) and light-response parameters. Mean GPP at the Burns site, $1\,111$ (range $475\text{--}1\,715$) $\text{g CO}_2 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$, was nearly 30% lower than mean GPP of $1\,602$ (range $963\text{--}2\,162$) $\text{g CO}_2 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ at the Dubois site. Mean RE at Burns, $1\,029$ (range $581\text{--}1\,544$) $\text{g CO}_2 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ was approximately proportionately lower than at Dubois, $1\,349$ (range $786\text{--}1\,778$) $\text{g CO}_2 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$. Particularly strong differences between the 2 sites were observed in net carbon balance. NEE at Burns was positive in only 4 of 7 years, while Dubois had a net accumulation of carbon 5 of 6 years. Long-term mean NEE rates at Burns ($82 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$) were about 70% lower than those at Dubois ($253 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$).

A significant linear relationship of GPP to hydrological year precipitation was observed at both sites (Fig. 9A). Sensitivity of GPP to precipitation at Dubois ($5.40 \text{ g CO}_2 \cdot \text{mm}^{-1} \text{ H}_2\text{O}$) was substantially higher than at Burns ($3.15 \text{ g CO}_2 \cdot \text{mm}^{-1} \text{ H}_2\text{O}$). Plots of RE vs. PCPN_{hyd} (Fig. 9B) are also characterized by positive correlation coefficients ($r = 0.33$ for Burns and $r = 0.79$ for Dubois), but only the Dubois linear regression of RE on precipitation was significant.

Table 4. Parameters of linear regressions for weekly daytime ecosystem respiration on nighttime respiration ($r_{d,wk} = a + b r_{n,wk}$) at the Burns and Dubois sites calculated for individual years and for data combined across years for each site.

Year	$a \pm s_a$	$b \pm s_b$	Testing hypothesis	
			$(b - 1)/s_b$	Significance
Burns, Oregon				
1995	0.00237 ± 0.0005	1.36 ± 0.22	1.636	*
1996	0.0 ± 0.0019	1.21 ± 0.14	1.500	*
1997	0.0046 ± 0.0029	1.31 ± 0.25	1.240	
1998	0.0041 ± 0.0017	1.02 ± 0.11	0.182	
1999	-0.00082 ± 0.00015	1.055 ± 0.008	6.875	***
2000	0.00078 ± 0.00037	1.3 ± 0.12	2.500	***
2001	-0.0012 ± 0.00026	1.21 ± 0.20	1.050	
1995–2001 combined	0.00177 ± 0.00029	1.172 ± 0.047	3.660	***
Dubois, Idaho				
1996	-0.0019 ± 0.0089	1.12 ± 0.28	0.429	
1997	0.0046 ± 0.0024	1.17 ± 0.14	1.214	
1998	-0.0052 ± 0.0041	1.06 ± 0.14	0.429	
1999	0.0116 ± 0.0016	0.91 ± 0.15	-0.600	
2000	-0.0031 ± 0.001	1.137 ± 0.078	1.756	**
2001	0.0052 ± 0.0027	1.19 ± 0.22	0.864	
1996–2001 combined	0.00177 ± 0.00077	1.126 ± 0.052	2.423	***

* $p < 0.10$; ** $p < 0.05$; *** $p < 0.01$.

DISCUSSION

Rangelands cover 40% of the Earth's surface and of the land area of the United States (White et al. 2000; WRI 2000). Given the tremendous extent of this land type, it will be difficult to document global carbon cycles fully without an understanding

of carbon dynamics on rangelands. Pacala et al. (2001) estimated that there is a substantial terrestrial carbon sink in the United States, and that half that sink was in nonforested areas. In this study we confirmed previous findings (Gilmanov et al. 2003a, 2004b) that sagebrush-steppe communities could be a carbon sink across multiple years.

Evaluating annual CO_2 fluxes (and thus source/sink status) requires continuous measurement of CO_2 gradients using "tower-based" micrometeorological techniques. At present, BREB and eddy correlation (EC) are the 2 approaches in use. Each approach provides an estimate of net CO_2 flux on a 24-hour basis during the measurement period. Net CO_2 flux has distinct phases: 1) during daylight hours, CO_2 is both acquired by photosynthesis and released by plant and soil respiration, and 2) during the night, photosynthesis is zero, and plant and soil respiration drive CO_2 flux. As photosynthesis declines through the season, daytime fluxes can also be negative (respiration is greater than photosynthesis). In the sagebrush steppe we found that there are brief periods of net CO_2 uptake followed by relatively long periods of low CO_2 losses (Figs. 7C, 8C).

Although our 2 study sites were dominated by sagebrush and had generally similar climatic characteristics, they differed in their seasonal patterns of precipitation. At Burns, a substantial portion of annual precipitation is received during fall, winter, and spring months (Fig. 1A). In contrast, the greatest proportion of the precipitation at Dubois occurs during May and June when water may be most efficiently used for biomass production. This resulted in marked differences in efficiency of water use for production between the 2 sites: $3.15 \text{ g CO}_2 \cdot \text{mm}^{-1} \text{ H}_2\text{O}$ vs. $5.40 \text{ g CO}_2 \cdot \text{mm}^{-1} \text{ H}_2\text{O}$ for Burns and Dubois, respectively (Fig. 9A). A significant linear relationship of RE to PCPN_{hyd} was also observed at Dubois where precipitation overlaps with the growing season (Fig. 9B). A close relation of annual respiration to precipitation is lacking at Burns and was apparently associated with the higher proportion of fall to spring precipitation at this site.

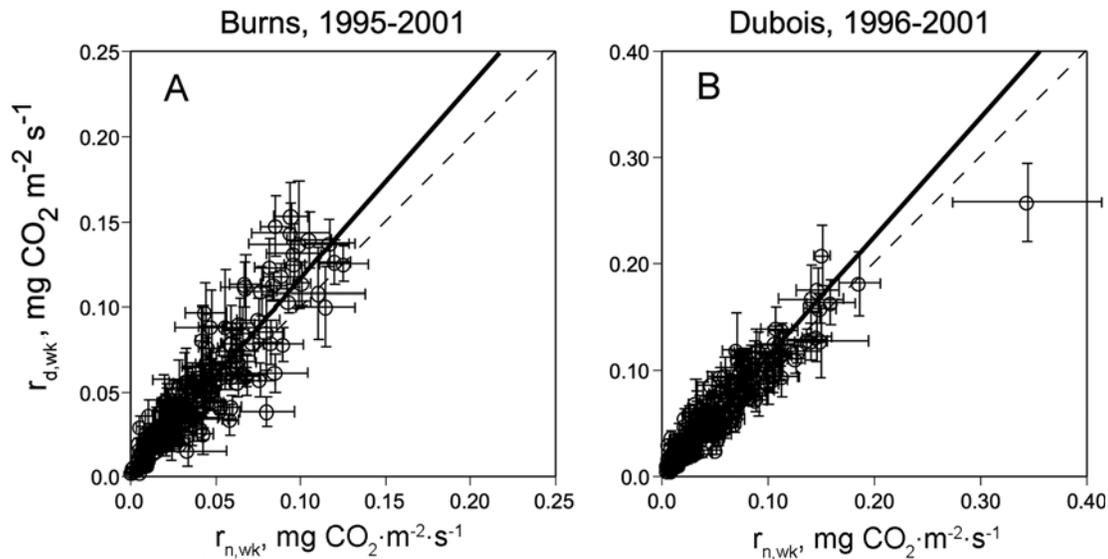


Figure 6. Linear regressions of daytime ecosystem respiration ($r_{d,wk}$) on nighttime ($r_{n,wk}$) ecosystem respiration for combined data at **A**, Burns 1995–2001, and **B**, Dubois 1996–2001. Dots show mean weekly data; error bars depict errors of the means in both x and y directions; solid lines show regressions with parameters presented in Table 3; and dashed lines show 1:1 relationships. Note differences in scale between panels A and B.

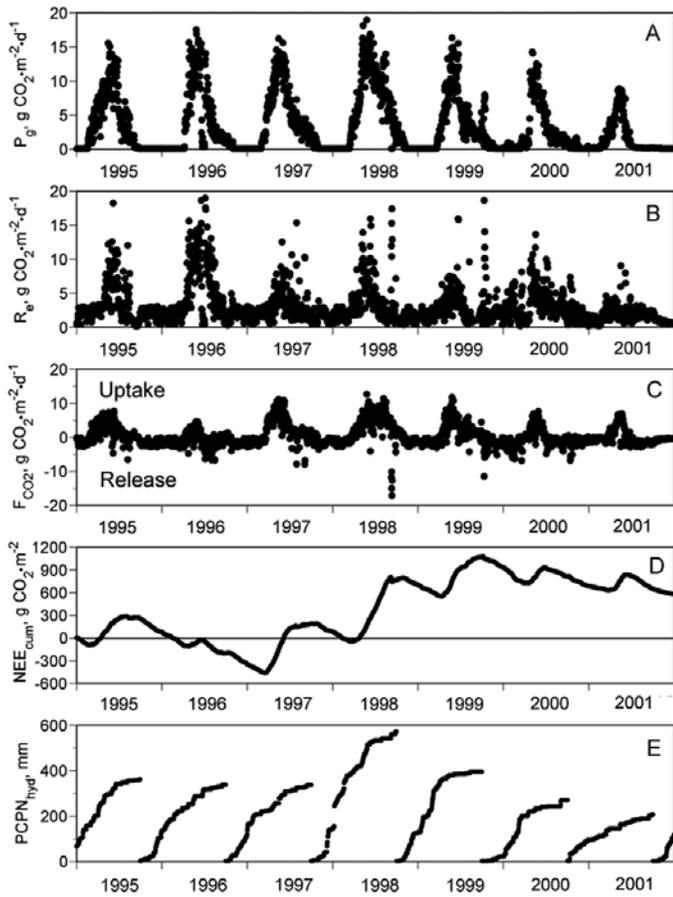


Figure 7. Seasonal and year-to-year dynamics of: **A**, gross primary productivity P_g ; **B**, ecosystem respiration R_e ; **C**, net ecosystem CO_2 exchange F_{CO_2} ; **D**, cumulative net ecosystem CO_2 exchange NEE_{cum} ; and **E**, accumulated precipitation of the hydrologic year $\text{PCPN}_{\text{hydr}}$ at the Burns site during 1995–2001. Note differences in scale between Figs. 7 and 8.

Data in Table 6 allow comparison of GPP and RE values for the sagebrush steppe with other nonforested ecosystems. The production and respiration estimates from our study for the sagebrush steppe of the Intermountain West were similar to published values for the shortgrass and mixed prairies of the Northern Great Plains and the High Central Plains of North America. However, they are lower than values of GPP and RE for more productive ecosystems in the United States including the mixed and tallgrass prairies of the Central and Southern Great Plains, Mediterranean grasslands in California, and warm-temperate grasslands of the East Coast.

During the course of this study (1995–2001), both the Burns and Dubois sites were carbon sinks, taking up from the atmosphere more CO_2 than they released. Because the slopes of the trend lines of the GPP–PCPN plots are higher than on RE–PCPN plots (Fig. 9), we observe predominance of CO_2 -sink activity in years with more precipitation and source activity in drier years (Fig. 7, 8). These patterns are in agreement with data for mixed prairies of the Northern and Central Great Plains, where both the BREB and the EC tower measurements demonstrated predominance of CO_2 -source activity in drought years (Meyers 2001; Gilmanov et al. 2003b, 2005b). During the entire study period, NEE at Burns and Dubois averaged 82

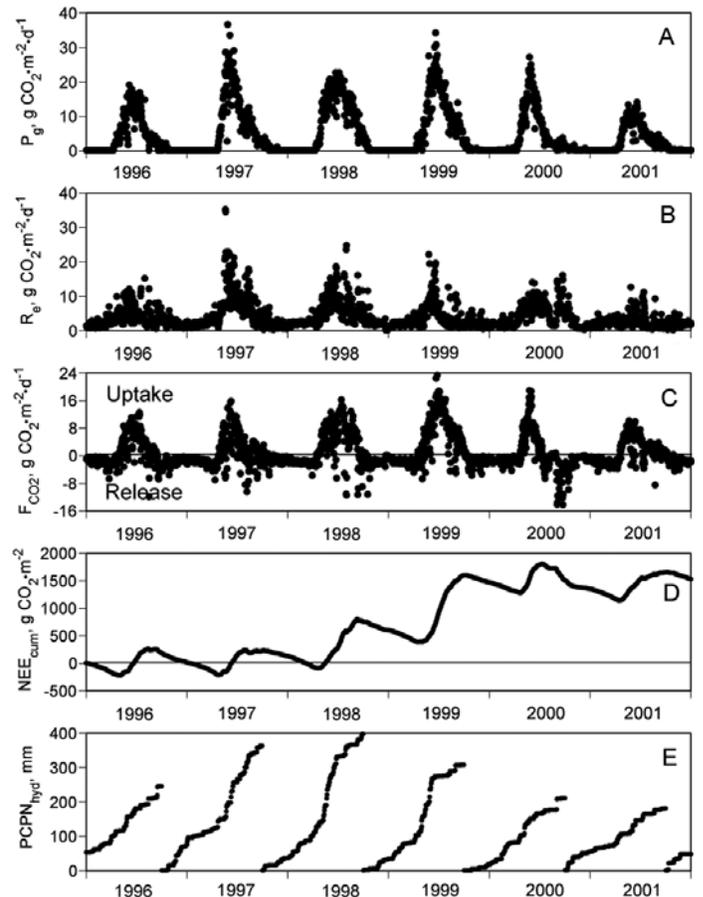


Figure 8. Seasonal and year-to-year dynamics of: **A**, gross primary productivity P_g ; **B**, ecosystem respiration R_e ; **C**, net ecosystem CO_2 exchange F_{CO_2} ; **D**, cumulative net ecosystem CO_2 exchange NEE_{cum} ; and **E**, accumulated precipitation for the hydrologic year $\text{PCPN}_{\text{hydr}}$ at the Dubois site during 1996–2001. Note differences in scale between Figs. 7 and 8.

and $253 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$, respectively. We would expect relatively large accumulations of organic carbon at these sites (especially Dubois) given these sink strengths. It is possible that these water-stressed sites have become more active sinks as atmospheric CO_2 has increased during the past 100+ years (Morgan et al. 2001, 2004; Mielnick et al. 2001). It is also possible that combustion of aboveground biomass played a role in carbon dynamics.

The Dubois site was a sink for CO_2 with average $\text{NEE} \sim 0.7 \text{ t C} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$. An estimate of the total amount of organic carbon in this ecosystem is about $116 \text{ t C} \cdot \text{ha}^{-1}$. If we assume that the NEE level of $0.7 \text{ t C} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$ is maintained at the Dubois site, it would take less than 200 years to accumulate this amount of organic carbon. However, an alternative scenario would be to assume variations in the NEE dynamics when high values ($\sim 0.7 \text{ t C} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$) occur as bursts during favorable periods, with lower or even negative NEE values in between. This suggests an accumulation of $116 \text{ t C} \cdot \text{ha}^{-1}$ may take 1 000 or more years. Why, with such a high CO_2 -sink potential at Dubois, is there no substantial accumulation of organic carbon? The explanation may be partially due to wildfires, which ensure periodic mineralization of organic matter. Wildfires are a natural part of sagebrush-steppe eco-

Table 5. Annual totals of climatic and CO₂ exchange characteristics for the 2 sagebrush-steppe sites during the study period: PCPN_{hyd} (hydrologic year precipitation), T_{yr} (mean annual air temperature), GPP (gross primary production), RE (ecosystem respiration), and NEE (net ecosystem CO₂ exchange).

Year	PCPN _{hyd} mm·yr ⁻¹	T _{yr} °C	GPP g·CO ₂ · m ⁻² ·y ⁻¹	RE g·CO ₂ · m ⁻² ·y ⁻¹	NEE g·CO ₂ · m ⁻² ·y ⁻¹
Burns 1995–2001					
1995	360	8.23	1 147	1 074	73
1996	336	7.96	1 120	1 544	-424
1997	334	7.61	1 343	918	426
1998	569	7.78	1 716	1 095	621
1999	394	8.19	1 152	924	227
2000	268	7.71	828	1 069	-245
2001	205	7.90	475	581	-106
Mean	352	7.91	1 111	1 029	82
SE	106	0.22	360	266	344
Dubois 1996–2001					
1996	244	5.24	1 185	1 176	9
1997	361	5.05	1 892	1 778	114
1998	396	5.36	2 162	1 690	472
1999	307	5.11	2 075	1 209	867
2000	210	5.36	1 335	1 453	-118
2001	181	5.77	963	786	177
Mean	283	5.32	1 602	1 349	253
SE	78	0.23	461	336	328

systems in the Intermountain West, with estimates of fire intervals ranging from 2–28 to 60–110 years (Whisenant 1990; Knapp 1995; Miller and Rose 1999). Fires substantially affect structure and composition of the ecosystem with consequences for CO₂, water, and energy fluxes (Johnson et al. 1999; West and Yorks 2002; Obrist et al. 2003).

Assuming that 1 t of phytomass corresponds to 0.45 t C, we may conclude that with a NEE of 253 g CO₂·m⁻²·y⁻¹ (= 0.69 t C·ha⁻¹·y⁻¹), it would take less than 7 years to renew the total (above + belowground) biomass of 10 t·ha⁻¹ (4.5 t C·ha⁻¹) (West 1983; West et al. 1994) for the sagebrush steppe. With a more realistic assumption of variable NEE between fires, we

would estimate a biomass turnover period of about 13 years, which is within the estimate of the average fire interval of 12–15 years in the sagebrush steppe of south-central Oregon (Miller and Rose 1999). Using a NEE of 82 g CO₂·m⁻²·y⁻¹ (= 0.224 t C·ha⁻¹·y⁻¹) estimated for Burns, and variable NEE rates between fires, we obtain a biomass turnover time of 40 years or more. This is closer to the fire interval estimate of 60–100 years suggested by Whisenant (1990).

The Dubois site was dominated by three-tip sagebrush and had shrub canopy cover of 40%, whereas the Burns site was dominated by Wyoming big sagebrush and had shrub cover of about 10%. In much of the Intermountain West, fire return intervals for communities at the high end of shrub cover (e.g., 40%) would be 15–25 years, whereas those with low cover (e.g., 10%) would have fire return intervals of 50–75 years. From a historical perspective, sites with higher productivity experienced a short fire return interval, and the less productive sites had slower fuel accumulation and burned less frequently.

The range of values for ecosystem-scale, light-response parameters { α , A_{max} , r_d } for sagebrush-steppe sites in our study (Figs. 4, 5; Table 3) were similar to parameters estimated for ecosystems of the Northern Great Plains in North America. This includes values for the northern short-mixed grass prairies in Lethbridge, Alberta, Canada ($\alpha_{wk} = 17$ mmol CO₂·mol photons⁻¹, $A_{max,wk} = 0.6$ mg CO₂·m⁻²·s⁻¹, $r_{d,wk} = 0.11$ mg CO₂·m⁻²·s⁻¹), Fort Peck, Montana, USA ($\alpha_{wk} = 18$ mmol CO₂·mol photons⁻¹, $A_{max,wk} = 0.56$ mg CO₂·m⁻²·s⁻¹, $r_{d,wk} = 0.20$ mg CO₂·m⁻²·s⁻¹), Miles City, Montana, USA ($\alpha_{wk} = 17$ mmol CO₂·mol photons⁻¹, $A_{max,wk} = 0.40$ mg CO₂·m⁻²·s⁻¹, $r_{d,wk} = 0.20$ mg CO₂·m⁻²·s⁻¹), and Mandan, North Dakota, USA ($\alpha_{wk} = 20$ mmol CO₂·mol photons⁻¹, $A_{max,wk} = 0.57$ mg CO₂·m⁻²·s⁻¹, $r_{d,wk} = 0.15$ mg CO₂·m⁻²·s⁻¹) (Flanagan et al. 2002; Gilmanov et al. 2005b). This is not surprising because of similar climates and grass cover in the northern mixed prairies (though they lack a significant shrub component). The light-response parameters for our sagebrush-steppe study sites were lower than those for more productive mixed prairie sites, such as the one at Cheyenne, Wyoming, USA ($\alpha_{wk} = 34$ mmol CO₂·mol photons⁻¹, $A_{max,wk} = 1.25$ mg CO₂·m⁻²·s⁻¹, $r_{d,wk} = 0.28$ mg CO₂·m⁻²·s⁻¹), or tallgrass prairies and agricultural crops (Luo et al. 2000; Gilmanov et al. 2003b; Gilmanov et al.

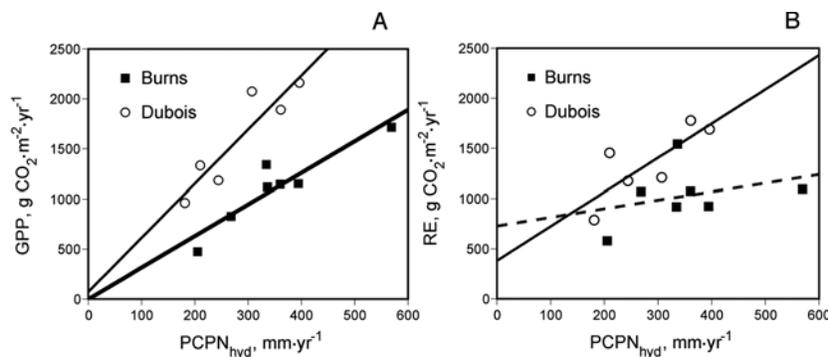


Figure 9. Gross primary production, GPP (A), and total ecosystem respiration, RE (B) (g CO₂·m⁻²·y⁻¹) for the Burns and Dubois sites in relation to hydrologic year precipitation, PCPN_{hyd} (mm·y⁻¹). Burns: GPP = 3.15·PCPN_{hyd} + 1.74, R² = 0.85, $p = 0.003$; RE = 0.85·PCPN_{hyd} + 729, R² = 0.11, $p = 0.12$ (nonsignificant); Dubois: GPP = 5.40·PCPN_{hyd} + 72.15, R² = 0.84, $p = 0.01$; RE = 3.41·PCPN_{hyd} + 382, R² = 0.63, $p = 0.06$.

Table 6. Gross primary production (GPP), ecosystem respiration (RE), and net ecosystem CO₂ exchange (NEE) in various nonforest ecosystems (g CO₂ · m⁻² · period⁻¹).

Ecosystem, site	GPP	RE	NEE	Source	Period, days
<i>Bouteloua gracilis</i> stand in shortgrass prairie, Colorado, United States	550	—	—	Detling et al. 1979	365
Northern temperate grassland, Lethbridge, Alberta, Canada	1 026	1 021	+5	Flanagan et al. 2002	365
Northern mixed prairie, Fort Peck, Montana, United States	459–1 455	996–1 293	–537–+162	Gilmanov et al. 2005b	91–305 138–302
Northern mixed prairie, Miles City, Montana, United States	913–1 239	1 130–1 437	–198–217	Gilmanov et al. 2005b	118–307 1–327
Sagebrush-steppe, Burns, Oregon, United States	1 111 475–1 716	1 029 581–1 544	82 –424–+621	This study	365
Sagebrush steppe, Dubois, Idaho, United States	1 602 963–2 162	1 349 786–1 778	253 –118–+867	This study	365
Shortgrass prairie, control, Colorado, United States	1 945	1 545	400	Andrews et al. 1974; Coupland and Van Dyne 1979; Schultz 1995	365
Pasture in mixed/tallgrass prairie, Little Washita, Oklahoma, United States	2 333	2 175	158	Meyers 2001; Gilmanov et al. 2003b	90–300
Tallgrass prairie, moderate seasonal grazing, Osage, Oklahoma, United States	2 787	3 039	–252	Risser et al. 1981	365
Tallgrass prairie, ungrazed, Osage, Oklahoma, United States	2 821	2 872	–51	Risser et al. 1981	365
Mediterranean grassland, Lone, California, United States	2 926 2 673–3 179	2 737 2 695–2 779	189 –106–484	Xu and Baldocchi 2004	365
Mixed prairie, winter grazing Woodward, Oklahoma, United States	3 037	2 517	520	Sims and Bradford 2001; Gilmanov et al. 2003b	365
Tallgrass prairie, moderate year-round grazing, Osage, Oklahoma, United States	3 678	3 698	–19	Risser et al. 1981	365
Warm temperate grassland, Durham, North Carolina, United States	4 407	4 763	–356	Novick et al. 2004	365
Tallgrass prairie, after spring burn, Shidler, Oklahoma, United States	5 223	3 964	1 259	Gilmanov et al. 2003b	365

2004b; Suyker et al. 2004). With respect to light-response parameters derived from flux-tower measurements, sagebrush-steppe ecosystems fall into the low-to-medium portion of the spectrum for semiarid terrestrial ecosystems. This agrees with rankings related to their biomass/productivity characteristics (West 1983; West et al. 1994).

We observed close visual correlation (R^2 coefficient cannot be calculated when both variables have errors; see Harrison 1996) between r_d and r_n . This was especially true for weekly grouped data (Figs. 6A, B) with $r_d > r_n$ on average. This agrees with Kansas tallgrass prairie chamber measurements, which established $r_d > r_n$ (Grahammer et al. 1991). Regarding factors affecting daytime respiration compared to nighttime respiration, it was suggested that respiration of green phytomass may be inhibited by light (see Wohlfahrt et al. 2005) causing decrease of r_d relative to r_n . Stomatal closure under drought stress may act in a similar manner (Amthor 1989). The average higher r_d than r_n rates observed in our study were similar to patterns observed for mixed and tallgrass prairies in Oklahoma (Gilmanov et al. 2003b), typical steppe in Kazakhstan (Gilmanov et al. 2004a), and mixed grass prairies of the Northern Great Plains (Chimner and Welker 2005; Gilmanov et al.

2005b). These patterns agree with the increase of autotrophic and heterotrophic respiration due to higher daytime temperature and light-dependent processes (e.g., Megonigal et al. 1999; Kuzyakov 2002; Lu et al. 2002), which apparently compensate for any decrease of r_d caused by light inhibition and stomatal regulation.

Previous results for grasslands of the Northern Great Plains of the United States demonstrated that soil water content (W_s) was a significant factor of CO₂ exchange (Gilmanov et al. 2005b). Higher precipitation and an increase of soil moisture at the end of the growing season when temperatures are still high enough and the substrate for decomposition in the form of dead phytomass is readily available may be responsible for the second peak on the $r_d(t)$ curves for Dubois. A second maximum of $r_d(t)$ did not occur at Burns when stronger soil desiccation in summer was combined with lower early fall precipitation (Fig. 4, 5). Phenology also may have played a significant role in determining the seasonal dynamics of gross primary productivity, especially during the early portion of the growing season (Burns site, 1996, 1998). More comprehensive multivariate analyses are needed for the relationships between CO₂ flux components (especially P_g and R_e) and various ecological

factors (Gilmanov et al. 2003a; Wylie et al. 2003; Gilmanov et al. 2005b). Opportunities for such analyses are increasing as more complete data sets for carbon, water and energy fluxes, and ancillary onsite and remotely sensed variables become available from various CO₂ flux networks (Law et al. 2002; Baldocchi 2003; Gilmanov et al. 2005a).

CONCLUSIONS AND IMPLICATIONS

Long-term BREB measurements of CO₂ exchange in the sagebrush-steppe ecosystem at the Burns and Dubois sites demonstrated a high seasonal and yearly variability. For both sites during our study period, there were years when NEE was positive (a CO₂ sink) and years when NEE was negative (a CO₂ source). During 7 years of study at Burns, the sagebrush-steppe ecosystem was a weak sink for atmospheric carbon, approaching carbon balance. However, the Dubois site was a substantial carbon sink during the 6 years of our study, accumulating 1 520 g CO₂·m⁻². Data from our 2 study sites confirmed conclusions made earlier with data from the steppes of Central Asia and Northern Great Plains grasslands that analysis of ecosystem-scale, light-response functions can be used to obtain measurement-based estimates of daytime ecosystem respiration. These values are consistent with direct nighttime tower CO₂ fluxes and suggest the utility and accuracy of the partitioning F_c into P_g and R_e components. Such separation of the net flux into its physiologically specific components allowed quantitative prediction of seasonal and yearly dynamics of CO₂ fluxes. Light-response parameters (α , A_{max} , r_d), daily productivity and respiration rates (P_g , R_e), as well as the mean values and ranges of GPP and RE for sagebrush-steppe ecosystems were consistent with literature values for shortgrass and northern mixed prairie ecosystems under similar geographical and climatic conditions. Our results support conclusions by Follett et al. (2001) about the high potential of grazing lands to fix and store atmospheric carbon. Given the large land area occupied by rangelands, attempts to balance global carbon cycles will require a better understanding of carbon fluxes on rangelands, of which sagebrush steppe alone occupies about 40 million hectares. There are several important points that arose from our research: 1) the 2 sites were both sinks for atmospheric CO₂ during the study period, 2) either site could be a sink or source in any given year, 3) precipitation was a good predictor of carbon sequestration within a site, and 4) total yearly precipitation level was not a good predictor of carbon sequestration across sites. The last point suggests that precipitation timing (rain at the right time) may be critical in determining productivity and thus carbon sequestration of sagebrush-steppe rangelands.

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