Carbon Fluxes on North American Rangelands

Tony Svejcar,¹ Raymond Angell,² James A. Bradford,³ William Dugas,⁴ William Emmerich,⁵ Albert B. Frank,⁶ Tagir Gilmanov,⁷ Marshall Haferkamp,⁸ Douglas A. Johnson,⁹ Herman Mayeux,¹⁰ Pat Mielnick,¹¹ Jack Morgan,¹² Nicanor Z. Saliendra,¹³ Gerald E. Schuman,¹⁴ Phillip L. Sims,¹⁵ and Kereith Snyder¹⁶

Authors are ¹Research Leader and ²Rangeland Scientist, USDA-ARS, Eastern Oregon Agricultural Research Center, Burns, OR 97720, USA; ³Plant Physiologist and ¹⁵Research Leader (retired), USDA-ARS, Southern Plains Range Research Center, Woodward, OK 73801, USA; ⁴Resident Director and Professor, and ¹¹Postdoctoral Research Associate, Texas Agricultural Experiment Station–Blackland Research Center, Temple, TX 76502, USA; ⁵Soil Scientist, USDA-ARS, Southwest Watershed Research, Tucson, AZ 85719, USA; ⁶Plant Physiologist (retired), USDA-ARS, Northern Great Plains Research Laboratory, Mandan, ND 58554, USA; ⁷Professor, South Dakota State University, Brookings, SD 57007, USA; ⁸Rangeland Scientist (retired), USDA-ARS, Livestock and Range Research Lab, Miles City, MT 59301-9202, USA; ⁹Plant Physiologist, USDA-ARS, Forage and Range Research Laboratory, Utah State University, Logan, UT 84322-6300, USA; ¹⁰Research Leader (retired), USDA-ARS, Grazinglands Research Plant Physiologist, US (USA; ¹²Research Leader, USDA-ARS Rangeland Resources Research Unit, Ft. Collins, CO 80526-2083, USA; ¹³Research Plant Physiologist, US (Plant Physiologist, USDA-ARS, High Plains Grasslands Research Station, Cheyenne, WY 82009, USA; and ¹⁶Ecologist, USDA-ARS, Exotic and Invasive Weeds Research Unit, 920 Valley Rd, Reno NV 89512, USA.

Abstract

Rangelands account for almost half of the earth's land surface and may play an important role in the global carbon (C) cycle. We studied net ecosystem exchange (NEE) of C on eight North American rangeland sites over a 6-yr period. Management practices and disturbance regimes can influence NEE; for consistency, we compared ungrazed and undisturbed rangelands including four Great Plains sites from Texas to North Dakota, two Southwestern hot desert sites in New Mexico and Arizona, and two Northwestern sagebrush steppe sites in Idaho and Oregon. We used the Bowen ratio-energy balance system for continuous measurements of energy, water vapor, and carbon dioxide (CO₂) fluxes at each study site during the measurement period (1996 to 2001 for most sites). Data were processed and screened using standardized procedures, which facilitated across-location comparisons. Although almost any site could be either a sink or source for C depending on yearly weather patterns, five of the eight native rangelands typically were sinks for atmospheric CO_2 during the study period. Both sagebrush steppe sites were sinks and three of four Great Plains grasslands were sinks, but the two Southwest hot desert sites were sources of C on an annual basis. Most rangelands were characterized by short periods of high C uptake (2 mo to 3 mo) and long periods of C balance or small respiratory losses of C. Weather patterns during the measurement period strongly influenced conclusions about NEE on any given rangeland site. Droughts tended to limit periods of high C uptake and thus cause even the most productive sites to become sources of C on an annual basis. Our results show that native rangelands are a potentially important terrestrial sink for atmospheric CO_2 , and maintaining the period of active C uptake will be critical if we are to manage rangelands for C sequestration.

Resumen

Los pastizales nativos constituyen casi la mitad de la superficie terrestre y pueden desempeñar un papel importante en el ciclo global del carbón (C). El objetivo de esta investigación fue estudiar el intercambio neto de carbono dentro del ecosistema (NEE) en ocho sitios de pastizales de Norteamérica durante un período de seis años. Las prácticas de manejo y grados de disturbio pueden influenciar el NEE, pero para consistencia, se compararon pastizales con y sin pastoreo. Se usaron cuatro sitios de las Grandes Planicies desde Texas a Dakota del Norte, dos sitios del desierto al sudoeste de New México y Arizona y dos sitios del noroeste del desierto de arbustivas en Idaho y Oregon. Se utilizo el sistema proporción-energía de Bowen para las medidas continuas de energía, de vapor de agua y de los flujos del CO_2 en cada sitio (1996 a 2001 para la mayoría de los sitios). Se examinaron los datos usando procedimientos estandarizados que facilitaron comparaciones entre sitios. Aunque casi cualquier sitio podría actuar como reservorio o fuente de C dependiendo de los patrones anuales. Cinco de los ocho pastizales nativos típicamente demandaron CO₂ atmosférico durante el período del estudio. Ambos sitios del desierto arbustivo y tres de cuatro sitios de las Grandes Planicies demandaron CO2. En contraste, los dos sitios secos del desierto del sudoeste fueron fuentes del carbón anualmente. La mayoría de los pastizales se caracterizaron por períodos cortos de alta absorción de C (2 a 3 meses) y largos periodos del balance de C o bien pequeñas pérdidas por respiración. Las condiciones ambientales durante el período de evaluación influenciaron fuertemente las conclusiones sobre NEE en todos los sitios evaluados. Las sequías limitaron períodos de alta absorción de C y la productividad de los sitios para convertirse anualmente en fuentes de C. Estos resultados demostraron que los pastizales nativos son potencialmente un reservorio terrestre para el CO2 atmosférico y el mantenimiento del período de absorción de C activo será crítico si se manejan los pastizales para el secuestro de C.

Key Words: carbon flux, grasslands, sequestration, shrub steppe

Authors are listed in alphabetical order after senior author

Correspondence: Tony Svejcar, USDA-ARS, 67826-A Hwy 205, Burns, OR 97720, USA. Email: tony.svejcar@oregonstate.edu

Manuscript received 26 September 2007; manuscript accepted 3 May 2008.

INTRODUCTION

There is considerable interest in potential effects of increasing atmospheric carbon dioxide (CO₂) on global climate, and consequently in maximizing terrestrial and oceanic sinks for carbon (C) as a means of ameliorating negative impacts. Attempts to balance known sources and sinks of the global C cycle often result in a "missing sink" of 1.3 Gt C \cdot yr⁻¹ to 1.4 Gt C \cdot yr⁻¹ (Woodwell et al. 1998). Carbon sequestration by terrestrial ecosystems may account for a portion of the missing C, although direct evidence for the terrestrial sink, from either plant or soil-based measurements, has not been forthcoming (Schimel 1995). However, there is indirect evidence for a strong net sink in the Northern Hemisphere (Canadell et al. 2000).

From the standpoint of C cycling, the more arid rangeland biomes of the world (i.e., savannas, grasslands, shrub steppes, and deserts) have received less research attention than forests, although at one time rangeland biomes occupied more than 50% of the earth's terrestrial land surface (Knapp et al. 1998). The high levels of organic carbon in many grassland soils suggest that these biomes have experienced positive net ecosystem exchange of carbon (NEE) over time. Much of this accumulation of soil carbon probably occurred at a time when atmospheric CO₂ was considerably lower than today's levels (Schimel 1995). There is evidence that compared to the preindustrial period, today's atmospheric CO₂ levels will reduce plant water stress (Morgan et al. 2004), potentially stimulating productivity and NEE.

There is increasing interest in rewarding land management practices that enhance sequestration of C. In the past, agricultural and forestry practices were targeted, but recently the Chicago Climate Exchange developed a carbon credit program for rangelands (www.chicagoclimatex.com). Carbon sequestration (and NEE) reflects the balance between CO_2 uptake via plant photosynthesis and CO_2 loss via plant and soil respiration.

 Table 1. Dominant species and land use history of study locations.

To gain a better understanding of rangeland NEE, the US Department of Agriculture–Agricultural Research Service (USDA-ARS) established a rangeland carbon flux network. Eight North American native rangeland sites were used in this study. Given the size and complexity of the study, we chose ungrazed and otherwise unmanaged rangeland for our initial comparisons. At most sites, measurements were initiated in 1995 and, for many sites, continue to the present. Most of the data presented here were collected during 1996 to 2001. Throughout the paper we use positive NEE to indicate C sequestration, and negative NEE to indicate C efflux.

Our objectives are to 1) provide a comparison of annual CO_2 flux patterns among a variety of rangeland biomes, and 2) estimate whether the various biomes are likely to be sources or sinks for atmospheric CO_2 .

MATERIALS AND METHODS

Study Sites

Eight individual sites were used in this study. Specific location, vegetation type, dominant species, and general site characteristics are presented in Tables 1 and 2. The sites were selected to represent native rangeland in the area. All sites were considered to be in good ecological condition (based on species composition) and were not managed (grazed by livestock, burned, or fertilized) during the course of the study. The one exception was the tallgrass prairie in Temple, Texas, which was burned in 1995.

Micrometeorological Measurements

We used the Bowen ratio–energy balance (BREB; model 023/ CO₂ Bowen Ratio; Campbell Scientific, Inc, Logan, UT) system for continuous measurements of energy, water vapor, and CO₂ fluxes at each study site. The theory and operation of the BREB technique have been described in detail (Dugas 1993; Campbell

Location	Dominant species	Land use history
Las Cruces, New Mexico	Bouteloua eriopoda, Larrea tridentata, and Prosopis glandulosa.	Not grazed since 1984.
Tucson, Arizona	Acacia constricta, Flourensia cernua, Larrea tridentata, Muhlenbergia porteri, and Zinnia pumila.	Not grazed since mid-1960s, not burned in 20+ yr, no herbicides applied in 21+ yr (had herbicide in 1981), no fertilizers, never plowed.
Burns, Oregon	Artemisia tridentata subsp. wyomingensis, Stipa thurberiana, Pseudoroegneria spicata, and Poa sandbergii.	Grazed moderately until start of study.
Dubois, Idaho	Artemisia tridentata subsp. rupicola, Pseudoroegneria spicata, and Balsamorhiza sagittata.	Grazed moderately until start of study.
Mandan, North Dakota	Bouteloua gracilis, Stipa comata, Schizachyrium scoparium, and Bouteloua curtipendula.	Never fertilized, no herbicides applied, last grazed in 1992.
Nunn, Colorado	Bouteloua gracilis and Buchloe dactyloides.	Grazed season-long (May to October) at moderate stocking rate for many years prior to the study; not grazed during the study. No record of burning or plowing. Atrazine applied at 1.12 kg \cdot ha ⁻¹ biannually from 1976 to 1989.
Woodward, Oklahoma	Schizachyrium scoparium, Andropogon halli, Bouteloua gracilis, Sporobolus cryptandrus, and Ambrosia psilostachya.	Light grazing during January and February 1995–1998. Moderate year-round grazing in 1999. Brush removed with herbicides periodically since 1960.
Temple, Texas	Andropogon gerardii, Schizachyrium scoparium, Sorghastrum nutans, and annual herbs.	Never plowed; no grazing, haying, or fertilizer or herbicide use in more than 20 yr; not burned in the 50 yr prior to a burn in February 1995.

Location	Vegetation type	Average annual precipitation (cm)	Elevation (m)	Lat/long	Slope (%)	Soil
Las Cruces, New Mexico	Desert grassland	22.7	1 230	lat 32°60′N, long 106°75′W	0	Onite–Pajarito complex; fine sandy loam to sandy loam, mixed thermic Typic Haplargid.
Tucson, Arizona (Lucky Hills)	Desert shrub	35.6	1 372	lat 31°44′N, long 110°03′W	3–15	Luckyhills; coarse-loamy, mixed, thermic, Ustochreptic Calciorthids.
Burns, Oregon	Sagebrush steppe	29.8	1 380	lat 43°29′N, long 119°43′W	2	Holte–Milcan complex; coarse to fine sandy loam aridic Duric Halpoxerolls & Orthidic Durixerolls.
Dubois, Idaho	Sagebrush steppe	34.0	1 700	lat 44°16′N, long 112°08′W	0–12	Maremma–Pyrenees complex; Maremma; fine-loamy mixed, superactive, frigid Calcic Pachic Argixerolls; Pyrenees; loamy- skeletal, mixed, superactive, frigid Typic Calcixerolls.
Mandan, North Dakota	Mixed-grass prairie	48.2	518	lat 46°46′N, long 100°55′W	2–10	Werner-Sen-Chama complex; loam, silt loam, and silty clay loam, Entic and Typic Haploborolls.
Nunn, Colorado	Short-grass prairie	48.9	1 660	lat 40°41′N, long 104°45′W	0–5	Olney; fine-loamy, mixed, mesic, Ustollic Haplargids.
Woodward, Oklahoma	Southern grass prairie	72.8	219	lat 36°36′N, long 99°35′W	5–45	Tivoli; mixed, thermic Typic Ustipsamments.
Temple, Texas	Tallgrass prairie	81.9	208	lat 31°06'N, long 97°20'W	0–15	Houston Black Clay; fine montmorillonitic, thermic Udic Pellustert.

 Table 2. Vegetation type and site characteristics for study locations.

Scientific, Inc 1998). Water vapor and CO₂ concentrations were measured with an infrared gas analyzer (IRGA; model LI-6262; Li-Cor Inc, Lincoln, NE) in differential mode with the CO₂ and water vapor scrubbed on the chopper input. Air samples from two heights (about 1 m and 2 m above the soil surface) were drawn and routed to the IRGA, which measured the difference in water vapor and CO₂ concentrations between the two heights. These two air sampling heights were above the vegetation surface. A low-power pump (model TD-3LSC; Brailsford and Co, Inc, Rye, NY) aspirated the air through 1um Teflon filters (model Acro 50; Gelman Sciences, Ann Arbor, MI), which prevented dust and liquid water contamination in the air tubes and IRGA. A solenoid valve (model 236-102B; Numatics Inc., Highland, MI) was programmed to reverse the air drawn through the IRGA sample and reference cells every 2 min. Another solenoid valve was programmed to control the flow of air stream at the beginning of each hour, when the IRGA sample cell was scrubbed to determine absolute concentrations of CO₂ and water vapor. The difference in air temperature between the two heights was measured with finewire, chromel-constantan thermocouples (model FW3; Campbell Scientific, Inc). Differences in temperature and water vapor and CO_2 concentrations between the two heights were simultaneously measured every 2 s and the average differences were calculated and stored every 20 min with a data logger (models 21X and SM912; Campbell Scientific, Inc).

Temperature and water vapor differences at 20-min averaging intervals were used to calculate the Bowen ratio (β):

$$\beta = (c_{\rm p}/\lambda 0.622)(\Delta T/\Delta W_{\rm f})$$
 [1]

where c_p is the specific heat at constant pressure $(J \cdot g^{-1} \cdot K^{-1})$, λ is the latent heat of vaporization $(J \cdot g^{-1})$, 0.622 is the ratio of molecular weights of water and air, ΔT is the difference in air temperature (K), and ΔW_f is the difference in mole fraction of water vapor (mmol \cdot mol⁻¹) between the two heights.

Sensible energy flux (H, $J \cdot m^{-2} \cdot s^{-1}$) was calculated as

$$H = (R_{\rm n} - G) / (1 + \beta^{-1})$$
[2]

where R_n (J · m⁻² · s⁻¹) is net radiation (model Q*7.1 net radiometer; REBS, Seattle, WA), and G (J · m⁻² · s⁻¹) is soil heat flux at the soil surface calculated from measurements with soil heat flux plates (model HFT3, REBS) and averaging soil temperature probes (model TCAV; Campbell Scientific, Inc). Two soil heat flux plates were installed 1 m apart at a 0.08-m depth, and two pairs of soil temperature probes were installed above each soil heat flux plate at depths of 0.02 m and 0.06 m. Volumetric soil water content at 0.05-m depth was measured every hour with a soil moisture content reflectometer (model CS615; Campbell Scientific, Inc), and soil bulk density was determined periodically by sampling the top 0.05 m of the soil surface. We calculated G according to the soil heat flux plate method described elsewhere (Sauer 2002).

Table 3. Average daily CO_2 flux for the winter (or nongrowing) season.

Site	Winter Period	No. of days measured	Mean daily CO_2 flux (g CO_2 \cdot m^{-2} \cdot d^{-1})
Burns, Oregon	2000: 1 October–31 December; 2001: 1 January–24 March	108	0.68
Dubois, Idaho	2000: 1 January–31 March, 1 October–31 December	165	1.31
Mandan, North Dakota	2001: 1 January–15 April, 15 November–31 December; 2002:	197	1.06
	1 January–15 April		
Nunn, Colorado	2001: 1 January–15 April, 15 November–31 December; 2002: 1 January–15 April	206	0.97
Woodward, Oklahoma	2001: 1 January–15 April, 15 November–31 December	137	2.11
Mean	—	—	1.23

The eddy diffusivity for heat $(K_b, m^2 \cdot s^{-1})$ was calculated as

$$K_{b} = (H/\rho_{a}C_{p}) \cdot (\Delta z/\Delta T)$$
[3]

where ρ_a is air density $(\mathbf{g} \cdot \mathbf{m}^{-3})$ and $\Delta \mathbf{z}$ is the height difference (usually 1 m) between the upper and lower thermocouples. Assuming that the eddy diffusivity for CO₂ (K_c) was equal to K_b , CO₂ flux was calculated as

$$F_{\rm CO_2} = K_b \cdot (\Delta \rho_c / \Delta z)$$
 [4]

where $\Delta \rho_c$ is gradient of CO₂ density (g · m⁻³). The CO₂ flux was corrected for the difference in water vapor density at the two heights (Webb et al. 1980). Corrections of CO₂ flux for the effects of heat density were not applied because fine-wire thermocouple measurements indicated that the temperatures of the two air streams were the same as they entered the sample and reference cells of the IRGA (Dugas et al. 1999; Angell et al. 2001).

Fluxes for the BREB method are most suspect at night when the temperature/humidity gradients are small and may have signs opposite of the flux (Ohmura 1982). When this occurs, BREB cannot be used to calculate turbulent diffusivity. Also, when the Bowen ratio nears -1, the method can indicate erroneous fluxes. This generally occurs at sunrise or sunset, during times when CO₂ fluxes are low. When that occurred, we estimated flux rate by linear interpolation. Additionally, daily plots of 20-min data were visually inspected. When individual 20-min CO₂ fluxes, a check was conducted on the measured data used to calculate CO₂ flux. If there were obvious problems with the measured data, the point was removed and again, linear interpolation was used to replace the 20-min flux data.

Data Processing

To ensure uniformity, data from all locations were sent to the Blackland Research and Extension Center in Temple, Texas, for initial quality control screening, summarization, and storage. We quantified the amount of linear interpolation of the 20-min data sets by randomly selecting 435 d across locations and years and summed to total number of interpolated data points (each data point represents a 20-min period). Of the 31 320 measurement periods (435 d \times 72 periods per day) evaluated, there were 188 (0.6%) interpolations during the daytime hours (0800 hours to 1800 hours) and 629 (2.01%) during nondaytime hours. When daily fluxes were measured for 10 or more days per month, monthly CO₂ fluxes

were calculated by obtaining the average daily flux and multiplying by the number of days for the month. When less than 10 d of daily fluxes were measured in a month, we interpolated the fluxes between 2 mo whose daily fluxes were measured for 10 or more days. Continuous micrometeorological measurements of fluxes during the dormant season (cold, winter months) were not made for the more northerly sites. For five study sites, we measured the daily fluxes during an entire winter (or nongrowing) season; an empirical modeling procedure that used soil temperature, snow depth, and/or wind speed as independent variables (Gilmanov et al. 2004) was developed to estimate daily CO₂ fluxes for each study site during winter months when BREB systems were not operated (Table 3). The values presented in Table 3 are comparable to chamber and eddy covariance measurements on similar plant communities (Gilmanov et al. 2004). Annual NEE values were the sums of January to December monthly NEE for each site during each year. The degree of gap-filling necessary for the annual estimates is presented in Tables 4 and 5.

Portions of the CO_2 flux data have been published previously (e.g., Frank and Dugas 2001; Sims and Bradford 2001; Emmerich 2003; Gilmanov et al. 2006). These publications contain additional descriptions of data collection and handling, and in several cases, also describe CO_2 fluxes for community types not included in the present analysis.

Empirical Support for CO₂ Flux Measurements

The two primary means of measuring diurnal CO_2 fluxes are the BREB system that we used in our study and the eddy

Table 4. Number of years and days measured and the percentage of days measured for eight study sites.

Site	No. of years	No. of days measured	Percentage of days measured (%)
Las Cruces, New Mexico	6	1 242	57
Lucky Hills, Tucson,			
Arizona	6	1 661	76
Burns, Oregon	6	1 045	48
Dubois, Idaho	6	1 346	61
Mandan, North Dakota	7	1 508	59
Nunn, Colorado	5	1 022	56
Woodward, Oklahoma	6	1 314	60
Temple, Texas	7	1 693	66
Total	49	10831	—
Mean	_	1 354	60

		No. of months	Gap-	filled months	No. of months measured	Percentage of months measured
Site	No. of years		Linearly interpolated	Using daily average in Table 3		
Las Cruces, New Mexico	6	72	25	_	47	65
Lucky Hills, Tucson, Arizona	6	72	12	_	60	83
Burns, Oregon	6	72	6	26	40	56
Dubois, Idaho	6	72	3	20	49	68
Mandan, North Dakota	7	84	14	19	51	61
Nunn, Colorado	5	60	5	16	39	65
Woodward, Oklahoma	6	72	5	15	52	72
Temple, Texas	7	84	16	_	68	81
Total	49	588	86	96	406	_
Mean	_	_	_	_	50.8	69

Table 5. Number of years, months that were gap-filled by using the average daily flux for the growing season and/or interpolation, months measured, and percent months measured for eight study sites.

covariance (EC) technique. At the time the USDA-ARS rangeland carbon flux network was initiated, the only commercially available system for measuring large-scale CO₂ fluxes was the BREB system. A recent comparison of BREB and EC systems on rangeland suggests that results of the two systems are reasonably similar when the appropriate data processing algorithms are used (Wolf et al. 2008). Each system has deficiencies under specific environmental conditions, and even with appropriate data processing, EC estimates of CO₂ flux tend to be slightly lower than those produced by BREB. Because there is no true "standard" CO2 flux to use for calibration, the values presented by either technique are estimates and should not be viewed as absolute. However, fluxes calculated using the BREB method have been shown to be similar to seasonal fluxes estimated from biomass differences (Dugas et al. 1999); to daytime soil CO₂ fluxes measured on a bare soil using a soil respiration chamber (Dugas 1993); to daytime canopy fluxes calculated from leaf gas exchange measurements for three C4 grasses (Dugas et al. 1997) and mesquite savannas (Ansley et al. 2002); to values calculated from small canopy chamber measurements above sagebrush (Angell et al. 2001); to measurements by several methods above sorghum (Twine et al. 2000); to nighttime fluxes calculated from the sum of measured soil respiration and estimated plant respiration (Frank et al. 2001); and to daytime and nighttime fluxes measured using EC instrumentation (Dugas et al. 2001).

Statistical Analysis

Linear regression analysis of annual NEE and annual precipitation across locations was conducted using Sigmaplot version 10 (Systat Software, Inc., San Jose, CA). Annual precipitation was considered the independent and NEE the dependent variable.

RESULTS AND DISCUSSION

Five of the eight rangeland sites that we studied typically functioned as sinks for atmospheric CO_2 during the study period, but sink strength varied among biomes and years (Table 6). The sagebrush steppe sites in the northwestern United States were surprisingly strong sinks for C during the

study period (Fig. 1; Table 6). Grassland sites on the US Great Plains were variable, with most sites either weak or moderate sinks for atmospheric CO₂ (Figs. 2 and 3; Table 6). In the sagebrush steppe, positive NEE was observed during 9 of 12 site years (years summed across sites within a region), whereas for the Great Plains sites 17 of the 25 total site years had positive NEE. Any site could function as a C source during drought, but sites in the Southwestern hot desert (Fig. 4; Table 6) had a strong tendency to be sources for C during the period of record. On an annual basis, net C efflux (C loss) was observed during 10 of 12 total site years for the Southwest. The primary source of C from these sites is unknown and may vary depending on precipitation patterns (Huxman et al. 2004), but inorganic C from carbonates (Emmerich 2003) or microbial respiration of organic compounds are likely sources. Globally, soil carbonates are the third largest C pool after oceanic and soil organic C (Monger and Martinez-Rios 2001). Net uptake of C in these arid Southwestern hot deserts is strongly driven by large rainfall events that were infrequent during the study; much of this region experienced extended drought during this period. Jasoni et al. (2005) found that a Mojave Desert shrubland in southern Nevada was a significant sink for atmospheric CO₂ during an average precipitation year.

Few annual estimates of NEE had been reported for arid and semiarid biomes (Canadell et al. 2000) until relatively recently; but those available are similar to values we measured. For example, Suyker and Verma (2001) measured NEE of 268 g $C \cdot m^{-2} \cdot yr^{-1}$ for a tallgrass prairie site in north-central Oklahoma. We observed an average NEE of 252 g $C \cdot m^{-2} \cdot yr^{-1}$ for our tallgrass prairie site in Texas. The study of Suyker and Verma (2001) involved annual burning. When they subtracted loss of C from combustion from annual NEE, the tallgrass was neutral or in balance with respect to C. Our tallgrass site was burned only in 1995, and that year was excluded from our calculations of NEE in Table 6. Other recent multiyear NEE estimates include 37.3 g C \cdot m⁻² \cdot yr⁻¹ for a northern mixed prairie in Alberta, Canada (Flanagan et al. 2002) and 51.5 g C \cdot m⁻² \cdot yr⁻¹ for a Mediterranean annual grassland in California (Xu and Baldocchi 2004). Both of these studies also found that their sites were either sinks or sources of C depending on precipitation patterns. Recent work suggests that even very arid communities can act as C sinks during

	Table 6. Aver	rage annual net ec	osystem exchange	(NEE) for rangeland	sites involved in the study.
--	---------------	--------------------	------------------	---------------------	------------------------------

Location and		Annual NEE (g	$C \cdot m^{-2} \cdot yr^{-1})^1$	No. of years with positive NEE	Total measurement years
measurement years	Vegetation type	Average	Range		
Las Cruces, New Mexico 1996–2001	Desert grassland	-160	-254 to 94	1	6
Lucky Hills, Arizona 1996–2001	Desert shrub	-93	-162 to 55	1	6
Burns, Oregon 1995–2000	Sagebrush steppe	73	-61 to 229	4	6
Dubois, Idaho 1996–2001	Sagebrush steppe	83	-47 to 260	5	6
Mandan, North Dakota 1995–2001	Northern mixed prairie	53	-27 to 119	6	7
Nunn, Colorado 1996, 1998–2001	Shortgrass prairie	107	4 to 227	5	5
Woodward, Oklahoma 1995–2001	Southern mixed prairie	-11	-134 to 138	3	7
Temple, Texas 1993, 1994, 1996–1999	Tallgrass prairie	99	-147 to 439	3	6

¹Positive flux values indicate accumulation of C in vegetation and soil, negative numbers indicate release of C.

nondrought years (Hastings et al. 2005). These authors found that a desert shrub community, which receives average annual precipitation of 17.4 cm, was a C sink during two near-average precipitation years.

Increasing evidence suggests that intact terrestrial ecosystems have accumulated C in recent years. Schimel et al. (2001) postulate that the terrestrial biosphere was neutral in terms of NEE during the 1980s, but became a C sink during the 1990s. They cited longer growing seasons, CO_2 fertilization, and regrowth of disturbed systems as possible explanations for the terrestrial sink pattern observed in the 1990s. Evidence also exists that during the late 1900s, both precipitation (Nemani et al. 2002) and net primary productivity (NPP; Hicke et al. 2002) increased in North America. These general increases coincided with the period of our study. The study of Hicke et al. (2002) was particularly striking because they found a 30% increase in NPP from 1982 to 1998. An increase in NPP and above average precipitation would help explain the generally positive NEE values that we observed for sagebrush steppe and Great Plains grassland sites.

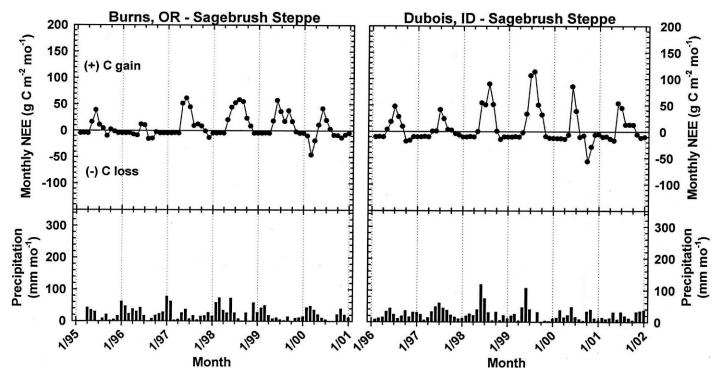


Figure 1. Monthly net ecosystem exchange of carbon (NEE) and monthly precipitation for rangelands in the northwestern United States.

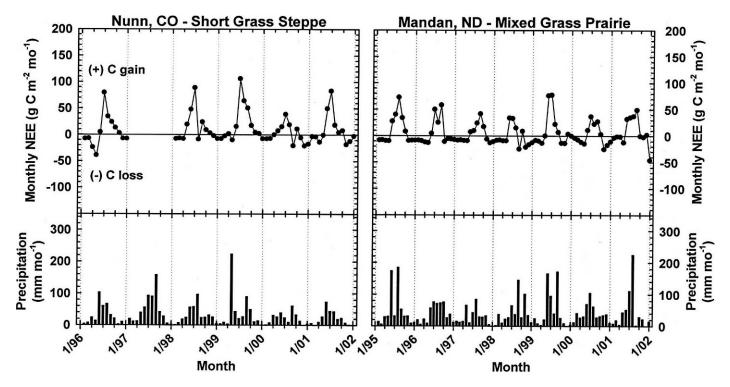


Figure 2. Monthly net ecosystem exchange of carbon (NEE) and monthly precipitation for rangelands in the Northern Plains of the United States.

Many of the rangeland sites we studied are water-limited ecosystems and exhibit increased NPP with timely precipitation (Schwinning and Sala 2004). Our sites often exhibited brief periods of positive NEE followed by long periods of either neutral or slightly negative NEE (Figs. 1–4). Any change in the period of positive NEE would likely determine whether a biome was a sink or source for atmospheric C. The primary impact of drought was to reduce peak NEE and shorten the duration of positive NEE; examples of drought include 2000 at Nunn, Colorado (Fig. 2); 2001 at Woodward, Oklahoma (Fig. 3); and 2001 at Dubois, Idaho (Fig. 1). Conversely, increased precipitation and a longer period of positive NEE could shift these sites to C sinks.

Land-use history is important in evaluating NEE of terrestrial biomes. Regrowth of disturbed forests and conver-

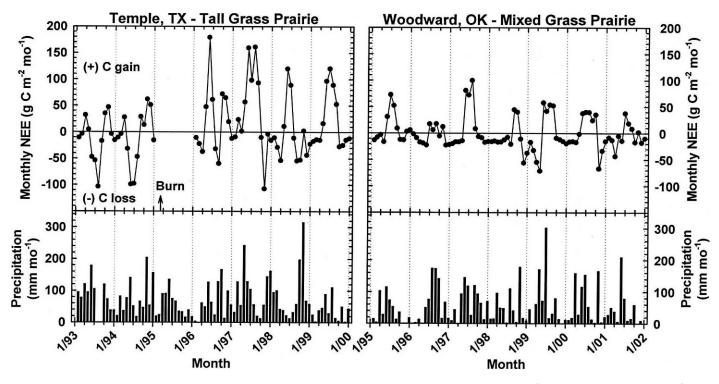


Figure 3. Monthly net ecosystem exchange of carbon (NEE) and monthly precipitation for rangelands in the Southern Plains of the United States.

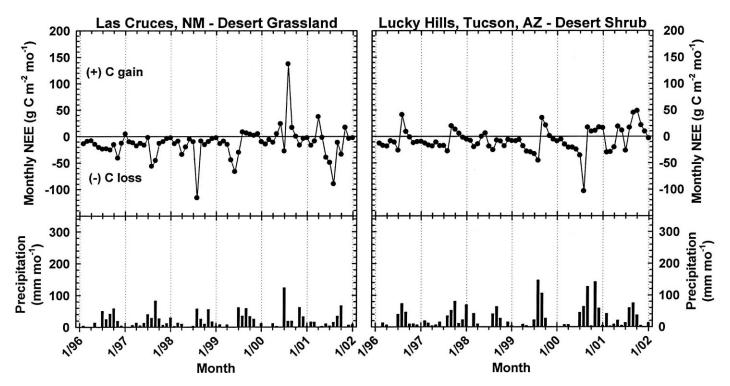


Figure 4. Monthly net ecosystem exchange of carbon (NEE) and monthly precipitation for rangelands in the southwestern United States.

sion of cropland to perennial vegetation can influence sink strength of terrestrial vegetation (Schimel et al. 2001). Similarly, the historical management of rangelands can dramatically influence current C dynamics. The rangeland sites we studied were considered to be in good ecological condition (that is, they were dominated by the appropriate mix of native species and protected from excessive disturbance prior to and during the time of the study). However, many US rangelands, and indeed rangelands around the world, have experienced periods of intense disturbance (such as extended drought, overgrazing, or species invasions). In relatively mesic and productive rangelands, accumulation of litter can limit growth (Knapp and Seastedt 1996). Intensive early grazing of tallgrass prairie can increase photosynthetic efficiency, and applying this grazing strategy helped maintain carbon stores (Owensby et al. 2006). However, recent research demonstrated that heavy grazing can have a negative impact on NEE (P. Sims, unpublished data, 2007). If grazing reduces leaf area and there is no protection from grazing during the active growth period, the net effect would probably be similar to drought, with a lower NEE peak and shorter period of positive NEE. Risch and Frank (2006) found no effect of grazing on growing season NEE in the grassland they studied. We suspect that grazing level and timing will control the impact of grazing on NEE, which is one reason we chose to take measurements on ungrazed rangeland for this study. Some locations within the network are studying grazing impacts.

Yearly weather variation is one of the major challenges to predicting NEE for any biome. We cannot assume that averaging yearly measurements will necessarily represent long-term NEE for a site or region. Linking NEE measurements to climate models will be a critical step in assessing carbon cycling in the terrestrial biosphere. Although annual precipitation amount is an important determinant of NEE, the relationship between these two variables is not simple. A cross-site regression of annual NEE on annual precipitation was low and not significant ($r^2 = 0.06$, P > 0.05). Annual precipitation was also a poor predictor of NEE when the analysis was restricted to the sagebrush steppe sites (Gilmanov et al. 2006). Precipitation timing can be more critical than precipitation amount in predicting NEE (Knapp et al. 2002). For example, peak monthly NEE at Dubois was influenced by growing-season precipitation (April to June) in 1998 and 1999 (Fig. 1). The availability of soil water at crucial times for plant growth probably controls the relationship between precipitation timing and seasonal NEE. On most of the rangelands we studied, the bulk of CO₂ uptake occurred over relatively short periods. A fundamental knowledge of plant community phenology and the independent responses of soil and plant CO2 fluxes will be needed to realistically scale such data to eco-regions and biomes. A second major challenge in developing biome-level NEE estimates is the spatial variation within individual biomes. One or two sites may not adequately characterize a biome.

Much of the research on C sequestration has been conducted in relatively mesic biomes. Although arid biomes have less potential for sequestering C on a given unit of land, they occupy a large proportion of the earth's surface. A recent meta-analysis suggests that increasing atmospheric CO_2 is increasing soil C in a variety of temperate ecosystems (Jastrow et al. 2005). Based on our results, it appears that efforts to improve the productivity and ecological health of rangeland biomes may also improve their potential for storing atmospheric C. It also appears that climatic shifts have great potential to influence the C balance of rangelands.

MANAGEMENT IMPLICATIONS

Although we did not test the impact of management practices on rangeland NEE, there are some important points to be gleaned from the annual NEE patterns. Because NEE and vegetation productivity are linked, these patterns have implications for managing rangelands. Most of the sites exhibited rapid CO_2 uptake for a short period (2 mo to 4 mo) and a longer period of low CO_2 loss (where ecosystem respiration exceeded photosynthesis). Drought reduced the period and magnitude of positive NEE. Ensuring that management does not routinely limit the period of active CO_2 uptake is a useful goal for maintaining the long-term productivity of rangeland biomes.

ACKNOWLEDGMENTS

The authors wish to thank the many individuals who provided technical and administrative support to this project. We also thank Joel Brown, Wayne Polley, several anonymous reviewers, and Associate Editor Robert Nowak for comments that improved the manuscript.

LITERATURE CITED

- ANGELL, R., T. SVEJCAR, J. BATES, N. Z. SALIENDRA, AND D. A. JOHNSON. 2001. Bowen ratio and closed chamber carbon dioxide flux measurements over sagebrush steppe vegetation. *Agricultural Forest Meteorology* 108:153–161.
- ANSLEY, R. J., W. A. DUGAS, M. L. HEUR, AND B. A. KRAMP. 2002. CO₂ fluxes over a burned and unburned Prosopis savanna. *Ecologicical Applications* 12:948–961.
- CAMPBELL SCIENTIFIC Inc. 1998. Instruction manual: 023/CO₂ Bowen ratio system with CO₂ flux. Available at: ftp://ftp.campbellsci.com/pub/outgoing/manuals/ co2bowen.pdf. Accessed 8 June 1998.
- CANADELL, J. G., H. A. MOONEY, D. D. BALDOCCHI, J. A. BERRY, J. R. EHLERINGER, C. B. FIELD, S. T. GOWER, D. Y. HOLLINGER, J. E. HUNT, R. B JACKSON, S. W. RUNNING, G. R. SHAVER, W. STEFFEN, S. E. TRUMBORE, R. VALENTINI, AND B. Y. BOND. 2000. Carbon metabolism of the terrestrial biosphere: a multi-technique approach for improved understanding. *Ecosystems* 3:115–130.
- DuGAS, W. A. 1993. Micrometeorological and chamber measurements of CO₂ flux from bare soil. *Agricultural Forest Meteorology* 67:115–128.
- DUGAS, W. A., R. EVANS, AND D. HOLLINGER. 2001. Eddy correlation and Bowen ratio/ energy balance measurements of sensible heat, latent heat, and CO₂ flux over a tallgrass prairie. Temple, TX, USA: Blackland Research Center. BRC Report No. 01-31. 16 p.
- DUGAS, W. A., M. L. HEUER, AND H. S. MAYEUX. 1999. Seasonal carbon dioxide fluxes over coastal bermudagrass, native prairie, and sorghum. *Agricultural Forest Meteorology* 93:121–139.
- DUGAS, W. A., D. C. REICOSKY, AND J. R. KINIRY. 1997. Chamber and micrometeorological measurements of CO₂ and H₂O fluxes for three C₄ grasslands. *Agricultural Forest Meteorology* 83:113–133.
- EMMERICH, W. E. 2003. Carbon dioxide fluxes in a semiarid environment with high carbonate soils. Agricultural Forest Meteorology 116:91–102.
- FLANAGAN, L. B., L. A. WEVER, AND P. J. CARLSON. 2002. Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. *Global Change Biology* 8:599–615.
- FRANK, A. B., AND W. A. DUGAS. 2001. Carbon dioxide fluxes over a northern semiarid, mixed-grass prairie. *Agricultural and Forest Meteorology* 108:317–326.
- FRANK, A., P. SIMS, J. BRADFORD, P. MIELNICK, W. DUGAS, AND H. MAYEUX. 2001. Carbon dioxide fluxes over three Great Plains grasslands. *In*: R. F. Follett, J. M. Kimble, and R. Lal [EDS.]. The potential of U.S. grazing lands to sequester carbon and mitigate the greenhouse effect. Boca Raton, FL, USA: CRC/Lewis Publishers. p. 167–188.
- GILMANOV, T. G., D. A. JOHNSON, N. Z. SALIENDRA, T. J. SVEJCAR, R. F. ANGELL, AND K. L. CLAWSON. 2004. Winter CO₂ fluxes above sagebrush-steppe ecosystems in Idaho and Oregon. *Agricultural Forest Meteorology* 126:73–88.
- GILMANOV, T. G., T. J. SVEJCAR, D. A. JOHNSON, R. F. ANGELL, N. Z. SALIENDRA, AND B. K. WYLIE. 2006. Long-term dynamics of production, respiration, and net CO₂

exchange in two sagebrush-steppe ecosystems. *Rangeland Ecology and Management* 59:585–599.

- HASTINGS, S. J., W. C. OECHEL, AND A. MUHLIA-MELO. 2005. Diurnal, seasonal and annual variation in the net ecosystem CO₂ exchange of a desert shrub community (Sarcocaulescent) in Baja California, Mexico. *Global Change Biology* 11:927–939.
- HICKE, J. A., G. P. ASNER, J. T. RANDERSON, C. TUCKER, S. LOS, R. BIRDSEY, J. C. JENKINS, AND C. FIELD. 2002. Trends in North American net primary productivity derived from satellite observations, 1982–1998. *Global Biogeochemical Cycles* 16:1018.
- HUXMAN, T. L., K. SNYDER, D. TISSUE, J. LEFFLER, K. OGLE, W. T. POCKMAN, D. R. SANDQUIST, D. L. POTTS, AND S. SCHWINNING. 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* 141:254–267.
- JASONI, R. L., S. D. SMITH, AND J. A. ARNONE, III. 2005. Net ecosystem CO₂ exchange in Mojave Desert shrublands during the eighth year of exposure to elevated CO₂. *Global Change Biology* 11:749–756.
- JASTROW, J. D., R. M. MILLER, R. MATAMALA, R. J. NORBY, T. W. BOUTTON, C. W. RICE, AND C. E. OWENSBY. 2005. Elevated atmospheric carbon dioxide increases soil carbon. *Global Change Biology* 11:2057–2064.
- KNAPP, A. K., S. L. CONARD, AND J. M. BLAIR. 1998. Determinants of soil CO₂ flux from a sub-humid grassland: effect of fire and fire history. *Ecological Applications* 8:760–770.
- KNAPP, A. K., P. A. FAY, J. M. BLAIR, S. L. COLLINS, M. D. SMITH, J. D. CARLISLE, C. W. HARPER, B. T. DANNER, M. S. LETT, AND J. K. MCCARRON. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* 298:2202–2205.
- KNAPP, A. K., AND T. R. SEASTEDT. 1996. Detritus accumulation limits productivity in tallgrass prairie. *BioScience* 36:662–668.
- MONGER, H. C., AND J. J. MARTINEZ-RIOS. 2001. Inorganic carbon sequestration in grazing lands. *In:* R. F. Follett, J. M. Kimble, and R. Lal [EDS.]. The potential of U.S. grazing lands to sequester carbon and mitigate the greenhouse effect. Boca Raton, FL, USA: CRC/Lewis Publishers. p. 87–117.
- MORGAN, J. A., D. E. PATAKI, C. KÖRNER, H. CLARK, S. J. DEL GROSSO, J. M. GRÜNZWEIG, A. K. KNAPP, A. R. MOSIER, P. C. D. NEWTON, P. A. NIKLAUS, J. B. NIPPERT, R. S. NOWAK, W. J. PARTON, H. W. POLLEY, AND M. R. SHAW. 2004. Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO₂. *Oecologia* 140:11–25.
- NEMANI, R., M. WHITE, P. THORNTON, K. NISHIDA, S. REDDY, J. JENKINS, AND S. RUNNING. 2002. Recent trends in hydrologic balance have enhanced the terrestrial carbon sink in the United States. *Geophysical Research Letters* 29:106-1–106-4.
- OHMURA, A. 1982. Objective criteria for rejecting data for Bowen ratio flux calculations. *Journal of Applied Meteorology* 21:595–598.
- OWENSBY, C. E., J. M. HAM, AND L. M. AUEN. 2006. Fluxes of CO₂ from grazed and ungrazed tallgrass prairie. *Rangeland Ecology and Management* 59:111– 127.
- RISCH, A. C., AND D. A. FRANK. 2006. Carbon dioxide fluxes in a spatially and temporally heterogeneous temperate grassland. *Oecologia* 147:291–302.
- SAUER, T. J. 2002. Heat flux density. *In:* G. C. Topp and J. H. Dane [EDS.]. Methods of soil snalysis. Part 4—physical methods. SSSA Book Series 5. Madison, WI, USA: Soil Science Society of America. p. 1233–1248.
- SCHIMEL, D. S. 1995. Terrestrial ecosystems and the carbon cycle. *Global Change Biology* 1:77–91.
- Schimel, D. S., J. I. House, K. A. Hibbard, P. Bousquet, P. Ciais, P. Peylin, B. H. Braswell, M. J. Apps, D. Baker, A. Bondeau, J. Canadell, G. Churkina, W. Cramer, A. S. Denning, C. B. Field, P. Friedlingstein, C. Goodale, M. Heimann, R. A. Houghton, J. M. Melillo, B. Moore, III., D. Murdiyarso, I. Noble, S. W. Pacala, I. C. Prentice, M. R. Raupach, P. J. Rayner, R. J. Scholes, W. L. Steffen, and C. Wirth. 2001. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature* 414:169–172.
- SCHWINNING, S., AND O. E. SALA. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia* 141:211–220.
- SIMS, P. L., AND J. A. BRADFORD. 2001. Carbon dioxide fluxes in a southern plains prairie. Agricultural and Forest Meteorology 109:117–134.
- SUYKER, A. E., AND S. B. VERMA. 2001. Year-round observations of the net ecosystem exchange of carbon dioxide in a native tallgrass prairie. *Global Change Biology* 7:279–289.

- TWINE, T. E., W. P. KUSTAS, J. M. NORMAN, D. R. COOK, P. R. HOUSER, T. P. MEYERS, J. H. PRUEGER, P. J. STARKS, AND M. L. WESELY. 2000. Correcting eddy-covariance flux underestimates over a grassland. *Agricultural Forest Meteorology* 103:279–300.
- WEBB, E. K., G. I. PEARMAN, AND R. LEUNING. 1980. Correction of flux measurements for density effects due to heat and water vapor transfer. *Quarterly Journal Royal Meteorological Society* 106:85–100.
- Wolf, A., N. Saliendra, K. Akshalov, D. A. Johnson, and E. Laca. 2008. Effects of different eddy covariance correction schemes on energy balance closure and

comparisons with the modified Bowen ratio system. *Agricultural and Forest Meteorology* 148:942–952.

- WOODWELL, G. M., F. T. MACKENZIE, R. A. HOUGHTON, M. J. APPS, E. GORHAM, AND E. A. DAVIDSON. 1998. Biotic feedbacks in the warming of the earth. *Climate Change* 40:495–518.
- Xu, L., AND D. D. BALDOCCHI. 2004. Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. Agricultural Forest Meteorology 123:79–96.