Carbon Fluxes on North American Rangelands

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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 (CO_2) 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 CO_2 atmosférico durante el período del estudio. Ambos sitios del desierto arbustivo y tres de cuatro sitios de las Grandes Planicies demandaron CO_2. 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 CO_2 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

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INTRODUCTION

There is considerable interest in potential effects of increasing atmospheric carbon dioxide (CO_2) 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 CO_2 was considerably lower than today's levels (Schimel 1995). There is evidence that compared to the preindustrial period, today's atmospheric CO_2 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.

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/CO_2 Bowen Ratio; Campbell Scientific, Inc, Logan, UT) system for continuous measurements of energy, water vapor, and CO_2 fluxes at each study site. The theory and operation of the BREB technique have been described in detail (Dugas 1993; Campbell

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

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.

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

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.

Scientific, Inc 1998). Water vapor and CO_2 concentrations were measured with an infrared gas analyzer (IRGA; model LI-6262; Li-Cor Inc, Lincoln, NE) in differential mode with the CO_2 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 CO_2 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 1-μm 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 CO_2 and water vapor. The difference in air temperature between the two heights was measured with fine-wire, 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):

$$\beta = (c_p/\lambda 0.622)(\Delta T/\Delta W_f) \qquad [1]$$

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

$$H = (R_n - G)/(1 + \beta^{-1}) \qquad [2]$$

where R_n $(J \cdot m^{-2} \cdot s^{-1})$ is net radiation (model Q*7.1 net radiometer; REBS, Seattle, WA), and G $(J \cdot m^{-2} \cdot s^{-1})$ 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: 1 January–15 April	197	1.06
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, m² · s⁻¹) was calculated as

$$K_b = (H/\rho_a C_p) \cdot (\Delta z / \Delta T) \qquad [3]$$

where ρ_a is air density (g · m⁻³) and Δz is the height difference (usually 1 m) between the upper and lower thermocouples. Assuming that the eddy diffusivity for CO_2 (K_c) was equal to K_b, CO_2 flux was calculated as

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

where $\Delta \rho_c$ is gradient of CO_2 density (g · m⁻³). The CO_2 flux was corrected for the difference in water vapor density at the two heights (Webb et al. 1980). Corrections of CO_2 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 CO_2 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 CO_2 flux values fell outside the range of surrounding 20-min CO_2 fluxes, a check was conducted on the measured data used to calculate CO_2 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 × 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 CO_2 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 CO_2 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 CO_2 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	10 831	—
Mean	—	1 354	60

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.

Site	No. of years	No. of months	Gap-filled months		No. of months measured	Percentage of months measured
			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

covariance (EC) technique. At the time the USDA-ARS rangeland carbon flux network was initiated, the only commercially available system for measuring large-scale CO_2 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 CO_2 flux tend to be slightly lower than those produced by BREB. Because there is no true "standard" CO_2 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 CO_2 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 CO_2 (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 CO_2 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. Average annual net ecosystem exchange (NEE) for rangeland sites involved in the study.

Location and measurement years	Vegetation type	Annual NEE (g C $\cdot$ m^{-2} $\cdot$ yr^{-1})[1]		No. of years with positive NEE	Total measurement years
		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

[1]Positive 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.
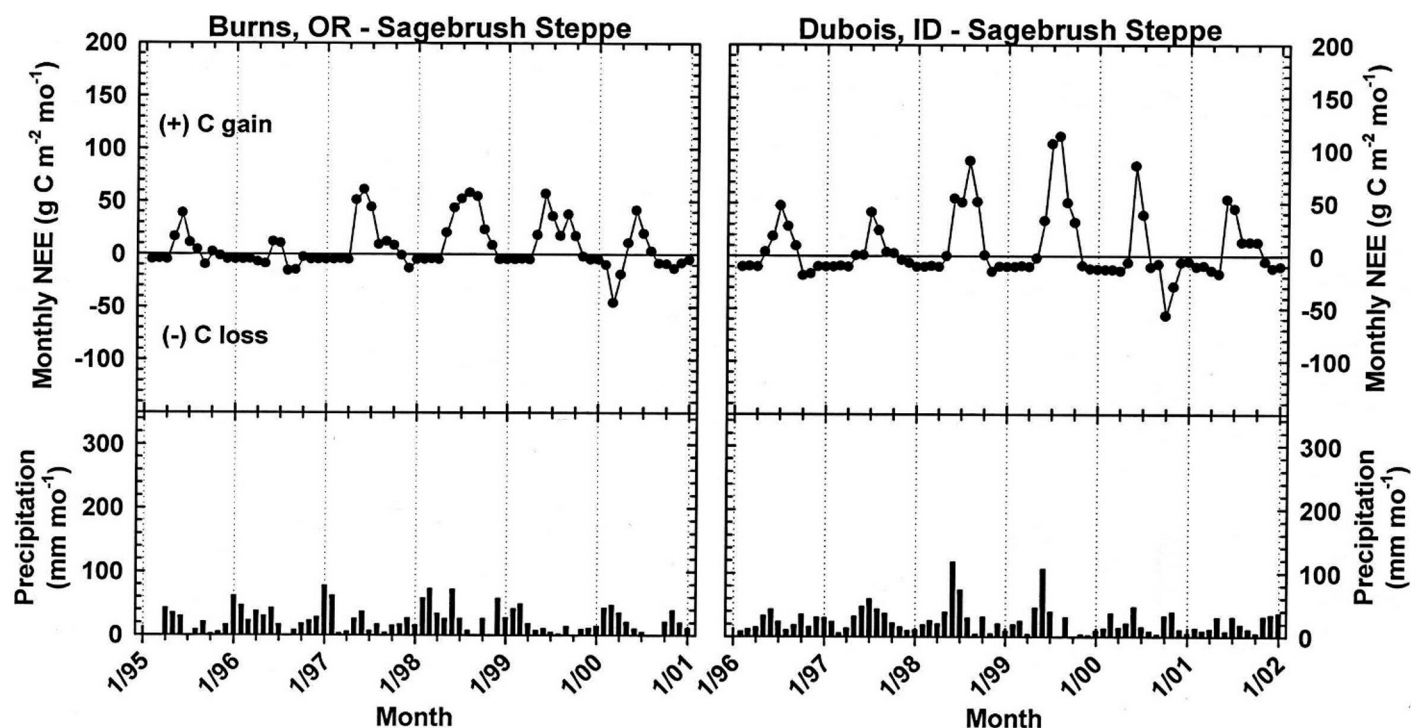
Figure 1. Monthly net ecosystem exchange of carbon (NEE) and monthly precipitation for rangelands in the northwestern United States.
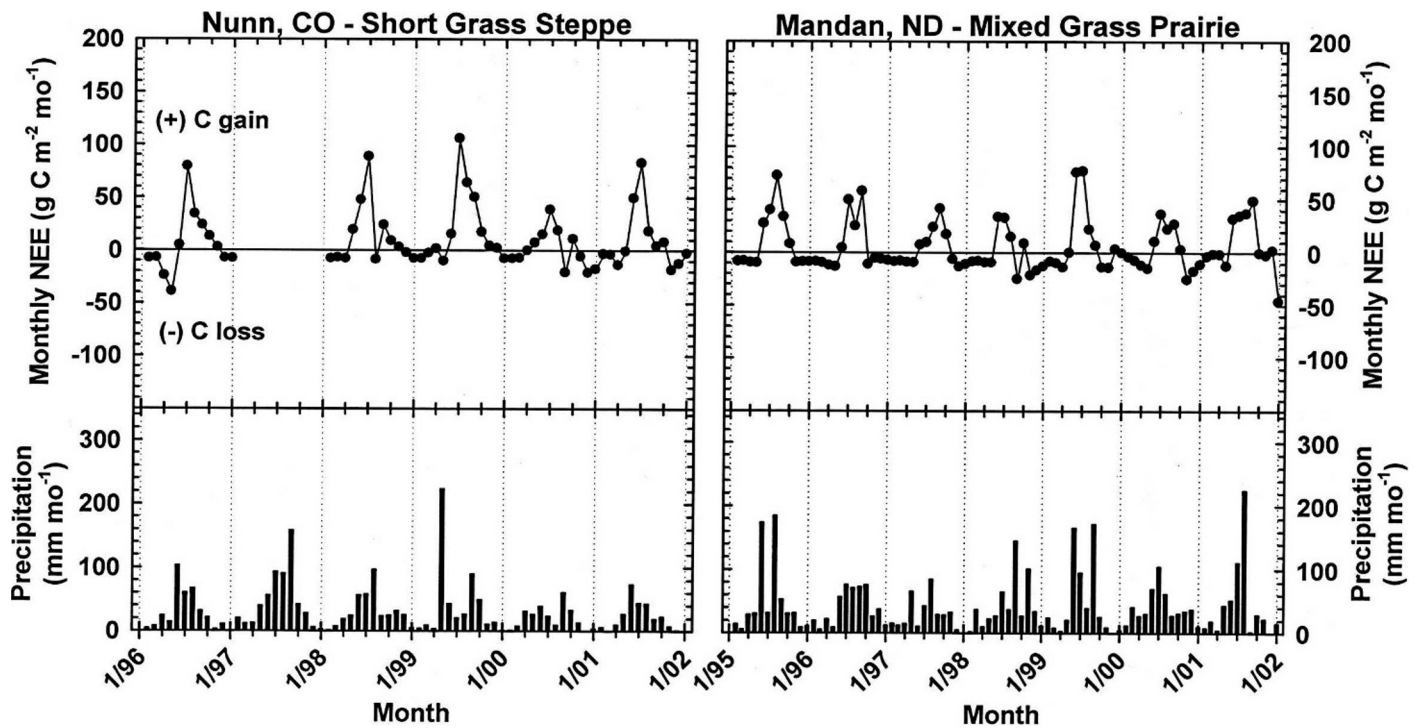
Figure 2. Monthly net ecosystem exchange of carbon (NEE) and monthly precipitation for rangelands in the Northern Plains of the United States.

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-
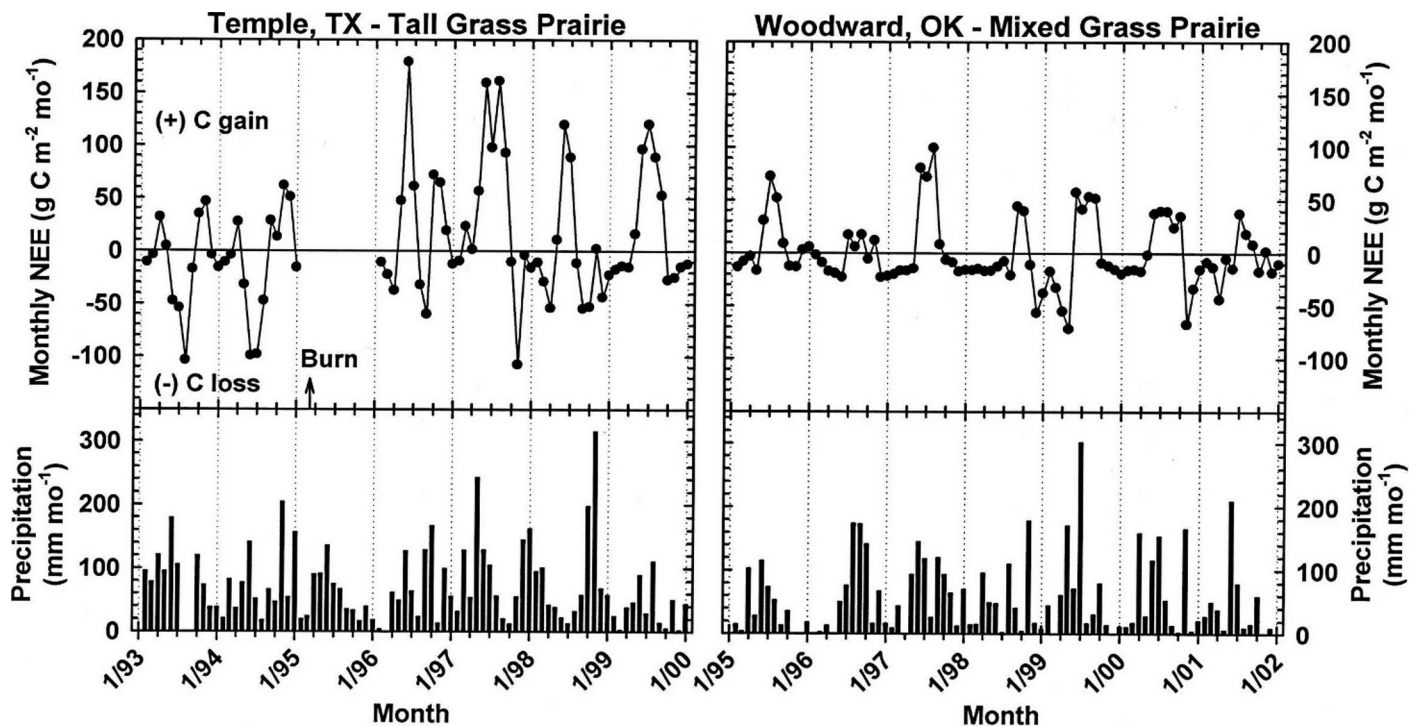

Figure 3. Monthly net ecosystem exchange of carbon (NEE) and monthly precipitation for rangelands in the Southern Plains of the United States.
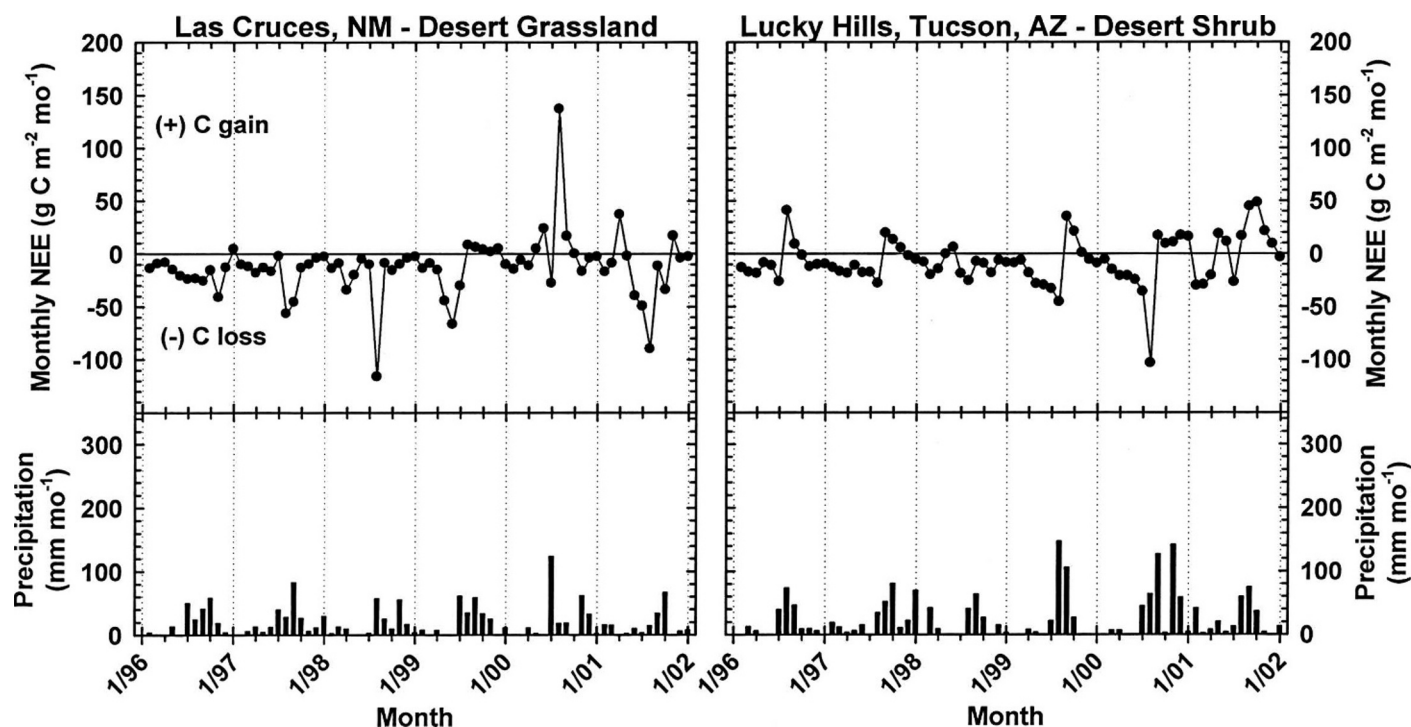
Figure 4. Monthly net ecosystem exchange of carbon (NEE) and monthly precipitation for rangelands in the southwestern United States.

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 CO_2 uptake occurred over relatively short periods. A fundamental knowledge of plant community phenology and the independent responses of soil and plant CO_2 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.

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