Soil CO₂ Efflux Responses to Soil Loss on Two Rangeland Ecosystems

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Abstract

A steady state in soil carbon (C) requires that the production of organic C compounds equal their losses through respiration and erosion. How accelerated rates of soil loss affect this balance in western rangelands, where rates of C accumulation without disturbance are relatively slow, is not well understood. The purpose of this study was to determine the effects of soil loss on total, bare soil, and plant respiration rates at shortgrass prairie and sagebrush steppe sites. The experimental design was a split-plot, randomized block, with a factorial arrangement of treatments. The factor levels consisted of 3 levels of soil removal (0, 11.2, and 22.4 t/ha) and 2 range condition classes (good and fair) with 3 replications each at the shortgrass site. Range condition class was not a factor considered at the sagebrush site. Soil CO₂ efflux was measured at weekly intervals during the 1999 and 2000 growing seasons at the shortgrass site but only during the 2000 season at the sagebrush site. Total, bare soil, and plant respiration rates at the sagebrush site varied little ($P > 0.10$) among the 3 soil removal treatments. While total respiration at the shortgrass site increased significantly ($P < 0.10$) as soil removal level increased, bare soil respiration did not vary ($P > 0.10$) among the 3 soil removal levels. Plant respiration rates at the shortgrass site generally increased as soil removal level increased, but this response was affected by environmental factors that influenced plant productivity. Increased total respiration rates observed on the shortgrass prairie resulted primarily from increased plant respiration rather than from changes in bare soil respiration. Thus, changes in plant respiration following disturbance may be more important to total soil CO₂ efflux than soil flora and faunal respiration that appeared to be more resistant to disturbance.

Resumen

Un estado balanceado del carbón (C) del suelo requiere de la que producción de compuestos de carbón orgánico sea igual a sus pérdidas sufridas a través de la respiración y erosión. Actualmente no está bien entendido como las tasas aceleradas de pérdida de suelo afectan este balance en los pastizales del oeste de Estados Unidos de América, donde las tasas de acumulación de carbón en condiciones sin disturbio son relativamente lentas. El propósito de este estudio fue determinar los efectos de la pérdida de suelo en las tasas de respiración total, del suelo desnudo y de la vegetación, en sitios de pastizal de zacates cortos y de estepa de "Sagebrush." El diseño experimental fue un bloque al azar en parcelas divididas con un arreglo factorial de tratamientos, los niveles de los factores consistieron en: 3 niveles de remoción de suelo (0, 11.2 y 22.4 t/ha) y 2 clases de condición del pastizal (buena y regular) la cual no se consideró como factor en el sitio de "Sagebrush"; se tuvieron 3 repeticiones por sitio de pastizal de zacates cortos. El efluente de CO₂ del suelo fue medido semanalmente durante las estaciones de crecimiento de 1999 y 2000 en los sitios de pastizal de zacates cortos y solo en el 2000 en el sitio de estepa de "Sagebrush." En el sitio de "Sagebrush las tasas de respiración total, del suelo desnudo y de la vegetación" variaron poco ($P > 0.10$) entre los 3 tratamientos de remoción de suelo; mientras que en el pastizal de zacates cortos la respiración total aumentó significativamente ($P < 0.10$) conforme el nivel de remoción de suelo se incrementó y la respiración de suelo desnudo no varió ($P > 0.10$) entre los niveles de remoción de suelo. Las tasas de respiración de las plantas en el pastizal de zacates cortos generalmente se incrementó conforme el nivel de remoción del suelo aumentó, pero esta respuesta fue afectada por factores ambientales que influyeron en la productividad de la planta. El aumento de las tasas de la respiración total observadas en el pastizal de zacates cortos resultó principalmente de un aumento en la respiración de las plantas y no de cambios en la respiración del suelo desnudo. Los cambios en la respiración de la planta después del disturbio pueden ser más importantes en el efluente total de CO₂ que la respiración de la flora y fauna del suelo que parecen ser más resistentes al disturbio.

Key Words: total respiration rates, plant respiration, bare soil respiration, shortgrass prairie, sagebrush steppe

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INTRODUCTION

Until recently, the turnover of the soil C pool of many ecosystems, including rangelands, has been difficult to quantify. Raich and Schlesinger (1992) noted that soil CO₂ efflux measurements give an estimate of total soil respiration and thus provide an alternative approach to estimate the turnover of the soil C pool. The coupling of soil respiration and photosynthetic rates also provides insight into the cycling of C through an ecosystem. Rangeland ecosystems have been considered important C sinks on a global scale (Svejcar et al. 1997). Therefore, understanding how soil loss affects net assimilation and respiration rates of CO₂ on western rangelands may provide both new information regarding the importance of rangelands to the global C cycle and incentives for improved management.

The efflux of CO₂ from the soil results in part from plant root respiration, microbial respiration as they decompose soil organic matter, faunal respiration, and the nonbiological, chemical oxidation of carbonate compounds (Witkamp 1966, 1969; Singh and Gupta 1977). Soil respiration can thus be divided into 2 basic sources: that which is inherent to primary productivity (i.e., root respiration) and that which results from soil processes (i.e., microbial decomposition, faunal respiration, and chemical oxidation). However, these 2 sources of soil respiration are inescapably confounded. For example, primary production (above- and belowground) is the major contributor to soil organic matter (Charley and West 1975; Klemmedson 1989; Raich and Schlesinger 1992), which in turn is the energy source for microbial growth. Thus, separation of total ecosystem respiration into its plant and soil components facilitates understanding how various disturbances, such as soil erosion, affects the efflux of CO₂ from the system.

Accelerated erosion rates adversely affect many soil properties that promote plant growth. Erosion removes mineral particles, organic matter, and nutrients from the soil, reducing surface horizon thickness and water-holding capacity (Singer and Munns 1991). A decline in primary productivity coupled with a loss of soil organic matter and nitrogen through erosion may affect the efflux of CO₂ from the soil (Singh and Gupta 1977). The net production of biomass in terrestrial ecosystems contributes directly to the soil organic carbon (C) pool (Schlesinger 1997). Soil chronosequence studies show that soil organic matter accumulates at rates ranging between 1 and 12 g C · m⁻² · y⁻¹ during soil development (Schlesinger 1990; Chadwick et al. 1994; Schlesinger 1997). The net production of organic C compounds must equal their removal through erosion for soils to exhibit a steady state in soil C content (Schlesinger 1997). How accelerated rates of soil loss affect this balance in arid and semiarid rangelands, where rates of C accumulation without disturbance are relatively slow (0.8–2.2 g C · m⁻² · y⁻¹; Schlesinger 1990), is not well understood.

The concept that some level of erosion could be sustained without loss of productivity led to the establishment of soil loss tolerance values (T value) for all soils in the United States. Using the Universal Soil Loss Equation (USLE), the Natural Resource Conservation Service has assigned T values ranging between 4.5 and 11.2 t · ha⁻¹ · y⁻¹ (2–5 t · acre⁻¹ · y⁻¹) to all agricultural lands (Schmidt et al. 1982). The soil loss rate of 11.2 t · ha⁻¹ · y⁻¹ is considered to be the maximum sustainable

erosion rate at which productivity can be maintained (Wischmeier and Smith 1978; Schmidt et al. 1982; Wight and Siddoway 1982). It is assumed that beyond this threshold, rangeland plant cover and productivity decline as soil erosion rates increase (SRM-Task Group 1995; Rasmussen et al. 1998). Although there is little quantitative evidence for this assumption, management decisions on western rangelands are often based on this relationship (SRM-Task Group 1995; Rasmussen et al. 1998). Weltz et al. (1998) suggested, however, that since there had been no research linking changes in plant productivity and sustainability to erosion on rangelands, the current concept of T values for rangelands may not be valid.

The specific objective of this research was to determine the effects of 3 levels of soil loss on total, bare soil, and plant respiration rates within the shortgrass prairie and sagebrush steppe ecosystems. The soil loss levels chosen for comparison represent no soil loss (0 t/ha), a soil loss level that is widely accepted to be the maximum allowable T value (11.2 t/ha; Schmidt et al. 1982), and twice the maximum allowable T value (22.4 t/ha). It was hypothesized that 1) bare soil respiration rates in both ecosystems would decline with increasing soil loss, 2) plant respiration rates in both ecosystems would increase with increasing soil loss, and 3) total soil respiration rates in both ecosystems would remain constant with increasing soil loss.

MATERIALS AND METHODS

Study Sites

The shortgrass prairie site was located at the USDA–Agricultural Research Service, Central Plains Experimental Range (CPER, lat 40°50'N, long 104°43'W), a 6 280-ha research area in northeastern Colorado. The shortgrass prairie has a long history of grazing (Milchunas et al. 1992). Currently, CPER is moderately grazed by cattle during the growing season (May–October). The 10-ha study site, however, was fenced in the spring of 1998 to protect it from livestock grazing.

Long-term (1939–1990) annual temperature at CPER averaged about 9°C with an average annual precipitation of 321 mm (Lauenroth and Sala 1992). The soil at the shortgrass prairie site was formed from calcareous sandy alluvial and eolian material and was classified as a Vona Sandy Loam, which is a coarse-loamy, mixed, mesic Ustollic Haplargid (USDA 1982). The vegetation at the study site was representative of the shortgrass prairie ecosystem (Milchunas et al. 1989) and was dominated by blue grama (*Bouteloua gracilis* [Kunth] Lag. ex Steud.) and buffalograss (*Buchloë dactyloides* [Nutt.] Englem.). Western wheatgrass (*Pascopyrum smithii* [Rydb.] A. Love) is also an important component of the shortgrass ecosystem (Brown and Trlica 1977; Kemp and Williams 1980; Monson et al. 1982, 1986) and was present at our study site.

The sagebrush steppe site was located within the 10 000 ha Arapaho National Wildlife Refuge (ANWR, lat 40°36'N, long 106°16'W) approximately 15 km south of Walden, Colorado. The refuge is managed by the U.S. Fish and Wildlife Service as a bird sanctuary and has been protected from livestock grazing since 1967. However, between 200 and 500 head of elk (*Cervus elaphus nelsoni* Nelson) graze ANWR ranges annually in the winter (Mark Lanier, personal communication). The 5-ha sagebrush research site was fenced to exclude wildlife grazing during the project.

Average annual temperature near ANWR at Walden is 3°C with a mean annual precipitation of 275 mm received mostly as snow in the winter (Western Regional Climate Center 2001). The research site was located on a Dry Mountain Loam range site representative of a sagebrush steppe (USDA 1981). The soil at the site was formed in gravelly alluvium and was classified as a Cabin Sandy Loam, which is a fine-loamy over sandy or sandy-skeletal, mixed, Argic Cryoboroll (USDA 1981). Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* [Beetle and Young] Welsh) was the dominant shrub component, with numerous C₃ grass species, including western wheatgrass, bluebunch wheatgrass (*Pseudoroegneria spicata* [Prush] A. Love), and sheep fescue (*Festuca ovina* L.) in the understory and interspaces.

Experimental Design

At the shortgrass site, the experimental design was a split-plot randomized complete block with a factorial arrangement of treatments. Factor levels at the shortgrass site consisted of 2 (split-plot) range condition classes (NRCS 1997), good (51%–76% of the climax community plants present) and fair (26%–50% of the climax community plants present), and 3 (whole-plot) levels of soil removal (0, 11.2, and 22.4 t/ha), with 3 replications of each level (18 experimental units). Only the good range condition class was present at the sagebrush site, so the experimental design was reduced to a randomized complete block with whole-plot treatments comprised of the 3 soil removal levels, with 3 replications of each (9 experimental units).

Treatment and Data Collection

At the shortgrass site, 9 (3 soil removal levels $\times$ 3 replications) permanent, 0.6 $\times$ 2-m steel-frame plots (1.2 m²) were randomly placed within each of the good and fair range condition classes (18 total plots) in the spring of 1998. Nine similar plots were installed at the sagebrush site in the spring of 1999. At both research sites, 1.34 and 2.68 kg of top soil were removed from each 11.2- and 22.4-t/ha treatment plot, respectively, using a vacuum and a collection bag. At the shortgrass site, treatments were imposed during the summer of 1998, while at the sagebrush site, treatments were conducted in the early summer of 1999.

Within each plot at both sites, 4 permanent 5-cm-deep $\times$ 10-cm-diameter polyvinylchloride rings were inserted to a depth of 2.5 cm into the soil leaving 2.5 cm of headspace between the soil surface and the top of the ring. The rings were inserted into the plots at the shortgrass site in May 1999 and in September at the sagebrush site. At both study sites, 2 of the 4 rings were placed in natural gaps in the vegetative cover for measuring bare soil respiration. The remaining 2 rings were placed within the vegetative cover for measuring total soil respiration rates.

Respiration measurements were made on all 4 rings within each plot with a Li-Cor 6400-09 Soil CO₂ Flux Chamber at weekly intervals throughout the growing season. At each sampling period, 3 consecutive measurements of respiration were taken on each ring. Respiration rates were sampled for both the 1999 and the 2000 growing seasons on the shortgrass site, while measurements at the sagebrush site were made only during the 2000 growing season. Plant respiration rates were then estimated by subtracting bare soil respiration from total respiration.

Because soil CO₂ efflux rate is influenced by soil and air temperature, relative humidity, and soil water content (Witkamp 1966, 1969; Wiant 1967; Singh and Gupta 1977; Raich and Schlesinger 1992; Craine et al. 1999), each of these variables was measured as a covariate with respiration during each sampling period. Soil temperature measurements were taken by inserting a soil probe 10 cm deep into the soil in the vicinity of each CO₂ flux ring at the time of sampling, and data were recorded by the Li-Cor 6400. The soil probe was inserted into either bare or vegetated soil to correspond with the area being sampled for CO₂ efflux. Air temperature and relative humidity were recorded by the Li-Cor 6400 in conjunction with each respiration measurement. Gravimetric soil water content was estimated at weekly intervals from soil cores removed from the vicinity of each plot at depths of 0–5 and 5–10 cm.

Statistical Analyses

Total, bare soil, and plant respiration rates ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) for the shortgrass site were analyzed using a repeated measures analysis of covariance procedure (Vonesh and Chinchilli 1997). Only air temperature met all assumptions concerning the use of covariates and also proved to be significant for all 3 response variables (Vonesh and Chinchilli 1997). Thus, air temperature was the only covariate used in the final analyses for the shortgrass site. For the sagebrush site, air temperature was not a significant covariate. Consequently, total, bare soil, and plant respiration rates for the sagebrush site were analyzed using a repeated measures analysis of variance (ANOVA) procedure (Vonesh and Chinchilli 1997). Repeated measures ANOVA was also used to test for differences in total, bare soil, and plant respiration rates between the shortgrass and sagebrush sites for the 2000 growing season. In all analyses, differences were considered significant at $P \leq 0.10$. Fisher's Least Significant Difference (LSD) test was used to separate group means when appropriate (Dowdy and Wearden 1991). Pearson's Correlation Analysis (Neter et al. 1996) was conducted to determine the type of relationship for total and bare soil respiration with soil and air temperature, soil water content (at 0–5- and 5–10-cm depths), and relative humidity as independent variables. Correlation coefficients (r) between variables were considered significant at $P \leq 0.01$.

RESULTS

Total soil respiration rates ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) for both years at the shortgrass site were significantly positively correlated with ambient air temperature ($r = 0.49$) and gravimetric soil water content at 5–10 cm ($r = 0.47$; Fig. 1). Relative humidity ($r = 0.26$), soil temperature ($r = 0.23$), and soil water content at 0–5 cm ($r = 0.28$) were also correlated ($P < 0.01$) with total respiration at the shortgrass site. Bare soil respiration rates at the shortgrass site were significantly positively correlated with ambient air temperature ($r = 0.44$), relative humidity ($r = 0.25$), soil water content at 0–5 and 5–10 cm ($r = 0.22$ and 0.45, respectively), and soil temperature ($r = 0.29$).

Total soil respiration rates at the sagebrush site were positively correlated ($P < 0.01$) with soil water content at the 0–5-cm depth ($r = 0.47$; Fig. 2) and relative humidity ($r = 0.43$). The correlation between total respiration and soil water content at the 5–10-cm depth ($r = 0.17$, $P < 0.01$) was low. Total soil

Figure 1. Weekly average ($\pm$ SE) total soil respiration rates ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; $n = 54$) for the good and fair condition classes and gravimetric soil water content (%; $n = 18$) at the 0–5- and 5–10-cm depths for the shortgrass prairie research area during the 1999 and 2000 growing seasons.

respiration rate at the sagebrush site was negatively correlated ($r = -0.17$, $P < 0.01$) with soil temperature but was not correlated with ambient air temperature ($P > 0.01$). Significant ($P < 0.01$) correlations existed between bare soil respiration at the sagebrush site and soil water content at 0–5- and 5–10-cm depths ($r = 0.56$ and 0.27 , respectively), relative humidity ($r = 0.18$), and soil temperature ($r = -0.30$). Ambient air temperature at the sagebrush site was not correlated ($P > 0.01$) with bare soil respiration.

Gravimetric soil water content (%) at the shortgrass research site varied ($P < 0.10$) by depth across sampling periods and years (Fig. 1). Generally, the 5–10-cm soil depth had a higher soil water content than the 0–5-cm depth. The differences in soil water content observed among periods between 1999 and 2000 at the shortgrass site were explained by differences in timing of precipitation events as well as total amount received. Peak soil water content in both years followed precipitation events but occurred at different times of the year.

Total precipitation received at the shortgrass site in 1999 (419 mm) was approximately 131% of the long-term average total annual precipitation of 321 mm (Lauenroth and Sala 1992). Conversely, in 2000, total precipitation (240 mm) was about 75% of the long-term average. This difference in total precipitation between years at the shortgrass site was reflected in the differences in average soil water content, which was

Figure 2. Weekly average ($\pm$ SE) total respiration rates ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; $n = 54$) and gravimetric soil water content (%; $n = 9$) at the 0–5- and 5–10-cm depths for the big sagebrush research area during the 2000 growing season.

approximately 28% lower in 2000 ($6.1 \pm 0.2\%$ SE, $n = 324$) than in 1999 ($8.5 \pm 0.2\%$ SE, $n = 324$).

In 2000, the sagebrush site received approximately 290 mm of precipitation, approximately 5% more than the long-term annual average of 275 mm (Western Regional Climate Center 2001). Of the 290 mm of precipitation received at the sagebrush site, 44% occurred between June and September 2000. However, June and July precipitation accounted for only 29 mm of the 128 mm received between June and September 2000. Most of the precipitation events that occurred during the 4 months of observation at the sagebrush site were short-duration, low-intensity storms that produced less than 2.5 mm of precipitation and consequently were not large enough to recharge the soil profile. This lack of adequate precipitation between June and September 2000 at the sagebrush research site resulted in droughty soils low in water content. In fact, the gravimetric soil water content varied by only 1% or 2% for both depths and never exceeded 5% of the total soil mass (Fig. 2). Nevertheless, gravimetric soil water content at the sagebrush site varied significantly ($P < 0.10$) between depths and across sampling periods. Soil water content in the 5–10-cm depth was generally greater than in the 0–5-cm depth and also less variable between weeks (Fig. 2). Weekly variation of soil water in the 0–5-cm depth likely resulted from higher evaporative losses in the upper 5 cm of the soil than in the 5–10-cm depth. For example, significant losses in soil water content in the 0–5-cm depth were observed from week 26 through week 29, but in the 5–10-cm depth, soil water did not decrease significantly until week 32.

Between-Site Differences

Total, bare soil, and plant respiration rates during the 2000 growing season were significantly different between the shortgrass and sagebrush sites, but these differences varied across sampling periods ($P < 0.10$). In general, total respiration rates were greater at the shortgrass site than at the drier sagebrush site (Figs. 1 and 2). Likewise, bare soil and plant respiration rates in 2000 were greater ($P < 0.10$) at the shortgrass site than at the sagebrush site.

Figure 3. Average ($\pm$ SE; covariate = ambient air temperature) total respiration rate ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) at the shortgrass prairie research area for 0- ($n = 644$), 11.2- ($n = 648$), and 22.4- ($n = 648$) t/ha soil removal levels (years and range condition classes combined). Similar letters above bars are not significantly different (Fisher's LSD = 0.256 [adjusted], $t = 1.782$, MSE = 6.724).

Respiration Rates at the Sagebrush Site

Soil removal level had little effect ($P > 0.10$) on total, bare soil, or plant respiration rates at the sagebrush site. Total respiration averaged ($\pm$ SE, $n = 54$) 1.73 ± 0.075 , 1.76 ± 0.071 , and $1.66 \pm 0.075 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at the sagebrush site during weeks 24, 25, and 26, respectively (Fig. 2). During this same period, plant respiration accounted for 45%, 44%, and 46% (weeks 24, 25, and 26, respectively) of the total CO₂ efflux at the sagebrush site. Significant decreases in the average total respiration rates from those observed in weeks 24, 25, and 26 occurred during weeks 28, 29, 31, and 32 (Fig. 2). Over this same period, the contribution of plant respiration to total CO₂ efflux also declined to 42%, 40%, 34%, and 35% for these last 4 weeks.

Respiration Rates at the Shortgrass Prairie Site

When adjusted for ambient air temperature, total respiration at the shortgrass prairie site increased ($P < 0.10$) with increasing soil removal (Fig. 3). This effect of soil removal level (0, 11.2, and 22.4 t/ha) on total respiration varied little ($P > 0.10$) between condition class, year, or sample periods, nor was it affected ($P > 0.10$) by 3- or 4-way interactions involving these variables. However, differences in total respiration rates between condition classes (good and fair) did vary ($P < 0.10$) among years (1999 and 2000) and sample periods but showed no consistent trend.

Bare soil respiration at the shortgrass site varied little between condition class ($P > 0.10$) or soil removal level ($P > 0.10$), nor was there a condition class $\times$ soil removal level interaction ($P > 0.10$). Average ($\pm$ SE, $n = 972$) bare soil respiration rate in 1999 ($3.8 \pm 0.033 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) was greater ($P < 0.10$) than in the drier 2000 ($1.93 \pm 0.027 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) growing season. Efflux of CO₂ from bare soil accounted for more than 65% of the total respiration rate in the 0- and 11.2-t/ha soil removal levels but declined to 59% in the 22.4-t/ha level. However, since bare soil respiration rates at the shortgrass site were relatively constant among soil removal treatments for both the good and the fair condition classes and between years (averaging $2.87 \pm 0.03 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ SE,

Figure 4. Weekly average ($\pm$ SE, $n = 36$) plant respiration rates ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) for the 0-, 11.2-, and 22.4-t/ha soil removal treatments at the shortgrass prairie research area during the 1999 and 2000 growing seasons.

$n = 1940$, with $< 0.2 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ between any 2 soil removal levels), they did not contribute to the increases observed in total respiration as soil removal level increased.

Differences in plant respiration rates between the good and fair condition classes varied across sample periods ($P < 0.10$) but not between years ($P > 0.10$). The response of plant respiration rates to soil removal level varied little between condition classes ($P > 0.10$) but did vary between sample periods and years ($P > 0.10$; Fig. 4). Plant respiration at the shortgrass site was 35% and 36% of the total CO₂ efflux in the 0- and 11.2-t/ha soil removal levels, respectively, but increased to 42% in the 22.4-t/ha level.

DISCUSSION

A direct comparison between the rates of total and bare soil respiration observed for the shortgrass and sagebrush sites with other studies is difficult because of the variety of methods and definitions used and conditions under which soil respiration is often measured (Clark and Coleman 1972; Raich and Schlesinger 1992; Bowden et al. 1993; Craine et al. 1999; Chen and Stark 2000). Nevertheless, we found that rates of total and bare soil respiration at the shortgrass and sagebrush research sites were usually within the range of values reported in the literature when similar methods were used in similar ecosystems (Clark and Coleman 1972; Craine et al. 1999; Lecain et al. 2000;

Mielnick and Dugas 2000). For example, in a study in the shortgrass prairie, Clark and Coleman (1972) reported rates of total respiration ranging from 0.3 to 4.4 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ depending on the season and soil environment. Craine et al. (1999) reported rates of total respiration as high as 9.3 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ for a tallgrass prairie site in Minnesota, and similar rates were reported by Mielnick and Dugas (2000) for a Kansas tallgrass prairie study. Total soil respiration rates reported by Lecain et al. (2000) for shortgrass prairie sites in Wyoming, however, were lower (0.43–0.66 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) than those observed in this study (0.8–8.8 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$).

Total, bare soil, and plant respiration rates at the shortgrass site were considerably greater than at the sagebrush site during the 2000 growing season. These differences between the 2 sites can be explained, in part, by the greater productivity at the shortgrass site than at the sagebrush site (Thorne 2002). Ecosystems with greater net primary production typically have larger soil C pools and, consequently, higher rates of total CO_2 efflux (Charley and West 1975; Klemmedson 1989; Raich and Schlesinger 1992; Ham and Knapp 1998). The higher rate of total soil CO_2 efflux in ecosystems with greater productivity results not only from increased root respiration but also from increased microbial activity because of greater soil C availability. For example, Klein (1977) reported that microbial activity was positively correlated with the soil organic matter of shortgrass soils. Thus, a larger soil C pool at the shortgrass site would support a larger and more active microbial population than at the sagebrush site (Insam 1990) and undoubtedly would account for a portion of the higher total and bare soil respiration rates observed at the shortgrass site than at the sagebrush site.

Plant and bare soil respiration rates declined sharply at both sites as soil water content decreased, indicating increased plant and microbial stress. Wiant (1967), Witkamp (1969), Klein (1977), and Insam (1990) noted that along with primary production, CO_2 efflux was suppressed during periods when soil water content was low and air and soil temperatures were high. Plant and microbial stress occurs when environmental conditions, such as air and soil temperatures, and soil water content are not optimal for growth and consequently results in reduced soil respiration rates (Witkamp 1969; Clark and Coleman 1972; Klein 1977; Insam 1990). Thus, as the soil dried at the shortgrass and sagebrush research areas, the contribution of plant and microbial respiration to the total efflux of CO_2 decreased. This resulted in the lower total respiration rates observed at both sites during weeks when soil water content was low (Figs. 1 and 2).

The characteristic seasonal trend in total respiration for both sites followed the fluctuations in soil water content and can be attributed to differences in the timing, amount, and frequency of precipitation received at both sites (Figs. 1 and 2). Similar results were found by Clark and Coleman (1972). For example, they found that the soil CO_2 efflux rate in shortgrass prairie soils increased from 0.6 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in June when soil water content (0–10-cm depth) was 2% to 4.4 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in July when soil water content was 10%. The study by Clark and Coleman (1972) also showed that 85% of the daily CO_2 efflux from shortgrass prairie soils occurred in the top 10 cm. This would help explain the strong correlation observed in this study for total and bare soil respiration rates

with soil water content at the 5–10-cm depth at the shortgrass site. At the sagebrush site, however, respiration rates were more strongly correlated with soil water content at the 0–5-cm depth. This, coupled with the likely shallow distribution of soil organic matter at the sagebrush site (Thorne 2002), would suggest that soil within the 0–5-cm depth contributed most of the CO_2 respired at the sagebrush site.

The lack of adequate precipitation to support herbaceous production at the sagebrush site resulted in a relatively short growing season in 2000 compared to the shortgrass site. While plant growth began at both sites during week 24 (June 11–17), herbaceous production ended at the sagebrush site during week 29 (July 16–22) but continued at the shortgrass site through week 36 (September 3–9; Figs. 1 and 2). Over this same period, total respiration at the sagebrush site was highest ($> 1 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) early in the growing season when soil water content in the 0–5-cm depth was greatest (3%–3.5%), but total respiration declined ($< 1 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) as the soil dried (2%–2.5%). This trend in total respiration at the sagebrush site was coincident with the loss of herbaceous production beginning in week 29 and was reflected in the decline in the contribution of plant respiration to the total CO_2 efflux rate. For example, plant respiration decreased from a high of 46% of total respiration in week 26 to a low of 34% in week 31. Plant respiration, therefore, contributed significantly to the total CO_2 efflux at the sagebrush site when conditions supported herbaceous growth (i.e., weeks 24–28).

Total respiration rate at the shortgrass site showed a different seasonal trend in 2000 than at the sagebrush site, reflecting a different pattern in precipitation received. Nevertheless, total respiration rates at the shortgrass site also declined as soil water content decreased (Fig. 1). However, a major difference between the shortgrass and sagebrush sites was the response of their total, bare soil, and plant respiration rates to the soil removal treatments.

Differences in plant respiration rates among the soil removal treatments across periods and between years can be explained by fluctuations in soil water content at the shortgrass site (Figs. 1 and 4). Higher plant respiration rates were observed for all soil removal levels when soil water content was greatest. Generally, during sample periods with adequate soil water content to support plant growth, plant respiration increased with increasing soil removal. This relationship did not hold, however, when respiration rates were low, such as when plant growth was limited by low soil water content, air temperature, or some other environmental factor. For example, conditions were cold (mean temperature = 19.4°C) and cloudy (mean photosynthetically active radiation = 490 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) the day samples were taken during week 25 in 2000 at the shortgrass site (Figs. 1 and 4). Consequently, because plant growth was limited, respiration rates at that time were low ($< 0.5 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) despite nearly 8% soil water content. In addition, for both years early in the growing seasons (weeks 24–32), proportionally less soil water was required to support plant respiration than during the late season periods (weeks 33–34). During these late season periods, the increased response of plant respiration to soil removal that had been observed during the early season was not as well defined (Fig. 4), and total respiration rates declined in all 3 soil removal treatments. This suggests that as the

growing season progressed, plant growth rate slowed; thus plant respiration rates were reduced, and this resulted in lower total CO₂ efflux.

At the shortgrass site, plant respiration accounted for 35%, 36%, and 41% of the total respiration rate for the 0-, 11.2-, and 22.4-t/ha soil removal levels, respectively, when averaged across both years. This is consistent with the observed increase in total respiration with increasing soil removal level. Moreover, plant photosynthetic rates observed at the shortgrass site during the same times showed similar increases with increasing soil removal (Thorne 2002). It appears, therefore, that the response of total respiration to the soil removal treatments at the shortgrass site was driven by a plant physiological response to the treatments. Indeed, plant respiration rates become elevated in response to increased use of metabolic energy for growth, ion uptake and transport, or stress (Chapin et al. 1987; Coyne et al. 1995; Larcher 1995).

Roots account for a significant portion (50%–80%) of the annual dry matter production of most rangeland plants, and only through continual growth can roots explore sufficient soil volume to meet the nutritional needs of the plant (Chapin et al. 1987). It is possible that the removal of soil in the 11.2- and 22.4-t/ha treatments altered one or more soil properties that generally supports plant growth (i.e., soil nutrient and organic matter content, water-holding capacity; Singer and Munns 1991). If alteration of these soil properties was not severe but was sufficient enough to create a deficiency within the rooting zone, then more C might be allocated for root growth to maintain plant function (Ares 1976; Bloom et al. 1985; Chapin et al. 1987). Thus, the general trend for plant respiration rates to be higher in the 11.2- and 22.4-t/ha soil removal treatments than in the control at the shortgrass site may have resulted from increased root growth, although this was not measured.

Since the response of total respiration to soil removal at the shortgrass site was probably a function of primary production, it is likely that the culmination of low production, low soil water content, and a shorter growing season at the sagebrush site resulted in no detectable responses in total, bare soil, and plant respiration to soil removal treatments. Differences among soil removal levels were generally less than 0.1 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ for all 3 responses at the sagebrush site, and at no time did total respiration exceed 2 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. When total respiration rates at the shortgrass site were less than 2 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, plant respiration rates varied little among soil removal levels. Thus, primary production at the sagebrush site was likely not great enough to contribute a significant quantity of respired CO₂ to the total efflux. Consequently, unlike at the shortgrass site where respiration rates often exceeded 2 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, differences in total respiration among soil removal levels at the sagebrush site could not be detected.

MANAGEMENT IMPLICATIONS

The objective of this study was to determine if soil loss at 0, 11.2, and 22.4 t/ha affected total, bare soil, and plant respiration rates within shortgrass prairie and sagebrush steppe ecosystems. Total and bare soil respiration rates were measured directly using a soil respiration chamber. Plant respiration rates

were estimated by subtracting bare soil respiration from the total CO₂ efflux. It was hypothesized that as soil loss increased in both ecosystems: 1) bare soil respiration rates would decline, 2) plant respiration rates would increase, and 3) total respiration rates would remain constant.

Bare soil respiration rates for both the shortgrass and sagebrush sites were unaffected by soil removal level. Therefore, the hypothesis that bare soil respiration rates would decrease with increasing soil removal level was rejected. Since bare soil respiration rates remained unchanged among soil removal levels, plant respiration rates likely accounted for most of the differences observed in total respiration rates at the shortgrass site as soil removal level increased.

Plant respiration rates on the shortgrass site generally increased with increasing soil removal level. This was dependent on environmental conditions that favored plant activity such as adequate soil water content, light, and temperature. When conditions were not favorable for plant growth, plant respiration rates were low, and few differences in CO₂ flux among soil removal levels were found. Since favorable growing conditions at the sagebrush site were relatively brief and likely did not adequately support plant growth, a plant respiration response to increasing soil removal similar to that found at the shortgrass site was not observed. Therefore, the hypothesis that plant respiration rates would increase with increasing soil loss was not rejected on the basis of the observations at the shortgrass site. However, this response was dependent on seasonal variations in growing conditions and, thus, would likely change with seasonal fluctuations in primary productivity.

For the shortgrass site, total respiration rates increased with increasing soil removal level. This was not observed for the sagebrush site; the lack of response for this site can probably be explained by the culmination of low soil moisture levels, low primary productivity, and a short growing season. Consequently, results for total respiration rates at the sagebrush site were inconclusive and, therefore, neither supported nor disproved the assumption regarding the response of total respiration to soil removal. Thus, the hypothesis that total respiration would remain constant as soil removal rate increased was rejected on the basis of observations from the shortgrass prairie site.

Based on these results, it appears that total respiration rates on the shortgrass prairie can be expected to increase with increasing soil loss. This increase in total respiration, however, will be driven by a plant physiological response to conditions imposed by the loss of soil. Bare soil respiration rates, on the other hand, contributed little to the total respiration response and in fact were relatively stable when compared with plant respiration rates. It is possible that because of this stability, more severe soil removal levels than those imposed in this study and that are repeated through time may be needed to cause a response in bare soil respiration rates. This poses 2 important questions for future study: 1) would more severe levels of soil loss than those imposed in this study result in different responses in total, bare soil, and plant respiration rates than what was observed in the present study, and 2) what would the response of total, bare soil, and plant respiration rates be to annual soil removal treatments? Answers to these questions would further our understanding of the effects of soil losses on rangeland productivity and carbon budgets.

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