

BOWEN RATIO/ENERGY BALANCE AND SCALED LEAF MEASUREMENTS OF CO₂ FLUX OVER BURNED *PROSOPIS* SAVANNA

R. J. ANSLEY,¹ W. A. DUGAS,² M. L. HEUER,² AND B. A. KRAMP¹

¹Texas Agricultural Experiment Station, P.O. Box 1658, 11708 Highway 70 South, Vernon, Texas 76385 USA

²Texas Agricultural Experiment Station, Blackland Research and Extension Center, Temple, Texas 76502-9622 USA

Abstract. Prescribed fire is used as a management practice to maintain grassland dominance and reduce woody plant encroachment on grasslands and rangelands. Little is known regarding effects of these fires on CO₂ fluxes and their potential contribution to atmospheric CO₂. The objectives of this study were (1) to quantify the effect of fire on net ecosystem CO₂ flux above *Prosopis glandulosa* Torr. (honey mesquite) mixed-grass savannas using the Bowen ratio/energy balance (BREB) method, and (2) to compare these fluxes to fluxes determined by an empirical model that scaled measurements of leaf photosynthesis and leaf area of dominant species and soil CO₂ fluxes to the ecosystem level. Measurements were made during a wet year (1995) and a dry year (1996) with different savanna areas burned in late winter (February–March) each year. In the wet year, BREB-estimated daily (24-h) CO₂ flux averaged -0.1 , 14.6 , and 0.8 g/m² on the unburned plot, and 15.7 , 19.7 , and 15.2 g/m² on the burned plot during spring, summer, and fall periods, respectively, during the first growing season following the fire (positive values mean net CO₂ uptake). In the drought year, mean daily CO₂ flux during spring, summer, and fall was -9.2 , 4.1 , and 4.8 g/m² on the unburned plot, and 8.1 , -0.9 , and 4.6 g/m² on the burned plot, respectively. The increased carbon uptake following a fire when compared to the unburned plot was estimated to offset the initial carbon loss from combustion within 28 growing-season days in the wet year, while it took 82 d in the dry year. Empirically determined daylight (12-h) CO₂ fluxes, measured on two midsummer days each year, averaged 17.9 g/m² when determined by BREB, and 12.0 g/m² when calculated from scaled-up leaf-level measurements. By the end of the first growing season following the burn, it is likely that the amount of carbon emitted during the burn had been taken up by the regrowing vegetation, in both a wet and a drought year.

Key words: biomass; burning; carbon; fire; grassland; leaf area index; mesquite; *Prosopis glandulosa*; rangeland; scaling; woody plant encroachment.

INTRODUCTION

Woody plant encroachment onto grasslands and rangelands is a worldwide phenomenon (Buffington and Herbel 1965, Grover and Musick 1990, Archer et al. 1995) that can be attributed in part to a reduction of naturally occurring fires, enhanced seed distribution via livestock, reduced grass competition from livestock grazing, and increased global CO₂ (Archer 1989, Polley et al. 1994, Kramp et al. 1998). The use of fire to maintain grassland dominance and suppress woody plant encroachment is an ongoing practice because it is often considered the most cost-effective and ecologically sound treatment as compared to other options (Wright and Bailey 1982, Scholes and Archer 1997, Ansley and Jacoby 1998). Fire either kills or reduces the stature of woody plants and usually increases herbaceous production and species diversity (Collins and Barber 1985, Howe 1994, Collins and Steinauer 1998, Knapp et al. 1998a).

In the face of concerns regarding biomass burning

and increases in global atmospheric CO₂ (Levine 1991, Ryan 1991, Pyne et al. 1996), there is a need to quantify the effects of fire on CO₂ fluxes in different ecosystems (Dugas et al. 1997, Seastedt et al. 1998). Fire is initially a source of atmospheric CO₂ due to the combustion of organic matter (Auclair and Carter 1993, Dixon and Krankina 1993, Miranda et al. 1994), but, especially within grassland ecosystems, increased photosynthetic rates and vegetation growth following fires may quickly offset the initial carbon loss to the atmosphere (Towne and Owensby 1984, Knapp 1985, Svejcar and Browning 1988). In arid or semi-arid savannas or woodlands, where there is a mixture of herbaceous and woody species, burning may not increase net CO₂ uptake because carbon gain from increases in herbaceous species growth and photosynthesis may be offset by the reduction of leaf area and standing mass of the woody component.

In the southern Great Plains (USA), fire is used to manage the woody legume *Prosopis glandulosa* Torr. (honey mesquite) that has increased significantly in density and distribution during the last century (Archer et al. 1995, Ansley et al. 2001). *Prosopis* is not usually killed by fire and most often will sprout from stem

bases following aboveground mortality (i.e., top-kill) (Ansley and Jacoby 1998). Thus, repeated fires are required to maintain a grassland dominance and suppress *Prosopis* leaf area. Little is known regarding carbon fluxes in *Prosopis* savannas that are managed with fire.

Development of models that estimate fire effects on ecosystem carbon flux may be approached empirically by scaling leaf-level measurements to the stand or ecosystem level, although this method is subject to scaling errors (Jarvis and McNaughton 1986, Schimel et al. 1991). Measurement errors at the organismal scale are, of course, exacerbated when scaled to ecosystem level. However, the process of scaling is useful because it allows for better definition of components (Field and Ehleringer 1993) and treatments. Flux-gradient methods provide an ecosystem-level (e.g., 1–10 km²) net CO₂ flux measurement that integrates the spatially variable vegetation and soil components (Jarvis and Dewar 1993, Dugas et al. 1997, Frank et al. 2000). These methods provide an independent test of the scaling process (Caldwell et al. 1993).

Our objectives were (1) to quantify the effect of fire on net ecosystem CO₂ flux above *Prosopis* mixed-grass savannas using the Bowen ratio/energy balance (BREB) method, and (2) to compare these fluxes to fluxes determined by an empirical model that scaled measurements of leaf photosynthesis and leaf area of dominant species and soil CO₂ fluxes to the ecosystem level. These objectives allowed us to test the hypotheses (1) that burning will reduce net ecosystem CO₂ flux (i.e., less CO₂ uptake) because ecosystem leaf area index (LAI) is usually greater in unburned *Prosopis* savanna than in open grasslands (Asner et al. 1998a, b) and (2) that ecosystem CO₂ flux in burned and unburned sites could be accurately estimated using a simple empirical model (assuming the “check” to this model, the BREB estimate, was accurate). Data from this study will also provide some indication as to potential consequences of using fire as a management activity on net carbon loss in this grassland/savanna system.

METHODS

Study area and treatments

This study was conducted in 1995 and 1996 on a 100-ha southern mixed-grass savanna in north Texas, south of Vernon (33°51' N, 99°26' W; elevation 368 m, slope <1%). Mean annual rainfall of 665 mm is bimodally distributed, peaking in May (119 mm) and September (77 mm). Mean monthly air temperatures range from 29.1°C in July to 3.8°C in January, with an annual mean monthly temperature of 16.9°C (National Oceanic and Atmospheric Administration 1996). The mean number of days between last spring and first fall freeze is 218 (National Oceanic and Atmospheric Administration 1987–1996). Soils are fine, mixed, thermic Typic Paleustolls of the Tillman series that are alluvial

clay loams to 3–4 m depth and underlain by Permian sandstone/shale parent material (Koos et al. 1962). Livestock grazing was excluded beginning in 1988.

Vegetation was dominated by a mixture of native grasses and a *Prosopis* overstory with a 40–60% canopy cover. Other woody species comprised <2% of the species composition by mass. Dominant perennial grasses were C₃ midgrass *Nassella leucotricha* ([Trin. and Rupr.] Pohl.; Texas wintergrass) and C₄ shortgrass *Buchloe dactyloides* ([Nutt.] Englem.; buffalograss). Grasses were distributed nonuniformly with shortgrasses and midgrasses dominating interstitial spaces between *Prosopis*, and midgrasses dominating the understory beneath *Prosopis* canopies. *Bromus japonicus* (Thunb.; Japanese brome), a C₃ annual grass, occurred throughout the site.

Three plots were used in this study, all within 1300 m of each other on similar soils. The unburned plot (used in both 1995 and 1996) was 3.3 ha in size (130 m east to west × 250 m north to south). *Prosopis* trees were 3 to 4 m tall and averaged six basal stems per tree. The two other plots were burned, one on 6 February 1995 and the other on 19 March 1996. Each burned plot was 6.3 ha (250 × 250 m). Oven-dry herbaceous fine fuel was estimated prior to each burn by clipping all herbaceous material within 20 0.25-m² quadrats located along two transect lines in each plot, drying the samples at 60°C for 48 h and weighing. Herbaceous fine fuel averaged 317 and 412 g/m² for the 1995 and 1996 fires, respectively.

BREB-determined CO₂ flux

The BREB instrumentation (Model 023/CO₂ Bowen ratio system; Campbell Scientific, Logan, Utah, USA) and methods of calculating CO₂ flux used in the current study have been described (Dugas et al. 1997, Frank et al. 2000). Fluxes from this system have been shown to be within 10% of those from eddy covariance instrumentation (Dugas et al. 2001).

One BREB system was used in the unburned and one in the burned plot in each year. Each system was located 50–80 m south of the north edge of each plot. Prevailing winds were from the southeast and fetch was >200 m. Measurements were made during spring (period 1), summer (period 2), and fall (period 3) in 1995 and 1996 (Table 1). Twenty-minute means of CO₂ flux between the atmosphere and the surface were calculated from BREB measurements (Dugas 1993, Dugas et al. 1997). Twenty-minute Bowen ratios were calculated from the mean temperature and humidity gradients that were measured every 2 s between 3.1 and 4.1 m above the soil surface. The lower Bowen ratio arm was below the tops of some of the taller trees, but was above mean canopy height. Net radiation (R_{net}) was measured at 3.5 m using a Model Q*6 net radiometer (REBS, Seattle, Washington, USA) and soil heat flux (G) was calculated from heat flux measured by heat flux plates (three per plot) buried at 50 mm (Model

TABLE 1. Dates of Bowen ratio/energy balance measurements during three measurement periods in 1995 and 1996.

Year	Spring (period 1)	Summer (period 2)	Fall (period 3)
1995	5–7 April (days 95–97)	27 June–16 July (days 178–197)	5–6 September (days 248–249)
1996	24 April–28 May (days 115–149)	8 July–5 August (days 190–218)	24 September– 16 October (days 268–290)

HFT; REBS, Seattle, Washington, USA) and from soil temperatures above the plates. Sensible and latent heat fluxes (the latter being equal to the evaporation rate) were calculated (Tanner 1960) from the Bowen ratio and 20-min means of R_{net} and G . Soil heat capacity, used in the calculation of G , was calculated from periodic volumetric soil moisture measurements in each plot. R_{net} and G were representative because of the sensor height (for R_{net}) and the multiple soil heat flux plates and soil thermocouples that were used. Previous work also demonstrated little differences in R_{net} when measured at different locations in a *Prosopis* savanna (Dugas and Mayeux 1991).

The turbulent diffusivity, assumed to be equal for heat, water vapor, and CO_2 , was calculated using the mean 20-min sensible heat flux and temperature gradient. Twenty-minute means of the CO_2 flux, corrected for vapor density differences at the two heights (Webb et al. 1980), were calculated as a product of the turbulent diffusivity and mean CO_2 gradient that also was measured for the same two heights by the BREB instrumentation. Twenty-minute fluxes were summed for daylight (0700 through 1900 Central Standard Time [CST]) and daily periods. Some fluxes were missing due to broken thermocouples used for temperature gradient measurement or equipment malfunction. If Bowen ratios were near -1 or if the directions of temperature gradient and sensible heat flux were of opposite sign (Ohmura 1992), the diffusivity was calculated (Dugas et al. 1997) from wind speed and canopy height. This method for estimation of diffusivity was used $\sim 5\%$ of the time, mostly during nighttime hours. In addition, fluxes were linearly interpolated when the Bowen ratio was near -1 .

Moisture and CO_2 gradients measured by the two BREB systems used in this study were similar to one another when they were side by side in a bare soil field in March 1994 (Dugas et al. 1997). Net radiometers used in the current study were calibrated against a laboratory standard in the early spring of 1995 and 1996. Thus, there were no systematic differences between the two BREB systems. Frequent storms in 1995 broke thermocouples and limited the number of sample days in which both systems were recording to 3 and 2 d in spring and fall periods, respectively (Table 1).

Ancillary measurements.—Diurnal photosynthetic photon flux density (PPFD) was measured on each day

BREB measurements were made. To estimate the amount of energy intercepted by the *Prosopis* canopy, PPFD also was measured below and above the canopy in each plot on 22 May 1995 using two cross-calibrated Li-Cor Model 191SA line quantum sensors (Li-Cor, Lincoln, Nebraska, USA). The PPFD was measured within 2 h of solar noon simultaneously above and below the *Prosopis* canopy for 15 s at each of 48 locations in each plot. Measurements were made every 2 m along three, east–west, 30 m long transects that were south of the Bowen ratio system. Intercepted PPFD was not measured in the 1996 burned plot because it was assumed, given the small amount of *Prosopis* leaf area in this plot, the PPFD intercepted by *Prosopis* was very small and similar to that measured in the 1995 burned plot. The below/above canopy ratio of PPFD was 0.87 for the burned plot and 0.63 for the unburned plot. Thus, there was a high percentage of radiation incident upon the top of the herbaceous canopy in both plots, but it was lower in the unburned plot due to greater *Prosopis* leaf area. Wind speed (used for calculation of diffusivity when the Bowen ratio method failed) was measured in unburned and burned plots at 3.8 m height. Wind direction was measured.

Empirically determined CO_2 flux and comparison to BREB-fluxes

A 12-h time interval during daylight hours (0700 through 1900 CST) was used to compare BREB and empirically determined CO_2 flux on 6 and 7 July 1995 (days 187 and 188) and 8 and 19 July 1996 (days 190 and 201) in both treatments. No attempt was made to compare the two techniques at night or in any month other than July.

Empirically determined CO_2 flux was calculated by measuring leaf-level photosynthesis, patch-level leaf area for vegetation components and patch-level soil CO_2 flux and scaling these to the ecosystem level as follows:

$$F_{\text{unburned}} = \sum (A_{\text{herb}(1\dots n)} \times \text{LAI}_{\text{herb}(1\dots n)}) + \sum (A_{\text{prgl}(\text{layer}\dots 3)} \times \text{LAI}_{\text{prgl}(\text{layer}\dots 3)}) + F_{\text{soil}} \quad (1)$$

$$F_{\text{burned}} = \sum (A_{\text{herb}(1\dots n)} \times \text{LAI}_{\text{herb}(1\dots n)}) + \sum (A_{\text{prgl}(\text{class}1\dots 5)} \times \text{LAI}_{\text{prgl}(\text{class}1\dots 5)}) + F_{\text{soil}} \quad (2)$$

where F = ecosystem CO₂ flux, $A_{\text{herb}(1\dots n)}$ = leaf photosynthesis of herbaceous species 1– n , $\text{LAI}_{\text{herb}(1\dots n)}$ = ecosystem LAI of herbaceous species 1– n , $A_{\text{prgl}(\text{layer } 1\dots 3)}$ = *Prosopis* leaf photosynthesis in canopy layers 1–3, $\text{LAI}_{\text{prgl}(\text{layer } 1\dots 3)}$ = *Prosopis* ecosystem LAI in shade layers 1–3, $A_{\text{prgl}(\text{class } 1\dots 5)}$ = *Prosopis* leaf photosynthesis in fire damage classes 1–5, $\text{LAI}_{\text{prgl}(\text{class } 1\dots 5)}$ = *Prosopis* ecosystem LAI in fire damage classes 1–5, and F_{soil} = soil CO₂ flux. Components of Eqs. 1 and 2 are as follows:

$$\text{LAI}_{\text{herb}(1\dots n)} = \sum (P_{\text{herb}(1\dots n)} \times C_{\text{herb}(1\dots n)}) \quad (3)$$

$$\text{LAI}_{\text{prgl}(\text{unburned})} = \sum (\text{LA}_{\text{stem}(1\dots n)} \times D_{\text{stem}}) \quad (4)$$

$$\text{LAI}_{\text{prgl}(\text{burn})} = \sum (\text{LA}_{\text{plant}(\text{class } 1\dots n)} \times D_{\text{plant}(\text{class } 1\dots 5)}) \quad (5)$$

where $P_{\text{herb}(1\dots n)}$ = patch LAI of herbaceous species 1– n , $C_{\text{herb}(1\dots n)}$ = patch percent cover of herbaceous species 1– n , $\text{LA}_{\text{stem}(1\dots n)}$ = *Prosopis* leaf area per basal stem of stems 1– n , D_{stem} = *Prosopis* basal stem density per land area, $\text{LA}_{\text{plant}(\text{class } 1\dots n)}$ = *Prosopis* leaf area per plant in fire damage classes 1–5, and D_{plant} = *Prosopis* plant density in fire damage classes 1–5. Following are procedures for determining components of empirically determined CO₂ flux.

Ecosystem LAI determination.—Ecosystem LAI was determined at a single time period in midsummer each year. Herbaceous ecosystem LAI in both treatments was determined (Eq. 3) as follows: percentage of ground area occupied by each grass species, herbaceous dicots, bare ground, and undefined litter was visually estimated within 0.25-m² quadrats placed along six 50 m long transects in each plot (Daubenmire 1959). Live leaf area of *Nassella* and *Buchloe* in each plot was estimated during midsummer each year by harvesting standing crop in five 0.25-m² quadrats located within monoculture patches of each species. Oven-dry live leaf mass, specific leaf area (SLA), live leaf area, and LAI were determined for each patch. Patch LAI of each warm-season midgrass (wsm) was determined by harvesting total biomass within monoculture patches of each of several wsm species and visually estimating percent live tissue. *Buchloe* SLA was used to convert wsm patch live leaf mass to patch LAI. Ecosystem LAI of each species was determined by multiplying patch LAI by percent cover as determined from the line transects.

Prosopis ecosystem LAI in the unburned plot (Eq. 4) was determined by measuring stem density and diameter of each basal support stem within 12, 9-m² (3 × 3 m) quadrats arranged in a fixed grid pattern at a 25-m spacing. In adjacent areas (also unburned), 35 *Prosopis* basal support stems of various diameters (5–25 mm) were harvested during midsummer of each growing season following diameter measurement. All leaves supported by each stem were removed, oven dried, and weighed. Prior to oven-drying, leaf area of subsamples was measured to determine SLA, and total leaf area per stem was then determined using total leaf

mass and the SLA. Regressions between stem diameter and total stem leaf area were developed for each growing season. Leaf area of each stem in each quadrat was estimated from stem diameter/leaf area regressions for each year and stem diameter and density measurement. Plot LAI for *Prosopis* was calculated by dividing total *Prosopis* leaf area per quadrat by 9 m².

It was not possible to use the same stem diameter/leaf area method to determine *Prosopis* ecosystem LAI in the burned plots because of the partial defoliation effects of the fires. Therefore, during the summer following each fire, *Prosopis* density was determined along six line transects using the point-centered quarter method (Cook and Stubbendieck 1986, Ludwig and Reynolds 1988). Along the same transects, ocular estimates were made of the percentage of *Prosopis* plants that were in each of five fire-damage classes: complete top-kill with basal sprouting, and 0–25%, 26–50%, 51–75%, and 76–100% of original foliage remaining on plants not top-killed. *Prosopis* density in each fire-damage class was then determined. All leaves of three randomly selected *Prosopis* plants within each fire-damage class were harvested, oven dried, and weighed. Prior to oven-drying, leaf area of subsamples was measured to determine SLA. Total leaf area per plant within each fire-damage class was then determined. Total *Prosopis* leaf area and LAI were estimated for each burned plot by multiplying *Prosopis* density by leaf area per tree within each fire-damage class and summing leaf areas of all fire-damage classes (Eq. 5).

Leaf and ecosystem-level photosynthesis measurements.—Leaf-level photosynthesis (leaf A ; $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \text{ leaf area} \cdot \text{s}^{-1}$) was measured in burned and unburned plots on 6 and 7 July 1995 and 8 and 19 July 1996 using two Li-Cor LI-6200 photosynthesis systems. Measurements were made during four or five sample periods per day between 0800 and 1600 CST. Leaf A was measured on three species per plot (*Prosopis*, *Nassella*, and *Buchloe*) and six individuals per species. All measurements were made on sunlit leaves similar to Ansley et al. (1991). In the 1995 burned plot, *Prosopis* leaf A measurements were made on regrowth of three top-killed plants and on three partially top-killed plants in each sample period. In the 1996 burned plot, leaf A measurements were made only on regrowth plants.

Daylight (12-h) ecosystem photosynthesis (ecosystem A ; $\text{g} \cdot \text{m}^{-2} \text{ ground area} \cdot 12 \text{ h}^{-1}$) for *Prosopis* and the herbaceous component was determined by multiplying leaf A by ecosystem LAI (Eqs. 1 and 2). *Prosopis* ecosystem A in the unburned plot was further adjusted to account for intracanalopy shading effects (Eq. 1). Data from an earlier study (R. J. Ansley, unpublished data) conducted on the same site and on trees similar in size to those in the current study were used to determine percent reduction in leaf A in shaded layers relative to fully sunlit leaves. *Prosopis* leaf A was measured diurnally on four leaves within each of three canopy lay-

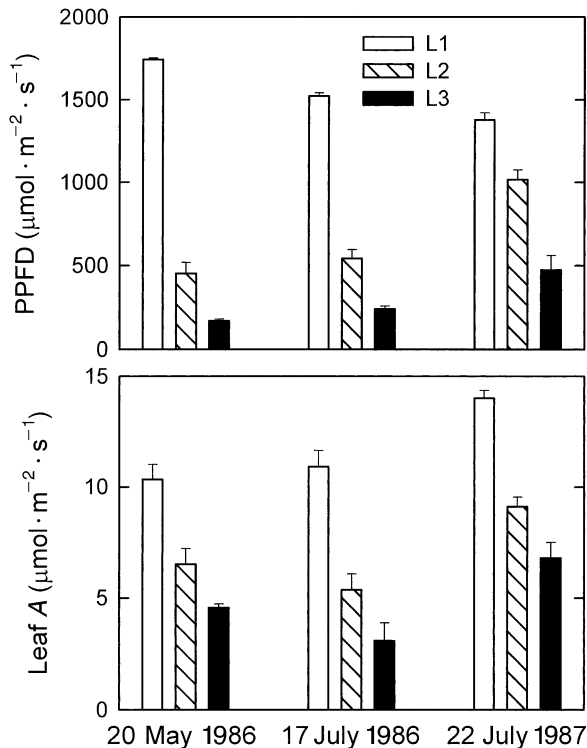


FIG. 1. Mean daylight (12-h) photosynthetic photon flux density (PPFD) and leaf photosynthesis (*A*) within *Prosopis* canopy layers L1 (sunlit), L2, and L3. Error bars represent 1 SE ($n = 4$).

ers (each layer represented roughly one third of total canopy foliage) using a LI-6200 in a similar manner as previously described with leaves oriented horizontally. PPFD was measured (Model 200S quantum sensor, Li-Cor) with each leaf *A* measurement. Layer 1 (L1) represented sunlit leaves, layer 2 (L2) the canopy middle, and layer 3 (L3) the most shaded layer. Leaf *A* in layers L2 and L3 was 60 and 41%, respectively, of that in L1 when averaged over three sample days (Fig. 1). Mean daily PPFD in L2 and L3 was 43 and 19%, respectively, of that in L1.

Percentage of *Prosopis* ecosystem LAI allocated to each shade layer was arbitrarily divided into three equal portions, but later adjusted as part of the modeling exercise. Because of the short stature of both *Nassella* and *Buchloe*, leaf *A* of sunlit leaves was used to represent all live leaf responses in the herbaceous layer. Leaf *A* of sunlit leaves was also used to represent all *Prosopis* leaves in the burned plots because there was very little shading within remaining foliage.

Soil CO_2 flux measurements.—Soil CO_2 flux was measured by a 0.001-m^3 chamber (inside diameter = 0.1 m), attached to Li-Cor 6200 photosynthesis system, and set on PVC collars placed in the soil (Dugas 1993, Nay et al. 1994, Dugas et al. 1997). Eight collars were placed in each treatment plot. Measurements were made every 90 min during daylight hours on 6 and 7

July 1995 and on 8 July 1996. The mean soil CO_2 flux measured on 8 July 1996 was used for both dates of leaf gas exchange measurements in 1996.

Comparisons (*t* tests) of leaf photosynthesis between treatments were made using subsamples within the burned and unburned plots as replicates. Because of an unequal number of sample dates within each period, annual means of CO_2 flux were based on the mean of each sample period. Throughout the paper, positive CO_2 flux values indicate a net downward movement of CO_2 , which represents net CO_2 uptake by the ecosystem.

RESULTS

Precipitation

Annual precipitation was markedly different in the two study years. In 1995, the annual precipitation was 954 mm, or 143% of the long-term mean, with especially high monthly totals in June, August, and October (Fig. 2). The growing season total (April through October) was 833 mm, which compares with the long-term mean of 501 mm. In 1996, by contrast, the annual precipitation total was 435 mm, or 65% of normal. Monthly totals were well below the mean from April through July. The April through October total was 342 mm.

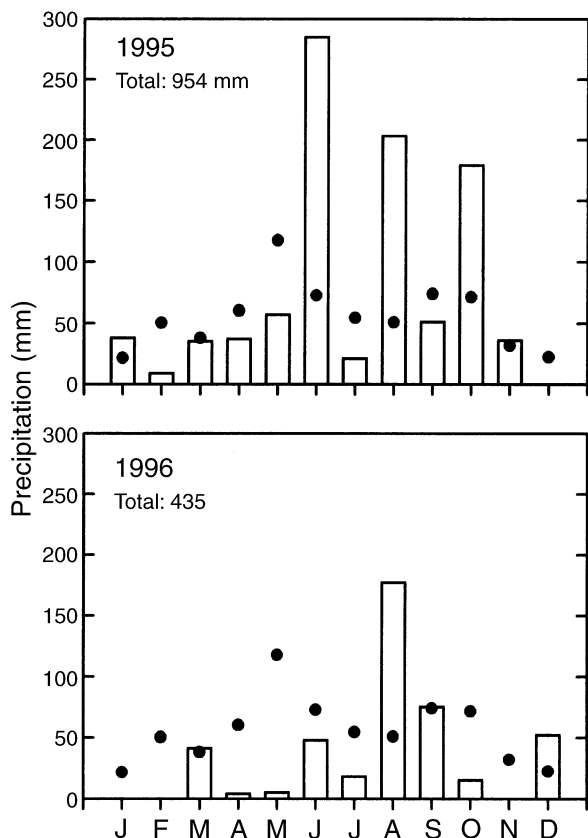


FIG. 2. Monthly precipitation totals (bars) at the research site in 1995 and 1996. Circles are 30-yr means from a NOAA site near Vernon, Texas, USA.

General fire effects and vegetation phenology

The 1995 fire caused complete aboveground mortality (top-kill) to 69% of *Prosopis* but yielded no whole plant mortality. Less than one-third of the trees not completely top-killed retained >50% of preburn foliage levels when measured the growing season following the fire. The 1996 fire was more intense, due to drier and warmer conditions and greater fine fuel, and *Prosopis* aboveground and whole-plant mortality were 97% and 3%, respectively.

In the unburned plot, *Prosopis* leaves emerged in April and canopies attained full development by mid-May and remained in full foliage until late October in both years. In burned plots, coppice growth in top-killed *Prosopis* began in May and attained a height of about 0.5 m by mid-July when leaf *A* measurements were made. Cool-season (*C*₃) grass growth began in late February and extended well into July in 1995 but stopped by early June in 1996 due to drought. Warm-season (*C*₄) grasses grew from May through September in 1995, but grew very little in 1996 due to drought.

BREB-determined CO₂ flux

Daily mean PPFD was lower in spring and fall when compared to the summer period in 1995 (Table 2). PPFD was high in both spring and summer 1996 and similar to the summer 1995 mean. Daily mean net radiation (*R*_{net}) differed by <10% among treatments during each sample period. Daily mean soil heat flux was typically <3% of daily mean *R*_{net} (data not shown) and soil heat flux differences between treatments were very small.

Mean 24-h CO₂ flux was greater in burned than unburned plots in all three seasonal periods in 1995 and during the spring of 1996 (Table 2). CO₂ flux was greater in the unburned than the burned plot in the summer of 1996, and there was little difference between treatments during the fall 1996. In both years, the growing season mean 24-h CO₂ flux was greater in burned than unburned plots and was greater for both treatments in 1995 than 1996. Trends were similar for 12-h daylight CO₂ fluxes.

A closer look at seasonal flux patterns within each year indicated that 24-h CO₂ fluxes were negative (net CO₂ loss to atmosphere) in the unburned plot during spring of both years (Table 2 and Fig. 3). Fluxes increased from the spring to summer period in both years, but declined to near zero from summer to fall in 1995 and did not change from summer to fall in 1996. In the burned plot in 1995, 24-h CO₂ flux was consistently high during all three periods with a maximum flux in summer. In 1996, 24-h CO₂ flux in the burned plot was greatest during spring, dropped to a negative value in the summer period, then increased in the fall.

The 12-h nighttime fluxes were more negative in the unburned than burned plots during each seasonal period in both years, indicating greater respiration rates in the

unburned plot. Thus, while trends were similar between 12-h daylight and 24-h fluxes, with respect to treatment differences, relative differences in 12-h daylight fluxes between treatments were lower than were differences in 24-h fluxes during all but the fall 1996 period.

While mean 24-h CO₂ flux was greater in the burned than the unburned plot throughout 1995, there was a 7-d period during summer (e.g., 5 to 11 July; days 186–192) when CO₂ flux was either similar between treatments or was substantially greater in the unburned plot (Fig. 3). Regressions indicated little relation between PPFD and CO₂ flux in either treatment or year (data not shown).

Components of empirically determined CO₂ flux

Ecosystem LAI.—*Prosopis* ecosystem LAI was greater in 1995 than in 1996 in both treatments and was much greater in the unburned than the burned plots in each year (Table 3). Herbaceous ecosystem LAI also was much greater in 1995 than in 1996 in both treatments (Table 4). The 1995 burned plot had the greatest herbaceous ecosystem LAI at 1.5. Adding *Prosopis* and herbaceous ecosystem LAI values from Tables 3 and 4 yielded a total ecosystem LAI of 3.1, 1.9, 2.2, and 0.1 in 1995 unburned, 1995 burned, 1996 unburned, and 1996 burned plots, respectively.

Variables used to calculate *Prosopis* and herbaceous ecosystem LAI are shown in Tables 3 and 4. Briefly, *Prosopis* SLA was greater in 1995 than in 1996 in both treatments, and was greater in the unburned than the burned plot each year (Table 3). Percent cover and patch live mass of *Nassella*, *Buchloe*, and warm-season midgrasses were greater in 1995 than 1996 in both treatments (Table 4). The percentage of nonphotosynthetic ground area (bare ground, litter, and dormant grass) was greater in both treatments in 1996 (61–64%) than in 1995 (9–32%).

The relationship between *Prosopis* basal stem diameter and leaf area in the unburned plot followed that of a power curve in both years (1995, $y = 0.34[x^{1.58}]$, $r^2 = 0.97$; 1996, $y = 0.26[x^{1.6}]$; $r^2 = 0.88$), although trees had more mean leaf area per stem in 1995 (6.4 m²) than 1996 (5.3 m²) (Table 3). In the 1995 burned plot, leaf area per tree of *Prosopis* ranged from 0.7 m² (1 SE = 0.2) in completely top-killed trees that exhibited only coppice growth to 16.7 m² (1 SE = 4.5) in trees that retained 76–100% of original foliage (data not shown). In the 1996 burned plot, all *Prosopis* were completely top-killed and leaf area per tree of coppice growth was also 0.7 m² (1 SE = 0.33).

Photosynthesis and soil CO₂ fluxes.—There were no significant differences in *Prosopis* mean daily leaf *A* between unburned and burned plots on the two days measured in July 1995 (Fig. 4). In 1996, *Prosopis* mean daily leaf *A* was two to three times greater in the burned than the unburned plot. Mean daily leaf *A* of *Nassella* and *Buchloe* was similar between burned and unburned plots in both years, but was much reduced in 1996 when

TABLE 2. Mean daily photosynthetic photon flux density (PPFD), mean 24-h net radiation (R_{net}), and mean 24-h daytime, and nighttime CO_2 flux for unburned and burned plots in 1995 and 1996.

Year and season	PPFD†	R_{net} (W/m ²)		24-h CO_2	
	Both	Unburned	Burned	Unburned	Burned
1995					
Spring ($n = 3$)	36.3 (6.3)	125 (23)	134 (25)	-0.1 (0.7)	15.7 (4.0)
Summer ($n = 17$)	47.3 (1.1)	195 (5)	200 (5)	14.6 (3.1)	19.7 (0.6)
Fall ($n = 2$)	34.7 (3.8)	132 (25)	133 (22)	0.8 (0.3)	15.2 (1.0)
Mean across seasons ($n = 3$)	39.4 (3.9)	151 (22)	156 (22)	5.1 (4.7)	16.8 (1.4)
Mean all sample dates ($n = 22$)	44.6 (1.5)	180 (8)	185 (8)	11.4 (2.7)	18.7 (0.7)
1996					
Spring ($n = 19$)	45.3 (2.2)	145 (8)	147 (8)	-9.2 (1.5)	8.1 (0.8)
Summer ($n = 25$)	43.6 (2.0)	164 (8)	152 (8)	4.1 (1.6)	-0.9 (1.0)
Fall ($n = 23$)	29.6 (1.6)	105 (6)	95 (5)	4.8 (1.1)	4.6 (0.9)
Mean across seasons ($n = 3$)	39.5 (5.0)	138 (17)	131 (18)	-0.1 (4.6)	3.9 (2.6)
Mean all sample dates ($n = 67$)	39.3 (1.4)	138 (5)	131 (5)	0.6 (1.1)	3.5 (0.7)

Notes: Data are from BREB measurements in spring, summer, and fall sample periods. Also reported are means across seasonal periods or all sample dates. Values in parentheses are 1 SE of the mean. CO_2 was measured in g/m² over 12 or 24 hours.

† PPFD measured for both burned and unburned plots.

compared to 1995. Mean daylight (12-h) soil CO_2 fluxes were more negative (greater loss to the atmosphere) on the burned than the unburned plot on 6 and 7 July 1995, but there were no differences between treatments in 1996 (Fig. 5).

BREB compared to empirically determined CO_2 fluxes

Empirically determined daylight (12-h) CO_2 fluxes on the two dates in July 1995 and 1996 were obtained by adding soil CO_2 fluxes, herbaceous ecosystem photosynthesis, and *Prosopis* ecosystem photosynthesis (Table 5). Empirically determined fluxes underestimated BREB estimates in both treatments, but were closer to BREB estimates in unburned than burned plots (Table 5 and Fig. 6). Averaged over all four sample days and both treatments, BREB-determined daylight CO_2 flux was 17.9 g·m⁻²·12 h⁻¹, and empirically determined flux was 12.0 g·m⁻²·12 h⁻¹.

Modifying the amount of *Prosopis* LAI allocated to each of the three canopy layers in the unburned plots to account for intracopy shading effects on *Prosopis* leaf A in some instances improved the empirically determined estimate (when compared to the BREB) relative to when LAI allocation was 33.3% in each layer (Table 6). The 50:25:25 allocation in L1, L2, and L3, respectively, appeared to generate the closest fit on three of the four days. The exclusion of adjustments for intracopy shading on *Prosopis* leaf A (i.e., using sunlit *Prosopis* leaf A for 100% of the canopy) increased the empirically determined CO_2 flux to >19% over the BREB estimates in 1995, but provided the closest fit to BREB estimates on the 19 July 1996 sample date.

DISCUSSION

Fire and CO_2 flux

While there is much concern regarding fire effects on carbon balance in many systems, in particular trop-

ical forests (Levine 1991, Ryan 1991), fire may be of benefit in temperate or subhumid grasslands and savannas (Knapp et al. 1998b, Pyne et al. 1996). Greater CO_2 uptake following burns has been shown in Great Plains grasslands (Frank et al. 2000) and in a Kansas tallgrass prairie (Knapp et al. 1998b). This is due in large part to a greater live/dead leaf ratio, increased nutrient availability and greater photosynthetic rates (Knapp 1985, Svejcar and Browning 1988, Schimel et al. 1991, Ojima et al. 1994). These increases in CO_2 flux may be offset somewhat by greater soil respiration in burned sites (Knapp et al. 1998c).

Less is known about fire effects on CO_2 flux in savannas where LAI in woody-dominated areas may be significantly greater than in open grasslands. Our hypothesis that reducing *Prosopis* canopy coverage with fire may lower ecosystem LAI and thereby lower CO_2 flux was based on work by Asner et al. (1998a, b), who found in south Texas that LAI in *Prosopis*-dominated areas was two to three times greater than in open grasslands. Based on our results, we reject our first hypothesis that fire decreases CO_2 flux in *Prosopis* savanna. While we found that ecosystem LAI was lower in burned plots than the unburned *Prosopis* stand, these differences were apparently not enough to reduce mean growing season CO_2 flux below that in the unburned plot. In this system, woodland areas are characterized by high *Prosopis* LAI and low herbaceous LAI due to competition from *Prosopis* (Bedunah and Sosebee 1984, Heitschmidt and Dowhower 1991, Scholes and Archer 1997). Reduction or removal of *Prosopis* by fire allowed an increase in herbaceous LAI to levels comparable to the *Prosopis* woodland in nondrought years. It was thus not possible for fire to substantially reduce LAI and CO_2 flux unless drought restricted grass growth, as occurred in 1996.

Fire and net carbon loss.—A rough estimate of the

TABLE 2. Extended.

Daylight (12-h) CO ₂		Nighttime (12-h) CO ₂	
Unburned	Burned	Unburned	Burned
5.2 (0.7)	18.4 (2.5)	-5.3 (0.8)	-2.8 (1.5)
18.9 (3.0)	23.2 (0.8)	-4.3 (0.4)	-3.5 (0.5)
6.4 (2.4)	18.1 (0.6)	-5.6 (2.2)	-3.0 (0.4)
10.2 (4.4)	19.9 (1.6)	-5.1 (0.4)	-3.1 (0.2)
15.9 (2.6)	22.1 (0.8)	-4.5 (0.4)	-3.4 (0.4)
1.5 (0.9)	9.2 (0.6)	-10.7 (0.9)	-1.1 (0.3)
9.0 (1.3)	3.3 (0.5)	-4.8 (0.6)	-4.2 (0.7)
12.4 (0.9)	10.5 (0.7)	-7.7 (0.6)	-5.9 (0.5)
7.6 (3.2)	7.7 (2.2)	-7.7 (1.7)	-3.7 (1.4)
8.0 (0.8)	7.4 (0.5)	-7.5 (0.5)	-3.9 (0.4)

net carbon exchange during the fire and the first growing season thereafter can be made. Preburn herbaceous mass, which was mostly litter, averaged 364 g/m² in the two burned plots. While there were differences in fire intensity between burns, which no doubt affected amount of biomass combusted, we assume a mean of 60% of this biomass (or 218 g/m²) was lost to combustion (McNaughton et al. 1998), although grass biomass combustion in savanna fires frequently reaches 90% or more (Shea et al. 1996). Carbon dioxide emitted from the fire through combustion was estimated to be 327 g/m², or 1.5 times the amount of herbaceous biomass combusted (Larcher 1975, Pyne et al. 1996). This resulted in a loss of 89.2 g/m² of carbon. *Prosopis* stems were killed from the heat but, because very little wood was consumed during these winter-season fires (Ansley et al. 1998a), contribution to atmospheric CO₂ was likely small. A further unknown contribution originated from the combustion of fallen twigs and leaf litter. The mean daily (24-h) CO₂ flux values of 16.8 and 5.1 g/m² (Table 2) in burned and unburned plots, respectively, during the 1995 growing season yielded a daily CO₂ flux difference of 11.7 g/m², and a daily carbon difference of 3.2 g/m². Thus, we estimate it would take ~28 d (327/11.7 or 89.2/3.2) to recover carbon lost from herbaceous layer combustion through increased CO₂ uptake in the burned plot. This is substantially less than the wet year growing season duration (~200 d). In the dry year, a daily CO₂-flux difference of 4.0

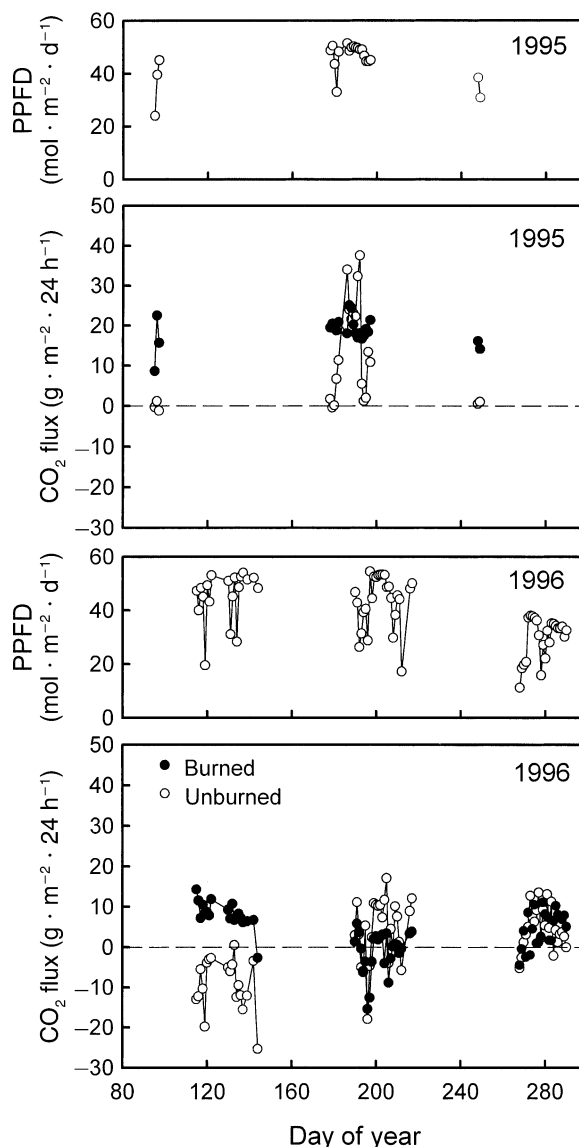


FIG. 3. Daily total photosynthetic photon flux density (PPFD) and 24-h CO₂ flux from Bowen ratio/energy balance (BREB) in the burned and unburned plots in 1995 and 1996.

TABLE 3. Specific leaf area (SLA), tree and stem density, mean stem diameter, mean leaf area per stem, and total plot (ecosystem) leaf area index (LAI) for *Prosopis* in unburned and burned plots in July 1995 and 1996.

Plot	SLA (m ² /kg ¹)	Tree density (tree/ha)	Stem density (stem/ha)	Stem diameter (cm)	Leaf area per stem (m ²)	<i>Prosopis</i> ecosystem LAI (m ² /m ²)
Unburned 1995	7.85	999	3704	5.93	6.37	2.36
Burned 1995	7.30	1642	0.41
Unburned 1996	6.90	999	3704	6.08	5.30	1.96
Burned 1996	5.29	506	0.04

TABLE 4. Percent cover, total mass, percentage live tissue, live mass, specific leaf area (SLA), and leaf area index (LAI) of vegetation patches, and ecosystem LAI for each species in unburned and burned plots in July 1995 and 1996.

Plot	Patch†	Cover (%)	Patch total mass (g/m ²)	Live tissue (%)	Patch live mass (g/m ²)	SLA (m ² /kg)	Patch LAI (m ² /m ²)	Eco-system LAI per species‡
1995 unburned	<i>Nassella</i>	22	232	43.8	102	8.6	0.88	0.19
	<i>Buchloe</i>	25	124	85.5	106	10.8	1.14	0.29
	wsm	18	280	50	140	10.8	1.51	0.27
	forbs	3						nd
	other	32						0
	total		100					0.75
1995 burned	<i>Nassella</i>	54	243	62.3	151	8.6	1.31	0.71
	<i>Buchloe</i>	9	129	83.6	108	10.8	1.17	0.11
	wsm	24	300	90	252	10.8	2.92	0.71
	forbs	4						nd
	other	9						0
	total		100					1.53
1996 unburned	<i>Nassella</i>	12	347	8.4	29	5.3	0.16	0.02
	<i>Buchloe</i>	9	205	25.4	52	11.6	0.60	0.05
	wsm	16	400	20	80	11.6	0.93	0.15
	forbs	2						nd
	other	61						0
	total		100					0.22
1996 burned	<i>Nassella</i>	20	45	25.9	12	6.6	0.08	0.02
	<i>Buchloe</i>	9	66	57.9	38	11.6	0.46	0.04
	wsm	3	120	50	60	11.6	0.72	0.02
	forbs	4						nd
	other	64						0
	total		100					0.08

† Abbreviations are: wsm, warm-season midgrasses; other, litter + bare ground + dormant cool-season annuals.

‡ nd = no data.

g·m⁻²·d⁻¹ (3.9 vs. -0.1 in burned and unburned plots, respectively) suggests it would take ~82 d (327/4) to recover lost CO₂.

These results, while approximate, suggest that the carbon emitted during the fire is probably recovered within the first year of post-fire regrowth, in both a wet and drought year. However, until measurements are made during dormant-season months and during subsequent post-fire growing seasons, further speculation about effects of fire on long-term net carbon flux or net contributions to atmospheric CO₂ are not possible. We would expect carbon losses to the atmosphere from respiration to be greater in *Prosopis*-dominated areas than in open grasslands during dormant-season months (November–March) because of the greater standing biomass of *Prosopis*, which can range from 9 to 20 Mg/ha on clay loam uplands (Felker et al. 1983). We would also expect burned grasslands to have lower CO₂ flux in succeeding years when compared to the first growing season following fire as standing dead grass tissue and litter accumulate, assuming equal precipitation among years and no further defoliation (Knapp et al. 1998a).

Mechanisms underlying CO₂ flux response to fire

Mechanisms that account for overall CO₂ flux responses to fire include differences in leaf-level pho-

tosynthesis, LAI, and soil respiration. In this study, CO₂ fluxes were very dependent on precipitation, and were much greater in both treatments during the wet year due to a combination of increased leaf photosynthesis and LAI.

Prosopis mean daily leaf photosynthesis (*A*) in the unburned plot was considerably lower in the drought year than the wet year (3.2 vs. 6.9 μmol·m⁻²·s⁻¹; Fig. 4). This indicates a sensitivity of this species to drought conditions, and confirms earlier research that suggested *Prosopis* in this region depend on shallow lateral roots for much of their moisture (Ansley et al. 1991, 1992a). In other regions, such as the Sonoran desert of southern California, *Prosopis* exhibit more phreatophytic tendencies and leaf water relations and photosynthesis are largely decoupled from soil moisture status at shallow depths (Nilsen et al. 1987). Increased *Prosopis* leaf *A* in response to precipitation explains in part why CO₂ flux in the unburned plot was greater in 1995 than in 1996.

Leaf *A* of coppice *Prosopis* in the burned plot in 1996 was up to three times greater than leaves on unburned mature *Prosopis* (Fig. 4). Coppice plants likely had an abnormally high root : shoot ratio that may have increased water and nutrient availability per unit leaf area (Knapp et al. 1998b). However, the increased leaf *A* of coppice *Prosopis* did not contribute much toward

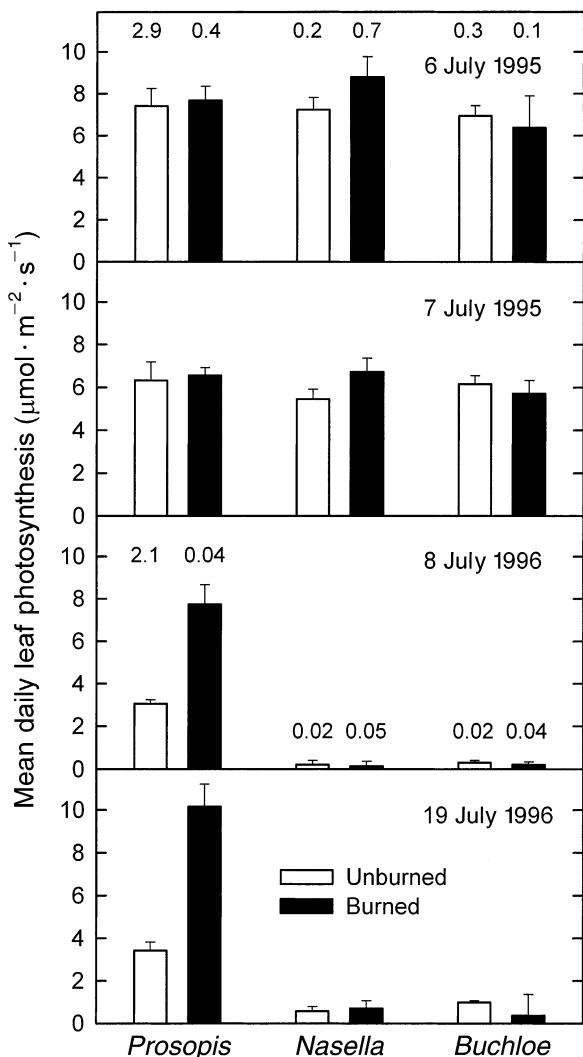


FIG. 4. Mean daily leaf photosynthesis on sunlit leaves of each species in burned and unburned plots. Error bars represent 1 SE. Ecosystem leaf area indices (LAI) for each species and treatment (data from Tables 3 and 4) are shown above photosynthesis bars.

increasing ecosystem CO₂ flux in the burned plot because *Prosopis* ecosystem LAI was extremely low. Differences in *Prosopis* leaf A between treatments were not as great in 1995 due to wetter conditions that increased *Prosopis* leaf A in both treatments and because many *Prosopis* plants in the 1995 burned plots were only partially top-killed and may not have had as great an imbalance in root : shoot ratio as in 1996, thus limiting the potential for maximizing leaf A.

Changes in the relative balance of *Prosopis* and herbaceous LAIs may also explain differences in CO₂ fluxes among seasonal sample periods and years. For example, greater 24-h CO₂ flux in the burned than the unburned plot in the spring of both years (Table 2 and Fig. 3) was because *Prosopis* leaves in the unburned plot were still immature and not assimilating CO₂ and

there was likely greater herbaceous live/dead ratios and less litter in the burned plot (Knapp 1985, Svejcar and Browning 1988).

Prosopis leaf area is usually at maximum in early to mid-summer, and declines in the fall (Ansley et al. 1992b). Live herbaceous leaf area in this region normally is greatest in spring (Heitschmidt et al. 1986). However, 1995 was atypical in that abundant rainfall in August stimulated herbaceous and possibly *Prosopis* leaf growth during fall (Nilsen et al. 1987). Thus, 24-h CO₂ fluxes in the 1995 burned plot were only slightly less in the fall than in summer (Table 2). In the unburned plot, the presence of *Prosopis* limited herbaceous growth and, as a result, created a large contrast in fluxes between summer and fall periods in 1995. *Prosopis* leaf A probably declined from summer to fall as indicated in other studies (Ansley et al. 1998b), but this was not measured.

The sharp increase in 24-h CO₂ flux in the unburned plot for a few days during the summer 1995 sample period (Fig. 3) merits further discussion because it provides an indication of the relationship between fire effects, precipitation, and CO₂ flux. A closer look at daylight (12-h) CO₂ fluxes in both treatments during this period reveals that CO₂ flux in the unburned plot increased shortly after a 21-mm precipitation event on day 183 (2 July; Fig. 7). The storm broke thermocouples in both treatments, so flux data were not available on days 183 to 185, but from days 186 to 192, CO₂ flux in the unburned plot was elevated relative to the burned plot when compared to flux levels in both treatments prior to the precipitation. This increase in flux in the unburned plot is most likely due to increases in *Prosopis* leaf A, combined with a relatively large *Prosopis* LAI that was maintained (see Table 3), and indicates a strong ability of this species to exploit a moisture event during an otherwise dry period, as other studies have shown (Nilsen et al. 1987, Ansley et al. 1992a). In contrast, CO₂ flux in the burned plot did not increase because

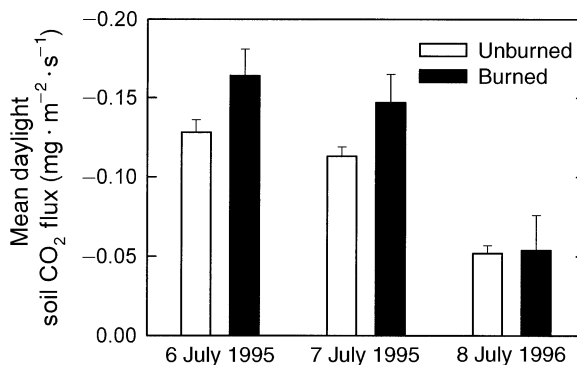


FIG. 5. Mean daylight (12-h) soil CO₂ flux in burned and unburned plots in 1995 and 1996. Error bars represent 1 SE (n = 8). Negative values indicate a CO₂ flux away from the soil.

TABLE 5. Empirically determined and Bowen ratio/energy balance (BREB) estimates of daylight (12-h) ecosystem CO₂ flux in unburned and burned plots on selected July days, 1995–1996. Empirically determined estimates include soil CO₂ flux (*S*) and ecosystem photosynthesis (Ecosys-A) for herbaceous (*H*) and *Prosopis* (*P*) components.

Date	Treatment	Empirically determined flux components (g·m ⁻² ·12 h ⁻¹)			Daylight CO ₂ flux (g·m ⁻² ·12 h ⁻¹)	
		Soil flux	Herbaceous Ecosys-A	<i>Prosopis</i> Ecosys-A	Empirical (<i>S</i> + <i>H</i> + <i>P</i>)	BREB
6 July 1995	unburned	-5.6	10.0	22.2	26.7	30.4
	burned	-7.1	21.5	6.0	20.5	29.0
7 July 1995	unburned	-4.9	8.5	18.9	22.6	28.1
	burned	-6.3	17.8	5.1	16.6	28.0
Mean 1995	unburned	-5.2	9.3	20.6	24.7	29.3
	burned	-6.7	19.6	5.6	18.6	28.5
8 July 1996	unburned	-2.2	0.1	7.6	5.5	5.9
	burned	-2.3	0.03	0.5	-1.8	3.7
19 July 1996	unburned	-2.2	0.4	8.5	6.7	13.8
	burned	-2.3	0.1	0.7	-1.5	3.8
Mean 1996	unburned	-2.2	0.3	8.1	6.1	9.9
	burned	-2.3	0.1	0.6	-1.6	3.8

Note: Positive values indicate downward flux (i.e., CO₂ uptake).

it was already at a high level (about 25 g·m⁻²·12 h⁻¹) prior to the precipitation event (Fig. 7).

A similar CO₂ flux response to midsummer precipitation was found in July 1996. One 4-mm event on day 193 and a larger 17-mm event on day 196 caused an increase in CO₂ flux in the unburned plot but not in the burned plot when compared to flux levels prior to the events (Fig. 7). Leaf *A* of grasses in the burned plot likely increased in response to these events, but overall LAI in this treatment was so low that the precipitation did not increase CO₂ flux.

Nighttime CO₂ flux (i.e., 1900 to 0700 CST) was more negative (greater CO₂ loss to the atmosphere) in the unburned plot in both years (Table 2), suggesting greater respiration maintenance costs, likely due to greater standing *Prosopis* biomass and more surface litter. Daylight soil CO₂ flux was more negative in the burned than the unburned plot during the wet year, but this variable was measured only during two midsummer days and may not be a reflection of trends for the entire growing season. More negative soil CO₂ fluxes on burned plots in 1995 may be due to increased soil microbial respiration (Knapp et al. 1998c), increased root respiration from greater root production (Seastedt and Ramundo 1990) and higher soil water content due to precipitation (Mielnick and Dugas 2000).

BREB vs. empirically determined CO₂ flux estimates

Responses from the four days in July selected for comparison of BREB and empirically determined CO₂ flux support our second hypothesis that a relatively simple empirical model, consisting of measurements made at the organism level and scaled to the ecosystem level, can be used to accurately estimate ecosystem fluxes, although empirically determined fluxes were lower than BREB estimates. During these four days, daylight CO₂ fluxes were actually greater in unburned than burned plots, which is opposite that of growing season trends between treatments, shown in Table 2. As discussed in the previous section, elevated CO₂ fluxes in the unburned plots on 6 and 7 July 1995 (days 187, 188) and on 19 July 1996 (day 201) were in response to precipitation (Fig. 7). Slightly greater CO₂ flux in unburned than burned plots on the 8 July 1996 (Table 5) was due to extreme drought which reduced both herbaceous leaf *A* and LAI in the burned plot.

Empirically determined flux values in the unburned plot were similar on 8 and 19 July 1996 (5.5 and 6.7

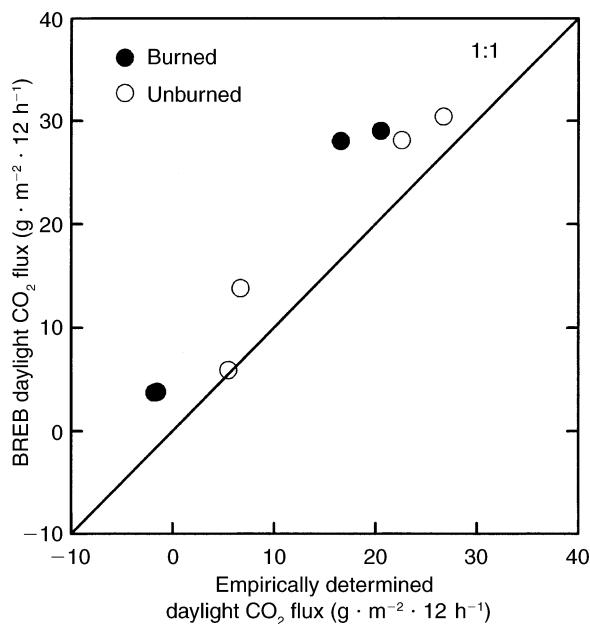


FIG. 6. Twelve-hour CO₂ flux from Bowen ratio/energy balance (BREB) and empirically determined measurements on four sample dates in the unburned and burned plots in July 1995 and 1996. The 1:1 line is also shown.

TABLE 6. Empirically determined estimates of daylight (12-h) ecosystem CO₂ flux in the unburned plot in response to variations in percentage LAI allocated to *Prosopis* canopy layers L1 (top), L2 (middle), and L3 (bottom), and compared to BREB-measured flux.

Type of flux measure	Leaf area (%)			Daylight ecosystem CO ₂ flux (g·m ⁻² ·12 h ⁻¹)			
	L1	L2	L3	6 July 1995	7 July 1995	8 July 1996	19 July 1996
	Empirically determined	100	0	0	37.7	32.0	9.2
	50	25	25	29.4	25.0	6.4	7.7
	33	33	33	26.7	22.6	5.5	6.7
	25	50	25	26.1	22.1	5.3	6.4
BREB				30.4	28.1	5.9	13.8

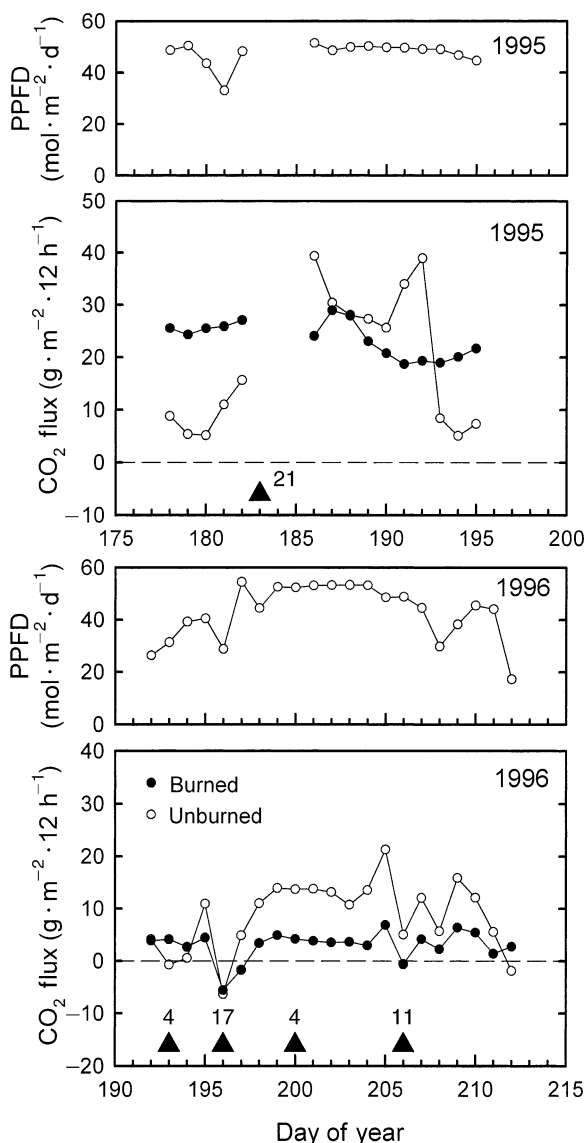


FIG. 7. Daily total photosynthetic photon flux density (PPFD) and 12-h daylight CO₂ flux from Bowen ratio/energy balance (BREB) in the burned and unburned plots during the summer sample period in 1995 and 1996. Black triangles and numbers above each triangle indicate a precipitation event and amount (mm), respectively.

g/m², respectively; Table 5), yet the BREB estimate detected more variation between these two days (5.9 and 13.8 g/m²). Rainfall occurred between the two days (Fig. 7) so it seems likely that CO₂ flux values would be greater on 19 July than on 8 July. The variation detected by the BREB measurements may have been due to increased photosynthesis, but the empirically determined estimate accounted for this. Ecosystem leaf area may also have increased from grass growth, and this was not considered in the empirically determined estimate as the same LAI was used for both dates. However, it is unlikely that significant growth occurred in 11 days during this time of the year with daily air temperatures exceeding 35°C.

The estimate of *Prosopis* ecosystem-level photosynthesis in unburned plots was based on four factors: (1) leaf A of sunlit leaves, (2) ecosystem-level LAI, (3) reduction of leaf A from shading within the *Prosopis* canopy, and (4) amount of *Prosopis* ecosystem LAI allocated to each shade layer. Values for leaf A of sunlit leaves and ecosystem LAI were based on field measurements and changed each year. Effects of intracopy shading on leaf A (factor 3) was based on an older data set and was not measured during the current study. This data set provided an indication of the degree of reduction of leaf A we might expect within the *Prosopis* canopy, and thus served as a basis from which to start. While we used the same percentage reduction of leaf A for each year, this likely would vary from year to year, especially in these contrasting moisture years.

The fourth factor, LAI allocation to shade layers, was arbitrarily determined. The fact that changes in LAI allocation (Table 6) generated a good match between BREB and empirically determined estimates in one year or the other, but not in both years suggests that canopy shading effects differed each year. Leaf area per *Prosopis* stem in the unburned plot was 20% greater in 1995 than in 1996 (Table 3). Thus, intracopy shading probably had less of an effect on leaf A in 1996.

CONCLUSIONS

In conclusion, greater 24-h CO₂ flux in burned than unburned plots during the first growing season following fire was in response to both greater daytime net

uptake of CO₂ (especially in 1995, the wet year) and lower nighttime loss of CO₂. Lower 24-h CO₂ flux in the burned than the unburned plot in the summer of 1996 apparently resulted from drought conditions that reduced herbaceous leaf photosynthesis and LAI. In the unburned plot, *Prosopis* maintained leaf area during drought and exploited precipitation events through increased photosynthesis.

Empirically determined 12-h daylight CO₂ flux, based on measurements of leaf photosynthesis, leaf area, and soil respiration and scaled to the ecosystem level, compared well with the BREB-determined values and provided explanation for variability in CO₂ flux between treatments. From an ecosystem management perspective, burning within this savanna ecosystem did not appear to cause a net increase in carbon to the atmosphere during the first growing season following fire, either in a wet or a drought year. It is acknowledged that these two years represented climatic extremes in this ecosystem and responses may be different in an average precipitation year.

ACKNOWLEDGMENTS

This research was funded by a grant from USDA-NRIRC Agricultural Systems (No. 94-04256); the E. Paul and Helen Buck Waggoner Foundation, Vernon, Texas; and from University of Texas Surface Leasing (UT-Lands), Midland, Texas. The W. T. Waggoner Estate provided the research site for this project. David Jones, Tim Tunnell, and Julie Huddle assisted in data collection. We thank Richard Teague, Sam Fuhlendorf, and Wayne Polley for comments on earlier versions of this manuscript.

LITERATURE CITED

- Ansley, R. J., and P. W. Jacoby. 1998. Manipulation of fire intensity to achieve mesquite management goals in north Texas. Pages 195–204 in T. L. Pruden and L. A. Brennan, editors. *Fire in ecosystem management: shifting the paradigm from suppression to prescription*. Tall Timbers Fire Ecology Conference Proceedings, Number 20. Tall Timbers Research Station, Tallahassee, Florida, USA.
- Ansley, R. J., P. W. Jacoby, and R. A. Hicks. 1991. Leaf and whole plant transpiration in honey mesquite following severing of lateral roots. *Journal of Range Management* **44**: 577–583.
- Ansley, R. J., P. W. Jacoby, C. H. Meadors, and B. K. Lawrence. 1992a. Soil and leaf water relations of differentially moisture-stressed honey mesquite (*Prosopis glandulosa* Torr). *Journal of Arid Environments* **22**:147–159.
- Ansley, R. J., D. L. Jones, T. R. Tunnell, B. A. Kramp, and P. W. Jacoby. 1998a. Honey mesquite canopy responses to single winter fires: relation to herbaceous fuel, weather and fire temperature. *International Journal of Wildland Fire* **8**: 241–252.
- Ansley, R. J., D. L. Price, S. L. Dowhower, and D. H. Carlson. 1992b. Seasonal trends in leaf area of honey mesquite trees: determination using image analysis. *Journal of Range Management* **45**:339–344.
- Ansley, R. J., B. A. Trevino, and P. W. Jacoby. 1998b. Intraspecific competition in honey mesquite: leaf and whole plant responses. *Journal of Range Management* **51**:345–352.
- Ansley, R. J., X. B. Wu, and B. A. Kramp. 2001. Observation: long-term increases in mesquite canopy cover in north Texas. *Journal of Range Management* **54**:171–176.
- Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? *American Naturalist* **134**:545–561.
- Archer, S., D. S. Schimel, and E. A. Holland. 1995. Mechanisms of shrubland expansion: land use, climate or CO₂? *Climate Change* **29**:91–99.
- Asner, G. P., C. A. Wessman, and S. A. Archer. 1998a. Scale dependence of absorption of photosynthetically active radiation in terrestrial ecosystems. *Ecological Applications* **8**:1003–1021.
- Asner, G. P., C. A. Wessman, and S. A. Archer. 1998b. Heterogeneity of savanna canopy structure and function from imaging spectrometry and inverse modeling. *Ecological Applications* **8**:1022–1036.
- Auclair, A. N. D., and T. B. Carter. 1993. Forest wildfires as a recent source of CO₂ at northern latitudes. *Canadian Journal of Forestry Research* **23**:1528–1536.
- Bedunah, D. J., and R. E. Sosebee. 1984. Forage response of a mesquite–buffalograss community following range rehabilitation. *Journal of Range Management* **37**:483–487.
- Buffington, L. C., and C. H. Herbel. 1965. Vegetational changes on a semi-desert grassland range from 1858 to 1963. *Ecological Monographs* **35**:139–164.
- Caldwell, M. M., P. A. Matson, C. Wessman, and J. Gamon. 1993. Prospects for scaling. Pages 223–230 in J. R. Ehleringer and C. B. Field, editors. *Scaling physiological processes—leaf to globe*. Academic, San Diego, California, USA.
- Collins, S. L., and S. C. Barber. 1985. Effects of disturbance on diversity in mixed-grass prairie. *Vegetatio* **64**:87–94.
- Collins, S. L., and E. M. Steinauer. 1998. Disturbance, diversity, and species interactions in tallgrass prairie. Pages 140–156 in A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. *Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, New York, New York, USA.
- Cook, C. W., and J. Stubbendieck. 1986. *Range research: basic problems and techniques*. Society for Range Management, Denver, Colorado, USA.
- Daubenmire, R. F. 1959. A canopy coverage method of vegetational analysis. *Northwest Science* **33**:43–64.
- Dixon, R. K., and O. N. Krankina. 1993. Forest fires in Russia: carbon dioxide emissions to the atmosphere. *Canadian Journal of Forestry Research* **23**:700–705.
- Dugas, W. A. 1993. Micrometeorological and chamber measurements of CO₂ flux from bare soil. *Agricultural and 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. Blackland Research Center Report Number 01-31. Blackland Research Center, Temple, Texas, USA.
- Dugas, W. A., and H. S. Mayeux, Jr. 1991. Evaporation from rangeland with and without honey mesquite. *Journal of Range Management* **44**:161–170.
- 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 and Forest Meteorology* **83**:113–133.
- Felker, P., G. H. Cannell, P. R. Clark, J. F. Osborn, and P. Nash. 1983. Biomass production of *Prosopis* species (mesquite), leucaena and other leguminous trees grown under heat/drought stress. *Forest Science* **29**:592–606.
- Field, C. B., and J. R. Ehleringer. 1993. Introduction: questions of scale. Pages 1–4 in J. R. Ehleringer and C. B. Field, editors. *Scaling physiological processes—leaf to globe*. Academic, San Diego, California, USA.
- Frank, A. B., P. L. Sims, J. A. Bradford, P. C. Mielnick, W. A. Dugas, and H. S. Mayeux. 2000. Carbon dioxide fluxes for three Great Plains grasslands. Pages 167–188 in R. F. Follett, J. M. Kimble, and R. Lal, editors. *Potential of U.S.*

- grazing lands to sequester carbon and mitigate the greenhouse effect. CRC, Boca Raton, Florida, USA.
- Grover, H. D., and H. B. Musick. 1990. Shrubland encroachment in southern New Mexico, U.S.A.: an analysis of desertification processes in the American southwest. *Climatic Change* **12**:305–330.
- Heitschmidt, R. K., and S. L. Dowhower. 1991. Herbage response following control of honey mesquite within single tree lysimeters. *Journal of Range Management* **44**:144–149.
- Heitschmidt, R. K., R. D. Schultz, and C. J. Scifres. 1986. Herbaceous biomass dynamics and net primary production following chemical control of honey mesquite. *Journal of Range Management* **39**:67–71.
- Howe, H. F. 1994. Managing species diversity in tallgrass prairie: assumptions and implications. *Conservation Biology* **8**:691–704.
- Jarvis, P. G., and R. C. Dewar. 1993. Forests in the global carbon balance: from stand to region. Pages 191–221 in J. R. Ehleringer and C. B. Field, editors. *Scaling physiological processes—leaf to globe*. Academic, San Diego, California, USA.
- Jarvis, P. G., and K. G. McNaughton. 1986. Stomatal control of transpiration: scaling up from leaf to region. *Advances in Ecological Research* **15**:1–49.
- Knapp, A. K. 1985. Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. *Ecology* **66**:1309–1320.
- Knapp, A. K., J. M. Briggs, J. M. Blair, and C. L. Turner. 1998a. Patterns and controls of aboveground net primary production in tallgrass prairie. Pages 193–221 in A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. *Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, New York, New York, USA.
- Knapp, A. K., J. M. Briggs, D. C. Hartnett, and S. L. Collins. 1998b. Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, New York, USA.
- Knapp, A. K., S. L. Conard, and J. M. Blair. 1998c. Determinants of soil CO₂ flux from a subhumid grassland: effect of fire and fire history. *Ecological Applications* **8**:760–770.
- Koos, W. M., J. C. Williams, and M. L. Dixon. 1962. Soil survey of Willbarger County, Texas. United States of America Department of Soil Conservation Service, Soil Survey Series 1959, Number 18. Fort Worth, Texas, USA.
- Kramp, B. A., R. J. Ansley, and T. R. Tunnell. 1998. Survival of mesquite seedlings emerging from cattle and wildlife feces in a semi-arid grassland. *Southwestern Naturalist* **43**:300–312.
- Lacher, W. 1975. *Physiological plant ecology*. Springer-Verlag, Berlin, Germany.
- Levine, J. S., editor. 1991. *Global biomass burning: atmospheric, climatic and biospheric implications*. MIT Press, Cambridge, Massachusetts, USA.
- Ludwig, J. A., and J. F. Reynolds. 1988. *Statistical ecology*. John Wiley and Sons, New York, New York, USA.
- McNaughton, S. J., N. R. H. Stronach, and N. J. Georgiadis. 1998. Combustion in natural fires and global emissions budgets. *Ecological Applications* **8**:464–468.
- Mielnick, P. C., and W. A. Dugas. 2000. Soil CO₂ flux in a tallgrass prairie. *Soil Biology and Biochemistry* **32**:221–228.
- Miranda, A. I., M. Coutinho, and C. Borrego. 1994. Forest fire emissions in Portugal: a contribution to global warming. *Environmental Pollution* **83**:121–123.
- Nay, S. M., K. G. Mattson, and B. T. Bormann. 1994. Biases of chamber methods for measuring soil CO₂ efflux demonstrated with a laboratory apparatus. *Ecology* **75**:2460–2463.
- Nilsen, E. T., M. R. Sharifi, R. A. Virginia, and P. W. Rundel. 1987. Phenology of warm desert phreatophytes: seasonal growth and herbivory in *Prosopis glandulosa* var. *torreyana* (honey mesquite). *Journal of Arid Environments* **13**:217–229.
- National Oceanic and Atmospheric Administration (NOAA). 1987–1996. Climatological data, Texas. Volumes 92 to 101. National Oceanic and Atmospheric Administration National Climatic Data Center, Asheville, North Carolina, USA.
- Ohmura, A. 1982. Objective criteria for rejecting data for Bowen ratio flux calculations. *Journal of Applied Meteorology* **21**:595–598.
- Ojima, D. S., D. S. Schimel, W. J. Parton, and C. E. Owensby. 1994. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry* **24**:67–84.
- Polley, H. W., H. B. Johnson, and H. S. Mayeux. 1994. Increasing CO₂: comparative responses of the C₄ grass *Schizachyrium* and grassland invader *Prosopis*. *Ecology* **75**:976–988.
- Pyne, S. J., P. L. Andrews, and R. D. Laven. 1996. *Introduction to wildland fire*. Second edition. John Wiley and Sons, New York, New York, USA.
- Ryan, K. C. 1991. Vegetation and wildland fire: implications of global climate change. *Environment International* **17**:169–178.
- Schimel, D. S., T. G. F. Kittel, A. K. Knapp, T. R. Seastedt, W. J. Parton, and V. B. Brown. 1991. Physiological interactions along resource gradients in a tallgrass prairie. *Ecology* **72**:672–684.
- Scholes, R. J., and S. R. Archer. 1997. Tree–grass interactions in savannas. *Annual Review of Ecological Systems* **28**:517–544.
- Seastedt, T. R., B. P. Hayden, C. E. Owensby, and A. K. Knapp. 1998. Climate change, elevated CO₂, and predictive modeling. Pages 283–300 in A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. *Patterns and controls of aboveground net primary production in tallgrass prairie*. Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, New York, USA.
- Seastedt, T. R., and R. A. Ramundo. 1990. The influence of fire on belowground processes of tallgrass prairies. Pages 99–117 in S. L. Collins and L. L. Wallace, editors. *Fire in North American tallgrass prairies*. University of Oklahoma Press, Norman, Oklahoma, USA.
- Shea, R. W., B. W. Shea, J. B. Kaufmann, D. E. Ward, C. I. Haskins, and M. C. Scholes. 1996. Fuel biomass and combustion factors associated with fires in savanna ecosystems of South Africa and Zambia. *Journal of Geophysical Research* **101**:551–568.
- Svejcar, T. J., and J. A. Browning. 1988. Growth and gas exchange of *Andropogon gerardii* as influenced by burning. *Journal of Range Management* **41**:239–244.
- Tanner, C. B. 1960. Energy balance approach to evaporation from crops. *Soil Science Society Annual Proceedings* **24**:1–9.
- Towne, G., and C. E. Owensby. 1984. Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. *Journal of Range Management* **37**:392–397.
- Webb, E. K., G. I. Pearman, and R. Leuning. 1980. Correction of flux measurements for density effects due to heat and water vapour transfer. *Quarterly Journal of the Royal Meteorological Society* **106**:85–100.
- Wright, H. A., and A. W. Bailey. 1982. *Fire ecology—United States and southern Canada*. John Wiley and Sons, New York, New York, USA.