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Net grassland carbon flux over a subambient to superambient CO_2 gradient

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Abstract

Increasing atmospheric CO_2 concentrations may have a profound effect on the structure and function of plant communities. A previously grazed, central Texas grassland was exposed to a 200-μmol mol^{-1} to 550 μmol mol^{-1} CO_2 gradient from March to mid-December in 1998 and 1999 using two, 60-m long, polyethylene-covered chambers built directly onto the site. One chamber was operated at subambient CO_2 concentrations (200–360 μmol mol^{-1} daytime) and the other was regulated at superambient concentrations (360–550 μmol mol^{-1}). Continuous CO_2 gradients were maintained in each chamber by photosynthesis during the day and respiration at night. Net ecosystem CO_2 flux and end-of-year biomass were measured in each of 10, 5-m long sections in each chamber. Net CO_2 fluxes were maximal in late May (*c.* day 150) in 1998 and in late August in 1999 (*c.* day 240). In both years, fluxes were near zero and similar in both chambers at the beginning and end of the growing season. Average daily CO_2 flux in 1998 was 13 g CO_2 m^{-2} day^{-1} in the subambient chamber and 20 g CO_2 m^{-2} day^{-1} in the superambient chamber; comparable averages were 15 and 26 g CO_2 m^{-2} day^{-1} in 1999. Flux was positively and linearly correlated with end-of-year above-ground biomass but flux was not linearly correlated with CO_2 concentration; a finding likely to be explained by inherent differences in vegetation. Because C_3 plants were the dominant functional group, we adjusted average daily flux in each section by dividing the flux by the average percentage C_3 cover. Adjusted fluxes were better correlated with CO_2 concentration, although scatter remained. Our results indicate that after accounting for vegetation differences, CO_2 flux increased linearly with CO_2 concentration. This trend was more evident at subambient than superambient CO_2 concentrations.

Keywords: Canopy CO_2 flux, CO_2 gradient, grassland

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Introduction

The direct and indirect effects of increasing atmospheric CO_2 may have profound implications for the structure and function of plant communities. Vegetation, in turn, plays a crucial role in the global carbon balance (Woodward *et al.* 1998). Although numerous greenhouse and growth chamber studies have been conducted on plant response to superambient atmospheric CO_2 concentrations (Diemer 1994; Polley *et al.* 1996; Field *et al.* 1997; Schapendonk *et al.* 1997; Bunce 1998; Diaz *et al.* 1998), processes controlling plant response to CO_2 on these smaller scales (e.g. greenhouse pot studies) may be quite different than those controlling plant responses on a larger scale, such as in the field. The complex effects of competitive resource acquisition (e.g. soil nutrients, light

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and water) in a natural ecosystem are not easily duplicated in smaller scale studies. Few studies have been undertaken on whole ecosystem response to superambient CO_2 (Jackson *et al*. 1994; Fredeen *et al*. 1997; Hamerlynck *et al*. 1997; Vasseur & Potvin 1998), and even less research has been directed towards the effects of subambient CO_2 concentrations on vegetation (Polley 1992a, 1992b; Polley *et al*. 1996). Evaluating plant responses in the field under both subambient and superambient CO_2 concentrations will help interpret effects of past CO_2 changes on vegetation, and may improve prediction of future responses of ecosystems to CO_2 concentrations.

Two commonly used facilities for outdoor CO_2 studies, open top chambers and Free Air Carbon Dioxide Enrichment (FACE) devices, use a limited number of CO_2 concentrations (Diemer 1994; Jackson *et al*. 1994; Lewin *et al*. 1994; Fredeen *et al*. 1997; Hamerlynck *et al*. 1997; Hungate *et al*. 1997a, 1997b). Covered chambers have been used in a greenhouse to evaluate plant responses over a wide range of subambient CO_2 concentrations (Polley *et al*. 1992a, 1992b). Here, we extended the use of a covered chamber outdoors to a Texas grassland to measure net ecosystem CO_2 flux continuously for two growing seasons. Our study is, we believe, the first to investigate plant responses over a continuum of subambient to superambient atmospheric CO_2 concentrations in a natural plant community. The canopy level flux measurements in this study complement concomitant work at the leaf-level scale (Anderson *et al*. 2001).

The objective of this study was to quantify relationships between CO_2 flux and both CO_2 concentration and biomass for a Texas grassland exposed to a 200–550 μmol mol^{-1} CO_2 gradient from early March to mid-December in 1998 and 1999.

Materials and methods

Johnson *et al*. (2000) present a complete description of the experimental apparatus and sampling protocol. A brief summary is presented here.

Chamber and site description

The research site was a previously grazed grassland at the Grassland, Soil and Water Research Laboratory in central Texas, USA (31°05′ N, 97°20′ W). Vegetation is dominated by the C_4 perennial grass *Bothriochloa ischaemum* (L.) Keng (King Ranch bluestem) and the C_3 perennial forbs *Solanum dimidiatum (Raf.)* (Western horsenettle) and *Ratibida columnaris* (Sims) D. Don (Mexican hat). Soil is in the Austin series (a mollisol) and is classified as a fine-silty, carbonatic, thermic, Udorthentic Haplustoll with 35–55% clay in the top 40 cm. Inclusions of the Houston Black series (a vertisol defined as a fine, smectitic, thermic Udic Haplustert) are common. Extensive sampling has shown that the soil varies horizontally and vertically over short distances, a characteristic of this soil type. Prior to fabrication of the chambers, soil cores (depth 1.7 m, diameter 40 mm) were taken at the centre of each section (n = 20, see below). Roots were removed from each core and total root biomass was determined. Measured rooting depth exceeded one meter throughout both chambers. To examine if soil variation affected root biomass, we regressed total root biomass against subsequent CO_2 concentration. Regression slopes were not significantly different from zero ($P > 0.2$ and $P > 0.6$ over subsequent superambient and subambient concentration gradients, respectively). Thus, we conclude that soil variation did not affect root biomass prior to CO_2 treatments.

Two, parallel, 60-m long chambers, enclosed by polyethylene film, were built 1.5 m apart on the site in a north–south orientation. The film transmitted 90% of incident photosynthetically active radiation (Johnson *et al*. 2000). Each chamber was divided into a series of 5-m long sections (numbered 1 through 10, south to north, in the superambient chamber, and 11 through 20 in the subambient chamber), separated by l-m long metal ducts containing chilled-water cooling coils that regulated air temperature and humidity. Chamber soil was isolated with a 1-m deep plastic liner extending vertically into the soil.

CO_2 uptake by plants during daylight depleted the CO_2 concentration of air as it was blown with a fan through each chamber from south to north, thus creating a continuous CO_2 gradient with highest concentrations at the south end and lowest concentrations at the north end. In the superambient chamber, CO_2 was injected into entering air during daylight hours to enrich the CO_2 concentration to 550 μmol mol^{-1} in section 1. The air exited at the north end at 360 μmol mol^{-1} (section 10). Ambient air was introduced to the south end of the subambient chamber to initiate a 360 (section 11) to 200 μmol mol^{-1} (section 20) gradient.

The direction of air flow was reversed at night and CO_2 concentration increased along each chamber because of plant and soil respiration. CO_2 was injected at night at the north end of the superambient chamber to increase the initial CO_2 concentration to 550 μmol mol^{-1}. Nighttime CO_2 concentrations were maintained in each section at 150 μmol mol^{-1} above daytime levels. The CO_2 concentration gradient was imposed from April through mid-December in 1997 and from March through mid-December in 1998 and 1999.

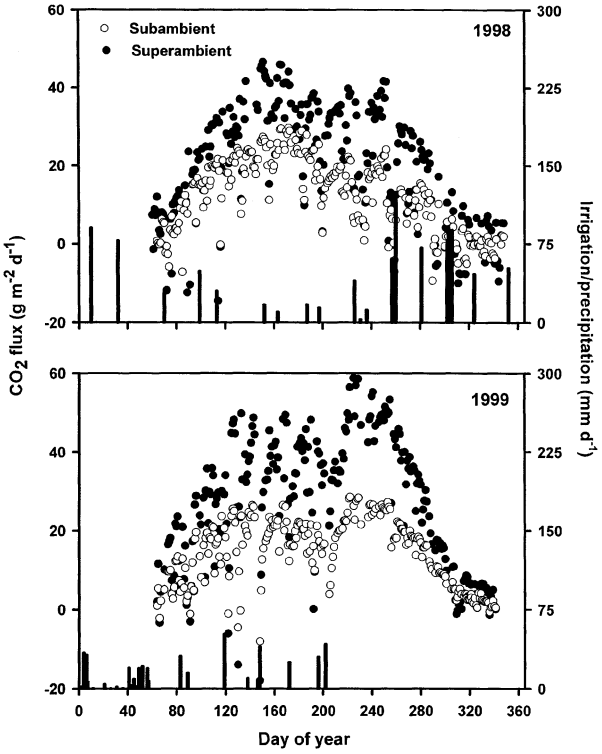

Fig. 1 Daily CO_2 flux for subambient and superambient chambers and daily irrigation or precipitation in 1998 and 1999. Fluxes are averages of 10 sections per chamber.

Precipitation/irrigation

The chambers received any precipitation that fell when they were uncovered (i.e. from mid-December to early March and during a single, daylight period each month for vegetation measurements); all other water was supplied by irrigation. The total amount of water applied (irrigation plus precipitation) was 996 mm in 1998 and 337 mm in 1999. The 87-year annual average precipitation at the site is 864 mm.

CO_2 flux measurements

Twenty-minute averages of net ecosystem CO_2 flux (positive = CO_2 uptake) for each 5-m section were calculated as a product of the average CO_2 gradient and average air flow rate in each section. The gradient was the difference in CO_2 concentration between the south and north ends of each section. Concentrations were measured, sequentially, within each chamber, once every 20 minutes during the final 20 s of a 1 minute sampling period using an infra-red gas analyser (Model 6262, Li-Cor, Inc, Lincoln, NE, USA). A separate analyser was used for each chamber. Air flow rate (L s^{-1}) was the product of the fan revolutions and a set of regression coefficients calculated for each section and flow direction. Coefficients were calculated during periodic calibrations using independent volumetric flow calculations at varying fan speeds. The same set of coefficients was used for each section for both years because coefficients varied by less than 10% between calibrations.

Net ecosystem CO_2 flux was calculated from day 60 to day 348 in 1998 and from day 64 to day 341 in 1999. Total daily fluxes were calculated as the sum of 20-minute fluxes. Fewer than 1% of seasonal 20-minute fluxes were linearly interpolated, usually due to spurious fluxes that sometimes occurred at dawn and dusk when flow direction changed. Occasionally, daily fluxes were unavailable due to malfunctioning equipment or when chambers were uncovered for vegetation measurements. Across all sections, flux was measured for an average of 254 and 236 days in 1998 and 1999, respectively. Average daily fluxes for the season were calculated from all daily fluxes; missing days (due to tunnel maintenance, calibrations, or temporary equipment malfunction) were ignored.

Above-ground biomass and vegetative cover

Above-ground biomass (including live and standing dead but excluding litter) in each section was harvested (to 5 cm), oven-dried and weighed in December of 1998 and 1999. The percentage green vegetative cover, by species, was determined monthly by visual inspection in two 1×1 m quadrats per section. Species were grouped into either C_3 or C_4 functional classes. The seasonal average percentage C_3 cover was used as an index of vegetative differences between sections and years.

Data analysis

For each 5-m section, average daily CO_2 flux for the season was regressed against average daytime CO_2 concentration and end-of-season above-ground biomass. To validate measured CO_2 fluxes, we compared seasonal average daily CO_2 flux for each section with an equivalent CO_2 flux calculated from end-of-season biomass measurements in each section using the following assumptions: above-ground live biomass was zero at the beginning of each year, 1 g of oven-dried organic matter equals 1.5 g of CO_2 (Larcher 1975), and the average root : shoot ratio was 3 : 1 (based upon root measurements in an adjacent grassland; Dugas, unpublished data 2000). This is consistent with measured ratios in grasslands that range from 2 : 1 and 4 : 1 (Svejcar 1990).

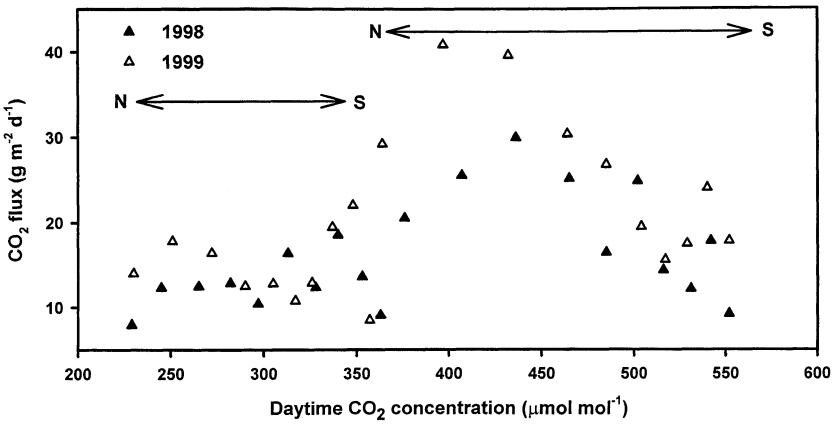

Fig. 2 Average daily CO_2 flux vs. average daytime CO_2 concentration in 1998 and 1999. Averages are for all days in a year. North and south ends of subambient and superambient chambers are indicated.

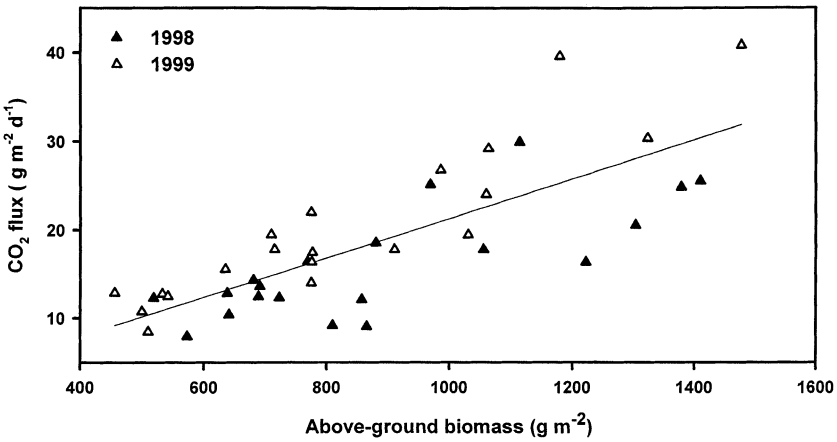

Fig. 3 Average daily CO_2 flux vs. end-of-year, above-ground biomass for all sections of both chambers in 1998 and 1999. $R^2 = 0.60$.

Results

Daily CO_2 fluxes

Daily CO_2 fluxes (averaged across 10 sections in each chamber) were lower over subambient than superambient CO_2 concentrations during much of the growing season in both 1998 and 1999 (Fig. 1). Most day-to-day variability in flux reflected changes in radiation, whereas seasonal changes in flux were related to changes in leaf area, phenology or soil moisture. At the beginning and end of each growing season, fluxes were near zero and were similar over both superambient and subambient CO_2 concentrations. As the season progressed, fluxes increased and there was a widening separation between superambient and subambient fluxes. Maximum flux occurred in late May (*c.* day 150) in 1998 and in late August (*c.* day 240) in 1999.

Recovery time of net CO_2 uptake following exposure to high temperatures or drought differed between subambient and elevated concentrations in both years. Daily CO_2 fluxes at superambient CO_2 concentrations recovered faster from heat and drought stress than fluxes at subambient CO_2 concentrations. For example, in 1998, following a 2-h exposure to temperatures >45 °C on day 199, fluxes at superambient CO_2 concentrations recovered 30% faster over the next 5 days than did fluxes at subambient CO_2 concentrations. In 1999, following a total irrigation of 72 mm on days 196 and 202 (mid-July) after a 24-day drought, net CO_2 uptake increased 25% faster over the next 6 days at superambient compared to subambient CO_2 concentrations.

The decline in daily CO_2 flux after day 240 in both 1998 and 1999 (Fig. 1) can be attributed to senescing vegeta-

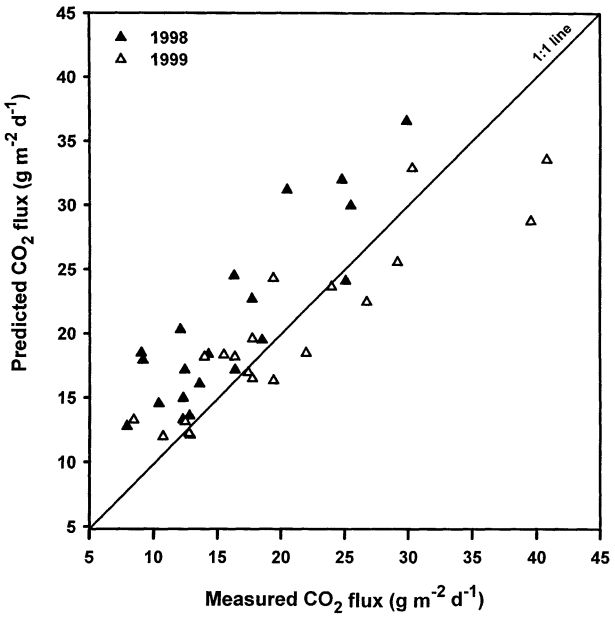

Fig. 4 Predicted vs. measured CO_2 flux in 1998 and 1999. Measured fluxes are averages for all days in a year. Predicted fluxes were calculated from end-of-year above-ground biomass and a root : shoot ratio of 3 : 1 (see text).

tion. The decrease is steeper in 1999, a situation likely to have been caused by soil moisture declining more rapidly in this year because of late season drought. Average daily CO_2 flux in 1998 was 13 and 20 g CO_2 m^{-2} day^{-1} in the subambient and superambient CO_2 chambers, respectively. In 1999, comparable averages were 15 and 26 g CO_2 m^{-2} day^{-1}.

Flux vs. CO_2 concentration

There was a greater than three-fold difference in average daily flux among chamber sections in both years (Fig. 2). In 1998, average daily CO_2 flux ranged from 8 g CO_2 m^{-2} day^{-1} at 229 μmol mol^{-1} to 30 g CO_2 m^{-2} day^{-1} at 436 μmol mol^{-1}. In 1999, flux ranged from 8 g CO_2 m^{-2} day^{-1} at 357 μmol mol^{-1} CO_2 to 41 g CO_2 m^{-2} day^{-1} at 397 μmol mol^{-1} CO_2. Generally, fluxes in each section were greater in 1999 than 1998.

There was a parabolic relationship between flux and CO_2 concentration with a maximum flux at about 400 μmol mol^{-1} CO_2 in both years. Over subambient CO_2 concentrations, fluxes increased with increasing CO_2 concentration, especially above 300 μmol mol^{-1}. However, flux decreased with CO_2 concentration >450 μmol mol^{-1} in the superambient chamber, a result opposite that which was expected.

Flux vs. above-ground biomass

In both years, average daily CO_2 flux was linearly and positively correlated with end-of-year, above-ground biomass (Fig. 3). Measured CO_2 fluxes were similar to biomass-predicted fluxes in 1999 and slightly less than predicted fluxes in 1998 (Fig. 4). The close relationship between measured and predicted CO_2 fluxes gives additional support to the accuracy of these fluxes, especially considering that our estimated 3 : 1 root : shoot ratio is consistent with published root : shoot measurements in grasslands.

Vegetation heterogeneity

Relative abundances of C_3 and C_4 species varied both spatially and temporally (Fig. 5). Clearly, over time, C_3 vegetation increased at the expense of C_4 vegetation. From 1997 to 1999, cover of C_3 species increased by 71% and 63%, while cover of C_4 species decreased by 77% and 52% over subambient and superambient CO_2 concentrations, respectively. Variation in vegetation among sections was great in each year; coefficients of variation among sections were greater than 30% and 40% for C_3 and C_4 species, respectively, in all three years. Aggressive, tall, early growing and relatively long-lived C_3 species like *R. columnaris, Solidago canadensis* (L.) (goldenrod) and *S. dimidiatum* increased in cover from 1997 to 1999 (results not shown). Over subambient CO_2 concentrations, percentage cover of the initially dominant C_4 grass *B. ischaemum* declined from an average of 46% in 1997 to less than 9% in 1999, and at superambient concentrations cover declined from 40% to 17%. However, another C_4 grass, *Sorghum halepense* (L.) Pers. (Johnsongrass), was one of a quartet of dominant species (including *R. columnaris, S. canadensis* and *S. dimidiatum*) in some sections in the superambient chamber. The total number of species in this grassland varied between 11 and 29 per section. The turnover rate of species (ratio of appearance to disappearance of species from year to year) was high between years, but was not related to CO_2 flux, above-ground biomass or CO_2 concentration (data not shown).

Adjusting flux

To standardize fluxes for vegetation changes among sections within each year, we divided the average daily flux by the percentage cover of C_3 plants, the dominant vegetative group at both the subambient and superambient CO_2 concentrations (Fig. 5). Average daily CO_2 fluxes were positively related to percentage C_3 cover ($P < 0.0001$) over all concentrations (results not shown). This standardization improved the relationship between

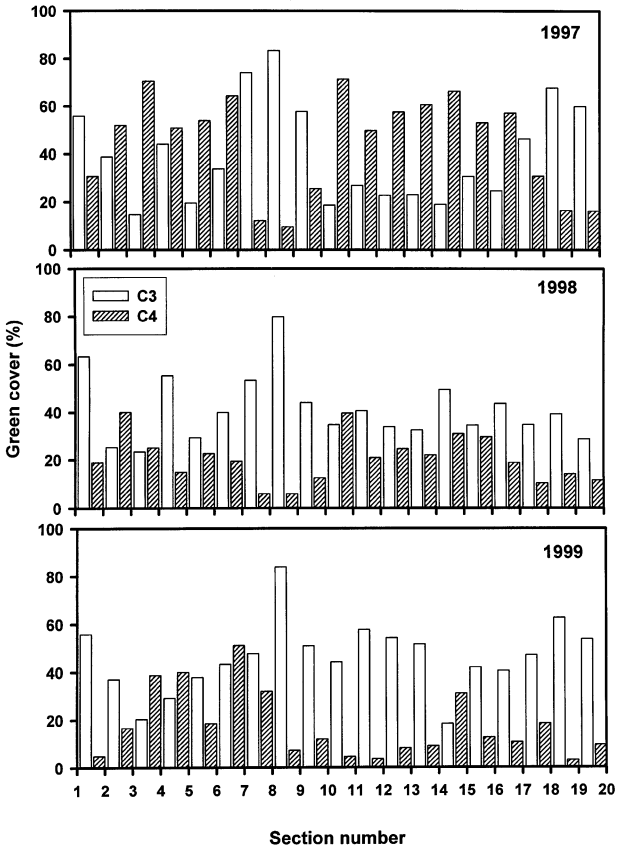

Fig. 5 Percentage green C_3 and C_4 vegetation cover in 1997, 1998 and 1999 for each section. (CO_2 concentration varied from 550 μmol mol^{-1} in section 1 to 230 μmol mol^{-1} in section 20). Percentage cover is an average of all monthly vegetation observations within a year.

flux and CO_2 concentration across the full CO_2 gradient (Fig. 6), although substantial scatter remained.

Discussion

After accounting for some of the variability in vegetation in this grassland, results show that CO_2 flux increased with increasing CO_2 concentration. Some of the remaining scatter may reflect differences in C_4 composition or other vegetation and/or soil differences not accounted for by this procedure (although initial root biomass did not differ with section position). There was a good relationship between CO_2 flux and above-ground biomass in both years, and between measured and predicted fluxes (Figs 3 and 4), although fluxes were high compared to CO_2 fluxes measured in other grasslands. For example, fluxes of 9.3 g CO_2 m^{-2} day^{-1} and 11.4 g CO_2 m^{-2} day^{-1} were measured during July and August in a C_4 grassland in Kansas under ambient and superambient CO_2 concentrations, respectively (Ham *et al.*

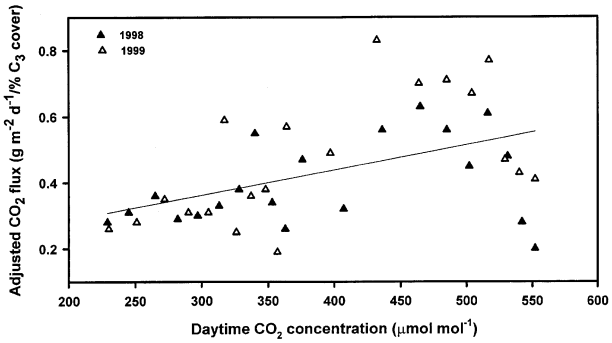

Fig. 6 Average daily CO_2 flux, adjusted for average percentage C_3 cover vs. average daytime CO_2 concentration in 1998 and 1999. $R^2 = 0.23$.

1995). Two-year average CO_2 fluxes in this study over the same time period (Fig. 1) were 21 g and 35 g CO_2 m^{-2} day^{-1} over subambient and superambient CO_2 concentrations, respectively. Our fluxes likely were high because of the protective environment inside the covered chambers compared to the outside environment (i.e. reduced wind and vapour pressure deficit, increased diffuse light (Johnson *et al.* 2000) and reduced insect herbivory) and a long growing season.

Community-level flux response to increasing CO_2 levels was strongly influenced by vegetation differences. We suggest the non-linear relationship of flux to CO_2 concentration (Fig. 2) was due to initial differences in vegetation and differences that developed with time (Fig. 5). C_3 and C_4 species have different growth and rooting patterns, plant architecture, seasonal production cycles and physiological parameters (Bazzaz & McConnaughay 1992; Owensby *et al.* 1993; Poorter 1993; Coviella & Trumble 1998), and may respond differently to CO_2 treatments (Campbell *et al.* 1995; Drake & Gonzales-Meler 1997; Collatz *et al.* 1998; Wand *et al.* 1999). The C_3 species at our site appeared to be more competitive for light, water and nutrients, regardless of CO_2 treatment. These characteristics led to an alteration in the C_3 and C_4 dominance hierarchy that manifested itself, over time, as a consistent decline in the proportion of C_4 species relative to C_3 species (Fig. 5). Among C_4 species, only *S. halapense*, a grass species that possesses many competitive attributes such as early growth and tallness, appeared to proliferate. Some of the highest CO_2 fluxes in both years occurred at 397 μmol mol^{-1}, where vegetation has maintained a consistently high and stable proportion of percentage C_3 cover (section 9, Fig. 5) and where the dominant C_3 species *Lippia nodiflora* (L.) Michx. (frogfruit) and *R. columnifera* changed little over time.

Accounting for differences in C_3 composition improved the fit of the relationship between CO_2 flux

and CO_2 concentration (Fig. 6). The relatively strong relationship between adjusted flux and CO_2 concentration at subambient concentrations suggests fluxes at these concentrations may have been limited by atmospheric CO_2.

The variability in species composition at this site is not unusual and reflects conditions often found in natural grasslands (Hungate *et al*. 1997a, 1997b; Reynolds *et al*. 1997; Braakhekke & Hooftman 1999) and probably in other ecosystems as well. Some of the variation in vegetation in this experiment could have resulted from CO_2 treatment as well as site history. The relationship between ecosystem CO_2 fluxes and CO_2 concentration differed from that of leaf-level fluxes and CO_2 treatment. Anderson *et al*. (2001) found a positive, linear photosynthetic response of leaves of 3 species to CO_2 over subambient to superambient concentrations. Canopy level flux measurements cannot, however, detect a species-specific response to CO_2 treatment. Thus, canopy fluxes may have been influenced by a disproportionate response of a few, highly responsive species (Navas 1998). Nevertheless, these results clearly illustrate that one must use caution when scaling up results from CO_2 experiments at the leaf- or single-plant level to intact, multi-species ecosystems.

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