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ECOSYSTEMS

Primary Productivity and Water Balance of Grassland Vegetation on Three Soils in a Continuous CO_2 Gradient: Initial Results from the Lysimeter CO_2 Gradient Experiment

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ABSTRACT

Field studies of atmospheric CO_2 effects on ecosystems usually include few levels of CO_2 and a single soil type, making it difficult to ascertain the shape of responses to increasing CO_2 or to generalize across soil types. The Lysimeter CO_2 Gradient (LYCOG) chambers were constructed to maintain a linear gradient of atmospheric CO_2 ($\sim$250 to 500 $\mu l\ l^{-1}$) on grassland vegetation established on intact soil monoliths from three soil series. The chambers maintained a linear daytime CO_2 gradient from 263 $\mu l\ l^{-1}$ at the subambient end of the gradient to 502 $\mu l\ l^{-1}$ at the superambient end, as well as a linear nighttime CO_2 gradient. Temperature variation within the chambers affected aboveground biomass and evapotranspiration, but the effects of temperature were small compared to the expected effects of CO_2. Aboveground biomass on Austin soils was 40% less than on Bastrop and Houston soils. Biomass differences between soils resulted from variation in biomass of *Sorghastrum nutans, Bouteloua curtipendula, Schizachyrium scoparium* (C_4 grasses), and *Solidago canadensis* (C_3 forb), suggesting the CO_2 sensitivity of these species may differ among soils. Evapotranspiration did not differ among the soils, but the CO_2 sensitivity of leaf-level photosynthesis and water use efficiency in *S. canadensis* was greater on Houston and Bastrop than on Austin soils, whereas the CO_2 sensitivity of soil CO_2 efflux was greater on Bastrop soils than on Austin or Houston soils. The effects of soil type on CO_2 sensitivity may be smaller for some processes that are tightly coupled to microclimate. LYCOG is useful for discerning the effects of soil type on the CO_2 sensitivity of ecosystem function in grasslands.

Key words: carbon dioxide; climate change; grassland; hydrology; net primary productivity; photosynthesis; soil moisture; soil respiration; *Solidago canadensis*.

INTRODUCTION

Atmospheric CO_2 concentration (C_A) has increased by about 100 $\mu l\ l^{-1}$ over the last 250 years to approximately 380 $\mu l\ l^{-1}$, its highest value since

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the pre-industrial era. Further, C_A has increased more quickly in the last 30 years than in the prior 200 years (Forster and others 2007). Increasing C_A affects many ecosystem processes. Typically, field studies have examined only two or a few experimental levels of C_A, making it difficult to detect the presence of non-linear or threshold responses to C_A. These field experiments also have typically been constrained to one soil type. However, CO_2 change is continuous, and soils differ in hydrologic and biogeochemical properties that can constrain ecosystem responses to increasing C_A. For example, soil texture mediates the distribution of water in the soil profile (Noy-Meir 1973), its availability to plants (Brady and Weil 2002), the availability of organic substrates to decomposers (Jenkinson 1977; Oades 1988), and the accumulation of organic matter (Hassink 1996). Therefore, the impacts of multiple levels of C_A on ecosystem function must be understood on different soil types to resolve the shape of ecosystem productivity, carbon cycling, and community structure as a function of C_A, to understand variation in these and other responses across soils, and ultimately to predict spatial variation in ecosystem structure and function under future climate scenarios (Ainsworth and Long 2005; Rogers and others 2006).

The Lysimeter CO_2 Gradient (LYCOG) facility was constructed to impose a continuous gradient of C_A representing pre-industrial to mid twenty-first century levels ($\sim$250 to 500 $\mu l\ l^{-1}$) on multiple soil types. LYCOG consists of outdoor chambers suited for grassland or other short-statured ($\leq \sim$1 m tall) vegetation. The design objectives were to maintain the prescribed gradient in C_A while also controlling air temperature (T_A) and precipitation inputs near ambient values. LYCOG evolved from previous C_A gradient systems (Mayeux and others 1993; Johnson and others 2000) but incorporates several new features, (1) intact, hydrologically isolated soil monoliths from three soil series initially planted to the same species of native perennial grasses and forbs, (2) weighing lysimeters, and (3) a system to sample drainage water exiting the bottom of the monoliths. These features allow more precise evaluation of soil type effects on ecosystem processes and resolution of the effect of CO_2 on the water and carbon budgets of these soils than would be possible in field plots.

Here our objectives are to (1) review the lineage of CO_2 gradient facilities that led to the LYCOG facility and the major results each provided, (2) document chamber function in terms of control of CO_2 and air temperature, (3) quantify the pre-CO_2 treatment plant species assemblages and soil C and N concentrations, (4) evaluate preliminary responses to C_A in aboveground net primary productivity, leaf photosynthesis, soil respiration, and the ecosystem water budget.

PREVIOUS CO_2 GRADIENT FACILITIES

LYCOG is the third generation of CO_2 gradient facilities. It was preceded by a prototype gradient experiment that established the viability of the technique, and then by a field facility. All three CO_2 gradient facilities rely on the simple concept that sunlit plants photosynthesizing in an enclosed linear chamber will deplete CO_2 from parcels of air moving directionally through the chamber. This linear chamber approach results in continuously varying C_A, and a unique capacity to evaluate plants and soils for linear, non-linear, and threshold responses to changing C_A.

Prototype Subambient to Ambient Gradient

Mayeux and others (1993) constructed the first CO_2 gradient facility at the USDA laboratory at Temple, Texas, USA. It consisted of a 38 m long × 45 cm wide serpentine chamber constructed in a greenhouse. The upper portion of the chamber was a clear polyethylene tube enclosing the aerial growth of plants, fixed to a 76 cm deep lower portion filled with soil. The chamber was supplied with ambient air, which during daylight was depleted to approximately 200 $\mu l\ l^{-1}$. Air temperature was controlled by a system of chilled water cooling coils and electrical resistance heaters. The system was well suited for leaf-level physiological studies of plant responses to subambient variation in CO_2 concentrations.

Monocultures and simple mixtures of species including *Triticum aestivum*, *Avena sativa*, *Brassica kaber, and Schizachyrium scoparium* were successfully grown in this chamber to examine the effects of increases in C_A from subambient to ambient values on vegetation function. Most species examined showed increases in total biomass, photosynthetic carbon assimilation, water and nitrogen use efficiencies, and decreased stomatal conductance in C_4 species (Polley and others 1992a, 1992b, 1993a, 1993b, 1994, 1995, 1996). These results suggested that sizeable changes in ecosystem function and plant growth may already have occurred in response to rising C_A, including increased vegetation productivity (Johnson and others 1993; Polley and others 1993a) and increased growth of woody species over dominant grasses (Polley and others

1994) because of reduced water limitation (Polley and others 1995).

The Prairie CO_2 Gradient (PCG)

The PCG facility was the first field implementation of a self-maintaining CO_2 gradient, on perennial C_4 grassland at Temple, Texas, USA (31°05′ N, 97°20′ W). Advancements of PCG over the greenhouse prototype included (1) extension of the gradient to superambient concentrations, (2) a nighttime C_A gradient, created by reversing the direction of air flow, and allowing nighttime plant + soil respiration to progressively increase C_A. PCG achieved gradients of about 550–200 $\mu l\ l^{-1}$ during daytime, and approximately 720–370 $\mu l\ l^{-1}$ at night using two linear chambers enclosing 100 linear m of intact grassland (Johnson and others 2000).

PCG's subambient to superambient gradient allowed for evaluation of the shape (linear or nonlinear) of ecosystem responses under conditions representing a continuum from past to future C_A. Responses varied among the ecosystem processes that were studied. For example, plant water status, leaf carbon assimilation and water use efficiency increased linearly across the gradient (Anderson and others 2001). However, during the 4 years of the PCG study, aboveground net primary productivity increased linearly with C_A in some years, but the increase was nonlinear in others, showing less increase at superambient C_A (Polley and others 2003). Soil organic carbon content also increased from subambient to ambient C_A but not beyond, and decomposition of older soil C increased at superambient C_A, whereas N mineralization rates decreased (Gill and others 2002). These results were consistent with N limitation of ANPP at above-ambient C_A. Together, the studies from the PCG facility suggested that linear increases in plant water status or productivity may not translate into increased soil C if N or other resources limit ecosystem function (Gill and others 2006).

The Lysimeter CO_2 Gradient (LYCOG)

LYCOG is the second field implementation of a self-maintaining CO_2 gradient. LYCOG built on PCG by incorporating multiple soils and the capacity to completely close ecosystem water budgets. The overarching goal of LYCOG is to test the hypothesis that soil properties will influence, and could even override, the effects of C_A on NPP, decomposition (Epstein and others 2002; Jenkinson 1977; Oades 1988), C accumulation in soil (Hagedorn and others 2003), and plant community structure among other processes.

METHODS

Study Site

LYCOG is located on the same site as PCG. The original native vegetation was Blackland Prairie, which is the southern extension of the North American tallgrass prairie. Intact Blackland Prairie plant communities are dominated by C_4 grasses accounting for most of the biomass, accompanied by numerous forb species. Less than 5% of this ecosystem remains in Central Texas, but it is an important benchmark for the structure and function of the diverse native grassland ecosystems in this region. The climate is classified as subtropical, and LYCOG is in an area of transition between humid and sub-humid zones. Mean annual precipitation is 914 mm (1971–2000), falling in a bimodal distribution with growing season wet periods in May–June and September–October, and a pronounced July–August dry period. Precipitation patterns are governed by interactions between onshore flows of tropical maritime air from the Gulf of Mexico and colder continental air masses. Temperatures range from a July–August mean maximum of 35°C to a December mean minimum of 2.9°C. The mean frost free period is approximately 250 days, from mid March to late November.

Chamber Design

LYCOG uses the aboveground chamber, CO_2 enrichment, temperature control, and monitoring systems from PCG to enclose a CO_2 gradient over intact soil monoliths. There are again two linear chambers, arranged in parallel on a north–south axis (Figure 1). Each chamber is 1.2 m wide, 1.5 m tall, and 60 m long, divided into 10–5 m long sections. Each section houses a steel container $5 \times 1.2 \times 1.6\ m^3$ deep buried to 1.5 m. Each container accommodates four 1 × 1 × 1.5 m deep intact soil monoliths housed in water-tight steel boxes (Polley and others 2008). Adjacent containers are joined by a 1-m sheet-metal plenum housing a chilled-water cooling coil. The coils are supplied by a 161.4 kW refrigeration unit that circulates coolant at 10°C.

Eighty intact soil monoliths were excavated in 2002 from three soil series: Houston Black clay (32 monoliths), a vertisol (Udic Haplustert) typical of lowlands; Austin (32 monoliths), a high carbonate, silty clay mollisol (Udorthentic Haplustol) typical of

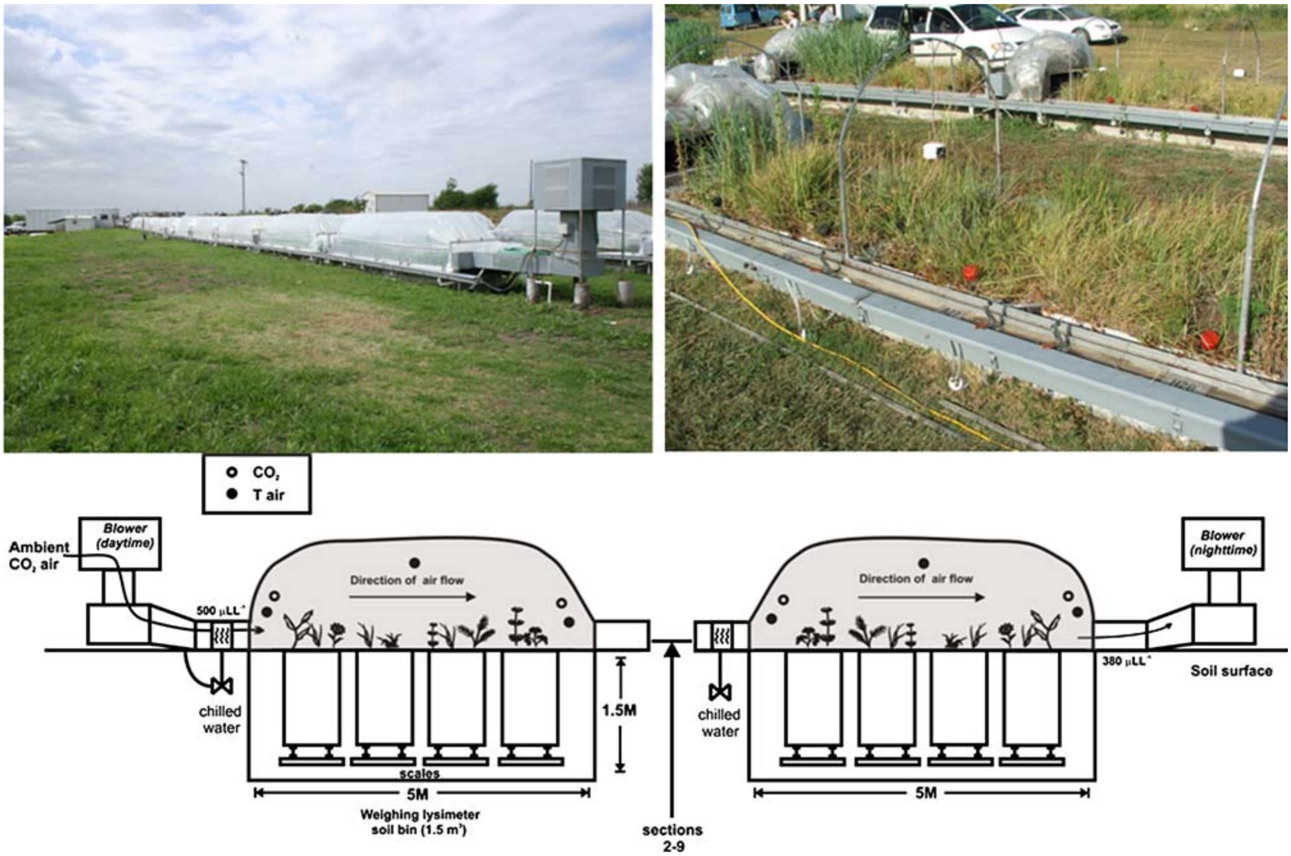

Figure 1. The LYCOG facility for maintaining a continuous gradient of atmospheric CO_2 concentration on vegetation growing in enclosed soil monoliths. View of the superambient chamber looking from the daytime air exit toward the chamber entrance. The white building at left houses the monitoring, control, and data logging equipment. The subambient chamber runs parallel to the superambient chamber, and is mostly obscured in this view (*Upper left*). One 5-m section of the superambient chamber (*Upper right*). Schematic of the entry (Section 1) and exit (Section 10) sections on the superambient chamber, depicting weighing lysimeters and scales, placement of CO_2, temperature, and dew point monitoring locations, and the inputs for controlling the CO_2 gradient and air temperature (*Lower*).

uplands, and Bastrop (16 monoliths), an alluvial sandy loam alfisol (Udic Paleustalf). These soils were chosen because they represent the broad range of texture, N and C content, and hydrologic properties of grasslands in the southern portion of the U.S. Central Plains. Two monoliths each of two of the soil types were placed randomly in each of the 20 containers. Bastrop soils were included in the pairings in even numbered sections. Sixty of the 80 monoliths (all Bastrop, 22 each of Austin and Houston) are weighed continuously on scales (4500 kg capacity, 450 g precision; Avery Weigh-Tronix, Fairmont, Minnesota, USA). The remaining monoliths serve as non-weighing lysimeters. Water that has drained to the bottom of the monoliths is channeled through a fiberglass wick into a 10 l reservoir attached to the bottom of each steel box. The reservoir is connected to a drainage water measurement system. A vacuum extracts each reservoir's contents for gravimetric determination of drainage volume and for collection of a water sample.

The vegetation is enclosed with clear polyethylene (.006″/.15 mm; Figure 1). This film transmits more than 90% of incident light with minimal effects on spectral quality, and is similar to polyethylene films used in other global change experiments (Fay and others 2003). The polyethylene is fitted with zippers backed by draft flaps to allow access to the monoliths for sampling. The polyethylene is replaced at the beginning of each growing season to minimize the effects of photodegradation on light transmittance. The polyethylene is removed during winter and the vegetation is exposed to ambient conditions.

CO_2 Treatment

There were three treatment objectives. (1) Maintain a constant linear daytime gradient in C_A from

500 to 380 µl l^{-1} in the superambient chamber, and from 380 to 250 µl l^{-1} in the subambient chamber (nighttime: ~720–500 and 500–380 µl l^{-1}, respectively), (2) maintain constant T_A along the length of the chambers and track the daytime ambient air temperature outside the chambers, and (3) provide precipitation inputs representative of an average year in total amount and seasonal distribution. The CO_2 treatment was first applied in May 2006, and is applied for that portion of each growing season when the photosynthetic capacity of the vegetation is adequate to maintain the C_A gradient, usually late April to early November. CO_2 treatments were applied with a system consisting of infrared gas analyzers (IRGAs; Li 6262, LiCor Biosciences, Lincoln, Nebraska, USA), filtered air sample lines at the entry and exit of each linear 50 m chamber, a quantum sensor for measuring ambient photosynthetic photon flux (PFD) densities, and a mass flow controller for injecting precise volumes of CO_2 at the superambient chamber entrance. The gradient endpoints were controlled by measuring chamber entry and exit C_A at 2-min intervals. At the entrance to the superambient chamber, the mass flow controller adds the appropriate amount of pure CO_2 to enrich the incoming air to 500 µl l^{-1}. The enriched air is advected through the chamber by a blower fan mounted at the entrance to section 1, supplemented by fans in sections 3, 5, and 7. The desired exit C_A (380 µl l^{-1}) is controlled by adjusting the blower speed. If the exit C_A is below the set point, blower speed is increased, resulting in less time for plant uptake and a higher exit C_A. Likewise, blower speed is decreased if exit C_A is above the set point. Fan speed is also continuously adjusted for diurnal and cloud-induced variation in PFD using inputs from the quantum sensor to an algorithm relating the direction and magnitude of PFD changes to the deviation in C_A from the set point. Air flow at the chamber entrance at maximum blower speed (800 rpm) is 380 l s^{-1}, decaying to 160 l s^{-1} (~0.5–0.2 m s^{-1}) at the chamber exit because of leaks and internal resistance. C_A and dew point temperature (T_{DP}) at the entry and exit of each section are measured on separate monitoring IRGAs and values stored at 20-min intervals. Nighttime control of C_A is identical to daytime control except the flow of air is reversed using nighttime blowers (Figure 1), CO_2 is injected into the opposite end of the superambient chamber, and nighttime respiration progressively increases C_A. The CO_2 treatment requires an external CO_2 source of approximately 3,700 l per month, a small supply requirement compared to other methods of ecosystem-level CO_2 manipulation, such as free air CO_2 exchange or open top chambers (Kimball 1992; Rogers and others 2006).

T_A is controlled so that the midpoint of each section tracks ambient air temperature. An aspirated thermistor is suspended mid-section at 0.75 m above the monoliths. The thermistor controls the flow of coolant through the cooling coil at the entrance of each section. Separate control of temperature in each section is necessary because evapotranspiration differs among sections, causing differences in energy balance. T_A at each section entry and exit is measured with shielded fine wire thermocouples.

Water from an onsite well is applied to the monoliths by a metered drip irrigation system in volumes and temporal patterns that replicate an average precipitation year. Applications are controlled and logged by a data logger and are verified by the measurements of monolith mass.

Pre-Treatment Soil Texture, C, and N

Soil texture was quantified using the rapid method of Kettler and others (2001) on 1 m deep × 4.2 cm diameter soil cores collected in 2002 during excavation of the monoliths. Soils from 0–10, 10–20, 20–30, 30–50, and 50–100 cm segments were homogenized, and 15 g of soil was suspended in 3% sodium hexametaphosphate. Sand was separated from the suspension by passage through a 0.05 mm sieve. The remaining material was resuspended and allowed to settle for 6 h. The supernatant containing suspended silt was discarded. Clay and sand fractions were weighed after drying to constant mass at 105°C. Silt mass was determined by difference, and all masses expressed as a percentage of the total mass. An additional 0.5–1.0 g of homogenized soil was analyzed at 900°C for total %N and %C and at 600°C for organic %C on a combustion gas chromatograph (Variomax CN, Elementar Instruments, Hanau, Germany).

Plant Establishment and Pre-Treatment Plant Biomass

To establish experimental plant communities on the three soils, the original vegetation on the monoliths was killed with a non-residual herbicide (glyphosate), and planted in spring 2003 with seedlings of perennial grass and forb species characteristic of Central Texas Blackland prairie. Eight plants of each of five grass species [*Bouteloua curtipendula* (side-oats grama), *Panicum obtusum* (vinemesquite), *Schizachyrium scoparium* (little bluestem), *Sorghastrum nutans* (Indiangrass), and *Tridens albescens* (white tridens)] and three forb species [*Salvia azurea* (pitcher sage), *Solidago canadensis* (Canada goldenrod), and the legume *Desmanthus illinoensis* (Illinois bundleflower)] were transplanted into each monolith at a total density of 64 plants per m^2 during May 2003. Seedlings were planted in a Latin Square design that was re-randomized for each monolith. Transplants were watered during the initial 2 months to promote establishment, but thereafter received only rainfall until CO_2 treatments began. Other species that emerged in the monoliths were removed. The grass *P. obtusum* proved to be highly aggressive and was removed in 2004 by cutting each plant beneath the crown. In addition, grubs (Coleoptera: Scarabaeidae) infested 20 monoliths of Houston and Austin soils. These were replanted in spring 2007 with well-watered and fertilized monocultures of *Panicum virgatum* (switchgrass) to maintain the assimilation capacity of the gradient, and to examine the response of this species to the C_A gradient. The *Panicum* monocultures are not considered further here.

Aboveground net primary productivity (ANPP) was measured each November. All current year growth of each species was clipped from the entire 1 m^2 monolith at 10 cm above the soil surface, dried to constant mass, and weighed. ANPP was measured similarly in subsequent years. Vertical profiles of volumetric soil water content (vSWC) in the top meter of each monolith were measured biweekly with a calibrated neutron attenuation probe (503DR Hydroprobe, CPN International, Concord, California, USA) in permanently installed access tubes. Soil temperature at 10 and 30 cm depth was measured with fine wire thermocouples in a total of 18 monoliths, pairs of each soil type at high, intermediate, and low C_A.

Monolith C and N pools were measured again after the 2005 growing season (early January 2006) prior to the CO_2 treatment and after the third growing season for the experimental plant communities. The monoliths were cored (1 m deep × 2.5 cm) and divided into 0–5, 5–10, 10–20, 20–30, 30–50, and 50–100 cm segments. Roots were separated from soil, dried to constant mass at 60°C, and weighed. Total %N, %C, and organic %C were measured as before.

Preliminary Responses to CO_2 Treatments

Leaf-level carbon and water exchange were measured on the forb *Solidago canadensis* and grass *Sorghastrum nutans* in 12 of the 20 sections, on one or two leaves on two plants per species per chamber section. The plants chosen had typical vigor for that soil type and CO_2, and the chosen leaves were recently fully expanded, and also of typical vigor. Leaves were measured for net carbon assimilation (A_{CO_2}) and transpiration rate (E) with an infrared gas analyzer (LI-6400 LiCor Biosciences, Inc., Lincoln, Nebraska, USA) using a 2 × 3 cm leaf cuvette, CO_2 mixer, and 85:15 red:blue light source. Leaf chamber illumination was controlled at 1500 $\mu mol\ m^{-2}\ s^{-1}$ photon flux density, leaf temperature at 30°C, and leaf cuvette H_2O mole fraction and $[CO_2]$ to the conditions maintained at that position along the gradient. The plants were measured on a day when the chamber was opened for monthly sampling (13 June 2007) during the period of rapid plant growth. In preliminary sampling, leaves (both species) measured with the chamber open and the leaf cuvette simulating closed chamber conditions gave readings indistinguishable from leaves measured with the chamber closed ($P = 0.10$–0.90). Surface (0–10 cm) volumetric soil water content (vSWC) during the gas exchange measurements was measured with a time domain reflectometry (TDR) probe (Fieldscout TDR 200, Spectrum Technologies, Plainfield, Illinois, USA). vSWC was computed from soil-specific calibrations.

Soil CO_2 efflux (J_{CO_2}) was also measured when the chambers were open (13 June 2007) on the 60 monoliths planted to mixtures of prairie species. J_{CO_2} was measured with a LiCor LI 6400 IRGA fitted with a soil respiration chamber. Two measurements were taken per monolith by placing the chamber on 10-cm deep PVC collars inserted in the soil to 7.5 cm depth. Each measurement was based on a 20 $\mu l\ l^{-1}$ change in CO_2 centered on ambient C_A. This technique provides an estimate of how combined root + microbial respiration differed among soils because of preceding CO_2 treatments. Rates were corrected for soil chamber insertion depth using SoilRecomp Version 1.3 software (LI-COR, Inc., Lincoln, Nebraska).

A water balance was tabulated for the month of May 2008, a period of rapid plant growth. Total irrigation inputs for this month were determined by summing the increases in monolith mass on the days when water was applied. Evapotranspiration (ET) was determined by summing the decreases in monolith mass on non-watering days. The portion of ET that was greater than irrigation inputs was classified as ET from storage, and represented depletion of prior soil moisture stores. Deep drainage was determined by summing the water removed from the reservoirs at the base of the monoliths during this period.

Data Analysis

C_A, T_A, and T_{DP} from mid April to early November 2007 were examined to characterize daytime (0830–1730) and nighttime (2100–0530) control of these parameters in the chambers. Vapor pressure deficit (VPD) was computed from T_A and T_{DP}. ANPP, ET (June 1–July 18 2006), 0–20 cm vSWC (neutron probe), and soil temperature at 10 and 30 cm were averaged by monolith position within the sections to evaluate their association with T_A variation within sections. The estimated effect of monolith position on ANPP was compared to the effect of CO_2 on ANPP by fitting a second order polynomial to the ANPP data, and then adjusting the resulting predicted ANPP curve for the effect of position within section on biomass.

Pre-treatment differences in aboveground biomass between soil types were evaluated for statistical significance using linear mixed model procedures with the monolith as the experimental unit. Soil type was a fixed effect, and species was considered a spatially repeated measure, because the species biomasses within a monolith are not independent. This enabled computation of a covariance matrix to determine correlations between species in biomass changes during establishment. Differences among soils in ET, leaf physiology, soil respiration, and 0–10 cm vSWC (TDR) were evaluated for statistical significance using linear mixed model procedures, again with the monolith as experimental unit, soil type as fixed effect, and C_A as a covariate. All analyses were conducted using SAS v9.1.3 (SAS Institute Inc. 2003).

RESULTS

Chamber Function: CO_2, Temperature, and VPD

Mean growing season daytime C_A was 502 µl l^{-1} at the entrance to the superambient chamber (target value 500 µl l^{-1}), declining to 370 µl l^{-1} at the exit (Figure 2A). Mean C_A of ambient air at the subambient entrance was 372 µl l^{-1}, declining to 263 µl l^{-1} at the subambient exit. The mean growing season daytime C_A gradient for the two chambers combined was linear ($R^2 = 0.99$, $P < 0.0001$), as was the mean growing season nighttime C_A gradient ($R^2 = 0.97$, $P < 0.0001$). Nighttime C_A averaged 143 µl l^{-1} greater than during daytime (Figure 2A), but with a slightly lower slope of C_A versus distance along chambers (nighttime = −1.8 µl l^{-1} m^{-1}; daytime = −2.1 µl l^{-1} m^{-1}).

There was day-to-day variability during the growing season in the mean C_A in both chambers, but 90% of the daily mean C_A values fell within 20–50 µl l^{-1} of the growing season mean (Figure 3A). Day-to-day variability in C_A was greater in the superambient chamber than in the subambient chamber. Variability at the superambient chamber entrance was greater than at the subambient chamber entrance. Variability in C_A increased with distance downstream in both chambers.

Mean growing season values of daytime T_A were 23–30°C at the entrance of each 5-m section (Figure 2B), and increased by 3–8°C (mean: 5.5 ± 0.4°C) within each section. The cooling coils at the exit of each 5-m section were generally effective at lowering T_A. As a result, the mean daytime temperature in each section tracked the mean ambient temperature (26.7°C) except in the last two sections of each chamber, which ran 2–4°C warmer. Mean nighttime T_A was essentially constant between 19 and 20°C in the superambient chamber (Figure 2B), and declined from 19 to 17°C along the subambient chamber. Daytime and nighttime VPD along the chambers showed the same pattern as their respective T_A values (Figure 2C).

The increased daytime T_A within each 5-m section was associated with lower 0–20 cm soil water content (12%) and aboveground biomass (20%), and higher T_{SOIL} (1.2–2.3°C) and ET (25%; $2.8 \leq F \leq 13.3$, $0.05 \geq P > 0.0001$, Table 1). However, the variation in biomass expected from within-section differences in T_A was small compared to the variation in biomass associated with soils or the C_A gradient (Figure 3B).

Pre-Treatment Soil Texture, C, and N

Houston soils were uniform in texture through the first meter of the profile, with 49–55% clay and 36–39% silt (Table 2). Austin soils were also uniform in texture, with higher silt (46–48%) than the Houston or Bastrop soils, and 40–45% clay. The Bastrop series showed more vertical variation in texture than the Austin or Houston soils, with 60–72% sand and 7–14% clay from 0 to 50 cm, but 48% sand and 26% clay from 50 to 100 cm.

The soils differed in total C, organic C, and total N when monoliths were collected in 2002 (Table 2). The Austin soils contained 8.2–8.7% total C, compared to 4.0–5.0% in the Houston soils and 0.2–0.8% in the Bastrop soils. Organic C was 0.4–2.0% for Austin, 1.0–2.4% for Houston, and 0.2–0.7% for Bastrop. Houston and Austin soils were higher in total N (0.03–0.21%), than the Bastrop soils

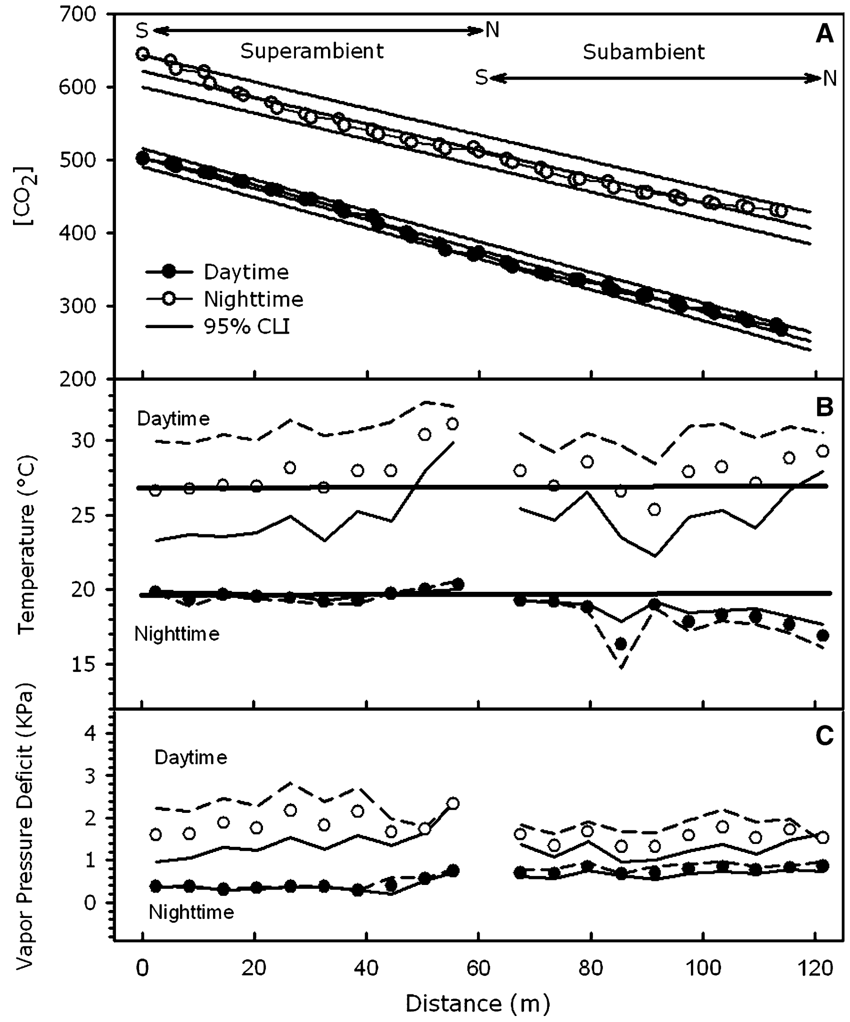

Figure 2. Gradients maintained in LYCOG superambient and subambient chambers during April–November, 2007. Daytime and nighttime, growing-season averages for **A** CO_2 concentration, **B** air temperature, and **C** vapor pressure deficit along the CO_2 gradient. In **B**, heavy *horizontal lines* denote ambient mean temperatures. In **B** and **C**, *solid lines* denote air temperature/VPD at the entrance of each 5-m section, and *dashed lines* the values at the exit of each 5-m section.

(0.02–0.08%). These C and N concentrations yielded a wide range of total C:N for these soil profiles, from 57 to 289 in the Austin profiles, to 4.8–9.6 in the Bastrop profiles. The C:N was much less variable for organic than total C, ranging from 5 to 10 in the Bastrop profiles, 12.5–14 in Austin profiles, and 11–20 in the Houston profiles.

Total C was essentially unchanged from 2002 to 2005, except for slight changes at 50–100 cm in Bastrop (a decrease) and Houston (an increase) soils ($.05 < P < .0001$, Table 2). Total % N declined from 2002 to 2005 by about 10% below 10 cm in Austin soils, but was unchanged in Bastrop and Houston profiles. Organic C below 10 cm depth decreased from 2002 to 2005 in Austin and Bastrop soils. The Austin soils had larger increases in C:N with depth compared to Bastrop and Houston profiles, reflecting greater decreases in total N with depth. There were no systematic changes from 2002 to 2005 in OC:N in the profiles.

Pre-Treatment Plant Biomass

After 3 years of plant establishment and growth, the soils differed in above and belowground biomass. Austin soils supported less aboveground biomass, 235 g m^{-2}, compared to 380–405 g m^{-2} on Bastrop and Houston soils (Table 3, Figure 4A). Soils also differed in 0–30 cm root biomass, but differences diminished with depth. vSWC differed among the soils, with highest vSWC in the Houston soil (35–39%) and intermediate vSWC in Austin soils (30%), both with little vertical variation. Bastrop soil had considerably lower vSWC throughout the profile (11–26%), especially in the top 40 cm of the profile (Table 3; Figure 4A).

The biomass of individual species differed among the three soils prior to CO_2 treatment (Table 3). *Sorghastrum nutans* was strongly dominant on Bastrop and Houston soils (Table 4), whereas *Solidago canadensis* and *S. nutans* were co-dominant on the

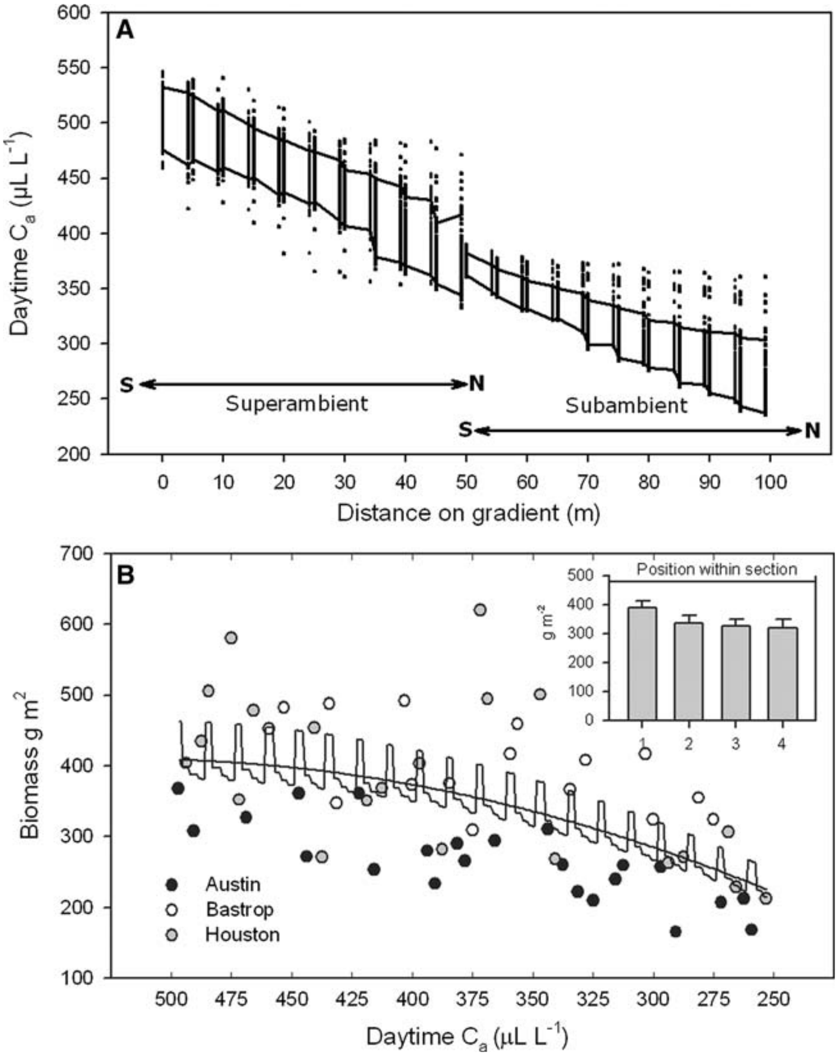

Figure 3. **A** Variability in daytime C_A in LYCOG during 2007. Each point marks 1 day's mean C_A for each sample point along the chambers. *Lines* represent 5th and 95th percentiles of daily mean C_A **B** Aboveground biomass for individual monoliths versus distance along the gradient, a proxy of C_A. Each point is the mean of 2006 and 2007. The *smooth line* represents the predicted biomass from regression analysis. The *varying line* represents the predicted biomass adjusted for the effect of T_A on biomass at each monolith position (inset).

Table 1. Biomass, Evapotranspiration, Soil Water Content, and Soil Temperature Within Chamber Sections

Position in section	Aboveground biomass (g m^{-2})*	ET (mm $H_2O\ d^{-1}$)*	Soil water content (% vol)*	T_{soil} 10 cm (°C)*	T_{soil} 30 cm (°C)*
1 (Entrance)	394.4 ± 19.6	3.66 ± 0.13	29.4 ± (0.4)	22.7 ± (0.4)	21.9 ± (0.3)
2	344.8 ± 21.7	4.26 ± 0.14	27.9 ± (0.4)	23.9 ± (0.4)	22.6 ± (0.2)
3	348.8 ± 20.2	4.50 ± 0.13	27.0 ± (0.4)	23.3 ± (0.6)	23.4 ± (0.3)
4 (Exit)	312.1 ± 21.2	4.56 ± 0.14	25.8 ± (0.4)	25.0 ± (0.5)	23.1 ± (0.3)
Effect	*F* (*P*)	*F* (*P*)	*F* (*P*)	*F* (*P*)	*F* (*P*)
Position	2.8 (0.05)	9.5 (<0.0001)	13.3 (<0.0001)	4.2 (0.02)	5.7 (0.009)
Soil	20.2 (<0.0001)	22.1 (<0.0001)	868.4 (<0.0001)	–	–
P × S	1.2 (ns)	1.6 (ns)	2.2 (0.06)	–	–

**Means ± 1 SE.*

less productive Austin soil. The covariance matrix of species biomass suggested there were negative associations among several species. The strongest negative covariance was between *S. nutans* and *S. canadensis* (Figure 4B), indicating that an increase in *S. nutans* was strongly associated with a

Table 2. Depth Profiles of Soil Texture and C and N in 2002 and 2005

2002

Depth (cm)	% Sand (se)	% Silt (se)	% Clay (se)	Total C, % (se)	Organic C, % (se)	Total N, % (se)	C:N	OC:N
Austin								
0–10	12.2 (0.4)	45.9 (0.7)	41.9 (0.6)	8.55 (0.08)	1.98 (0.04)	0.15 (0.01)	57.0	13.2
10–20	10.6 (0.4)	44.1 (0.7)	45.3 (0.7)	8.18 (0.14)	1.37 (0.03)*	0.11 (0.003)[†]	75.3	12.5
20–30	11.4 (0.6)	45.7 (0.9)	42.9 (0.9)	8.44 (0.17)*	0.99 (0.03)*	0.07 (0.003)**	124.3	14.1
30–50	11.9 (0.8)	46.3 (1.1)	41.8 (1.1)	8.69 (0.11)	0.69 (0.03)**	0.05 (0.002)[‡]	179.6	13.8
50–100	11.7 (0.7)	48.4 (1.3)	39.9 (1.6)	8.66 (0.09)	0.41 (0.03)**	0.03 (0.002)**	289.0	13.7
Bastrop								
0–10	72.8 (0.6)	19.7 (0.4)	7.5 (0.4)	0.77 (0.06)	0.71 (0.06)	0.08 (0.006)	9.6	8.8
10–20	70.2 (1.4)	22.9 (0.8)	6.8 (0.5)	0.35 (0.02)	0.36 (0.01)*	0.04 (0.005)	8.0	9.0
20–30	65.7 (0.2)	25.9 (0.3)	8.3 (0.4)	0.19 (0.01)	0.21 (0.01)	0.02 (0.002)	9.0	10.5
30–50	60.2 (2.8)	25.7 (0.7)	14.0 (3.3)	0.17 (0.01)	0.18 (0.02)*	0.03 (0.007)	5.0	6.0
50–100	48.2 (0.9)	25.7 (1.8)	26.1 (2.3)	0.21 (0.01)**	0.21 (0.02)[†]	0.04 (0.004)	4.8	5.3
Houston								
0–10	11.2 (0.5)	39.5 (1.0)	49.2 (1.2)	5.05 (0.16)	2.38 (0.07)	0.21 (0.009)	26.6	11.3
10–20	10.2 (0.9)	38.8 (1.0)	51.0 (1.7)	4.49 (0.13)	1.77 (0.03)	0.13 (0.005)	35.2	13.6
20–30	9.3 (0.8)	37.0 (1.0)	53.6 (1.1)	4.23 (0.16)	1.52 (0.04)	0.10 (0.005)	44.1	15.2
30–50	9.5 (0.8)	35.5 (0.9)	54.9 (0.9)	4.09 (0.05)	1.32 (0.05)	0.08 (0.004)	51.5	16.5
50–100	8.8 (1.0)	35.7 (0.8)	55.4 (0.7)	3.98 (0.05)**	0.99 (0.08)	0.05 (0.004)	81.4	19.8

2005

Depth (cm)	Total C, % (se)	Organic C, % (se)	Total N, % (se)	C:N	OC:N	Root mass, mg cm^{-3} (se)
Austin						
0–5	8.60 (0.16)	2.43 (0.11)	0.20 (0.01)	43.0	12.2	41.91 (7.45)
5–10	8.31 (0.10)	1.72 (0.05)	0.14 (0.006)	59.3	12.3	24.92 (3.21)
10–20	8.28 (0.10)	1.20 (0.03)	0.09 (0.004)	92.0	13.3	14.70 (1.41)
20–30	8.70 (0.14)	0.83 (0.04)	0.06 (0.003)	145	13.8	11.58 (1.49)
30–50	8.99 (0.08)	0.55 (0.03)	0.04 (0.002)	224	13.8	8.58 (0.80)
50–100	8.67 (0.06)	0.31 (0.05)	0.03 (0.002)	289	10.3	4.70 (0.56)
Bastrop						
0–5	1.15 (0.22)	1.17 (0.15)	0.11 (0.02)	13.7	10.6	77.61 (11.79)
5–10	0.49 (0.14)	0.47 (0.07)	0.05 (0.005)	6.1	9.4	30.25 (4.23)
10–20	0.32 (0.14)	0.31 (0.04)	0.03 (0.003)	10.3	10.3	19.94 (2.43)
20–30	0.18 (0.19)	0.17 (0.05)	0.02 (0.002)	9.0	8.5	11.84 (1.69)
30–50	0.15 (0.11)	0.14 (0.04)	0.02 (0.003)	2.5	7.0	8.99 (1.19)
50–100	0.19 (0.008)	0.18 (0.06)	0.04 (0.002)	4.8	4.5	5.90 (0.88)
Houston						
0–5	5.92 (0.16)	3.12 (0.11)	0.28 (0.01)	21.1	11.1	99.74 (21.65)
5–10	4.94 (0.10)	2.10 (0.05)	0.17 (0.008)	29.0	12.4	43.00 (4.82)
10–20	4.57 (0.10)	1.70 (0.03)	0.12 (0.004)	38.1	14.2	25.58 (2.21)
20–30	4.41 (0.14)	1.58 (0.04)	0.10 (0.005)	44.3	15.8	15.79 (1.74)
30–50	4.12 (0.08)	1.32 (0.03)	0.08 (0.003)	51.5	16.5	10.35 (0.86)
50–100	4.07 (0.06)	1.11 (0.05)	0.05 (0.002)	81.6	22.2	4.57 (0.47)

**$P \leq 0.05$, **$P \leq 0.01$, [†]$P \leq 0.001$, [‡]$P \leq 0.0001$ from paired t-tests of monoliths sampled in both 2002 and 2005.*

decrease in *S. canadensis*. This negative association was apparent in the biomass values (Table 4). On Bastrop and Houston soils the biomass of *S. canadensis* was relatively low compared to *S. nutans*, and on Austin soils *S. canadensis* biomass increased compared to *S. nutans*. Sizeable negative covariances were also found between *Schizachyrium scoparium* and both *S. nutans* and *S. canadensis*, and between *Bouteloua curtipendula* and *S. nutans*. Covariances near zero for the forbs *Tridens albescens*,

Table 3. Analysis of Variance Statistics for Aboveground and Root Biomass, Soil Water Content, Leaf Gas Exchange, Soil CO_2 Efflux, and Monolith Water Balance

Response	Effect	df	*F*	*P*-value
Aboveground biomass	Soil	2,77	67.1	<0.0001
	Species	6,72	613.3	<0.0001
	Soil × species	12,109	25.5	<0.0001
Root biomass (0–30 cm)	Soil	2,75	7.6	0.001
Soil water content (neutron probe)	Soil	2,77	832.4	<0.0001
	Depth	4,308	250.9	<0.0001
	Soil × depth	8,308	88.9	<0.0001
Solidago canadensis				
A_{CO_2}	Soil	2,12	1.30	0.3079
	Soil × C_A	3,12	5.58	0.0124
WUE	Soil	2,12	0.80	0.4711
	Soil × C_A	3,12	10.20	0.0013
Sorghastrum nutans				
A_{CO_2}	Soil	2,15	1.08	0.3658
	Soil × C_A	3,15	0.74	0.5437
WUE	Soil	2,15	1.46	0.2636
	Soil × C_A	3,15	1.62	0.2260
Soil water content (0–10 cm, TDR)	Soil	2,26	5.93	0.0076
	Soil × C_A	3,26	7.65	0.0008
Soil CO_2 efflux	Soil	2,54	3.03	0.0567
	Soil × C_A	3,54	3.18	0.0312
Evapotranspiration	Soil	2,37	10.20	0.0003
	Soil × C_A	1,37	6.18	0.0175
Storage loss	Soil	2,37	10.08	0.0003
	Soil × C_A	1,37	4.32	0.0446

Salvia azurea, and *Desmanthus illinoensis* indicated that variation among monoliths in biomass in these species was unrelated to the biomass of the other species.

Preliminary Plant and Soil Responses to CO_2

For *S. canadensis*, leaf A_{CO_2} and water use efficiency (WUE) increased at higher C_A (Figure 5A, B). The C_A sensitivity of A_{CO_2} and WUE in *S. canadensis* was greater on Houston and Bastrop than on Austin soils (Table 3). However, there was no significant main effect of soil type on A_{CO_2} or WUE. For *S. nutans*, there were no significant effects of soil type or C_A on A_{CO_2} or WUE. vSWC was lower in Bastrop than in Austin or Houston soils (Table 3, Figure 5C) and increased more with C_A on Austin than on Houston or Bastrop soils. Soil CO_2 efflux was 32% greater on Houston than on Austin or Bastrop soils (Table 3, Figure 5D), however, efflux increased with C_A more on Bastrop soils.

ET during May 2008 averaged 109 mm on Houston soils, compared to 91 mm on the Austin and Bastrop soils (Table 3, Figure 6). ET was 46 mm greater than irrigation on the Houston soils, and 26 mm greater on Austin and Bastrop soils, indicating that ET depleted previously stored soil water. ET from storage was correlated with changes in monolith soil moisture measured with the neutron probe ($R^2 = 0.73$, $P < 0.0001$). Both total ET and ET from storage increased with higher C_A (Table 3; Figure 6). The effects of C_A on ET and storage did not differ between soils ($P \geq 0.88$). Mean drainage from the monoliths was 1.39 ± 0.37 mm (max = 9.20 mm), which was a negligible portion of the water budget. Irrigation inputs to the monoliths averaged about 64 mm during May 2008 (Figure 6).

DISCUSSION

LYCOG extends the CO_2 gradient approach of Mayeux and others (1993) and Johnson and others (2000) to multiple soil types and allows for closure of monolith water budgets. Preliminary results support the hypothesis that soil properties will influence the effects of C_A on the productivity, soil CO_2 efflux, hydrology, and plant species composition of these grassland monoliths.

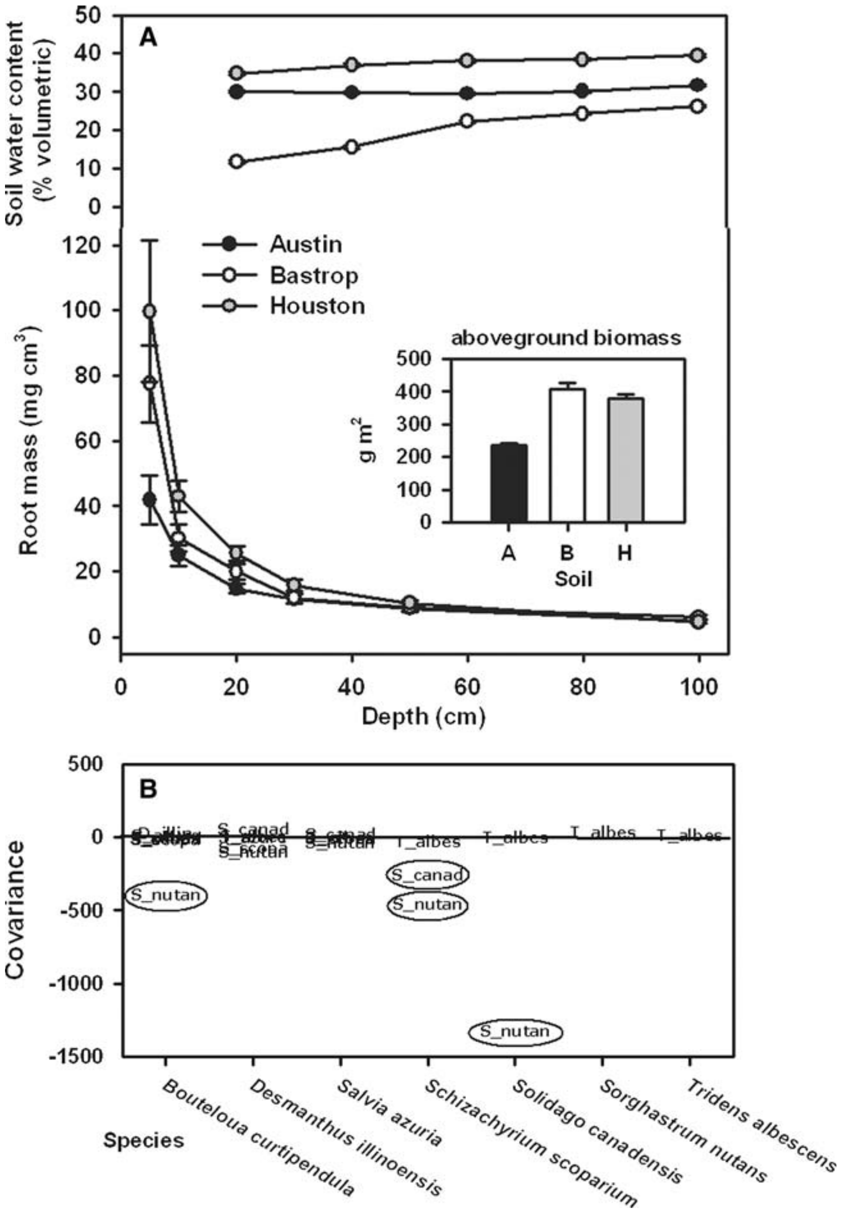

Figure 4. Soil moisture and plant biomass on the three soils in LYCOG following the 2005 growing season, after 3 years of growth in ambient conditions and prior to CO_2 treatment. **A** Mean growing season volumetric soil water content (neutron probe; SE falls within the symbols) and root mass mean ± 1 SE for the top 1 m of the soil profile; Inset: total aboveground biomass. **B** Covariance for species pairs in monolith-to-monolith variation in biomass.

Chamber Function

A goal of global change field experiments is to simulate the desired factor while minimizing confounding changes in other factors (Dunne and others 2004). LYCOG achieved the objective of linear daytime and nighttime C_A gradients. The system performed similarly to the Phase II version of the experiment, which used the same aboveground infrastructure and CO_2 monitoring and control systems (Johnson and others 2000). There were two main artifacts of the system noted in this study. First, day-to-day variability in mean C_A increased with distance along each chamber. This is due to the directional flow concept used in LYCOG, where upstream disturbances to C_A travel downstream, and may be magnified by subsequent downstream disturbances. C_A variation measured at the subambient chamber entry was caused by day-to-day variability in ambient C_A. Ambient C_A varies with soil moisture, temperature, and light because of their effects on photosynthesis. Variation in C_A entering the superambient chamber results primarily from variation in the function of the mass flow controller that regulates CO_2 injection. Factors contributing additional variability downstream may include patchy light levels due to partial cloud cover, illuminating some part of the 50 m chambers more than other parts, and opening chamber sections for sampling or maintenance. The second

Table 4. Mean Aboveground Biomass by Species in LYCOG After the 2005 Growing Season

Soil	Species	Aboveground biomass, g m^{-2} (SE)
Austin	*Solidago canadensis*	66.86 (5.87)
	Sorghastrum nutans	60.61 (9.95)
	Bouteloua curtipendula	54.43 (5.16)
	Schizachyrium scoparium	44.01 (5.76)
	Desmanthus illinoensis	7.49 (1.83)
	Salvia azurea	1.99 (0.43)
	Tridens albescens	1.41 (0.59)
	Total	236.79 (6.66)
Bastrop	*Sorghastrum nutans*	214.28 (23.22)
	Schizachyrium scoparium	104.65 (12.14)
	Solidago canadensis	70.78 (7.75)
	Bouteloua curtipendula	8.31 (1.42)
	Desmanthus illinoensis	7.97 (1.64)
	Salvia azurea	0.76 (0.23)
	Tridens albescens	0.13 (0.13)
	Total	406.88 (19.40)
Houston	*Sorghastrum nutans*	182.51 (14.54)
	Solidago canadensis	107.32 (5.77)
	Schizachyrium scoparium	39.13 (3.85)
	Desmanthus illinoensis	26.69 (3.20)
	Bouteloua curtipendula	19.30 (2.59)
	Tridens albescens	4.31 (0.92)
	Salvia azurea	0.40 (0.28)
	Total	379.65 (11.21)

artifact was the presence of within section daytime temperature gradients of about 1°C m^{-1}, similar to PCG (Johnson and others 2000). This rate of warming is greater than reported from other gradient facilities. For example, Rawson and others (1995) reported a temperature gradient of 0.6°C m^{-1} during midday full sun in their temperature gradient chamber, and Lee and others (2001) reported 0.25°C m^{-1}. Within section warming is greater on days with high radiation loads, and during periods of slow air flow caused by low photosynthetic rates (Johnson and others 2000). Within-section temperature variation was centered on ambient temperature except for the exit sections of the chambers, which trended warmer than the upstream sections.

Within-section warming measurably affected ET and aboveground biomass, but these effects were small compared to those of C_A and soil type (Figures 3, 4, and 6; Table 1). For example, previous CO_2 gradient studies found that decreasing C_A from 550 to 250 μl l^{-1} increased ET by 35% (Polley and others 2008), decreased aboveground biomass by up to 86% (Polley and others 2003) and decreased J_{CO_2} by 300% (Mielnick and others 2001). In contrast, an approximate 2°C increase in T_{SOIL} would cause a 15% increase in J_{CO_2}, assuming a Q_{10} of 2. Although a temperature gradient within sections of the chamber is not ideal, it should pose minimal problem in detecting and interpreting ecosystem effects of the C_A gradient, given that the temperature gradients are similar among 5-m sections in each chamber. Our primary interest is in comparing the averaged responses of monoliths within each section as a function of C_A and with

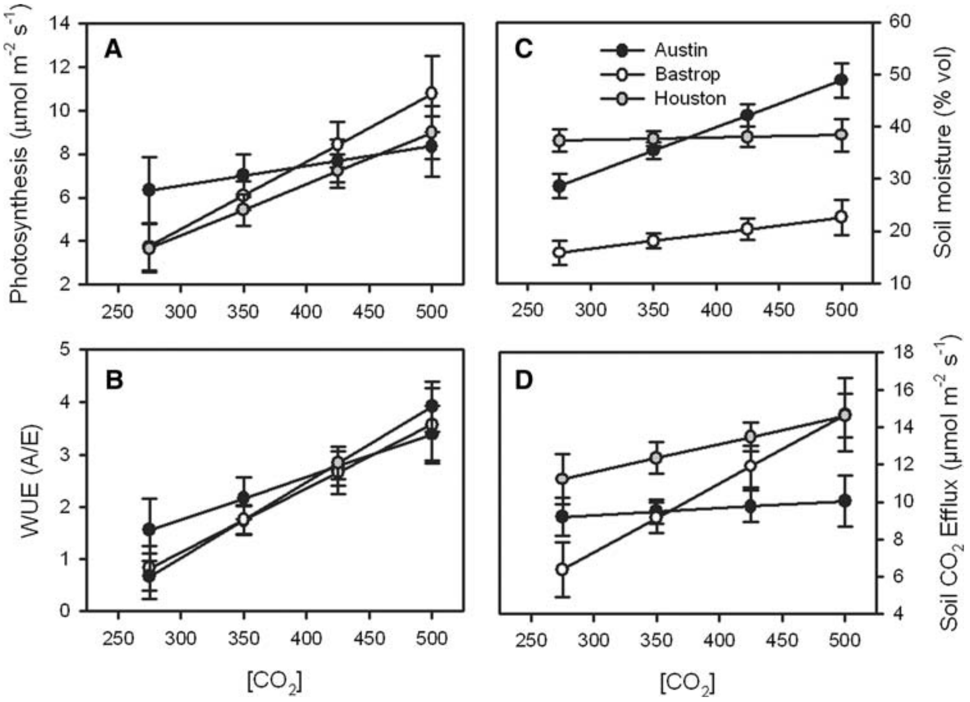

Figure 5. Leaf and soil responses to C_A on the three soil types in LYCOG. **A** Leaf carbon assimilation (A_{CO_2}), and **B** photosynthetic water use efficiency for *Solidago canadensis*. **C** 0–10 cm volumetric soil water content (vSWC) and **D** soil CO_2 efflux. Values are least squared means ± 1 SE from linear mixed models analysis.

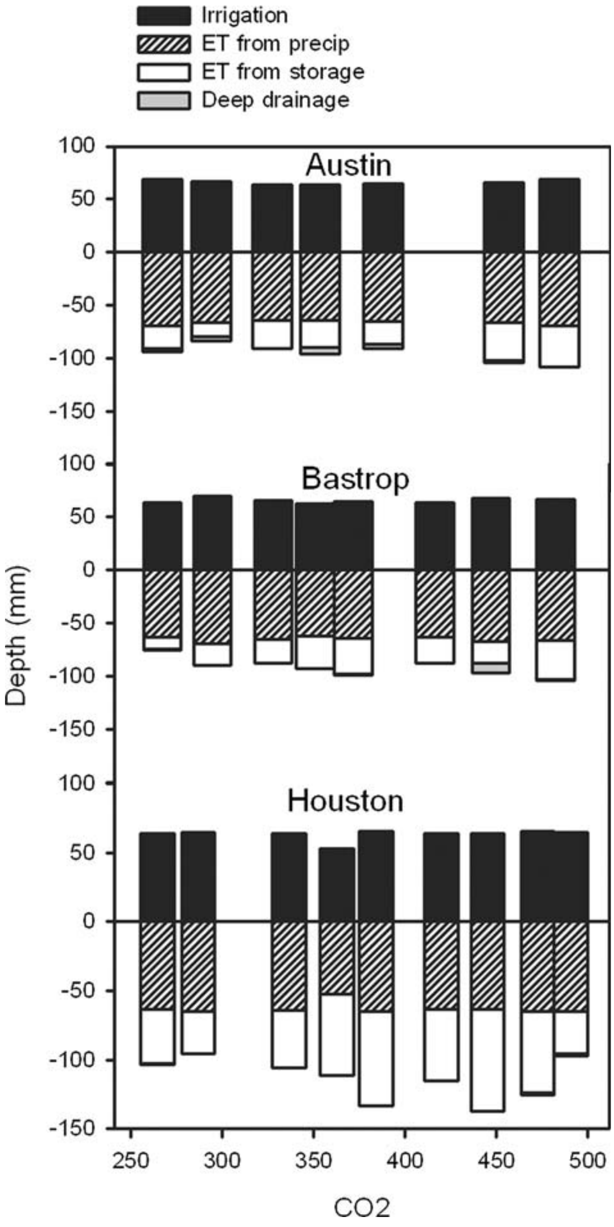

Figure 6. Water balance for the LYCOG soils along the CO_2 gradient for May 2008. Data shown are averages for the 2 monoliths of a given soil type in each 5-m section of the chambers.

determining effects of C_A and soil type within chambers, rather than comparing the chambers with outside conditions (Rawson and others 1995).

Pre-Treatment Soils and Plants

Soils differed markedly in texture and C:N pools. Bastrop soils had the lowest total C, organic C, total N, and soil moisture values, typical of sandy soils. Organic C (OC) accounted for nearly all the carbon in these soils, and the low OC:N despite high plant productivity suggested higher potential decomposition rates versus the other soils. The Houston soils were highest in total C, organic C, total N, and soil moisture. A strong increase in OC:N with depth suggested that decomposition rates are greatest in the top of the soil profile. Austin soils were highest in total C, because of high concentrations of carbonate (V. Jin, unpublished data), and intermediate in soil moisture, organic C and total N. OC:N was higher in Austin than Bastrop soil and comparable to that in the upper layer of Houston soils, implying that decomposition rates are slower in the clay soils compared to the Bastrop soil.

The soils exhibited substantial differences in pre-treatment aboveground and belowground biomass, with Austin soils much less productive than Bastrop and Houston soils. However, productivity did not correlate with either soil water or the pre-treatment C and N pools. Soil texture strongly influences both N and water availability to plants. Other things being equal, decomposition rates and therefore N availability to plants usually are greater in clay than C-poor sandy soils (Paul and others 2001; Johnson and others 2007). In contrast, soil water potential at a given soil water content is greater (less negative) and the permanent wilting point lower in sandy than fine textured soils, resulting in greater plant access to soil moisture (Brady and Weil 2002). This result suggests that productivity differences among soils will depend on soil-specific nutrient × water interactions and their variation with C_A.

The strong negative covariances among *Bouteloua*, *Sorghastrum*, *Solidago*, and *Schizachyrium* imply that CO_2 and soil effects on plant productivity and species composition will be mediated primarily through interactions among these dominant species. We expect to see different trajectories of community change among the soil types in response to the CO_2 gradient because of differential effects of CO_2 on the water budgets of these three soils. For example, we expect CO_2 enrichment to favor the C_3 component of the experimental communities, especially *S. canadensis*, more on the sandy Bastrop soil than on the clay soils. These species are likely to be the most active players in productivity responses to the CO_2 gradient. The differences among LYCOG soils in pre-treatment plant composition are comparable to differences in plant composition both among and within soil types in established tallgrass prairie (Diamond and Smeins 1984; Gibson and Hulbert 1987; Piper 1995). Precipitation may mediate the relationship between soil type and plant community composition. Diamond and Smeins (1984) reported that in

Texas coastal prairies, plant communities located where precipitation was higher showed less association with soil type than communities with lower precipitation.

Preliminary Responses to C_A

Leaf photosynthesis (A_{CO_2}) and photosynthetic water use efficiency (WUE) in *Solidago canadensis* increased with C_A more on the more productive Houston and Bastrop soils in this early summer assessment. A_{CO_2} and WUE are coupled to soil water and N availability, and to the radiation, temperature, and H_2O vapor pressure conditions surrounding the leaf. The vSWC differed substantially among soils during the leaf gas exchange measurements (Figure 5C), but the differences in vSWC sensitivity to C_A among soils did not correspond to the C_A sensitivity of A_{CO_2} and WUE in *S. canadensis*. This implies that leaf carbon assimilation and water loss for *S. canadensis* were regulated more strongly by the leaf microenvironment at this time. However, the relative importance of leaf microclimate versus availability of soil moisture or nutrients such as N is not static, and soil resources should become more important for leaf function when soil moisture is more limiting later in the season and at low C_A (Anderson and others 2001).

J_{CO_2} increased nearly 3-fold with C_A on Bastrop soils. The magnitude of the Bastrop J_{CO_2} response was similar to that reported by Mielnick and others (2001) in the PCG experiment. This large response to C_A may reflect tighter coupling of J_{CO_2} to vSWC on the Bastrop soils, as the C_A response of J_{CO_2} was smaller on the wetter Austin and Houston soils. The greater efflux response to C_A on the Bastrop than Austin and Houston soils suggests that there was a larger increase in root and microbial activity with higher C_A on the Bastrop soil. However, control of J_{CO_2} depends on vSWC, soil temperature, and substrate availability (Luo and Zhou 2006). The response of J_{CO_2} to C_A may decrease as the season progresses and photosynthesis decreases and labile soil C and soil moisture are depleted.

The water budgets showed that ET and the portion of ET supplied by pre-existing stores of soil moisture increased at higher C_A on all three soils. Stomatal closure at higher C_A typically reduces transpiration per unit leaf area (for example, Ward and others 1999; Anderson and others 2001). In this preliminary study, transpiration was not significantly affected by C_A for either species on any of the soils ($P = 0.15$–0.27). Increased aboveground biomass at higher C_A may be responsible for the higher ET. As with leaf carbon assimilation and J_{CO_2}, the effects of soil and C_A on ET are likely to change through the season as soil moisture becomes depleted.

CONCLUSIONS

The CO_2 gradient approach has been used successfully to study plant and soil responses to subambient-to-ambient (Mayeux and others 1993) and subambient-to-superambient (Johnson and others 2000) ranges of C_A. LYCOG maintained linear gradients of daytime and nighttime C_A, with good overall control of T_{air}. The facility advances our capability to discern effects of pre-industrial to mid-twenty-first century levels of C_A on ecosystem structure and function on soils that differ in water and nutrient availability, primary productivity, and plant species composition. The initial results of this study indicate that aboveground net primary productivity, ET, leaf C assimilation in an abundant C_3 forb, soil C efflux, and soil moisture depletion all increased with enriched C_A, particularly on the sandy soil. No counteracting effect of C_A on stomatal conductance was detected. These results suggest that increased C_A may accelerate rates of carbon cycling on these soils. Over the longer term, plant and soil responses to C_A may be mediated by differences in hydrologic properties among the soils and in particular by differences in both soil water content and the availability of soil water to plants and microbes. The larger implication is that variation in soil texture and other properties has the potential to cause considerable variation across the landscape in grassland responses to continuing CO_2 enrichment.

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