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Project : *Processes Affecting Carbon Fluxes of Grassland Ecosystems Under Elevated CO₂*

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Final Report

Fumigation with 2X ambient atmospheric CO₂ of a native tallgrass prairie ecosystem was done for 9 years. The elevated CO₂ plots were compared to chambered and unchambered plots with ambient CO₂. In order to better quantify the impact of reduced water use under elevated CO₂, six physiology chambers were modified to measure CO₂ and water vapor fluxes. The top-opening of existing CO₂-enrichment chambers were permanently covered to prevent any natural rainfall from entering the system. Additionally, two concentric, 1-m deep hydraulic barriers were installed beneath the chamber wall to disallow horizontal water movement between the enclosed plot and the unchambered soil profile. At the start of the growing season, natural rainfall was allowed onto the plots so that the soil water profile reached saturation. After this initial period, rainfall was withheld from the plots for several weeks until leaf water potentials and soil water contents from 0-30 cm reached threshold values. Once the target drying level was reached, 75 mm of water was added to the plots and the dry-down cycle was repeated. This procedure was continued throughout the season. At the end of the 1996 growing season, all chambers were removed from the long-term plots and intensive belowground sampling for microbial properties, mycorrhizal infection and activity, nematode populations, soil carbon partitioned by aggregate fraction, nitrogen cycle properties, and storage carbohydrates was done.

Results:

Long term biomass production and plant census - To determine the long-term impact of elevated CO₂ on primary production of native tallgrass prairie, we compared the responses of tallgrass prairie at ambient and twice-ambient atmospheric CO₂ levels over an 8-year period. Plots in open-top chambers (4.5 m dia) were exposed continuously (24 hr) to ambient and elevated CO₂ from early April to late October each year. Unchambered plots also were monitored. Aboveground peak biomass was determined by clipping each year in early August, and root growth was estimated by harvesting roots from root ingrowth bags. Plant community composition was censused each year in early June. In the last 2 years of the study, subplots were clipped on 1 June or 1 July, and regrowth was harvested on 1 October. Volumetric soil water content of the 0-100 cm soil layer was determined using neutron scattering, and was generally higher in elevated CO₂ plots than ambient. Peak aboveground biomass was greater on elevated CO₂ plots than ambient CO₂ plots with or without chambers during years with significant plant water stress. Aboveground regrowth biomass was greater under elevated CO₂ than under ambient CO₂ in a year with late-season water stress, but did not differ in a wetter year. Root ingrowth biomass was also greater in elevated CO₂ plots than ambient CO₂ plots when water stress occurred during the growing season. The basal cover and relative amount of warm-season perennial grasses (C₄) in the stand changed little during the 8-year period, but basal cover and relative amount of cool-season perennial grasses (C₃) in the stand declined in the elevated CO₂ plots and in ambient CO₂ plots with chambers. Forbs (C₃) and members of the Cyperaceae (C₃) increased in basal cover and relative amount in the stand at elevated compared to ambient CO₂. Greater biomass production under elevated CO₂ in C₄-dominated grasslands may lead to a greater carbon sequestration by those ecosystems and reduce peak atmospheric CO₂ concentrations in the future.

Water use under different atmospheric CO₂ concentrations - We measured leaf-level stomatal conductance, xylem pressure potential, and stomate number and size as well as whole

plant sap flow and canopy-level water vapour fluxes in a C₄-tallgrass prairie in Kansas exposed to ambient and elevated CO₂. Stomatal conductance was reduced by as much as 50% under elevated CO₂ compared to ambient. We found that greatest reductions in stomatal conductance occurred in those species with the highest potential growth rates. Moreover, during periods of dry soils, the CO₂-induced reduction in stomatal conductance was absent and in some species stomatal conductance was higher at elevated CO₂. This was attributed to more favorable water status in these plants. Thus, there are exceptions to the generalization that plants exposed to high CO₂ will always have reduced stomatal conductance. In addition, there was a reduction in stomate number of the C₄ grass, *Andropogon gerardii* Vitman, and the C₃ dicot herb, *Salvia pitcheri* Torr., under elevated CO₂ compared to ambient. The result was an improved water status for plants exposed to elevated CO₂ which was reflected by a less negative xylem pressure potential compared to plants exposed to ambient CO₂. Sap flow rates were 20 to 30% lower for plants exposed to elevated CO₂ than for those exposed to ambient CO₂. At the canopy level, evapotranspiration was reduced by 22% under elevated CO₂. The reduced water use by the plant canopy under elevated CO₂ extended the photosynthetically-active period when water became limiting in the ecosystem.

Leaf longevity - Responses to elevated CO₂ in leaf area, number, development and longevity were quantified for the tallgrass prairie dominant, *Andropogon gerardii*. Plants were grown in open-top chambers (OTCs) modified to limit water availability and maximize responses to elevated CO₂. In OTCs with elevated (2x ambient) levels of CO₂, aboveground biomass production and leaf water potentials were increased significantly compared to plants in OTCs with ambient CO₂. There were no differences in leaf area or leaf number per tiller in *A. gerardii* in elevated vs. ambient OTCs. However, leaf area in adjacent unchambered plots with greater water availability was significantly higher than in the OTCs. The time required for developing leaves to achieve maximum leaf area was reduced by 29%, and the period of time until leaves senesced was increased by 20% for plants exposed to elevated vs. ambient CO₂. Thus, leaves of this C₄ grass species expanded more rapidly (6 days) and remained green longer (9 days) when exposed to elevated CO₂. Such CO₂-induced increases in leaf longevity in the dominant species may allow this grassland to respond more opportunistically to temporally variable rainfall patterns in future high CO₂ environments. These responses should be included in leaf-based simulation models that attempt to mechanistically link physiological alterations to predicted canopy responses to increased CO₂.

Soil-surface CO₂ exchange - Twenty nine plots were subjected to three clipping treatments: no clip, early-clip, and full season clip. The magnitude and frequency of the clipping was designed to emulate the effect two grazing regimes (intense early stocking, full season stocking). Soil surface CO₂ flux was measured on a weekly basis with a surface chamber for the entire growing season. Soil water and soil temperature was also monitored in each plot. Clipping reduced soil CO₂ flux by 23 percent (1,000 g CO₂) over the season. Process-level analysis showed that biomass removal decreased canopy photosynthesis (P) in the clipped plots. Decreased canopy P caused a reduction in carbon translocation below ground, which reduced both root and microbial respiration. Measurement on land grazed by cattle and bison showed similar results. Grazing practices have a large impact on carbon dynamics. In comparison to data collected in the CO₂ enrichment experiment, the effect of grazing on soil CO₂ flux was three times larger than the effect of doubled CO₂.

Soil and microbial biomass C and N - Microbial biomass C and N were significantly higher ($p < 0.1$) in the elevated CO₂ chambers compared to ambient chambers at the 5 to 15 cm depth

during the 1992 - 94 field seasons. Available inorganic NH_4^+ and NO_3^- appeared to be unaffected by elevated CO_2 . In 1996 microbial biomass C was significantly higher ($p < 0.1$) in the elevated CO_2 chambers compared to ambient CO_2 chambers at the 5 to 15 cm depths. Microbial activity was significantly higher ($p < 0.05$) in the elevated CO_2 chambers for 1991 - 1996. Denitrification potential tended to be higher in elevated CO_2 , but variability among samples was extremely high. Nitrogen fixation by free-living microorganisms as measured by the acetylene reduction assay was not significantly different between treatments. Long-term mineralization of soil cores indicated significantly ($p < 0.05$) higher levels of active fraction C in elevated CO_2 . Most results particularly microbial activity were highly and positively correlated to higher soil moisture from increased plant WUE under elevated CO_2 . In late October, 1996 the CO_2 chambers were disassembled and intensive plant and soil sampling occurred. We were able to see statistically significant differences in whole soil C and N. Furthermore, there was no difference between the two controls (AC and NC avg=51.5 mgC/g soil) but the 2X had 56.0 mg/g ($P=0.0036$). These data are only for the top 5 cm. We have also identified some fractions where the C appears to be accumulating. We soaked the soil in sodium hexametaphosphate (Calgon) overnight and then put it on a wrist-action shaker for 4 hrs. This treatment disrupted macro- and microaggregates $>53\mu\text{m}$ in diameter. We put the soil solution through a $53\mu\text{m}$ sieve and collected the particulate OM (POM) and sand that remained on the sieve. Then we density fractionated the POM retained on the sieve using 1.8, 2.0, and 2.2 g/cm³ Na Polytungstate (SPT). This gave us fractions that represent increasing levels of degradation, based on visual examination and on C:N ratios (the avg for the $<1.8\text{g/cm}^3$ fraction is 22.4 and averages drop from there; the 1.8-2.0 fraction is 15.3, the 2.0-2.2 fraction is 13.5, and the >2.2 fraction is 11.4). Visually, the <1.8 includes large pieces of what still looks like roots, but as the density increases, the pieces become more amorphous and smaller. Of the 4.5 mgC/g soil increase in whole soil C due to elev. CO_2 , 1.9 mg/g of it is in the POM fractions ($P=0.0774$) and there is a statistically sig. increase in the 1.8-2.0 g/cm³ fraction that amounts to 1.7 g/cm³ ($P=0.0194$). The >2.2 g/cm³ fraction is also significantly greater in the 2X treatment and the 2.0-2.2 increases slightly under 2X (but is not statistically significant). However, the <1.8 is 0.5 mgC/g lower in the 2X trt than in the controls (but variable enough that the difference is not significant statistically). This suggests that if elev. CO_2 causes an increase in production which translates to greater belowground detrital inputs, then microbial activity may increase to the point where there is less readily decomposable POM (i.e., the $<1.8\text{g/cm}^3$ fraction) but an accumulation in the more rendered fractions. Furthermore, these more rendered fractions may be accumulating due to physical protection in aggregates. Support for this idea comes from the fact that the C:N ratios of the POM fractions with densities of 1.8-2.0 and >2.2 are significantly higher than the C:N ratios for the controls. In all of the analyses, there is no difference between the chambered and nonchambered controls. Furthermore, for whole soil there was a significant block (site slope) effect, but this was not present for any of the POM fractions suggesting that there was innate variability in whole soil C due to slope when the site was established but that the fractions we are isolating are indicative of CO_2 related effects rather than the original variability of the soils. Although, we don't know anything about the turnover and mean residence time for C in the fractions that are accumulating. At the same time, there is another 2.6 mg/g C that passed through the $53\mu\text{m}$ sieve with the mineral fraction of the soil and we are working on fractionating those pools (which are likely to be even more protected).

We determined the effects of elevated CO_2 on the quantity and quality of belowground biomass and various soil organic matter pools at the conclusion of an eight-year CO_2 enrichment experiment on native tallgrass prairie. Plots in open-top chambers (4.5-m diameter) were exposed continuously to ambient and twice-ambient CO_2 from early April through late October of

each year. Soil beneath and next to the crowns of C4 grasses in these plots and unchambered plots were sampled to a depth of 30 cm. Elevated CO₂ increased the standing crops of rhizomes (87%), coarse roots (46%), and fibrous roots (40%) but had no effect on root litter (mostly fine root fragments and sloughed cortex material). Soil C and N stocks also increased under elevated CO₂, with accumulations in the silt/clay fraction over twice that of particulate organic matter (POM). The mostly root-like, light POM ($\leq 1.8 \text{ g m}^{-2}$) appeared to turn over more rapidly while the more amorphous and rendered, heavy POM ($> 1.8 \text{ g m}^{-2}$) accumulated under elevated CO₂. Overall, the C:N ratios of rhizomes and roots were not greatly affected by CO₂ enrichment. However, elevated CO₂ increased root litter and POM C:N ratios in the surface 5 cm and induced small, but significant, increases in the C:N ratios of the silt/clay fraction to a depth of 15 cm. Our data suggest that elevated CO₂ may have affected elements of the N cycle (including mineralization, immobilization, and asymbiotic fixation) but that any alterations in N dynamics were not preventing significant plant growth responses to CO₂ enrichment after eight years.

Since N is a limiting nutrient in tallgrass prairie and most ecosystems, changes in N availability or N cycling could control the long-term response of ecosystems to elevated atmospheric CO₂. Alterations in N dynamics such as plant uptake, nitrogen fixation, nutrient cycling, microbial utilization, and partitioning of N into plant and soil fractions could ultimately affect the capability of ecosystems to sequester and store atmospheric CO₂. Treatments (replicated 3 times using a randomized complete block design) were ambient CO₂-no chamber (NC), ambient CO₂-chamber (AC), and 2X ambient CO₂-chamber (EC). Several short laboratory incubations were utilized to assess whether turnover rates of N in soil would be altered under elevated CO₂. Gross transformations of N were not significantly altered under elevated CO₂ compared to ambient conditions. To examine plant-microbial competition and altered allocation patterns of N under elevated CO₂, ¹⁵NH₄⁺-N was added to 25 cm diameter PVC cores in the field and destructively sampled after 8 months. Microbial biomass contained about 75% of the total ¹⁵N that occurred in the soil organic matter pool and thus appears to be a significant regulator of plant available N. Under elevated CO₂, the soil organic matter contained significantly more ¹⁵N compared to the ambient chamber. Plant roots and rhizomes had a significantly reduced % of recovered ¹⁵N under elevated CO₂ relative to the ambient chamber, but was not different from the no chamber treatment. Greater ¹⁵N in the SOM pool and greater %¹⁵N SOM/%¹⁵N plant suggests greater microbial demand for N under elevated CO₂ relative to ambient conditions.

Open-top Chambers Studies: Open-top chambers are an economical means of testing ecosystem-level responses to elevated CO₂. They provide the only feasible method of measuring canopy level trace gas fluxes on a continual basis. The effects of the chamber on micrometeorology are a serious drawback to their use. While chamber effects are unavoidable, knowing their impact allows for meaningful interpretation of the results. Our experience with open-top chambers indicates that certain precautions are necessary for their effective use, the most important of which are the use of a barrier in the soil and matching chamber pressure with atmospheric pressure.

Chamber design is particularly important when measuring the impact of elevated CO₂ on water relations. A watertight barrier must be placed beneath the chamber to prevent water exchange with the surrounding soil. Any difference in soil water status induced by different atmospheric CO₂ concentrations may be severely altered due to lateral movement of soil water in or out of the soil volume that is associated with the chamber. The chamber environment reduces water use and creates a lateral gradient in ambient chambers as well. Thus, ozone and other trace

gas studies should also use a barrier. The smaller the chamber area, the greater is the impact of lateral soil water movement in the soil. The magnitude of the soil water movement is dependent on the difference in soil water status between the chamber and the surrounding area and soil physical properties. Barriers should be as deep as the effective rooting zone of the major dominants in the plant community. Failure to incorporate a soil barrier partially negates the water savings induced by elevated CO₂, because water can move to the drier soil adjacent to the chamber. In ecosystems in which water is a primary limiting resource, the true impact of elevated CO₂ on ecosystem processes is greatly altered. For the chambers we used, the barrier was placed to a 1-m depth using a trenching machine and there was no disturbance to the chamber soil. The soil barrier was sealed to the chamber.

In order to accurately measure gas fluxes in open-top chambers, the atmospheric pressure inside the chamber must equal that outside. Relatively small increases in pressure inside the chamber can result in substantial movement of chamber air into the soil. Using a two-dimensional advection diffusion model, we simulated the impact of 0, 1, and 2 Pa pressure inside an open-top chamber on CO₂ from the soil surface and the volume flow of air into the soil (Table 1). The results indicate that soil-surface CO₂ flux was substantially reduced and that a large amount of air was forced into the soil. The average CO₂ flux from the soil is several times greater than that which is fixed by photosynthesis, and the pressure developed by the flow of air into the chamber greatly reduces the soil CO₂ flux. When chamber CO₂ flux under elevated CO₂ is measured, that air movement into the soil and the subsequent reduced soil CO₂ flux is interpreted as a sequestration by the plant canopy. In the absence of a soil barrier, there is a flow of air through the chamber soil to the outside soil and to the soil surface, where it is lost to the atmosphere. Indeed, the soil CO₂ flux adjacent to the chamber would be much greater than normal. Pressure inside the chamber can be adjusted using a variable speed fan (0.6 m dia.) in the top chamber orifice and a differential pressure transducer to measure pressure differences. During most of the day the shading from the fan falls outside the plot area, but does shade a small area during midday. When we used fans in the top of the OTCs to equalize pressure, we found no statistical difference in soil CO₂ flux between the ambient OTCs and control plots. We measured flux on a weekly basis over the entire growing season using a soil-surface chamber.

Table 1. Simulated values of CO₂ flux from the soil surface and the volume flow of air into the soil within an open-top chamber. Pressure inside the chamber was simulated at 0, 1, and 2 Pa above atmospheric pressure. The CO₂ concentrations at the upper boundary (aerial CO₂) was held constant at 14.5 $\mu\text{mol m}^{-3}$ (350 ppm) both inside and outside the chamber.

Pressure Differential $P_{\text{chamber}} - P_{\text{atmosphere}}$ (Pa)	Soil Surface CO ₂ Flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Volume Air Flow into the Soil within the Chamber ($\text{m}^3 \text{ air m}^{-2} \text{ area day}^{-1}$)
0	4.2	0
1	3.6	1.03
2	3.2	2.81

Changes in forage quality under elevated CO₂ - We collected diet samples from ambient and elevated CO₂ (2X ambient) plots using three esophageally-fistulated sheep at 2-week intervals throughout the growing season in 1989 by grazing one half of 4.5 m dia. plots. The diet samples were frozen immediately, freeze-dried, and acid detergent fiber (ADF) and N concentration

determined. We used the ADF and N values from the ambient and elevated CO₂ diet samples to estimate the growth response of yearling steers grazing tallgrass prairie. Chemical composition affects the energetic value of plant materials when used as feeds for livestock. Therefore, we estimated the magnitude of the impact on livestock gain that could result from the changes in chemical composition observed in response to enhanced CO₂ concentration. Weight gain projections were calculated for beef cattle that were assumed to be between 12 and 24 months of age and experiencing relatively rapid growth while grazing tallgrass prairie during the late spring and summer periods.

The initial step in the simulation process involved estimation of organic matter digestion (OMD) from the ADF concentration. Accuracy of OMD predictions using this approach has been quite good when compared with OMD values determined directly in cattle consuming tallgrass-prairie forage. Subsequently, digestible energy (DE) concentration was estimated from the OMD concentration and then the metabolizable energy (ME) concentration was predicted from the DE concentration. The efficiency of ME use for maintenance (k_m) and the efficiency of ME use for production (i.e., gain; k_{rp}) were estimated using the associated protein values and ME concentrations (expressed as a percentage of gross energy). Metabolizable energy values and their associated efficiencies were then used to estimate the gain that might be realized by a rapidly growing, yearling steer consuming a given amount of forage. Although weight would obviously be changing over the course of the grazing period, to simplify the simulations an average weight of 250 kg was used in all calculations and forage intake was assumed to be the same for cattle consuming forage from CO₂-enriched and ambient CO₂ environments (intake would likely be lower for cattle consuming forage produced in an elevated CO₂ environment). Amount of forage intake was assumed to decrease as season progressed based on measurements from previous studies at our location. The amount of net energy needed for maintenance was estimated by dividing the k_m into the sum of an estimate of fasting heat production (FHP) and activity. Once maintenance was accounted for, we estimated the amount of gain that could be supported from the remaining ME. This was determined by multiplying the ME available for gain by the k_{rp} . Finally, the calorific values of weight gain presented by Blaxter (1962) were used to convert megacalories of gross energy in the gain into weight gain values. Estimated gain for steers consuming forage produced under elevated CO₂ in 1989 was lower than that produced under ambient CO₂ summed over the 150-day growth period (2X CO₂ - 80.6 kg; 1X CO₂ - 99.6 kg), with the greatest reduction in gain coming in the early season. Since N and fiber concentrations in the diet of ruminants impact forage digestibility and utilization efficiency, the reported reduced N and increased fiber concentrations in plants grown under elevated CO₂ will likely impact ruminant productivity negatively. Data reporting reduced productivity or increased consumption for insects consuming diets of plants grown under elevated CO₂ support that conclusion. Contrary to the results from insect studies, where intake increased as diet quality decreased, ruminant intake declines as forage quality decreases. Therefore, there cannot be a compensatory intake response to maintain productivity levels comparable to current levels. For domestic livestock, diets can be supplemented to compensate for reduced forage quality, but with wild ruminants, or for ruminants in developing countries, diet supplementation is not an option. The result will be reduced growth and reproduction. Further, changes in climate may impact foraging by ruminants. High daytime air temperatures currently reduce total grazing time for cattle with little or no compensatory nighttime grazing.

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