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FINAL REPORT

Project: 84-ER-60253 Rangeland - Plant Responses to Elevated CO_2.

Study Site and Experimental Design

The experimental site for the tallgrass prairie research was located in pristine tallgrass prairie north of and adjacent to the Kansas State University campus. Vegetation on the site was a mixture of C_3 and C_4 perennial species and was dominated by big bluestem (*Andropogon gerardii* Vitman; C_4) and indiangrass [*Sorghastrum nutans* (L.) Nash; C_4]. Subdominants included Kentucky bluegrass (*Poa pratensis* L.; C_3), sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.; C_4], and tall dropseed [*Sporobolus asper* var. *asper* (Michx.) Kunth; C_4]. Members of the sedge family (C_3) made up 5-10% of the composition. Principal forbs included ironweed [*Vernonia baldwinii* subsp. *interior* (Small) Faust; C_3], western ragweed (*Ambrosia psilostachya* DC.), Louisiana sagewort (*Artemesia ludoviciana* Nutt.; C_3), and manyflower scurfpea [*Psoralea tenuiflora* var. *floribunda* (Nutt.) Rydb.; C_3]. Average peak biomass occurs in early August at 425 g m^{-2} of which 35 g m^{-2} is from forbs. Soils in the area are transitional from Ustolls to Udolls (Tully series: fine, mixed, mesic, montmorillonitic, Pachic Argiustolls). Slope on the area is 5%. Fire has been infrequent, occurring two to three times in 10 years. Past history has included primarily winter grazing by cow-calf pairs. The 30-year average annual precipitation is 84 cm, with 52 cm occurring during the growing season.

Nine circular plots were established in early May, 1989 on native tallgrass prairie. Each year in late February the area is mowed to a 5-cm height and the cut material removed. Treatments, replicated three times, were ambient CO_2-no chamber (**A**), ambient CO_2 plus chamber (**CA**), and double ambient (enriched) CO_2 plus chamber (**CE**) and have continued on the same plots through 1993. A nitrogen fertilizer study on the same area had twice-replicated treatment of ambient CO_2 plus nitrogen (**AN**), chamber plus ambient CO_2 plus nitrogen (**CAN**), and chamber plus CO_2-enriched plus nitrogen (**CEN**).

Nitrogen was applied as ammonium nitrate at 56 kg N ha^{-1} in late March of both years. Fumigation chambers were placed over the natural vegetation in late March, 1990 and retained on the same area for a two-yr period. On the unfertilized and fertilized studies, one half of each chamber was used to determine biomass accumulation, plant population dynamics, and nutrient status, and the remaining half was grazed by esophageally fistulated sheep to collect samples to determine forage quality differences among treatments.

RESULTS

Biomass Production

Owensby *et al.* (1993a) determined above- and belowground biomass production, leaf area, plant community species composition, and measured and modeled water status of a tallgrass prairie ecosystem exposed to ambient and twice-ambient CO_2 concentrations. Exposure was in open-top chambers during the entire growing season from 1989 through 1991. Compared to ambient CO_2 levels, elevated CO_2 increased production of C_4 grass species, but not of C_3 grass species. Belowground biomass production, estimated in 1990 and 1991 by root ingrowth bags, responded similarly to that of the aboveground, but the relative increase was greater than that above ground. Species composition of C_4 grasses did not change, but *P. pratensis* (C_3) declined, and C_3 forbs increased in the stand exposed to elevated CO_2 compared to ambient. The reduction in C_3 grasses was partly due to the lack of grazing which allowed the taller C_4 grasses to quickly overtop the shorter C_3 species, but the increased biomass and leaf area in CO_2-enriched plots was probably the primary forcing factor in the decline of the C_3 grasses. There was also drought in two of the initial three years in the study, which also favored the C_4 species. The taller C_3 forbs increased under elevated CO_2, supporting the hypothesis that canopy response (i.e. competition for light) associated with CO_2 enrichment affected interspecific competition.

Tallgrass prairie productivity is commonly limited by N and water availability (Owensby *et al.* 1969). Increased WUE under elevated CO_2 apparently had a greater impact on productivity of C_4 plants than photosynthetic pathway of C_3 species. We concluded that the lower the growing season precipitation the greater was production response of *A. gerardii* and total biomass to elevated CO_2. Field *et al.* (1992) indicated that the most limiting resource to ecosystem productivity would dominate even under elevated CO_2. Indications are that in the nutrient-poor tallgrass prairie under elevated CO_2 increased primary production resulted from reduced water stress and improved WUE.

The common speculation that in mixed C_3/C_4 plant communities C_3 species will gain a competitive advantage was not supported by observations during the 3-year period. The combination of increased biomass and leaf area under elevated CO_2, drought, and lack of grazing may preclude any increase in C_3 grass production or population increase in tallgrass prairie. Unpublished data from the following two years with above normal precipitation and the same treatments showed a further decline in C_3 grass production and population. We conclude that the normal limits to C_3 production continued to operate, but the reduced water stress for the C_4 grasses allowed them to increase production in years with substantial water stress.

Water Use Efficiency

Knapp *et al.* (1993a) measured responses in leaf xylem pressure potential (ψ) of *A. gerardii* plants within chambers with ambient and elevated CO_2 and from adjacent unchambered plots throughout the 1991 and 1992 growing seasons. 1991 was a year with below-average rainfall and 1992 was a very wet year. Midday ψ was significantly higher (less negative) in plants grown at elevated CO_2 in both years. When averaged over the growing season, ψ was 0.48 to 0.70 MPa lower in 1991 than 1992. In both years, stomatal conductance (g_s) was significantly reduced (21-51%) when measured at 700 vs. 350 $\mu l\ l^{-1}$ CO_2. These data support the contention that for C_4 grasses in the tallgrass prairie, positive responses on biomass production to elevated CO_2 may only occur in years with significant water stress and improved water status will allow for continued growth under elevated CO_2 while growth is abated in ambient CO_2 environments.

In addition to the reduced water stress under elevated CO_2, stomatal response to sunlight may impart additional water savings in *A. gerardii*, the dominant C_4 grass in tallgrass prairie (Knapp *et al.* 1993b). Within chambers with ambient and twice ambient atmospheric CO_2, or in adjacent unchambered plots, *A. gerardii*, was subjected to fluctuations in sunlight similar to that resulting from intermittent clouds or within canopy shading (full sun > 1500 μmol m^{-2} s^{-1} vs. shade 350 μmol m^{-2} s^{-1}) and stomatal conductance measured. Time constants describing stomatal responses were significantly reduced (29-33%) at elevated CO_2, As a result, water loss was reduced by 6.5% due to more rapid stomatal responses in twice-ambient CO_2 atmospheres. Leaf xylem pressure potential increased during periods of sunlight variability indicating that more rapid stomatal responses at elevated CO_2 enhanced plant water status. It is important to note that CO_2-induced alterations in the kinetics of stomatal responses to variable sunlight will likely amplify direct effects of elevated CO_2 and increase WUE in all ecosystems.

In 1993, we measured whole-chamber water vapor fluxes and net carbon exchange (NCE) in **CE** and **CA** plots using the method of Ham et al. (1993). Continuous data were collected over a 34-d period when the canopy was near peak biomass (LAI 4 to 5 m^2 m^{-2}) and soil water was not limiting. Results showed that 2 x ambient CO_2 reduced evapotranspiration by 22% and also increased NCE (Ham et al., 1994). However, the increases in NCE were primarily caused by delayed senescence in the **CE** plots rather than increased photosynthetic rates during vegetative growth. Reduced evapotranspiration and greater NCE under CO_2 enrichment resulted in higher ecosystem-level water use efficiency (**CA** - 1.7 g $_{CO2}$ kg^{-1} $_{H20}$, **CE** - 2.6 g kg^{-1}). Additionally, whole-chamber data collected on days with high evaporative demand showed that ecosystem quantum yield, (umol $_{CO2}$ umol $_{PAR}{}^{-1}$) in the CE plots remained high in the afternoon period, but decreased in the **CA** plots (e.g., **CA** - 0.021 umol

umol^{-1}, **CE** - 0.029 umol umol^{-1}). These data tend to confirm the leaf-level measurements of Knapp et al. (1993a) that showed more favorable leaf water potentials were maintained under CO_2 enrichment. Measurements of reduced sap flow and increased canopy resistance to water vapor transport in the **CE** plots provided further evidence that CO_2 strongly influenced the hydrology and plant water relations of the ecosystem (Ham *et al.* 1994). Data collected at the leaf, whole-plant, and ecosystem scale all suggested that C_4 plant communities exposed to elevated CO_2 will maintain a more favorable water status when subjected to periodic moisture stress.

Our data support the speculation that elevated CO_2 will increase WUE, and we conclude that, in ecosystems that experience moderate to severe water stress, primary production will increase, provided other resources are adequate. The data from Owensby *et al.* (1993a) and unpublished data from the following two years clearly indicate an increase in biomass production in years with water stress and no increase in wetter years. Natural ecosystems, particularly grasslands and shrublands, are often limited by water availability. In the event that global climate change reduces precipitation and increases temperature in a region, the increased WUE in a high-CO_2 world may serve as a buffer against substantial ecosystem change.

Photosynthetic Capacity

The research presented below is for photosynthetic capacity of *A. gerardii* under ambient and elevated CO_2 and address the speculation that C_4 photosynthetic capacity will be essentially unaffected by elevated CO_2. In 1991 and 1992, *A. gerardii* plants were grown in large pots (as intact soil cores with *A. gerardii* extracted from pristine tallgrass prairie) in the **A**, **CA**, and **CE** plots and periodically were moved to the laboratory, watered to field capacity, and net photosynthetic (A) measured over a range of CO_2 concentrations, light levels and air temperatures (Knapp *et al.* 1993a). In 1992, we also measured maximum photosynthetic capacity (A_{max}), apparent quantum requirement (Q_r), the photosynthetic light compensation point (LCP), and dark respiration (R_r). In 1991, a dry year, A and g_s were significantly reduced (A was 27%

lower regardless of measurement CO_2 level) in plants grown at ambient vs. elevated CO_2. Apparently, the more frequent water stress under ambient CO_2 reduced photosynthetic capacity of *A. gerardii.* Greater water stress also affected A over a broad range of temperatures (17-35 °C), with plants grown in **A** and **CA** plots having significant reductions in A (as much as 7.1 μmol m^{-2} s^{-1}) compared to those grown in **CE** plots. In 1992, a wet year, no differences in A, A_{max}, Q_r, LCP or R_d were detected when ambient and elevated CO_2 grown plants were compared. There was a trend for lower R_d and LCP in *A. gerardii* grown at elevated CO_2.

Although the photosynthetic capacity of C_4 species may not be directly enhanced under elevated CO_2, we conclude that water-stress related reductions in photosynthetic capacity are less likely to occur under elevated CO_2 compared to ambient CO_2 for C_4 grasses. Ultimately, this will lead to higher photosynthetic rates at elevated vs. ambient CO_2.

Nutrient Limitations

While it has often been speculated that increased biomass production under elevated CO_2 will wane as reduced nutrient availability is generated, increased nutrient use efficiency may negate that response. There are both short- and long-term implications regarding nutrient limitation and response to elevated CO_2. The short-term response reflects the inherent low N availability of most natural ecosystems which affects the ability of the ecosystem to increase productivity with increased carbon availability. The long-term response relates to reduced N availability results from slower decomposition of litter because of reduced litter quality. We studied the response of nitrogen-fertilized tallgrass prairie to ambient and twice-ambient CO_2 levels over a 2-year period (Owensby *et al.* 1993c). Comparisons were made with the results of the unfertilized companion experiments of Owensby *et al.* (1993a&b) at the same research site. Above- and belowground biomass production and leaf area were greater on **CEN** plots than on **CAN** or **AN** plots both years, with a much larger increase measured in 1991, a dry year. Tissue nitrogen concentration was lower for plants in **CEN** plots than for those in **CAN** and **AN** plots, but total standing crop N was greater on the **CEN** plots. The relative differences were the same as those in the unfertilized study, but N concentrations were 15-20% higher with N fertilization. Similar to the unfertilized area, increased root biomass under elevated CO_2 likely increased N uptake. The response of biomass production to elevated CO_2 on N-fertilized plots was much greater than in the unfertilized plots. Owensby *et al.* (1993c) concluded that response to elevated CO_2 was suppressed by N limitation.

These data were for the short term and do not reflect changes in nutrient cycling, but they do indicate the severity of N limitation in tallgrass prairie. If N availability is further reduced under elevated CO_2 by slower nutrient cycling, then the biomass production response to elevated CO_2 may be further limited. The speculation that N-limitation will be amplified under elevated CO_2 is supported by our short-term results from the tallgrass prairie.

Decomposition and Nutrient Cycling.

Owensby *et al.* (1993b) reported on N concentrations in *A. gerardii, P. pratensis,* and forb aboveground biomass in tallgrass prairie exposed to ambient and elevated CO_2 over the 3-year period. N concentration of root ingrowth bag biomass was also measured. Total N in above- and belowground biomass was calculated as a product of concentration and peak biomass by species groups. N concentration in *A. gerardii* and forb aboveground biomass was lower and total N higher in elevated CO_2 plots than in ambient CO_2 plots. N concentration in *P. pratensis* aboveground biomass was lower in elevated CO_2 plots than in ambient, but total N did not differ among treatments in 2 of 3 years. In 1990, N concentration in root ingrowth bag biomass was lower and total N greater in elevated CO_2 than in ambient CO_2 plots. Root ingrowth bag biomass N concentration did not differ among treatments in 1991, but total N in root ingrowth bag biomass was greater in elevated CO_2 plots than in ambient CO_2 plots.

The impact of elevated CO_2 on decomposition of aboveground biomass and soil microbial processes were also measured. Rice *et al.* (1993) determined the effects of elevated CO_2 in unfertilized and N-fertilized plots on amount of carbon and nitrogen stored in soil organic matter and microbial biomass and microbial activity in 1991 and 1992. The data were taken on the plots that had been exposed to elevated and ambient CO_2 since 1989 for the unfertilized plots and since 1990 for the fertilized. Soil organic C and N significantly increased after three seasons under enriched atmospheric CO_2. In 1991, a dry year, CO_2 enrichment significantly increased microbial biomass C and N compared to ambient, but in 1992, a wet year, microbial biomass C and N did not differ among CO_2 treatments. Added N increased microbial C and N and stimulated microbial activity under CO_2 enrichment. Microbial activity was consistently greater under CO_2 enrichment probably as a result of better soil water conditions. Ratios of microbial to organic C and N did not differ among treatments. Increased microbial N with CO_2 enrichment was another indication that plant production may become limited by N availability. In order to determine if the soil system could compensate for the limited N by increasing the labile pool to support increased plant production with elevated atmospheric CO_2, longer-term studies are needed to determine how tallgrass prairie will respond to increased C input.

Because translocation of N in late-season from the aboveground biomass to belowground storage made aboveground litter similar in tissue chemistry, decomposition of surface litter was unaffected by CO_2 treatment (Kemp *et al.* 1993). They collected standing dead and green foliage litter from *A. gerardii* (C_4), *S. nutans* (C_4), and *P. pratensis* (C_3) plants that had been grown under twice-ambient or ambient CO_2 and with or without nitrogen fertilization. The litter was placed in mesh bags on the soil surface of adjacent prairie and allowed to decay over a 2-year period. Litter bags, retrieved at intervals, showed that the CO_2 treatment had a relatively minor effect on the initial chemical composition of the litter or its subsequent rate of decay. However, there was a large difference among species in litter decomposition. *P. pratensis* leaf litter decayed more rapidly, had higher total N & P, and a different initial carbon chemistry than the C_4 grasses. These differences suggest that there could be an indirect effect of CO_2 on decomposition and nutrient cycling by way of CO_2-induced changes in species composition.

The increased microbial N, higher soil C content of the upper soil layer, and the increased microbial respiration with N addition all indicate that there is a reduction in soil organic matter decomposition under elevated CO_2. Since the addition on N to the ecosystem under elevated CO_2 substantially increased CO_2 evolution from the soil, Those data support the contention that in the long term N limitation may slow the biomass production response to elevated CO_2. Because surface litter chemistry does not appear to differ between ambient and elevated CO_2 treatments, it is not likely higher atmospheric CO_2 will cause significant change in surface litter decomposition.

Forage Quality

Acid detergent fiber (ADF) (primarily cellulose and lignin) of *A. gerardii, P. pratensis*, and forb aboveground biomass was estimated by periodic hand clipping of samples throughout the growing season in 1989 and 1990 (Owensby, unpublished data). In 1991, ADF in peak biomass was estimated by an early August harvest. ADF concentration was higher (indicating lower forage quality) in plots with elevated CO_2 than with ambient CO_2 for the C_4 grasses in 1989 and 1990. ADF concentration in *P. pratensis* was similar among treatments in 1989, but in 1990, elevated CO_2 reduced ADF concentration compared to ambient CO_2. Diet quality samples were collected using esophageally-fistulated sheep in 1989 and 1990. In both years, *In vitro* dry matter digestibility (IVDMD: disappearance of dry matter following anaerobic incubation in rumen fluid) was lower for sheep-collected samples from CO_2-enriched plots than that of samples from ambient-CO_2 plots, with the difference being greater with up to 32 hr exposure to rumen fluid. We conclude that elevated CO_2 may reduce forage quality and, therefore, reduce intake, and ruminant productivity. Since domestic livestock can be supplemented with harvested food resources, the impact will likely be greater for wild ruminants than for domestic.

SUMMARY AND CONCLUSIONS

A summary of the common speculations about ecosystem-level responses to elevated CO_2 is presented in Table 1. The primary impact of elevated CO_2 on the tallgrass prairie ecosystem will most likely be through changes in water use as a result of reduced stomatal conductance and concomitant reduction in water loss from leaves. Whole-chamber water flux measurements and whole-plant sap flow data show a substantial reduction in evapotranspiration, and less negative diurnal and midday xylem pressure potentials in years with water stress indicate an amelioration of water stress under elevated CO_2. Further, a more rapid stomatal response to sun/shade events also conserves water in plants under elevated CO_2. Soil moisture levels were consistently higher under elevated CO_2 indicating reduced water use by the plant community. Since tallgrass prairie is subjected to frequent water stress, biomass production will be enhanced under increased levels of atmospheric CO_2. Our data show that in years with water stress, biomass production of C_4 species is greater under elevated CO_2 than ambient.

Severe water stress reduces the photosynthetic capacity of *A. gerardii,* the dominant C_4 grass in tallgrass prairie. We found that plants grown under elevated CO_2 maintained a greater photosynthetic capacity across a range of air temperatures and CO_2 concentrations after exposure to natural water stress conditions. These data further support the contention that the reduced transpiration under elevated CO_2 attenuated the detrimental effects of water stress on carbon fixation.

Interspecific competition in natural ecosystems may not follow the conventional wisdom that C_3 species will gain a competitive advantage. In mixed C_3/C_4 communities, those resource limits that currently maintain plant composition may have a greater impact than the CO_2 fertilizer effect on C_3 photosynthesis. In the tallgrass prairie, water stress and time of N availability favor C_4 species, and the partial alleviation of water stress under elevated CO_2 likely gives the C_4 species a greater competitive advantage. Over the five years of CO_2 fumigation in tallgrass prairie, the C_3 grasses have declined in the stand. Speculation based on greenhouse studies that C_3 species will have a competitive advantage in natural ecosystems is likely an oversimplification and care should be taken regarding prediction of species composition changes.

A reduction in tissue N concentration under elevated CO_2 reported by others was also observed in tallgrass prairie exposed to elevated CO_2 for species with increased biomass production as well those without increased production. The reduction was likely from dilution of a fixed N supply as well as a reduced N requirement. The greater total N in above- and belowground biomass indicates increased availability or increased acquisition capability under elevated CO_2. The apparent reduced N requirement may allow for increased biomass production under elevated CO_2 without increased N availability, or the apparent improved N acquisition may allow for sustained increased biomass production under elevated CO_2. However, the potential reduction in N availability from reduced decomposition rates may result in a N limitation to increased biomass production under elevated CO_2. The addition of N fertilizer to tallgrass prairie shows that biomass production response to elevated CO_2 is limited already by N availability, and further reductions in N availability may preclude substantial response to elevated CO_2.

Whether natural ecosystems will be sources or sinks for carbon is of great importance to future atmospheric CO_2 concentrations. In tallgrass prairie, preliminary indications are that carbon is accumulating under elevated CO_2 in surface soils. It appears that at least a portion of that increased carbon is in the labile pool, since addition of N to the system results in a greater microbial respiration on areas with elevated CO_2. The increased soil microbial N content in CO_2-enriched plots indicates N immobilization due to increased carbon allocation below ground resulting in increased C/N ratios. In the absence of increased N availability to natural ecosystems, it is likely that soil carbon quantity will increase in tallgrass prairie and be a substantial sink for carbon as atmospheric CO_2 concentration rises.

Our research casts some doubt as to whether leaf- or plant-level responses to CO_2 enrichment measured under greenhouse conditions can be scaled to the ecosystem level. Certainly, the mechanisms involved in plant response to elevated CO_2 must be derived at the leaf and plant level and may be essential in understanding responses at the ecosystem level. However, our data indicate that ecosystem level responses must be measured under field conditions to avoid erroneous conclusions.

Table 1. Common speculations summarized from the literature concerning responses of natural ecosystems to elevated CO_2 and results from a CO_2-enriched C_4-dominated tallgrass prairie.

Common Speculation	Results from a CO_2-enriched C_4-dominated tallgrass prairie
Biomass production of C_3 species will increase more under elevated CO_2 than C_4 species and interspecific competition will favor C_3 species.	C_4 grass species had increased biomass production and C_3 grass species biomass production was unaffected by elevated CO_2. Elevated CO_2 favored C_4 species with C_3species declining in the stand.
Ecosystem-level water use efficiency will be enhanced under elevated CO_2.	Increased biomass production under elevated CO_2 in years with water stress indicated increased water use efficiency. In all years elevated CO_2 reduced water use at the ecosystem level.
Photosynthetic capacity of C_3 species will increase, but C_4 species will not have increased photosynthetic capacity under elevated CO_2.	Reduced water stress under elevated CO_2 appeared to protect the photosynthetic capacity in dry years compared to ambient, resulting in a greater capacity under those conditions.
Increased biomass production under elevated CO_2 will not be sustained due to nutrient limitations, particularly nitrogen.	Biomass production response to elevated CO_2 appeared to be nitrogen limited.
Nitrogen concentration in plant tissues will be reduced and fiber concentration increased under elevated CO_2 and that will slow decomposition and nutrient cycling.	Under elevated CO_2, nitrogen concentration was reduced and fiber concentration increased under elevated CO_2. Belowground organic matter decomposition appeared to be reduced.
Changes in forage quality under elevated CO_2 will affect ruminant herbivory.	Forage quality of sheep diet samples was reduced under elevated CO_2.

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