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Water vapour fluxes and their impact under elevated CO₂ in a C4-tallgrass prairie

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Abstract

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. In addition, there was a reduction in stomate number of the C4 grass, Andropogon gerardii Vitman, and the C3 dicot herb, Salvia picheri Tort, 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. The result was an increased above- and belowground biomass production in years when water stress was frequent.

Keywords: biomass production, elevated CO₂, sap flow, stomatal conductance, tallgrass prairie, water vapour flux

Introduction

The predicted increase in atmospheric CO₂ has fuelled both research and speculation with regard to its impact. The initial hypotheses were that there would be significant increases in both productivity and competitive ability of C3 plants compared to C4 in natural ecosystems resulting from increased photosynthetic capacity due to reduced oxygen competition (Bazzaz 1990). While there have been few ecosystem-level studies to test those hypotheses, there has been evidence to suggest that C4-dominated ecosystems may respond to elevated CO₂ with increased production due to improved water use efficiency and C4 dominance maintained or strengthened (Owensby et al. 1993). Ecosystem-level responses to elevated CO₂ will be mediated through the interaction of elevated CO₂ with those processes that normally limit productivity or competitive ability. If the ecosystem is normally limited by water or nitrogen availability (Owensby et al. 1969; Field et al. 1992), then the impact that elevated CO₂ has on water or nitrogen availability and/or requirement will determine ecosystem response. Only in those rare cases in natural ecosystems where atmospheric CO₂ is the primary limiting resource will the hypotheses that C3 species will benefit to the detriment of C4 species be true.

Water stress in grasslands is frequent, particularly in those dominated by C4 species (Doliner & Jolliffe 1979). Increased atmospheric CO₂ has the potential both to reduce water loss through changes in stomatal conductance (gₛ) (van Bavel 1974) and to increase water acquisition through increased root growth (Oechel & Strain 1985; Owensby et al. 1993). Coupled with increased carbon assimilation associated with elevated CO₂, reduced gₛ provides increased water use efficiency (WUE) (Eamus 1991; Newton 1991). Stomatal conductance under elevated CO₂ is typically reduced by 30–50% in both C3 and C4 plants (Eamus & Jarvis 1989; Woodward et al. 1991).
Eamus (1991) indicated that stomatal behaviour is optimal with respect to water loss and carbon gain. Therefore, reduced water loss under elevated CO$_2$ has the potential to forestall water stress thereby maintaining optimal carbon fixation, and in natural grassland ecosystems, which are often water-stressed, it is likely more important in its effect on primary production than the direct effect of elevated CO$_2$ on C3 or C4 photosynthesis.

The long-term impact of elevated CO$_2$ has been studied from 1989 to the present on a native tallgrass prairie north of Manhattan, KS, USA (39.12°N, 96.35°W, 324 m above mean sea level). Vegetation on the site was a mixture of C3 and C4 species, dominated by the C4 grasses, Andropogon gerardii Vitman and Sorghastrum nutans (L.) Nash. Subdominants included Poa pratensis L. (C3), Bouteloua curtipendula (Michx.) Torr. (C4), and Sporobolus asper var. asper (Michx.) Kunth (C4). Members of the sedge family (C3) made up 51% of the composition. Principal forbs (all C3) included Vernonia baldwinii var. interior (Small) Schub., Ambrosia psilostachya DC., Artemisia ludoviciana Nutt., and Psoralea tenuiflora var. floribunda (Nutt.) Rydb. Average peak above-ground biomass (dry wt.) of 425 g m$^{-2}$ occurs in early August, of which 35 g m$^{-2}$ is from forbs (Owensby & Anderson 1967). Soils in the area are transitional from Udolls to Ustolls (Tully series: fine, mixed, mesic, montmorillonitic, Pachic Argiudolls). Slope on the area is 5%. The 30-year average annual precipitation is 840 mm, with 520 mm occurring during the growing season.

Treatments, replicated three times, were ambient CO$_2$-no chamber (A), ambient CO$_2$-with chamber (CA), and 2x ambient CO$_2$-with chamber (CE). The open-top chambers used in the study were 4.5 m in diameter by 4 m in height, with a conetop baffle that reduced the top opening to 1.5 m. Precipitation that was intercepted by the cone-top baffle was collected in gutters and immediately applied to the plots using a sprinkler system. Carbon dioxide enrichment was continuous from April one until late October each year. The polyethylene film covering the chamber frame was removed in late October and replaced in late March of each year. All treatments were sustained on the same plots over the 7-year period. For a detailed description of the fumigation and data acquisition and control systems, see Owensby et al. (1993). In 1993, additional plots were added to the study area to determine carbon and water vapour fluxes under the same CO$_2$ treatments. These chambers were modified to meet the requirements for flux measurements (Ham et al. 1993).

In this report, we synthesize the impacts of elevated CO$_2$ on water relations in tallgrass prairie from results obtained to date, and we describe methodology required to accurately measure carbon and water vapour fluxes using open-top chambers. We have measured stomatal conductance, stomate size and density, stomatal response to sun/ shade events, xylem pressure potential, soil water, sapflow, canopy carbon and water vapour fluxes and above- and below-ground biomass. Using these measurements, we conclude that the primary response to elevated CO$_2$ in tallgrass prairie is mediated through reduced water use.

**Abbreviations**

A  ambient CO$_2$ treatment
CA  ambient CO$_2$ treatment with chamber
CE  twice ambient CO$_2$ treatment with chamber
ET  evapotranspiration
g$_s$  stomatal conductance
LAI  leaf area index
NCE  net carbon exchange
PAR  photosynthetically active radiation
Vleaf  leaf water potential
WUE  water use efficiency
Ψ  xylem pressure potential

**Open-top chambers**

Open-top chambers are an economical means of testing ecosystem-level responses to elevated CO$_2$. 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 (Owensby et al. 1993). 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.

**Soil barrier**

Chamber design is particularly important when measuring the impact of elevated CO$_2$ 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 CO$_2$ 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 (Quadri et al. 1994; Clothier et al. 1996). 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...
Table 1. Simulated values of CO_2 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. CO_2 concentrations at the upper boundary (aerial CO_2) were held constant at 345 ppm. Values of CO_2 flux to the atmosphere were derived using a two-dimensional advection diffusion model, we simulated the impact of 0, 1, and 2 Pa pressure inside an open-top chamber on CO_2 flux from the soil surface and the volume flux of air into the soil (Table 1). The results indicate that soil-surface CO_2 flux was substantially reduced and that a large amount of air was forced into the soil. The average CO_2 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 CO_2 flux. When chamber CO_2 flux under elevated CO_2 is measured, that air movement into the soil and the subsequent reduced soil CO_2 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 CO_2 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 diam.) 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 CO_2 flux between the ambient OTCs and control plots (Ham et al. 1995). We measured flux on a weekly basis over the entire growing season using a soil-surface chamber.

<table>
<thead>
<tr>
<th>Pressure differential</th>
<th>Soil surface CO_2 flux (umol m(^{-2}) s(^{-1}))</th>
<th>Volume air flow into the soil within the chamber (m(^3) air m(^{-2}) area d(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>(P_{\text{chamber}} - P_{\text{atmosphere}}) (Pa)</td>
<td>0</td>
<td>4.2</td>
</tr>
<tr>
<td>1</td>
<td>3.6</td>
<td>1.03</td>
</tr>
<tr>
<td>2</td>
<td>3.2</td>
<td>2.14</td>
</tr>
</tbody>
</table>

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 CO_2 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 CO_2 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.

Pressure adjustment

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 (Kanemasu et al. 1974; Nakayama & Kimball 1988). Using a two-dimensional advection diffusion model, we simulated the impact of 0, 1, and 2 Pa pressure inside an open-top chamber on CO_2 flux from the soil surface and the volume flux of air into the soil (Table 1). The results indicate that soil-surface CO_2 flux was substantially reduced and that a large amount of air was forced into the soil. The average CO_2 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 CO_2 flux. When chamber CO_2 flux under elevated CO_2 is measured, that air movement into the soil and the subsequent reduced soil CO_2 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 CO_2 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 diam.) 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 CO_2 flux between the ambient OTCs and control plots (Ham et al. 1995). We measured flux on a weekly basis over the entire growing season using a soil-surface chamber.

Effects of elevated CO_2 on water use

Stomatal conductance

Reductions in water use by plants under elevated CO_2 ultimately come from a reduced stomata1 conductance (g_s) of water vapour from the leaf. Changes in leaf area, canopy structure, and different stomata1 responses among species will modify the effects of elevated CO_2 on stomata1 conductance making scaling to the canopy level difficult. In order to determine the relationships of leaf-level stomata1 conductance to higher levels, we have measured g_s regularly for A. gerardii, and occasionally for S. nutans and various forb and woody species. In 1991 than 1992, A. gerardii g_s was significantly lower (by 21–51%) in CE than in CA or A plots during early, mid, and late growing season (Knapp et al. 1993a). In 1993, in conjunction with sap flow measurements, we showed that big bluestem g_s was 6.6 mm s\(^{-1}\) in CA and A plots and 3.2 mm s\(^{-1}\) in CE plots, and indiangrass g_s was 5.0 mm s\(^{-1}\) CA and A plots and 3.1 mm s\(^{-1}\) in CE plots (Bremer et al. 1996). Later in 1994, Knapp et al. (1996) measured seasonal responses in stomatal conductance (g_s) to elevated CO_2 among 12 tallgrass prairie species that differed in growth form and rate. During June, when water availability was high, elevated CO_2 resulted in decreased g_s in 10 of the 12 species measured. Lower g_s under elevated CO_2 (<< 50% lower) occurred in growth forms with the highest potential growth rates (C3 and C4 grasses, and C3 ruderals). In contrast, no difference was found in g_s of two C3 shrubs under elevated and ambient CO_2. During a dry period in September, lower g_s at elevated CO_2 was measured in only two species (a C3 ruderal and a C4 grass) and higher g_s at elevated CO_2 was measured in the shrubs and a C3 forb. The greater g_s at elevated CO_2 was attributed to enhanced leaf water potential (\(v_{\text{leaf}}\)) resulting from increased soil water availability and/or greater root biomass. After rainfall in September, only lower g_s was measured in response to elevated CO_2. Thus, there was significant interspecific variability in stomata1 responses to CO_2 that may be related to growth form or rate and to plant water relations. That the response was not uniform throughout the season nor among species confirms the need to consider interactions
between indirect effects of elevated CO₂ on plant water relations and direct effects of elevated CO₂ on gs, particularly for ecosystems in which water availability often limits productivity.

Stomatal response to sunny shade events
Stomates open and close in response to sun/ shade events (Knapp et al. 1993b), and the length of time that it takes for the stomate to close affects water loss. In those species for which stomata1 response time to the shade event is slow, water loss is greater than in those species with faster response times. Under elevated CO₂ stomata1 response to sunlight may impart additional water savings in A. gerardii, the dominant C4 grass in tallgrass prairie (Knapp et al. 1993b). In A, CA, and CE plots, A. gerardii was subjected to fluctuations in sunlight similar to that resulting from intermittent clouds or within canopy shading (full sun > 1500 umol m⁻² s⁻¹ vs. shade 350 umol m⁻² s⁻¹) and stomata1 conductance measured. Time constants describing stomata1 responses were significantly lower (29-33%) at elevated CO₂. Using a statistically based simulation model (Knapp 1992, 1993), the effect of different stomata1 response times between ambient and elevated CO₂ on transpiration were simulated. That simulation indicated that water loss was reduced by 6.5% due to more rapid stomata1 responses in elevated CO₂ treatments compared to ambient. Leaf xylem pressure potential increased during periods of sunlight variability, indicating that more rapid stomata1 responses at elevated CO₂ enhanced plant water status. It is important to note that CO₂-induced alterations in the kinetics of stomata1 responses to variable sunlight will likely amplify direct effects of elevated CO₂ and increase WUE in all ecosystems.

Stomata1 density, distribution, and size
Many authors have theorized that, as atmospheric CO₂ increases, stomatal density and/or size will decrease due to the reduced requirement for gas exchange. Those studies that have measured stomata1 density have not shown a consistent decline in density with increased atmospheric CO₂ and have largely not been conducted in intact ecosystems (Woodward 1987; Korner 1988; Woodward & Bazzaz 1988; Ferris & Taylor 1994). Knapp et al. (1994) measured stomata1 density, abaxial and adaxial distribution, and guard cell length of two common tallgrass prairie species, A. gerardii, and the C3 forb, Salvia pitcheri, in A, CA, and CE plots throughout the 1993 growing season. After full canopy development, stomata1 density on abaxial and adaxial surfaces and guard cell length were determined. High rainfall amounts during the 1993 growing season minimized water stress in these plants (leaf xylem pressure potential was usually > -1.5 MPa in A. gerardii) and also minimized differences in water status among treatments. In A. gerardii, stomata1 density was significantly higher (190 ± 7 mm⁻²; mean ± SE) in plants in A plots compared to plants in CA plots (161 ± 5 mm⁻²). Thus, there was a significant ‘chamber effect’ on stomata1 density. At elevated levels of CO₂, stomata1 density was even lower (P < 0.05; 121 ± 5 mm⁻²). Most stomata were on abaxial leaf surfaces in A. gerardii, but the ratio of adaxial to abaxial stomata1 density was greater at elevated levels of CO₂ than at ambient. In S. pitcheri, stomata1 density was also significantly higher for plants in A plots (235 ± 10 mm⁻²) compared to plants in CA plots (140 ± 6 mm⁻²). However, stomata1 density was greater in CE plots (218 ± 12 mm⁻²) compared to plants in CA plots. The ratio of stomata on adaxial vs. abaxial surfaces did not vary significantly in this herb. Guard cell lengths were not significantly affected by any treatment for either species. These results indicate that stomata1 density responses to elevated CO₂ are species specific.

Sap flow
Measurement of transpiration of the entire plant both improves estimates of elevated CO₂ effects on water use by plants and offers the opportunity to measure differences among species at the whole plant level. Heat balance sap flow gauges (Senock & Ham 1993, 1995) were used to measure transpiration in ironweed (Vernonia baldwynii var. inferior (Small) Schult.), a C3 forb, and on individual grass culms of A. gerardii and S. nutans, both C4 grasses, in CE, CA and A plots in 1993 (Bremer et al. 1996). Because of frequent rainfall during 1993, all data were collected under well-watered conditions. Comparisons of plants in the CE and CA plots showed that sap flow was reduced by 33% in ironweed, 18% in big bluestem, and 22% in indiangrass under CO₂-enrichment. Soil water was consistently highest under elevated CO₂, reflecting the lower transpiration with that treatment. During sap flow measurements, whole-plant stomata1 resistance to water vapour flux in big bluestem was 103 s m⁻¹ in CA plots and 194 s m⁻¹ in CE plots. Whole plant transpiration was considerably lower under elevated CO₂ than in ambient CO₂, but the difference between gs for CE and CA was even greater, indicating the need to measure transpiration at least at the whole plant level or measure gs for leaves throughout the plant canopy in order to adjust for differences in radiation and vapour pressure deficit.

Xylem pressure potential
Xylem pressure potential (ψ) reflects the water status of a plant at a given point in time and integrates the soil water and environmental impacts on plant water status. Therefore, ψ offers a better estimate of the effects of elevated

CO$_2$ on water status of plants growing in competition with others in the ecosystem. Owensby et al. (1993) measured the diurnal course of $\psi$ on 29 July 1991. Both midday $\psi$, between 12.00 and 13.00 hours, CST, and pre-dawn $\psi$ were estimated at approximately weekly intervals in CE, CA, and A plots from 30 May to 25 September 1991, a dry year. Midday $\psi$ indicated less moisture stress for A. gerardii plants in CE plots compared to those in CA or A plots. The seasonal mean midday $\psi$ of A. gerardii was $-1.89$ MPa $\pm 0.03$ (SE) for the CE plots, $-2.18$ MPa $\pm 0.03$ for the CA plots, and $-2.38$ MPa $\pm 0.04$ for the A plots. The diurnal $\psi$ on 29 July 1991 of A. gerardii was less negative in CE plots than in CA and A plots from 12.00 to 14.00 hours, CST, and A. gerardii $\psi$ was less negative at 20.00 hours in CE and CA plots than in CA and A plots from 12.00 to 14.00 hours, CST, and A. gerardii $\psi$ did not differ among treatments. Knapp et al. (1993a) measured midday $\psi$ of A. gerardii plants in the CE, CA, and A plots throughout the 1991 and 1992 growing seasons. Midday $\psi$ was significantly higher (less negative) throughout the season in plants grown at elevated CO$_2$ during both years. When averaged over the growing season, $\psi$ was $0.48-0.70$ MPa lower in 1991 than 1992. Elevated CO$_2$ improves plant water status of A. gerardii plants growing in a natural stand compared to ambient CO$_2$ levels.

Ecosystem-level water vapour fluxes

Whole chamber water vapour fluxes at the ecosystem level offer the best opportunity to scale estimates of the impact of elevated CO$_2$ on water use to the landscape level. In 1993, we measured whole-chamber water vapour 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-day period when the canopy was near peak biomass (LAI 4.5) and soil water was not limiting. Results showed that elevated CO$_2$ reduced evaporative transpiration by 22% and also increased NCE compared to ambient CO$_2$ (Ham et al. 1994).

Impacts of improved water status under elevated CO$_2$

The impact of the reduced stomatal conductance, the reduced transpiration (sap flow measurements), and the improved water status of the plant (xylem pressure potential) under elevated CO$_2$ are reflected by the lower ET at the ecosystem level. Daily ET was 22% lower with CO$_2$ enrichment compared to ambient, sap flow was 18–33% lower, and canopy resistance to water vapour flux was 24 s m$^{-1}$ greater with CO$_2$ enrichment than at ambient. Not surprisingly, greater NCE at the ecosystem level under elevated CO$_2$ was primarily caused by continued photosynthesis in the CE plots when water stress stopped leaf gas exchange in the CA plots. Greater NCE and lower ET resulted in higher daytime water use efficiency (WUE) in elevated CO$_2$ than in ambient (9.84 vs. 7.26 g CO$_2$ kg$^{-1}$ H$_2$O). Additionally, whole-chamber data collected on days with high evaporative demand showed that ecosystem quantum yield ($\mu$mol CO$_2$ mol PAR$^{-1}$) in the CE plots remained high in the afternoon period, but decreased in the CA plots (CA = 0.021 $\mu$mol mol$^{-1}$, CE = 0.029 $\mu$mol mol$^{-1}$). These data tend to confirm the leaf-level measurements of Owensby et al. (1993) and Knapp et al. (1993a) that showed more favourable leaf water potentials under elevated CO$_2$. Lower sap flow and greater canopy resistance to water vapour transport in the CE plots than in the CA plots provide further evidence that CO$_2$ strongly influenced the hydrology and plant water relations of the ecosystem. Data collected at the leaf, whole-plant, and ecosystem scale all suggest that C4 plant communities exposed to elevated CO$_2$ will maintain a more favourable water status when subjected to periodic moisture stress. However, if water availability is sufficient to not limit growth, there will not be an improved biomass production under elevated CO$_2$.

The improved water status of the ecosystem under elevated CO$_2$, when water limits ecosystem production, explains the increased above- and below-ground biomass production in dry years reported by Owensby et al. (1993, 1996) (Figs 1 and 2). Compared to ambient CO$_2$ levels, elevated CO$_2$ increased production of C4 grass species, but not of C3 grass species. Below-ground biomass production, estimated by root ingrowth bags, responded similarly to that of the above-ground, but the relative increase was greater than that above-ground during dry years. Relative amounts of C4 grasses did not change from 1989 to 1996, but P pratensis (C3) declined, and C3 forbs increased in the stand exposed to elevated CO$_2$ compared to ambient. It is likely that the reduction in C3 grasses was partly due to

Fig. 1 Mean total above-ground peak biomass (g m$^{-2}$) for native tallgrass prairie exposed to twice-ambient and ambient CO$_2$ concentrations for the indicated years. Means within species or species groups with a common letter do not differ [Duncan's Multiple Range Test, $P<0.10$].

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the lack of grazing, which allowed the taller C4 grasses to quickly overtop the shorter C3 species, but, since the C3 grass populations in the ambient CO2 treatments remained relatively high, the primary force behind the decline of the C3 grasses was probably the increased biomass and leaf area in CO2-enriched plots. There was also drought in two of the initial three years in the study, which favoured the C4 species. The taller C3 forbs increased under elevated CO2, supporting the hypothesis that canopy response (competition for light) associated with CO2 enrichment affected interspecific competition. The major limit to C3 grasses in the northern Kansas Flint Hills is nitrogen, while C4 grasses are limited more by water, and the relatively high, the primary force behind the decline of the C3 grasses was probably the increased biomass and leaf area in CO2-enriched plots. There was also drought in two of the initial three years in the study, which favoured the C4 species. The taller C3 forbs increased under elevated CO2, supporting the hypothesis that canopy response (competition for light) associated with CO2 enrichment affected interspecific competition. The major limit to C3 grasses in the northern Kansas Flint Hills is nitrogen, while C4 grasses are limited more by water, and the relatively greater impact of elevated CO2 on water relations made it unlikely that the C3 grasses would competitively displace the C4 grasses component.

Elevated CO2 in the tallgrass prairie increases water use efficiency, and in ecosystems in which water availability is a primary limiting resource, it will increase primary production until some other resource limits growth.

Acknowledgements

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