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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 stomata1 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 CO_2 . Stomata1 conductance was reduced by as much as 50% under elevated CO_2 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 pitcheri Tort, under elevated CO_2 compared to ambient. The result was an improved water status for plants exposed to elevated CO_2 which was reflected by a less negative xylem pressure potential compared to plants exposed to ambient CO_2 . Sap flow rates were 20 to 30% lower for plants exposed to elevated CO_2 than for those exposed to ambient CO_2 . At the canopy level, evapotranspiration was reduced by 22% under elevated CO_2 . The reduced water use by the plant canopy under elevated CO_2 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 CO_2 , sap flow, stomata1 conductance, tallgrass prairie, water vapour flux

Introduction

The predicted increase in atmospheric $\ensuremath{\text{CO}}_2$ 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

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water or nitrogen availability (Owensby *et al. 1969*; Field *et al.* 1992), then the impact that elevated CO_2 has on water or nitrogen availability and/or requirement will determine ecosystem response. Only in those rare cases in natural ecosystems where atmospheric CO_2 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 CO_2 has the potential both to reduce water loss through changes in stomatal conductance (g,) (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 CO_2 , reduced g_s provides increased water use efficiency (WUE) (Eamus 1991; Newton 1991). Stomatal conductance under elevated CO_2 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 CO2 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 510% of the composition. Principal forbs (all C3) included Vernonia buldwinii var. interior (Small) Schub., Ambrosia psilostachya DC., Artemesia ludovicianu 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 Ustolls to Udolls (Tully series: fine, mixed, mesic, montmorillonitic, Pachic Argiustolls). 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 CO2no chamber (A), ambient CO2-with chamber (CA), and 2x ambient CO₂-with chamber (CE). The open-top chambers used in the study were 4.5 m in diameter by 4 m in height, with a cone-top 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 stomata1

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	evatranspiration
gs	stomata1 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: Ham *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. Pressureinside the chamber was simulated at 0, 1, and 2 Pa above atmospheric pressure. The CO_2 concentrations at the upper boundary (aerial CO_2) was held constant at 14.5 umol m^{-3} (350 ppm) both inside and outside the chamber.

Pressure differential P _{chamber} - P _{atmosphere} (Pa)	Soil surface CO ₂ flux (µmol m ⁻² s ⁻¹)	Volume air flow into the soil within the chamber $(m^3 \text{ air } m^{-2} \text{ area } d^{-1})$
0.	4.2	0
1	3.6	1.03
2	3.2	2.81

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 l-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 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 CO_2 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

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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 CO₂ on water use

Stomata1 conductance

Reductions in water use by plants under elevated CO₂ 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 CO2 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 gs 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 gs 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 stomata1 conductance (g,) to elevated CO2 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 gs 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 $g_{s}\xspace$ of two C3 shrubs under elevated and ambient CO2. 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 CO₂ was measured in the shrubs and a C3 forb. The greater gs at elevated CO2 was attributed to enhanced leaf water potential (vleaf) 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 CO₂. Thus, there was significant interspecific variability in stomata1 responses to CO₂ 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 CO_2 on plant water relations and direct effects of elevated CO_2 on $g_{s\prime}$ particularly for ecosystems in which water availability often limits productivity.

Stomata1 response to sunlshade 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 stomatal 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

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Many authors have theorized that, as atmospheric CO_2 increases, stomata1 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 \pm 7 mm⁻²; mean \pm SE) in plants in A plots compared to plants in CA plots $(161 \pm 5 \text{ mm}^{-2})$. Thus, there was a significant 'chamber effect' on stomata1 density. At elevated levels of CO2, stomata1 density was even lower $(P < 0.05; 121 \pm 5 \text{ mm}^{-2})$. Most stomata were on abaxial leaf surfaces in A. gerardii, but the ratio of adaxial to abaxial stomatal 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 $(235 \pm 10 \text{ mm}^{-2})$ compared to plants in CA plots (140 \pm 6 mm⁻²). However, stomata1 density was greater in CE plots (218 \pm 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 baldwini var. inferior (Small) Schub.), 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, wholeplant 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 CO_2 than in ambient CO_2 , 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 g_s 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

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CO₂ on water status of plants growing in competition with others in the ecosystem. Owensby et al. (1993) measured the diurnal course of ψ on 29 July 1991. Both midday ψ , between 12.00 and 13.00 hours. CST, and pre-dawn ψ were estimated at approximately weekly intervals in CE, CA, and A plots from 30 May, to25 September 1991, a dry year. Midday ψ indicated less moisture stress for A. gerardii plants in CE plots compared to those in CA or A plots. The seasonal mean midday A. gerardii y was = 1.89 MPa ± 0.03 (SE) for the CE plots, -2.18 MPa ± 0.03 for the CA plots, and -2.38 MPa \pm 0.04 for the A plots. The diurnal ψ 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 ψ was less negative at 20.00 hours in CE and CA plots than in A plots. Predawn A. gerardii v did not differ among treatments. Knapp et al. (1993a) measured midday ψ of A. gerardii plants in the CE, CA, and A plots throughout the 1991 and 1992 growing seasons. Midday w was significantly higher (less negative) throughout the season in plants grown at elevated CO₂ during both years. When averaged over the growing season, ψ was 0.48-0.70 MPa lower in 1991 than 1992. Elevated CO2 improves plant water status of A. gerardii plants growing in a natural stand compared to ambient CO₂ levels.

Ecosystem-level water vapourfluxes

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 evapotranspiration by 22% and also increased NCE compared to ambient CO_2 (Ham *et al.* 1994).

Impacts of improved water status under elevated $\ensuremath{\text{CO}}_2$

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

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Fig. 1 Mean total above-ground peak biomass (g m⁻²) for native tallgrass prairie exposed to twice-ambient and ambient CO₂ 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].

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 H₂O). Additionally, whole-chamber data collected on days with high evaporative demand showed that ecosystem quantum yield (µmol CO₂ mol PAR⁻¹) in the CE plots remained high in the afternoon period, but decreased in the CA plots (CA $0.021 \ \mu mol \ \mu mol^{-1}$, CE = 0.029 ymol μ 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 CO₂. Lower sap flow and greater canopy resistance to water vapour transport in the CE plots than in the CA plots provide further evidence that CO₂ 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 CO₂.

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. 2 Root biomass (g m⁻²) in ingrowth bags to a 15 cm depth in tallgrass prairie exposed to twice ambient and ambient CO_2 concentrations for the indicated years. Data are means of four bags per plot in 1990 and eight bags per plot in the other years. Means with a common letter within year do not differ [Duncan's Multiple Range Test, P < 0.10].

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 CO_{2} , 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 CO_2 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.

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References

- Bazzaz FA (1990) The response of natural ecosystems to the rising global CO2 levels. Annual Reviews in Ecology and Systematics, 21, 167–196.
- Bremer DJ, Ham JM, Owensby CE (1996) Effect of elevated atmospheric carbon dioxide and open-top chambers on

transpiration in a tallgrass prairie. *Journal of Environmental Quality, 25,* 691-701

- Clothier BE, Green and SR, Katou H (1996) Multidimensional infiltration: points, furrows, basins, well, and disks. Soil Science Society of America Journal, 59, 286-292.
- Doliner LH, Jolliffe PA (1979) Ecological evidence concerning the adaptive significance of the C4 dicarboxylic acid pathway of photosynthesis. *Oecologia*, **38**, 23–34.
- Eamus D, Jarvis PG (1989) The direct effects of increase in the global atmospheric CO_2 concentration on natural and commercial temperate trees and forests. Advances in Ecological Research, 19, 1-57.
- Eamus D (1991) The interaction of rising CO₂ and temperatures with water use efficiency. *Plant, Cell and Environment*, **14**, 843-852.
- Field BF, Chapin III FS, Matson PA and Mooney HA (1992) Responses of terrestrial ecosystems to the changing atmosphere: A resource-based approach. Annual Reviews in Ecological Systematic, 23, 201–235.
- Ferris R, Taylor G (1994) Stomatal characteristics of four native herbs following exposure to elevated CO_2 . Annuls of Botany, 73, 447453.
- Ham JM, Owensby and CE, Coyne PI (1993) Technique for measuring air flow and CO_2 flux in large open-top chambers. Journal of Environmental Quality, 22, 759-766
- Ham JM, Owensby Coyne CE, DJ, Bremer PI (1995) Fluxes of CO₂ and water vapor from a prairie ecosystem exposed to ambient and elevated atmospheric CO₂. Agriculture and Forest Meteorology, 77, 73-93.
- Kanemasu ET, Powers and WL, Sij JW (1974) Field chamber measurements of CO₂ flux from soil surfaces. *Soil Science*, 118 (4), 233-237.
- Knapp AK, Hamerlynck and El', Owensby CE (1993a) Photosynthetic and water relations responses to elevated CO₂ in the C4 grass, Andropogon gerardii. International Journal of Plant Science, 154, 459–466.
- Knapp AK, Fahnestock and JT, Owensby CE (1993b) Elevated atmospheric CO_2 alters stomata1 response to sunlight in a C4 grass. *Plant, Cell and Environment,* **17**, 189–195.
- Knapp AK, Cocke M, Hamerlynck and EP, Owensby CE (1994) Effects of elevated CO₂ on stomata1 density and distribution in a C4 grass and a C3 forb under field conditions. *Annals* of *Botany*, 74, 595–599.
- Knapp AK, Hamerlynck El', Ham and JM, Owensby CE (1996) Responses in stomatal conductance to elevated CO_2 and opentop chambers in 12 grassland species that differ in growth form. *Vegetatio*, 125, 3141.
- Korner C (1988) Does global increase of CO_2 alter stomatal density? Flora, 181, 253–257.
- Nakayama FS, Kimball BA (1988) Soil carbon dioxide distribution and flux within the open-top chamber. *Journal* of *Agronomy, 80,* 394-398.
- Newton PCD (1991) Direct effects of increasing carbon dioxide on pasture plants and communities. New Zealand Journal of Agricultural Research, 34, 1-24.
- Oechel WC, Strain BR (1985) Native species responses to increased carbon dioxide concentration. In: Direct Effects of Increasing Carbon Dioxide on Vegetation (eds Strain BR, Cure JD), pp. 117–

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154. DOE/ER 0238. US Department of Energy, Washington, D.C.

- Owensby CE, Anderson KL (1967) Yield responses to time of burning in the Kansas Flint Hills, Journal of Range Management, 20, 12–16.
- Owensby CE, Hyde and RM, Anderson KL (1969) Effects of clipping and supplemental nitrogen and water on loamy upland bluestem range. *Journal of Range Management*, **23**, 341–346.
- Owensby CE, Coyne PI, Ham JM, Auen and LM, Knapp AK (1993) Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated levels of CO₂. *Journal of Applied Ecology*, **3**, 644-653.
- Owensby CE, Ham JM, Knapp AK, Rice CW, Coyne and PI, Auen LM (1996) Ecosystem-Level responses of Tallgrass Prairie to elevated *C02.* In: *Carbon Dioxide and Terrestrial Ecosystems* (eds Koch G, Mooney H), pp. 175-193. Physiological Ecology Series, Academic Press, New York.

- Quadri MB, Clothier BE, Angulo-Jaramillo R, Vauclin and M, Green SR (1994) Axisymmetric transport of water and solute underneath a disk permeameter: experiments and numerical model. *Soil Science Society American* Journal, 58, 696–703.
- Senock RS, Ham JM (1993) Heat balance sap flow gauge for small diameter stems. *Plant, Cell and Environment*, 16, 593-601.
- Senock RS, Ham JM (1995) Measuring water use by prairie grasses with heat balance sap flow gauges. Journal of Range Management, 48, 150-158.
- Van Bavel CHM (1974) Anti-transpirant action of carbon dioxide on intact sorghum plants. Crop Science, 14, 208–212.
- Woodward FI, Thompson and GB, McKee IF (1991) The effects of elevated concentrations of carbon dioxide on individual plants, populations, communities and ecosystems. *Annals of Botany*, **67**, 23–38.
- Woodward FI (1987) Stomata1 numbers are sensitive to increases in CO₂ from pre-industrial levels. *Nature*, 327. 617–618.

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