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ELEVATED ATMOSPHERIC CO₂ INCREASES WATER AVAILABILITY IN A WATER-LIMITED GRASSLAND ECOSYSTEM¹

Arthur L. Fredeen, James T. Randerson, N. Michele Holbrook, and Christopher B. Field²

ABSTRACT: Californian annual grassland on sandstone (moderately fertile) and serpentine (very infertile) soils at the Jasper Ridge Biological Preserve, Stanford, California, were exposed to ambient or elevated (ambient + 36 Pa CO₂) atmospheric CO₂ in open-top chambers since December 1991. We measured ecosystem evapotranspiration with open gas-exchange systems, and soil moisture with time-domain reflectometry (TDR) over 0-15 cm (serpentine) and 0-30 cm (sandstone) depths, at times of peak above ground physiological activity. Evapotranspiration decreased by 12 to 63 percent under elevated CO₂ in three consecutive years in the sandstone ecosystem ($p = 0.053$, $p = 0.162$, $p = 0.082$ in 1992, 1993, and 1994, respectively). In correspondence with decreased evapotranspiration, late-season soil moisture reserves in the sandstone were extended temporally by 10 ± 3 days in 1993 and by 28 ± 11 days in 1994. The effect of elevated CO₂ on soil moisture was greater in the drier spring of 1994 (419 mm annual rainfall) than in 1993 (905 mm annual rainfall). In the serpentine ecosystem, evapotranspiration and soil moisture reserves were not clearly affected by elevated CO₂. Soil water may be conserved in drought-affected ecosystems exposed to elevated CO₂, but the amount of conservation appears to depend on the relative importance of transpiration and soil evaporation in controlling water flux.

(**KEY TERMS:** elevated CO₂; annual grassland; evapotranspiration; soil moisture; water-use efficiency; time-domain reflectometry.)

INTRODUCTION

Some of the greatest challenges in global change research involve scaling CO₂ responses from the leaf to the ecosystem level (Field *et al.*, 1992; Field *et al.*, 1995; Körner, 1995). For example, physiologists have long known that increasing CO₂ concentration around

a leaf results in stomatal closing (Linsbauer, 1917) and decreased transpiration (see Ketellapper, 1963). Clear evidence that anthropogenic activities are resulting in increasing concentrations of atmospheric CO₂ (Keeling *et al.*, 1989) has stimulated major investments in CO₂ research, with foci on climatic and ecosystem effects. The role of elevated CO₂ in altering water balance through effects on stomatal conductance has received relatively little attention even though it has potential implications for both ecosystem and climatic processes (Field *et al.*, 1995).

Water flux from an ecosystem to the atmosphere can occur either through stomata (transpiration) or directly from soil or plant surfaces (evaporation). Transpiration is an important component of water flux in grasslands. Estimates of the percent of water movement to the atmosphere through transpiration range from 32 percent in Patagonian steppe (Paruelo and Sala, 1996) to 67 percent in Canadian prairie (De Jong and Hayhoe, 1984), with evaporation typically making up the majority of the difference. Leaf area index, stomatal conductance, and aerodynamic conductance of the soil surface are important variables in determining rates of evapotranspiration (Shuttleworth and Wallace, 1985).

To explore the effects of elevated CO₂ on ecosystem water flux, we examined evapotranspiration and soil moisture in two adjacent water-limited grassland ecosystems. The first, on a serpentine-derived soil, has relatively low plant productivity (100 to 200 g m⁻² yr⁻¹) and short-statured plants. The second

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ecosystem, on sandstone-derived soil, supports higher plant productivity (300 to 800 g m⁻² yr⁻¹) and taller plants (Field *et al.*, 1996). Leaf area indices are in the range of 1 to 2 in the serpentine grassland and 2 to 8 in the sandstone grassland (Turitzin, 1976). Soil surface characteristics also vary substantially between grasslands. The serpentine grassland has little standing litter during the growing season, while the sandstone grassland often has half as much standing litter as green biomass in the second year (Gamon *et al.*, 1993).

In the dominant species in the sandstone grassland, *Avena barbata*, leaf-level stomatal conductance and transpiration are strongly decreased in plants in high-CO₂ plots (Jackson *et al.*, 1994). The leaf-level CO₂ response of *Avena* is typical of observations on herbaceous plants (Morison, 1987) and somewhat larger than the mean for woody plants (Gunderson and Wullschlegel, 1994; Curtis, 1996). Here, we explore the implications of this leaf-level response for ecosystem water balance in cis-montane annual grassland in central California.

MATERIALS AND METHODS

Field Site and Open-Top Chambers

Sixty circular plots (0.65 m diameter) were selected on two adjacent annual grassland ecosystems on serpentine and sandstone derived soils at the Jasper Ridge Biological Preserve, Stanford, California. Ten plots on each soil type were left as controls (without chambers), ten received open-top chambers at ambient CO₂ and the remaining ten received open-top chambers at elevated CO₂ (ambient + 36 Pa CO₂). Air and elevated CO₂ open-top treatments were initiated in December of 1991 and have been maintained through the present. CO₂ fumigation was daytime only from December 1991 until June 1992. It has been continuous since October 1992. Additional information on the experimental setup and the plant species composition can be found in Field *et al.* (1996). Open-top chambers were polyethylene (0.1mm thick) cylinders with aluminum frames and overall dimensions of 1m height x 0.63 m diameter. Chambers sit on the soil surface and no barriers prevent roots from growing into or out of the chamber area. Air flow occurs at a rate of approximately 17 air changes min⁻¹, with a separate blower on each chamber. The higher than normal air flow makes it possible to maintain reliable CO₂ control without closing part of the chamber top with a frustrum, an important requirement for experiments watered by natural rainfall. Pure CO₂ is fed

into the blower inlet of each elevated CO₂ chamber and adjusted with needle valves. The CO₂ concentration in each elevated CO₂ chamber is monitored every 30 minutes with an IRGA (LI-6262, LICOR INC., Lincoln, Nebraska, USA).

Evapotranspiration

Measurements of ecosystem water flux were made with 'open' gas-exchange systems. In 1992, an open gas-exchange system modified from a leaf system was used (Fredeen and Field, 1995). This system, based on an IRGA (LI-6251, Li-COR Inc., Lincoln, Nebraska, USA) and a photosynthesis leaf chamber (PLC-3, ADC, Co., Hoddesdown, Herts, UK) moved air from the leaf chamber to a canopy chamber (0.3m height x 0.095 m diameter) in an open-system configuration. Pumps (Spectrex, Redwood City, California, USA) moved air through the canopy chamber at a rate equivalent to 1 air change min⁻¹. In 1993, we used the same canopy chamber but eliminated the leaf chamber, replacing its humidity sensors with a CO₂-H₂O IRGA (LI-6262, Li-COR Inc., Lincoln, Nebraska, USA). The 1993 system is described in greater detail in Fredeen *et al.* (1995).

The gas-exchange system used in 1994 measured CO₂ and H₂O flux from six entire open-top chambers every 45 minutes. Similar to the previous year, the 1994 system utilized an LI-6262 in differential mode for both CO₂ and H₂O vapor determinations. A second IRGA measured absolute concentrations of CO₂ and H₂O vapor. The system was open, with fluxes calculated from the difference between the quantity of CO₂ and H₂O transported into or out of the chamber volume. To minimize the effects of external turbulence on gas concentrations inside the systems, chambers were fitted with a clear polyethylene lid containing a 0.3 m tall by 0.03 m diameter chimney. The system operated with each chamber at a slight positive pressure (~200 Pa) possibly compromising the measurement of soil respiration. Air flow through each chamber was restricted approximately 40-fold to achieve measurable CO₂ and H₂O differentials between inlet and outlet gas streams. Approximately 4 to 5 minutes was required for a complete air change of the open-top chambers when fitted with the air restrictors and lids. Fluxes in each chamber were determined from 30 samples, collected at 1 second intervals, after sampling the gas from each chamber for 210 seconds. All data were recorded on a data logger (CR-10, Campbell Scientific, Logan, Utah, USA).

Since the gas exchange measurements led to substantial effects on air flow and chamber microclimate, the gas exchange system was in place on each chamber only one day out of four. For all gas-exchange

measurements, microclimate was similar for low and high CO₂ chambers. All the gas-exchange systems had substantial effects on photosynthetically active photon flux density, decreasing it by 15-20 percent. Air temperatures were often increased by several °C in the small chamber used in 1992 and 1993, while air and leaf temperatures were typically increased by 5°C in 1994, and sometimes by as much as 10°C.

Evapotranspiration was measured on Julian dates ranging from 93 to 112 (April 3 to April 22) coinciding approximately with times of peak above-ground biomass in both ecosystems. Gas-exchange was performed within two hours of solar noon. For 1992 and 1993, the data are one measurement from each of 10 chambers x 3 treatments x 2 soil types. For 1994, the data are from 12 chambers (2 CO₂ levels x 2 soil types x 3 replicates), using 20 to 30 measurements of water flux across the day from each chamber on two consecutive clear days. The chambers used for gas exchange in 1994 were selected to be characteristic of each treatment with respect to biomass.

Soil Moisture

Time-domain reflectometry (TDR) was used to determine the gravimetric moisture content of soils (Topp *et al.*, 1982). The TDR instrument consisted of a TDR cable tester (1502C, Tektronix Inc., Beaverton, Oregon, USA) and a coaxial cable (RG-58C) terminated in copper alligator clips. TDR clips were electrically shorted against one another to obtain a zero length location. Measurements of apparent wave guide length were made by mating the TDR clips with parallel vertical stainless steel (308) wave guides, 5 cm apart, protruding 1 cm from the soil surface. Two lengths of wave guides were used, 30 cm in the sandstone and 15 cm in the serpentine soil. The shorter wave-guide was used in the serpentine because the depth to bedrock was rarely much greater than 15 cm. Measurements were typically made at midday. Both grassland types were monitored in 1993. The sandstone alone was monitored in 1994.

The apparent length of the wave guide is related to soil water content because the speed of propagation of electromagnetic waves along wave guides is proportional to the inverse of the square root of the dielectric constant of the medium. Under non-saline conditions, the primary constituent affecting the dielectric constant of soils is water (Topp *et al.*, 1980). We developed an empirical calibration, which resulted in a third or fourth-order polynomial relationship between apparent wave guide length and gravimetric water content for each soil. This was achieved by sequentially adding water increments to the appropriate soil type, mixing soil and water thoroughly, replacing the

soil around the wave guides, and recording the apparent length of the wave guides on the TDR display. While this approach did not necessarily preserve the bulk density of the soil, later calibrations with controlled bulk densities produced similar relationships (Field, unpublished data).

Climate

A weather station, approximately 200 m away from the field chambers, continuously monitors temperature, relative humidity and precipitation. Total precipitation for the 1991-1992, 1992-1993, and 1993-1994 rainy seasons (October to April) was 695, 905, mm and 419 mm, respectively. Average relative humidity and air temperatures from the weather station were used in the modeling exercise below.

Modeling

Evapotranspiration was modeled with the Penman-Monteith equations for C3 plants implemented in PLANTMOD 2.1 (Greenhat Software, Armidale, NSW, Australia). Light curves were based on estimates for average canopy and climate conditions of the two grassland communities, serpentine and sandstone, at 35 and 70 Pa CO₂ on Julian date 105. We assumed a temperature of 25°C and a relative humidity of 29 percent, similar to monthly means for these variables at the nearby weather station for April of 1993 and 1994. We also assumed leaf area indices of 0.9 and 2.8, and canopy heights of 0.08 and 0.8 m for the serpentine and grassland communities, respectively, based on harvested biomass (Field *et al.*, 1996) and leaf area / biomass and height estimates (unpublished data).

RESULTS

Evapotranspiration

Evapotranspiration (ET) was measured at times of peak above ground biomass, approximately the first week of April in 1992 and 1994. In 1993, measurements were later than usual (at the end of the third week of April). Elevated CO₂ decreased ET in the sandstone from 12 to 63 percent, but had no effect or increased (not significant) ET in the serpentine relative to ambient controls in all three years (Table 1). The ET of canopies in non-chambered control locations was measured in 1993 only. Levels of ET were

57 and 23 percent higher in non-chambered sites relative to ambient CO₂ chambers in the serpentine and sandstone ecosystems in 1993, respectively (Table 1).

Canopy transpiration was simulated for C3 canopies with serpentine and sandstone grassland properties (Figure 1). Results suggest that both the absolute level of canopy transpiration and the relative effect of elevated CO₂ on canopy transpiration is reduced in a serpentine canopy relative to a sandstone canopy. At an average daily light level of 800 mol PAR m⁻² s⁻¹, the simulation suggests that canopy transpiration for the serpentine community would be approximately half that of the sandstone community. The relative decrease in canopy transpiration in response to elevated CO₂ was 42 percent lower on serpentine than on sandstone.

Soil Moisture

Soil moisture in the sandstone ecosystem was depleted more rapidly in open-top chambers receiving ambient CO₂, than in those receiving elevated CO₂ (Figures 2b, 2c). Moisture depletion in the control (no chamber) sites was similar to that in elevated CO₂ chambers (Figures 2b, 2c). In the sandstone ecosystem, soil moisture was significantly greater in elevated than in ambient CO₂ plots for three consecutive measurement dates, 21, 23, and 28 April (Julian dates 111, 113, and 118), 1993 (ANOVA followed by Tukey's HSD, $p < 0.05$) during the period when soil moisture depletion was most rapid (Figure 2b). In 1994, elevated CO₂ resulted in significantly higher soil moisture contents from Julian date 80 to 155 (ANOVA followed by Tukey's HSD, $p < 0.05$) (Figure 2c). Elevated CO₂ extended soil moisture temporally

by an average of 10 ± 3 days in 1993 and by 28 ± 11 days in 1994 from Julian dates 100 to 150 (~ April 10 to May 30). Soil moisture contents were not affected significantly by elevated CO₂ or chamber in the serpentine ecosystem at any point in the growing season (Figure 2a).

Figure 1. A Penman-Monteith Simulation of Canopy Transpiration, E (mm H₂O hr⁻¹) Versus Mean Daily Irradiance Incident on the Canopy ($\mu\text{mol PAR m}^{-2} \text{s}^{-1}$) Using Average Properties for Meteorological Inputs and Serpentine and Sandstone Community Canopies (see Materials and Methods) at 35 (ambient) and 70 (elevated) Pa CO₂.

TABLE 1. Effect of Elevated Atmospheric CO₂ (ambient + 35 Pa CO₂) and Ambient CO₂ in Comparison With Non-Chambered Controls on Evapotranspiration, ET (mm H₂O m⁻² h⁻¹) in Contiguous Serpentine and Sandstone Californian Annual Grassland Ecosystems. Means with standard errors shown. The percent effect of elevated CO₂ on ET relative to ambient CO₂ is shown for both ecosystems.

Grassland	Treatment	ET (1992)	ET (1993)	ET (1994)
Serpentine	Chamber Control	na	0.203 ± 0.067	na
	Ambient CO ₂	0.137 ± 0.032	0.129 ± 0.034	0.131 ± 0.021
	Elevated CO ₂	0.135 ± 0.032	0.140 ± 0.036	0.150 ± 0.025
	Percent CO ₂ Effect	-1	10	14
Sandstone	Chamber Control	na	0.192 ± 0.029	na
	Ambient CO ₂	0.176 ± 0.034	0.156 ± 0.038	0.211 ± 0.035
	Elevated CO ₂	0.139 ± 0.033	0.138 ± 0.025	0.129 ± 0.010
	Percent CO ₂ Effect	-21	-12	-39

Figure 2. Gravimetric Soil Moisture Content ($\text{g H}_2\text{O g}^{-1} \text{ soil}$) in Natural Californian Grassland Ecosystems on (a) Serpentine 1992-1993 and (b, c) Sandstone 1992-1993 and 1993-1994, Soils, Respectively; Grown Under Elevated Atmospheric CO₂ (ambient + 35 Pa CO₂: dashed line) and ambient CO₂ (solid line). Moisture was measured from 0-15 cm depth in the serpentine soil and from 0-30 cm in the sandstone soil. The mean standard error is shown.

DISCUSSION

Decreased transpiration and enhanced photosynthetic water use efficiency (decreases in water lost for carbon gained) are typically observed at the leaf level in plants after short-term (Morison, 1985) and long-term (e.g., Rogers *et al.*, 1983) exposure to elevated CO₂. This was certainly true for the biomass dominant in the sandstone ecosystem studied here. Both instantaneous and integrated measures of water-use efficiency were increased, and transpiration and conductance decreased, in leaves of *Avena barbata* exposed to elevated CO₂ in open-top chambers (Jackson *et al.*, 1994). Similar increases in leaf-level photosynthetic water-use efficiency and decreases in leaf and ecosystem transpiration were observed in container grown *Avena* exposed to elevated CO₂ (Fredeen and Field, 1995). In the sandstone grassland exposed to elevated CO₂, ecosystem evapotranspiration (ET) was decreased relative to the ambient CO₂ chamber control for three consecutive years (Table 1). In contrast, ET was unchanged or not significantly

increased by elevated CO₂ in contiguous serpentine grassland (Table 1).

Consistent with effects on ET, soil moisture reserves were extended for 10-28 days in the elevated-CO₂ chambers on sandstone, i.e., soil moisture levels in elevated-CO₂ chambers were reached 10-28 days after they were reached in ambient-CO₂ chambers (Figure 2). Decreases in ET and higher soil moisture levels have also been observed for C4-dominated tall-grass prairie exposed to elevated CO₂ (Bremer *et al.*, 1996). These results have important implications for production in drought-affected ecosystems, especially when conserved water coincides with fully developed photosynthetic surfaces, high photosynthetically active radiation and warm temperatures.

The ET in non-chambered control locations was measured in 1993. Levels of ET were 57 and 23 percent higher in non-chambered sites relative to ambient CO₂ chambers in the serpentine and sandstone communities, respectively (Table 1). The higher ET did not translate into lower moisture levels (Figure 2). On the contrary, moisture levels were higher in the non-chambered control as opposed to the ambient

CO₂ chamber. There are many possible reasons for this result. The most likely is that non-chambered control sites were not subjected to the continuous high air flow that was present within chambers. Thus, the instantaneous measures of ET (performed in a well-stirred chamber) would be much less reflective of the actual ET in non-chambered sites than in chambered sites.

In contrast with the sandstone, no extension of soil moisture by elevated CO₂ or chamber was observed in the serpentine grassland (Figure 2a). This result coincided with the absence of an effect of elevated CO₂ on ET in three years of serpentine measurements (Table 1). A possible explanation for this is that the lack of a root barrier in the chamber design may have allowed for greater lateral flow of soil moisture in the serpentine relative to the sandstone grassland chambers. This lateral transport might have been facilitated by reduced surficial litter, a large number of emergent rocks at the soil surface, and a shallow soil depth in the serpentine.

Another possibility is that the canopy characteristics of the serpentine community predispose it to evaporative as opposed to transpirational water loss, e.g., the canopy is sparse, short in stature (< 10 cm in height), shallow-rooted, and has a highly exposed soil surface. All of these factors would reduce the amount of transpiration, and therefore the relative importance of transpiration in the total evapotranspirational water loss from the ecosystem (Shuttleworth and Wallace, 1985). A simulation of the effects of elevated CO₂ on canopy transpiration in canopies with average properties of sandstone and serpentine communities supports this conclusion. The absolute level of canopy transpiration was halved and the relative decrease in canopy transpiration in response to elevated CO₂ was ~ 42 percent lower in communities with serpentine versus sandstone properties (Figure 1). Furthermore, modeled transpiration was a greater proportion of ET in sandstone than in the serpentine (see Table 1); i.e., assuming an average daily irradiance of 800 $\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$, modeled canopy transpiration was 45 and 74 percent of total ET in the serpentine and sandstone respectively at ambient CO₂. The $\delta^{13}\text{C}$ (Jackson, personal communication) and leaf level conductance (Field, personal communication) of leaves of serpentine species indicate an increase in water-use efficiency in response to elevated CO₂. Thus, it is likely that with an increased level of resolution in our measures of both soil moisture and ET, and without the severe edaphic limitations to growth in the serpentine, we might have also observed an extension of soil moisture reserves in the serpentine ecosystem in response to elevated CO₂.

At the canopy and regional scales, ET may be constrained by feedbacks related to energy balance and

the humidity of the planetary boundary layer (Jarvis and McNaughton, 1986; McNaughton, 1989; McNaughton and Jarvis, 1991; Kelliher *et al.*, 1993). These feedbacks potentially limit CO₂ effects on soil moisture, but only when the surface conductance (the combination of canopy and soil surface conductances) is large in relation to the boundary layer conductance. This can occur when vegetation is sparse and the soil surface is wet or when canopy conductance is very high, as in agricultural crops with abundant moisture and high leaf area indices. During the latter part of the growing season on Jasper Ridge, the soil surface is usually dry, leaf conductances are modest (Jackson *et al.*, 1994), and the leaf area indices are low. Under these conditions, canopy scale feedbacks on ET tend to be unimportant (Valentini *et al.*, 1995), and the results from the open-top chambers should be relevant at larger scales.

Only a small number of studies have quantified the effect of long-term CO₂ enrichment on water-use at the ecosystem level (Tissue and Oechell, 1987; Drake, 1989; Owensby *et al.*, 1993; Bremer *et al.*, 1996). This study is one of the first to report increased soil moisture in response to elevated CO₂, and the first to show it in a C3-dominated ecosystem. We provide evidence that elevated CO₂ can decrease ecosystem ET, and as a result, increase late-season soil water availability. Furthermore, decreased transpiration at the leaf level in the sandstone community (Jackson *et al.*, 1994) corresponds well with decreased ET at the ecosystem scale. Increased late-season soil water could have important implications for nutrient cycling, ability to set and fill seed, and species composition, especially the ratio and importance of early to late-season annuals in water limited ecosystems.

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