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Evapotranspiration and soil water content in a scrub-oak woodland under carbon dioxide enrichment

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Abstract

Leaf conductance often decreases in response to elevated atmospheric CO_2 concentration (C_a) potentially leading to changes in hydrology. We describe the hydrological responses of Florida scrub oak to elevated C_a during an eight-month period two years after C_a manipulation began. Whole-chamber gas exchange measurements revealed a consistent reduction in evapotranspiration in response to elevated C_a, despite an increase in leaf area index (LAI). Elevated C_a also increased surface soil water content, but xylem water deuterium measurements show that the dominant oaks in this system take up most of their water from the water table (which occurs at a depth of 1.5–3 m), suggesting that the water savings in elevated C_a in this system are primarily manifested as reduced water uptake at depth. Extrapolating these results to larger areas requires considering a number of processes that operate on scales beyond these accessible in this field experiment. Nevertheless, these results demonstrate the potential for reduced evapotranspiration and associated changes in hydrology in ecosystems dominated by woody vegetation in response to elevated C_a.

Keywords: elevated CO_2, evapotranspiration, hydrology, soil water content

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Introduction

Rising atmospheric CO_2 concentrations (C_a) will likely alter many aspects of ecosystem structure and function (Mooney *et al*. 1998). Plant photosynthesis increases with C_a (Drake *et al*. 1997), and this response can alter carbon cycling at the ecosystem level (Canadell *et al*. 1996). Elevated C_a, by increasing CO_2 concentrations within the leaf (Mott 1988), often decreases stomatal conductance (Morison 1987), though this effect is not universal (Saxe *et al*. 1998). The ecosystem consequences of reduced stomatal conductance in elevated C_a will depend on the degree of stomatal control over evapotranspiration (Jarvis & McNaughton 1986), as well as feedbacks operating at different spatial and temporal scales, including physiological acclimation (Medlyn *et al*. 2001), compensatory increases in leaf area index (LAI) (Jones *et al*. 1984; Samarakoon & Gifford 1995; Beerling *et al*. 1996) and soil evaporation (Wilson *et al*. 1999), increases in canopy temperature and vapour pressure deficit (Friend & Cox 1995), and entrainment by the surface and planetary boundary layers (Jacobs & DeBruin 1997; Wilson *et al*. 1999). Some of these feedbacks amplify, but most tend to reduce the consequences of reduced stomatal conductance at larger scales. Nevertheless, reduced stomatal conductance in response to elevated C_a can lead to reduced plant transpiration and evapotranspiration, changes with consequences ranging from increased soil water content and associated changes in soil processes (Hungate *et al*. 1997; Zaller & Arnone 1997; Arnone & Bohlen 1998; Niklaus *et al*. 1998) to increased water yield in watersheds (Idso & Brazel 1984; Hatton *et al*. 1992), to altered climate (Field *et al*. 1995; Sellers *et al*. 1996; Cox *et al*. 1999). Thus, determining the hydrological responses of terrestrial ecosystems to elevated C_a is critical for predicting ecosystem and landscape processes in a high C_a world.

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Reductions in evapotranspiration and/or increases in soil water content in response to elevated C_a have been documented in a number of herbaceous ecosystems, including annual grasslands (Field *et al*. 1997; Fredeen *et al*. 1997), tallgrass prairie (Ham *et al*. 1995; Bremer *et al*. 1996; Owensby *et al*. 1997), C3- and C4-dominated salt marsh stands (Arp 1991), alpine grassland (Diemer 1994), calcareous grassland (Niklaus *et al*. 1998; Stocker *et al*. 1999), and crop systems (Clifford *et al*. 1993; Kimball *et al*. 1999). Responses in woody systems are less clear. Stomatal conductance in coniferous trees tends to be less responsive to elevated C_a than in herbaceous species, and responses in deciduous tree species are intermediate (Curtis & Wang 1998; Saxe *et al*. 1998; Medlyn *et al*. 2001). Thus, in some forest ecosystems, small or nonexistent reductions in stomatal conductance may preclude a C_a-induced reduction in evapotranspiration. However, in the ecosystem considered here, Florida scrub oak, Lodge *et al*. (2001) measured 40% reductions in stomatal conductance in the dominant species, *Quercus myrtifolia* Willd., indicating the physiological potential for reduced evapotranspiration in response to elevated C_a.

Because trees are large, assessments of the effects of elevated C_a on evapotranspiration in forest ecosystems have primarily been confined to modelling approaches (Hatton *et al*. 1992; Friend & Cox 1995; Thornley & Cannell 1996). However, a number of studies have examined the effects of elevated C_a on sap flow rates in trees, and these show variable responses. For example, in a *Pinus taeda* forest, elevated C_a had no effect on stomatal conductance and whole-plant transpiration (Ellsworth *et al*. 1995; Pataki *et al*. 1998). While trees of *Quercus ilex* (Togentti *et al*. 1998) and *Quercus pubescens* (Togentti *et al*. 1999) growing near a natural CO_2 spring showed consistently lower rates of whole-tree water flux than paired trees growing away from the spring, this effect was primarily because trees growing near the spring had lower total leaf area rather than reduced water flux per unit leaf area. In 30-y-old *Pinus sylvestris* trees, elevated C_a reduced whole-tree transpiration by an average of 14.4% during a 32-d period, though the magnitude and statistical significance of the effect varied with weather conditions (Kellomäki & Wang 1998). Similarly, free-air CO_2 enrichment reduced whole-tree transpiration in *Liquidambar styraciflua* (sweetgum) by 13%, though the effect was significant only during periods when radiation and vapour pressure deficits were high (Wullschleger & Norby 2001). Thus, elevated C_a can reduce sap flow in trees grown in the field. Whether a reduction in transpiration translates to a reduction in evapotranspiration has, to our knowledge, never been experimentally tested in ecosystems dominated by woody vegetation. In this study, we investigated the hydrological responses to elevated C_a in a Florida scrub ecosystem dominated by oaks.

Materials and methods

This research occurred at the John F. Kennedy Space Center on Merritt Island on the east coast of central Florida (28°38′N, 80°42′W). The climate is warm and humid, with mean daily maximum temperatures of 22 °C in January and 33 °C in July, and an average annual precipitation of 131 cm.

Florida scrub oak is a low-statured shrub community with a fire disturbance cycle of 7–10 years (Schmalzer & Hinkle 1992). Three oak species – *Q. myrtifolia* Willd., *Q. chapmanii* Sargent, and *Q. geminata* Small – and saw palmetto (*Serenoa repens* Small) dominate the community. A total of 27 species of plants have been described in the scrub-oak community (Schmalzer & Hinkle 1992), including ericaceous shrubs (*Lyonia fruticosa*, *L. lucida*), a blueberry (*Vaccinium myrsinites*), and leguminous (*Gallactia eliottia*) and actinorhizal (*Myrica cerifera*) nitrogen-fixing plants.

The soils at the experimental site are Pomello (Arenic Haplahumod) and Paola (Spodic Quartzipsamment) sands, both moderately well drained sandy soils with low pH (pH 3.9–4.1). Organic matter is concentrated at the surface and negligible below 30 cm, except for a B_h horizon that occasionally occurs at the depth of the water table (typically 1.5–2.5 m below the surface). Roots are also concentrated in the surface (Day *et al*. 1996), but can be found at depths of 3.0 m.

We chose a mature stand of scrub-oak vegetation and selected plots dominated by the three oak species. Pre-treatment aboveground biomass and density were measured in each plot (as described in Dijkstra *et al*. 2001). Shoots of *Q. myrtifolia* dominated these plots, occurring at densities of 12.4 shoots m^{-2} and constituting 70% of the aboveground biomass. Densities of *Q. geminata* and *Q. chapmanii* shoots were lower, 4.3 m^{-2} and 1.6 m^{-2}, respectively. Together, the three oak species constituted 96% of the total aboveground biomass in the plots. Total aboveground biomass and densities of each of the three oak species were not significantly different between plots later assigned to the ambient and elevated C_a treatments (Dijkstra *et al*. 2001). After the pre-treatment characterization, plant material was returned to the plots from where it was removed and left to burn. Burning of the aboveground vegetation occurred in two phases – in August 1995 and in January 1996.

Sixteen plots were selected and divided between the ambient and elevated C_a treatments in a randomized block design ($n = 8$). Open-top chambers (octagonal, 3.45 m across and 1.76 m tall, covering 9.47 m^2 ground area) were erected on each plot and were constructed with a 4-inch PVC pipe frame covered with polyester film panels (Melinex 071, Courtaulds Performance Films, VA, USA), and topped with a frustum, leaving an opening of 5.9 m^2. Eight additional octagonal plots (also 9.42 m^2 in area) were selected within the burned area to serve as unchambered plots.

The experimental treatments began in May 1996. Air was blown into the open-top chambers with or without supplemental CO_2 in order to maintain either ambient or elevated (ambient + 350 μLL^{-1}) C_a over the enclosed vegetation. The rate of air flow was 24–30 $m^3 \, min^{-1}$, replacing the air volume in each chamber 1.3–1.6 times min^{-1}. C_a treatments were maintained continuously during 1998 – the period considered in this report – with average daytime C_a in the chambers of 376 $\mu L \, L^{-1}$ for the ambient treatment and 700 $\mu L \, L^{-1}$ for the elevated treatment.

Measurement of evapotranspiration

We measured whole-plot H_2O exchange with the atmosphere, evapotranspiration, using the open-top chambers as open gas exchange systems (Drake *et al*. 1989) during one week every month over an eight-month period, January–August 1998. During measurements, the open-top chambers were fitted with custom designed Lexan lids (Commercial Plastics, Orlando, FL, USA) to reduce backflow of ambient air, and air was blown into each open-top chamber at a rate of 27 $m^3 \, min^{-1}$, with the chamber volume being replaced 1.5 times a minute. Air entered the open-top chamber through 4 circular ducts each of 20.3 cm diameter, total surface area 1.23 m^2, and exited through exhausts in the lids with a total exit surface area of 0.96 m^2. This difference in entrance and exit area increased chamber air pressure to 5.5 P_a, reducing measurement errors caused by leaks. Two IRGAs (LI 6262; LI-COR, Lincoln NB) were calibrated using a dew point generator (LI 610) at a temperature of 25 °C. The IRGAs were plumbed to measure both a reference H_2O mol fraction from one of the 4 chamber inlet ducts and a sample H_2O mol fraction inside the chambers at canopy height. The first IRGA operated in differential mode. The second IRGA continuously measured absolute chamber inlet reference H_2O mol fraction and fed this value into the differential analyser. Both reference and sample air streams were drawn from the open-top numbers at a flow rate of 5 $L \, min^{-1}$. After exhausting, the sample was fed to the IRGAs at a rate of 1 $L \, min^{-1}$ after being individually mixed in flask volumes of 1.9 L. During measurement periods, all 16 open-top chambers were sampled once every 26 min. The flow rate through the chamber was determined at the end of each measurement period from the dilution of a known CO_2 flux injected into the blower. CO_2 mol fraction was measured before and after the blower. Evapotranspiration (ET, mmol $H_2O \, m^{-2} \, s^{-1}$) was calculated as

$$\mathrm{ET} = F(W_{\mathrm{i}} - W_{\mathrm{o}})/A,$$

where F is the rate of air flow through the chamber ($m^3 \, s^{-1}$), $W_{\mathrm{i}} - W_{\mathrm{o}}$ is the difference in water vapour concentration entering and exiting the chamber (mmol m^{-3}), and A is the ground area covered by the chamber (m^2).

In this humid climate, evaporation of water from condensation on the chamber walls often caused a large spike in evapotranspiration during the morning hours. Thus, we focused this analysis on data collected after the spike had subsided, integrating daily values from noon through the afternoon until evapotranspiration rates approached zero in the evening. Problems with condensation and water pooling in the ducts were also apparent during and immediately after rain events; these data were also excluded from this analysis. Because of extremely high ambient temperatures, which had the potential to damage plants during our experiments, the measurements of ecosystem gas exchange during July 1998 were terminated early, before any useful data could be obtained; thus, this measurement period is excluded here.

Short-term effects of C_a on ET

During the May measurement period, we conducted a short-term treatment reversal experiment in order to evaluate the direct physiological effects of elevated C_a on evapotranspiration. In this experiment, the chambers in the ambient C_a treatment were exposed to elevated C_a for a 24-h period, and the chambers in the elevated C_a treatment were exposed to ambient C_a during ths same time. Treatments were reversed for blocks 1–4 on May 12, and for blocks 5–8 on May 13. Meteorological conditions were quite similar for these days, so we combined data from all 8 blocks and evaluated the transition from ‘growth’ CO_2 concentrations (Day 1) to ‘reversed’ CO_2 treatments (Day 2) and back to ‘growth’ CO_2 concentrations (Day 3).

Soil water content

We measured surface soil water content continuously, using CS615 Water Content Reflectometers (Campbell Scientific Inc., Logan, UT). To account for soil- and probe-specific effects on the relationship between probe output and soil water content, we calibrated each probe individually in the following manner. Four large PVC cylinders were packed with soil (excavated from the field site) to approximate field bulk density and adjusted to water contents spanning 5–100% water holding capacity. Probes were inserted into each of the four cylinders, probe output was determined as the soil dried, and a quadratic relationship was developed between probe output and known water content (determined by weighing the entire column). One Water Content Reflectometer was placed in the center of each plot, inserted at a 30° angle such that the 30-cm long waveguides integrated over a depth of 0–15 cm. Probes were connected to a multiplexor (AM416, Campbell Scientific Inc.) and then to a computer-controlled datalogger (CR7, Campbell Scientific Inc.), such that automated measurements of surface soil moisture content were collected every 11 min.

We also measured soil water content at several depths in the soil using the Trase time-domain reflectometry system (Soil Moisture Equipment Inc., San Diego, CA). Again, because of the sandy soils at this site, we calibrated the Trase system in a manner analogous to that described above (though probe-to-probe variation was smaller in the Trase system, so only one calibration curve was used). Buriable waveguides were installed near the center of each plot in a vertical transect through the soil profile at depths of 3–10 cm, 15–30 cm, 45–60 cm, and 65–80 cm, and each probe was attached to a 2-m extension cable so that measurements could be taken without entering the chamber. Soil water content was determined once every two weeks. Again, because of the high sand content of the soil at our site, the relationship between water content and apparent dielectric constant for this soil differs from the standard calibration provided with the Trase TDR system. Thus, to calibrate the TDR system, five intact soil cores (15-cm diameter × 30-cm tall) were taken from the field in plastic cylinders and brought into the lab. One buriable TDR probe was installed into each core, and water was added to each core to bring it to field capacity. Total core weight and apparent dielectric constant were determined periodically during several drying cycles to develop the following relationship:

$$\mathrm{VWC} = -0.1 + 0.0487 \times K_a - 0.0035 \times K_a^2 + 0.0000745 \times K_a^3,$$

where VWC is the volumetric water content (cm^3 H_2O cm^{-3} soil) and K_a is the apparent dielectric constant.

Water table depth

We measured water table depth using pressure transducers described in Keeland *et al.* (1997). Submersible pressure transducers are encased in polyurethane resin and placed below the minimum level of the water table. Increasing mass of water (decreasing water table depth) increases pressure on the transducer, which is recorded every 11 min by a datalogger. To calibrate the sensor, we measured water table depth manually using inspection wells every two weeks during the summer of 1997. The signal from the pressure transducer was linearly related to water table depth ($r^2 = 0.99$).

Xylem deuterium

We measured the δD composition of water from the surface soil, the water table, and from the xylem of *Q. myrtifolia* and *Q. geminata* to determine the depth in the soil profile from where these dominant oaks obtained their water. In May of 1998, from each chamber, a 3–5-cm section of stem was collected from each of the two species (except in plots where the biomass of *Q. geminata* was too low to allow destructive sampling, in which case only *Q. myrtifolia* was sampled). Leaves from the section were removed immediately, and the stems were seated in a scintillation vial and stored in a freezer. Five replicate samples of soil and water table were collected from the area surrounding the chambers (to minimize disturbance to the plots). Water from the stem samples was extracted and analysed for δD at the Stable Isotope Ratio Facility for Environmental Research at the University of Utah.

Statistical analyses

We analysed evapotranspiration data by calculating the mean daily rate for each month for each plot and then conducting a Repeated Measures Analysis of Variance (ANOVA), with CO_2 as the main effect and month as the repeated measure. Analysing monthly rather than daily averages kept the number of measures below the number of replicates, thereby avoiding violating assumptions of sphericity in the Repeated Measures ANOVA. We also used Repeated Measures ANOVA to analyse soil water content.

For the switching experiment, we also used Repeated Measures ANOVA with growth C_a as the main effect and day (switched, unswitched, and switched conditions) as the repeated measure. This allowed testing whether ET would show instantaneous responses to changing CO_2 concentrations and would be apparent as a significant $C_a \times$ day interaction.

Results

Evapotranspiration

Daily evapotranspiration rates varied over the 8-month period (Fig. 1, Repeated Measures ANOVA, effect of time $P < 0.001$), increasing from the winter into the spring as temperature and irradiance increased, and decreasing into the summer, likely because of the drought that occurred during this period. Evapotranspiration rates dropped during March, the period of leaf senescence and abscission, but increased again in April with the growth of the new cohort of leaves.

Elevated C_a reduced mean daily ET rate over the 8-month period (Fig. 1, Repeated Measures ANOVA effect of C_a, $P = 0.014$), with average evapotranspiration rates of 3.15 ± 0.18 mmol m^{-2} s^{-1} (mean ± SE) at ambient C_a compared to 2.55 ± 0.16 mmol m^{-2} s^{-1} at elevated C_a, a 19% reduction in average mid-day evapotranspiration. Though evapotranspiration varied through time, there was no indication that the effect of elevated C_a varied seasonally (Fig. 1, Repeated Measures ANOVA, $C_a \times$ time interaction, $P > 0.050$).

Switching experiment

Reversing the C_a treatments in May caused the expected changes in evapotranspiration (Repeated Measures ANOVA, $C_a \times$ day term, $P = 0.002$). Exposing the chambers normally at ambient C_a to elevated C_a reduced evapotranspiration, and rates returned to levels typical of the ambient C_a treatment once the growth C_a level was restored (Fig. 2). The corresponding pattern was found for the elevated C_a-treated plots, where switching to ambient C_a increased evapotranspiration, and restoring the elevated C_a treatment caused evapotranspiration to decline (Fig. 2).

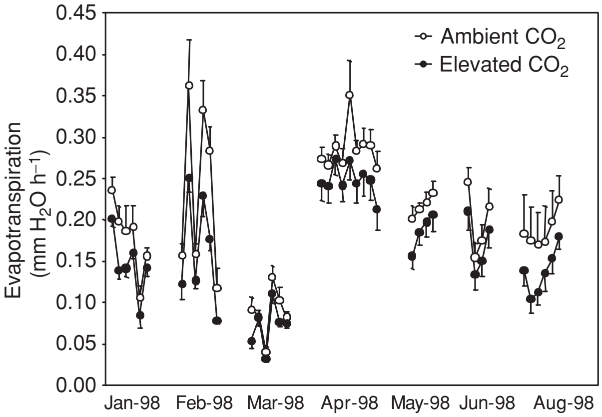

Fig. 1 Average daily evapotranspiration (mm H_2O h^{-1}) during the seven measurement periods. ET rates were measured continuously during the measurement periods, but only average values for the afternoon measurements are shown here (due to interference from condensation during the morning periods). Values shown are means for the ambient (open symbols, +1 standard error) and elevated (filled symbols, −1 standard error) CO_2 treatments, calculated from the average afternoon ET rates from the replicate plots.

Stem-water δD

Xylem δD measurements showed that the two dominant oaks take up most of their water from the water table (Fig. 3). A two-source mixing model to partition water uptake showed that reliance on the water table was greater in *Q. geminata* (95% of its water from the water table) compared to *Q. myrtifolia* (79% of its water from the water table), which relied somewhat more on surface soil water.

Rainfall, water table depth, and soil water content

Soil water content tracked rainfall throughout the measurement period (Fig. 4), high from February–April, decreasing as the drought progressed from May through July, and increasing again with greater rainfall in August, September and October. The depth-distributed measurements of soil water content did not begin until May, but revealed the same seasonal pattern as the continuous measurements in the surface soil, with water contents increasing at all depths from May into September as the drought ended (Fig. 5). Water table depth also tracked rainfall throughout this period, decreasing from March through August '98, reflecting the drought during this period. Recovery of the water table lagged behind soil water content; after the rains resumed, soil water content

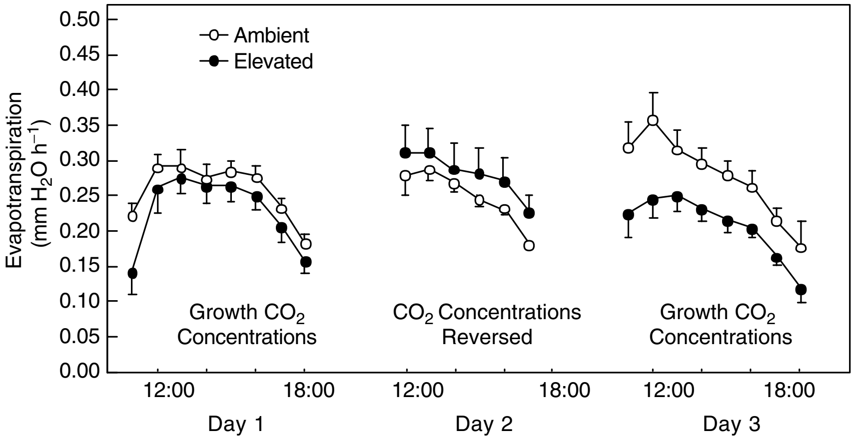

Fig. 2 Evapotranspiration rates (mm H_2O h^{-1}) during the May 'switching experiment', in which growth CO_2 concentrations were temporarily reversed on day 2. Symbols indicate growth CO_2 treatments, with ambient CO_2-grown plants indicated with open symbols and elevated CO_2-grown plants indicated with filled symbols. Hourly mean ET rates are shown for each day, beginning with hour on each day when interference from condensation was no longer evident.

recovered very quickly (by mid-July), whereas, even by October of '98, the water table was still at levels lower than before the drought in January and February of '98.

The continuous monitoring of soil moisture in the top 15 cm of soil revealed a trend toward wetter soils in elevated compared to ambient C_a (Fig. 4). While this effect was not significant for any of the continuous measurements ($P > 0.300$), soil water content in the 3–10 cm depth, as determined by manual TDR measurements every two weeks, was significantly greater in the elevated C_a treatment (RMA, $P = 0.023$; Fig. 5). Elevated C_a had no effect on water content in soil depths of 15–25 cm ($P = 0.370$), 45–60 cm ($P = 0.734$), nor 65–85 cm ($P = 0.570$).

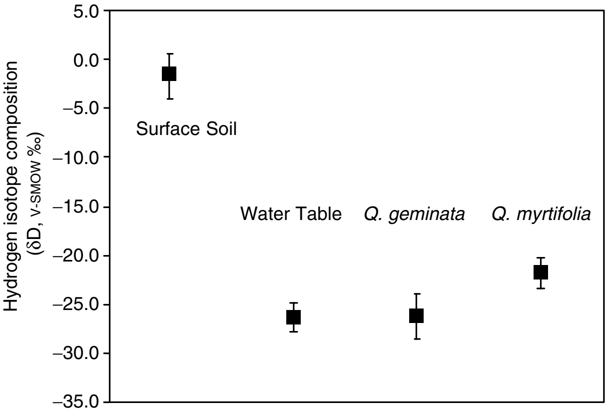

Fig. 3 Deuterium composition (expressed in the per mil notation on the V-SMOW scale) for water from the surface soil (0–10 cm depth), the water table (2 m depth), and xylem from *Q. geminata* and *Q. myrtifolia*. Values shown are means ± standard errors ($n = 10$).

Discussion

Elevated C_a has been shown to cause a 40% reduction in leaf conductance (Lodge *et al.* 2001) in *Q. myrtifolia*, the dominant oak species in this scrub-oak ecosystem. The 19% reduction in mid-day evapotranspiration rates and increase in soil water content reported here demonstrate some of the possible ecosystem consequences of this change in stomatal functioning. The effect of elevated C_a on evapotranspiration reported here is based on measurements at mid-day and does not consider evapotranspiration during the morning or after heavy rains, when evaporation from the chamber walls could have interfered with the measurements, or at night. Using $\text{PROXEL}_{\text{NEE}}$, a model of whole-system H_2O and CO_2 exchange, Reichstein (2000 and unpublished data) extrapolated measured rates of ET to estimate total ET during the 8-month period considered here, estimating total evapotranspiration to be 756 mm for the ambient and 673 mm for the elevated CO_2 treatments. This estimate of an 11% reduction in ET caused by elevated C_a is smaller than the 19% reduction observed during mid-day (Fig. 1), because the model included periods when effects of C_a on transpiration are likely to be reduced or to disappear entirely, for example during periods of low radiation (Wullschleger & Norby 2001).

While elevated C_a often reduces stomatal conductance in herbaceous species, responses in tree species have been less consistent and, in general, less pronounced (Field *et al.* 1995; Saxe *et al.* 1998). A recent meta-analysis (Medlyn *et al.* 2001) revealed an average decrease in stomatal conductance of 21% in woody species in response to elevated C_a, with broadleaved species showing larger reductions

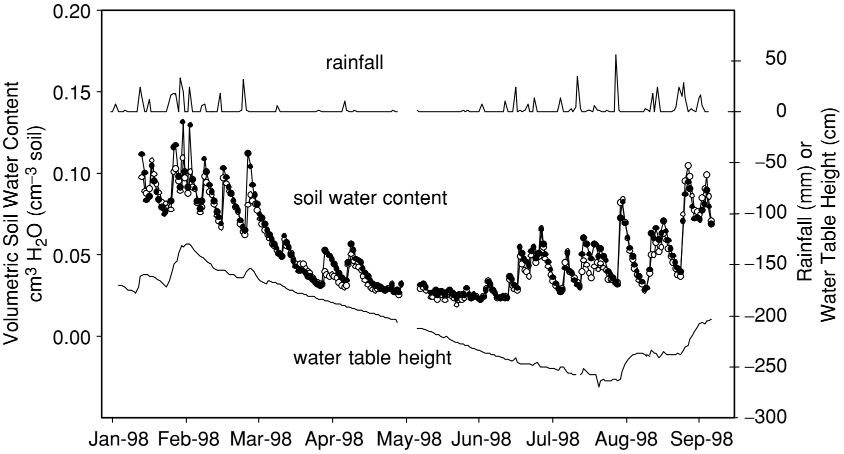

Fig. 4 Rainfall (right axis), surface soil water content (left axis), and water table depth (right axis) from 1 January to 1 October 1998. Rainfall measurements were collected on site using an automated rainfall gauge. Water table depth was measured using two submersible pressure transducers connected to a datalogger. Soil water content was measured every 11 min using Campbell CS-615 Water Content Reflectometers positioned in the top 15 cm of soil in each plot. Mean soil water contents for the ambient-CO_2 treated plots (open circles) and elevated-CO_2 treated plots (filled circles) are shown.

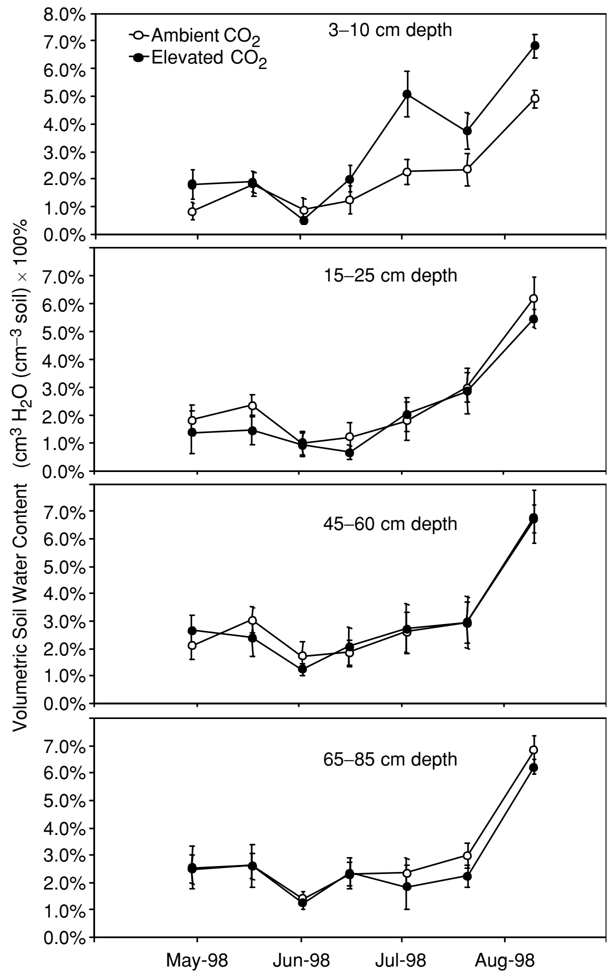

Fig. 5 Soil water content determined by time-domain reflectometry using the TRASE TDR system with buriable waveguides placed at 3–10 cm, 15–25 cm, 45–60 cm, and 65–85 cm depths. Values shown are means ± standard errors ($n = 8$) for the ambient (open symbols) and elevated (filled symbols) CO$_2$ treatments.

(25%) than evergreen (8%), and long-term exposure (>1 year) to elevated C_a causing larger (23%) and more consistent reductions than short-term exposure (10%). Clearly, changes in stomatal conductance in response to elevated C_a vary among species, and *Q. myrtifolia*, the dominant oak in the ecosystem examined here, appears to be among the more responsive woody species in which stomatal conductance has been examined under field conditions (Lodge *et al.* 2001; Medlyn *et al.* 2001).

Compared to the relatively high number of reports of the effects of elevated C_a on stomatal conductance, there are fewer reports on the effects of elevated C_a on transpiration of trees under field conditions, and very few reports of measurements of ET in elevated C_a. No effect of elevated C_a on transpiration measured at the whole-plant scale (sap flow) was found in a developing stand of *Pinus taeda* (Pataki *et al.* 1998), and small (on the order of 10–15%) reductions in sap flow have been found in *Q. ilex* (Togentti *et al.* 1998), *Q. pubescens* (Togentti *et al.* 1999), *Pinus sylvestris* (Kellomäki & Wang 1998), and *Liquidambar styraciflua* (Wullschleger & Norby 2001). Thus, responses appear to vary among studies, and, in general, elevated C_a-induced reductions in whole-plant transpiration tend to be smaller than those observed for stomatal conductance.

A number of processes can dampen the effect of elevated CO$_2$ on transpiration and evapotranspiration (Field *et al.* 1995), including a C_a-stimulation of LAI and thus an increase in the area of transpiring surface. We have observed large increases in total aboveground biomass in this ecosystem in response to elevated C_a, with 68% greater biomass in elevated C_a by the end of 1998 (Dijkstra *et al.* 2001). Based on several techniques which determined LAI using light penetration, reflectance, and hemispherical photographs, the effect of elevated C_a on LAI appears to be smaller, on the order of 20–40% greater LAI in elevated C_a for 1999–2000 (G Hymus and BG Drake, unpublished data). Increasing soil evaporation has also been proposed as a mechanism tending to counteract reduced transpiration in elevated C_a, a negative feedback to the reduction in evapotranspiration (Wilson *et al.* 1999), but our whole-plot measurements of evapotranspiration would have captured any such increase in soil evaporation in the elevated C_a treatment. Thus, the observed increase in LAI and the possible increase in soil evaporation (if it occurred) were not large enough to eliminate the reduction in evapotranspiration caused by elevated C_a (Fig. 2).

In canopies where aerodynamic conductance is low compared to stomatal conductance (as typically occurs in many agricultural crops and in some grasslands, with short, dense canopies), reductions in stomatal conductance tend to have relatively little influence on evapotranspiration (Jarvis & McNaughton 1986). In these so-called 'poorly coupled' canopies, effects of elevated C_a on stomatal conductance may be of little consequence for whole-system water fluxes (e.g. Shaer & van Bavel 1987). In the scrub-oak ecosystem considered here, the vegetation is patchy and clumped, particularly during this early phase in postfire stand development, suggesting closer coupling between plant stomata and the atmosphere (i.e. relatively high aerodynamic conductance compared to stomatal conductance), consistent with the reduction in evapotranspiration we observed in response to stomatal closure. Using eddy covariance in a similarly aged stand of scrub-oak vegetation, the decoupling coefficient (Ω) was estimated to be 0.2 (S. Dore, personal communication), indicating relatively strong stomatal control over evapotranspiration (Jarvis & McNaughton 1986).

Open-top chambers can modify the degree of coupling. In tallgrass prairie, open-top chambers reduced aerodynamic conductance, possibly diminishing the effect of reduced stomatal conductance in elevated C_a on transpiration and evapotranspiration in the chambers compared to the open prairie (Ham *et al*. 1995). Similarly, open-top chambers in a salt marsh reduced wind speed, suggesting lower aerodynamic conductance and a reduction in stomatal coupling with the atmosphere (Drake & Peresta 1993). In our study as well, preliminary measurements of aerodynamic conductance suggest that the chambers increase Ω to 0.22–0.41 (Monjes, personal communication). Thus, in our site, as in the tallgrass prairie and salt marsh, the open-top chambers may tend to underestimate the effects of elevated C_a on evapotranspiration.

Additional feedbacks operating at spatial scales larger than those accessible through field experiments could influence whether the reduction in evapotranspiration we observed in response to experimental C_a doubling alters regional H_2O fluxes in a future, high C_a world (Jacobs & DeBruin 1992; Field *et al*. 1995). Negative feedbacks could occur in which an initial reduction in evapotranspiration dries the canopy, surface layer, and ultimately the planetary boundary layer and increases surface temperature and sensible heat flux, together increasing vapour pressure deficit, the driving gradient for evapotranspiration (Wilson *et al*. 1999). By contrast, a positive feedback to the initial reduction in evapotranspiration could occur if stomatal conductance decreases in response to increased vapour pressure deficit (Field *et al*. 1995; Friend & Cox 1995). The relative importance of these changes depends on both stomatal sensitivity to vapour pressure deficit and on the degree of stomatal coupling with the atmosphere.

In grassland ecosystems, reduced evapotranspiration in elevated C_a often leads to increased soil moisture (Clifford *et al*. 1993; Rice *et al*. 1994; Field *et al*. 1995; Fredeen *et al*. 1997; Niklaus *et al*. 1998). The reduction in evapotranspiration at the whole-chamber level likely contributes to the increase in surface soil moisture we observed. Yet, the oaks' strong reliance on water from the water table suggests that this effect is smaller than it might be in ecosystems where plants rely more heavily on water from the surface soil, or that some other mechanism is involved. Litter accumulation – greater in the high C_a treatment due to increased aboveground production (Dijkstra *et al*. 2001; DW Johnson, unpublished data) – could also contribute to increasing surface soil moisture by causing a mulching effect, reducing soil evaporation and/or increasing soil water holding capacity. Increased LAI in elevated C_a could also reduce the amount of radiation reaching the soil surface, thereby reducing soil evaporation. Additionally, the oaks' reliance on the water table indicates that increased surface soil moisture is not the only possible consequence of reduced evapotranspiration in elevated C_a. In such ecosystems, where the distributions of soil water and plant roots are bimodal and where plants rely more heavily on the deeper water source, reduced ET in elevated C_a may cause increased water table height or increased lateral flow of groundwater. In a number of grassland ecosystems, elevated C_a has stimulated microbial processes through its effects on surface soil water content – microbial respiration (Rice *et al*. 1994), nitrogen mineralization (Hungate *et al*. 1997), denitrification (Arnone & Bohlen 1998), and earthworm activity (Zaller & Arnone 1997). However, because microbial activity and nutrient concentrations are typically concentrated in the surface soil layer, these effects are likely to be weaker in ecosystems where reduced ET in elevated C_a is manifest as reduced water uptake at depth.

Our results show that elevated C_a can reduce evapotranspiration and increase soil moisture in ecosystems dominated by woody vegetation. The extent and importance of this result for regional H_2O fluxes in a high C_a world will depend both on species differences in stomatal responses to elevated C_a and on the various feedback processes involved in scaling leaf to plot to regional responses. Nevertheless, the potential for reduced evapotranspiration demonstrated here calls attention to the need for additional studies on the effects elevated atmospheric C_a on the hydrology of forests and shrublands. Reduced evapotranspiration could alter a number of ecosystem processes and has implications for regional and global climate (Field *et al*. 1995).

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References

Arnone JA III, Bohlen PJ (1998) Stimulated N_2O flux from intact grassland monoliths after two growing seasons under elevated atmospheric CO_2. *Oecologia*, **116**, 331–335.

Arp WJ (1991) *Vegetation of a North American salt marsh and elevated atmospheric carbon dioxide*. Doctoral Thesis. Free University of Amsterdam.

Beerling DJ, Heath J, Woodward FA, Mansfield TA (1996) Drought-CO_2 interactions in trees: Observations and mechanisms. *New Phytologist*, **134** (2), 235–242.

Bremer DJ, Ham JM, Owensby CE (1996) Effects of elevated atmospheric carbon dioxide and open top chambers on transpiration in a tallgrass prairie. *Journal of Environmental Quality*, **25**, 691–701.

Canadell JG, Pitelka LF, Ingram JSI (1996) The effects of elevated CO_2 on plant-soil carbon below ground: a synthesis. *Plant and Soil*, **187**, 391–400.

Clifford SC, Stronach IM, Mohamed AD, Azam-Ali SN, Crout NMJ (1993) The effects of elevated atmospheric carbon dioxide and water stress on light interception, dry matter production and yields in stands of groundnut (*Arachis hypogaea* L.). *Journal of Experimental Botany*, **44**, 1763–1770.

Cox PM, Betts RA, Bunton CB, Essery RLH, Rowntree PP, Smith J (1999) The impact of new land surface physics on the GCM simulation of climate and climate sensitivity. *Climate Dynamics*, **15**, 183–203.

Curtis PS, Wang X (1998) A meta-analysis of elevated CO_2 effects on woody plant mass, form and physiology. *Oecologia*, **113**, 299–313.

Day FP, Weber EP, Hinkle CR, Drake BG (1996) Effects of elevated atmospheric CO_2 on fine root length and distribution in an oak-palmetto scrub ecosystem in central Florida. *Global Change Biology*, **2**, 143–148.

Diemer MW (1994) Mid-season gas-exchange of an alpine grassland under elevated CO_2. *Oecologia*, **98**, 429–435.

Dijkstra P, Hymus G, Colavito D, Vieglais DA, Cundari CM, Johnson DP, Hungate BA, Hinkle CR, Drake BG (2001) Elevated atmospheric CO_2 stimulates aboveground biomass in a fire-regenerated scrub-oak ecosystem. *Global Change Biology*, in press.

Drake BG, Leadley PW, Arp WJ, Nassiry K, Curtis PS (1989) An open top chamber for field studies of elevated atmospheric CO_2 concentration on saltmarsh vegetation. *Functional Ecology*, **3**, 363–371.

Drake BG, Long SP, Gonzalez-Meler M (1997) Increased plant efficiency: a consequence of elevated atmospheric CO_2? *Annual Review of Plant Physiology*, **48**, 609–639.

Drake BG, Peresta GJ (1993) Open top chambers for studies of the long-term effects of elevated atmospheric CO_2 on wetland and forest ecosystem processes. In: Design and Execution of Experiments on CO_2 Enrichment (eds Schultze ED, Mooney HA, E. Guyot SA, Rue Ransfort 25, 1080 Brussels. Ch 21. pp. 273–289.

Ellsworth DS, Oren R, Huang C, Phillips N, Hendrey GR (1995) Leaf and canopy responses to elevated CO_2 in a pine forest under free-air CO_2 enrichment. *Oecologia*, **104**, 139–146.

Field CB, Jackson RB, Mooney HA (1995) Stomatal responses to increased CO_2: implications from the plant to the global scale. *Plant Cell and Environment*, **18**, 1214–1225.

Field CB, Lund CP, Chiariello NR, Mortimer BE (1997) CO_2 effects on the water budget of grassland microcosm communities. *Global Change Biology*, **3**, 197–206.

Fredeen AL, Randerson JT, Holbrook NM, Field CB (1997) Elevated atmospheric CO_2 increases water availability in a water-limited grassland ecosystem. *Journal of American Water Resources Association*, **33**, 1033–1039.

Friend AD, Cox PM (1995) Modelling the effects of atmospheric CO_2 on vegetation–atmosphere interactions. *Agricultural and Forest Meteorology*, **73**, 285–295.

Ham JM, Ownesby CE, Coyne PI, Bremer DJ (1995) Fluxes of CO_2 and water vapor from a prairie ecosystem exposed to ambient and elevated atmospheric CO_2. *Agricultural and Forest Meteorology*, **77**, 73–93.

Hatton TJ, Walter J, Dawes WR, Dunin FX (1992) Simulations of hydroecological responses to elevated CO_2 at the catchment scale. *Australian Journal of Botany*, **40**, 679–696.

Hungate BA, Chapin FS III,, Zhong H, Holland EA, Field CB (1997) Stimulation of grassland nitrogen cycling under carbon dioxide enrichment. *Oecologia*, **109**, 149–153.

Idso SB, Brazel AJ (1984) Rising atmospheric carbon dioxide may increase streamflow. *Nature*, **312**, 51–53.

Jacobs CMO, DeBruin HAR (1992) The sensitivity of regional transpiration to land surface characteristics: significance of feedbacks. *Journal of Climate*, **5**, 683–698.

Jacobs C, DeBruin H (1997) Predicting regional transpiration at elevated atmospheric CO_2: influence of the PBL-vegetation interaction. *Journal of Applied Meteorologys*, **36**, 1663–1675.

Jarvis PG, McNaughton KG (1986) Stomatal control of transpiration: scaling up from leaf to region. *Advances in Ecological Research*, **15**, 1–49.

Jones P, Allen LH, Jones JW, Boote KJ, Campbell WJ (1984) Soybean canopy growth, photosynthesis, and transpiration responses to whole-season carbon dioxide enrichment. *Agronomy Journal*, **76**, 633–637.

Keeland BD, Dowd JF, Hardegree WS (1997) Use of inexpensive pressure transducers for measuring water levels in wells. *Wetlands Ecology and Management*, **5**, 121–129.

Kellomäki S, Wang KY (1998) Sap flow in Scots pine growing under conditions of year-round carbon dioxide enrichment and temperature elevation. *Plant, Cell and Environment*, **21**, 969–981.

Kimball BA, LaMorte RL, Pinter PJ, Wall GW, Hunsaker DJ, Adamsen FJ, Leavitt SW, Thompson TL, Matthias AD, Brooks TJ (1999) Free-air CO_2 enrichment and soil nitrogen effects on energy balance and evapotranspiration of wheat. *Water Resources Research*, **35**, 1179–1190.

Lodge RJ, Dijkstra P, Drake BG, Morison JIL (2001) Stomatal acclimation to increased CO_2 concentration in a Florida scrub oak species *Quercus myrtifolia* Willd. *Plant, Cell and Envrionment*, **24**, 77–88.

Medlyn BE, Barton CVM, Broadmeadow MSJ, Ceulemans R, De Angelis P, Forstreuter M, Freeman M, Jackson SB, Kellomäki S, Laitat E, Rey A, Roberntz P, Sigurdsson BD, Strassemeyer J (2001) Stomatal conductance of forest species after long-term exposure to elevated CO_2 concentration: a synthesis. *New Phytologist*, **149**, 247–264.

Mooney HA, Canadell J, Chapin FS III,, Ehleringer JR, Korner Ch, McMurtrie RE, Parton WJ, Pitelka LF, Schulze E-D (1998) Ecosystem physiology responses to global change. In: *The Terrestrial Biosphere and Global Change: Implications of Global Change for Natural and Managed Ecosystems* (eds Walker BH, Steffen WL, Canadell J, Ingram JSI), pp. 141–189. Cambridge University Press, Cambridge.

Morison JIL (1987) Intercellular CO_2 concentrations and stomatal responses to CO_2. In: *Stomatal Function* (eds Zeiger E, Farquhar GD, Cowan IR), pp. 229–251. Stanford University Press, Stanford.

Mott KA (1988) Do stomata respond to CO_2 concentrations other than intercellular? *Plant Physiology*, **86**, 200–203.

Niklaus PA, Spinnler D, Körner Ch (1998) Soil moisture dynamics of calcareous grassland under elevated CO_2. *Oecologia*, **117**, 201–208.

Owensby CE, Ham JM, Knapp AK, Bremer D, Auen LM (1997) Water vapour fluxes and their impact under elevated CO_2 in a C4-tallgrass prairie. *Global Change Biology*, **3**, 189–195.

Pataki DE, Oren R, Tissue DT (1998) Elevated carbon dioxide does not affect average canopy stomatal conductance of *Pinus taeda* L. *Oecologia*, **117**, 47–52.

Reichstein M (2000) *Drought effects on carbon and water exchange in semi-arid ecosystems – an analysis based on ecosystem gas exchange data and process modelling*. PhD Dissertation. University Bayreuth.

Rice CW, Garcia FO, Hampton CO, Owensby CE (1994) Soil microbial response in tallgrass prairie to elevated CO_2. *Plant and Soil*, **165**, 67–75.

Samarakoon AB, Gifford RM (1995) Soil water content under plants at high CO_2 concentration and interactions with the direct CO_2 effects: a species comparison. *Journal of Biogeography*, **22** (2–3), 193–202.

Saxe H, Ellsworth DS, Heath J (1998) Tansley Review No. 98: Tree and forest functioning in an enriched CO_2 atmosphere. *New Phytologist*, **139**, 395–436.

Schmalzer PA, Hinkle CR (1992) Species composition and structure of oak-saw plametto scrub vegetation. *Castanea*, **57**, 220–251.

Sellers PJ, Bounoua L, Collatz GJ, Randall DA, Dazlich DA, Los SO, Berry JA, Fung I, Tucker CJ, Field CB, Jensen TG (1996) Comparison of radiative and physiological effects of doubled atmospheric CO_2 on climate. *Science*, **271**, 1402–1406.

Shaer YA, van Bavel CHM (1987) Relative role of stomatal and aerodynamic resistances in transpiration of a tomato crop in a CO_2-enriched greenhouse. *Agricultural and Forest Meteorology*, **41**, 77–85.

Stocker R, Körner C, Schmid B, Niklaus PA, Leadley PW (1999) A field study of the effects of elevated CO_2 and plant species diversity on ecosystem-level gas exchange in a planted calcareous grassland. *Global Change Biology*, **5**, 95–105.

Thornley JHM, Cannell MGR (1996) Temperate forest responses to carbon dioxide, temperature and nitrogen: a model analysis. *Plant, Cell and Environment*, **19**, 1331–1348.

Tognetti R, Langobucco A, Miglietta F, Raschi A (1998) Transpiration and stomatal behaviour of *Quercus ilex* plants during the summer in a Mediterranean carbon dioxide spring. *Plant Cell and Environment*, **21**, 613–622.

Tognetti R, Langobucco A, Miglietta F, Raschi A (1999) Water relations, stomatal response and transpiration of *Quercus pubescens* trees during summer in a Mediterranean carbon dioxide spring. *Tree Physiology*, **19**, 261–270.

Wilson KB, Carlson TN, Bunce JA (1999) Feedback significantly influences the simulated effect of CO_2 on seasonal evapotranspiration from two agricultural species. *Global Change Biology*, **5**, 903–917.

Wullschleger SD, Norby RJ (2001) Sap velocity and canopy transpiration for a 12-year-old sweetgum stand exposed to free-air CO_2 enrichment. *New Phytologist*, **150**, 489–498.

Zaller JG, Arnone JA III (1997) Activity of surface-casting earthworms in a calcareous grassland under elevated atmospheric CO_2. *Oecologia*, **111**, 249–254.