

Future carbon dioxide concentration decreases canopy evapotranspiration and soil water depletion by field-grown maize

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Abstract

Maize, in rotation with soybean, forms the largest continuous ecosystem in temperate North America, therefore changes to the biosphere-atmosphere exchange of water vapor and energy of these crops are likely to have an impact on the Midwestern US climate and hydrological cycle. As a C₄ crop, maize photosynthesis is already CO₂-saturated at current CO₂ concentrations ([CO₂]) and the primary response of maize to elevated [CO₂] is decreased stomatal conductance (g_s). If maize photosynthesis is not stimulated in elevated [CO₂], then reduced g_s is not offset by greater canopy leaf area, which could potentially result in a greater ET reduction relative to that previously reported in soybean, a C₃ species. The objective of this study is to quantify the impact of elevated [CO₂] on canopy energy and water fluxes of maize (*Zea mays*). Maize was grown under ambient and elevated [CO₂] (550 $\mu\text{mol mol}^{-1}$ during 2004 and 2006 and 585 $\mu\text{mol mol}^{-1}$ during 2010) using Free Air Concentration Enrichment (FACE) technology at the SoyFACE facility in Urbana, Illinois. Maize ET was determined using a residual energy balance approach based on measurements of sensible (H) and soil heat fluxes, and net radiation. Relative to control, elevated [CO₂] decreased maize ET (7–11%; $P < 0.01$) along with lesser soil moisture depletion, while H increased (25–30 W m^{-2} ; $P < 0.01$) along with higher canopy temperature (0.5–0.6 °C). This reduction in maize ET in elevated [CO₂] is approximately half that previously reported for soybean. A partitioning analysis showed that transpiration contributed less to total ET for maize compared to soybean, indicating a smaller role of stomata in dictating the ET response to elevated [CO₂]. Nonetheless, both maize and soybean had significantly decreased ET and increased H , highlighting the critical role of elevated [CO₂] in altering future hydrology and climate of the region that is extensively cropped with these species.

Keywords: elevated [CO₂], maize, evapotranspiration, soil moisture, sensible heat, canopy temperature

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Introduction

Atmospheric carbon dioxide concentration ([CO₂]) is expected to double by the end of this century (Meehl *et al.*, 2007) and will likely have significant impacts on the growth and yield of many important agricultural crops (Long *et al.*, 2006). Decreased stomatal conductance (g_s) is one of the most consistent responses of leaves to growth at elevated [CO₂] (Medlyn *et al.*, 2001; Zheng & Peng, 2001; Ainsworth *et al.*, 2002; Wullschlegler *et al.*, 2002; Long *et al.*, 2004; Ainsworth & Long, 2005; Yoshimoto *et al.*, 2005; Kim *et al.*, 2006; Leipprand & Gerten, 2006; Bernacchi *et al.*, 2007). This decrease in g_s can alter the partitioning of available energy in and

out of an ecosystem primarily by altering fluxes of sensible (H) and latent heat (λET ; Sellers *et al.*, 1997). These energy fluxes dominate the influence of vegetation on biosphere-atmosphere exchange; therefore the stomatal response to rising [CO₂] may alter the climate and hydrological cycle of a given region, especially for continental interiors (Sellers *et al.*, 1997; Arnell *et al.*, 2001; Berry *et al.*, 2010).

The response of canopy evapotranspiration (ET) to elevated [CO₂] has been examined in growth chamber studies for various crops and has been found to vary with some showing an increase (Chaudhuri *et al.*, 1990; Hui *et al.*, 2001), no change (Jones *et al.*, 1985; Hileman *et al.*, 1994; Ellsworth, 1999) and a decrease (Burkart *et al.*, 2004; Li *et al.*, 2004; Kim *et al.*, 2006; Chun *et al.*, 2011) in ET under elevated [CO₂]. In contrast, numerous Free Air Concentration Enrichment

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(FACE) studies have shown a consistent ET reduction in irrigated crops grown under elevated [CO₂], ranging from 4% to 8% for wheat (Kimball *et al.*, 1999; Burkart *et al.*, 2011) and rice (Yoshimoto *et al.*, 2005); to 9–12% for winter barley (Burkart *et al.*, 2011); to 10–12% for sorghum (Conley *et al.*, 2001; Triggs *et al.*, 2004) and potato (Magliulo *et al.*, 2003); and up to 18% for sugar beet (Burkart *et al.*, 2011) with only one study showing no change for cotton (Kimball *et al.*, 1994).

Combined, these studies present strong evidence of decreased water loss from well-watered crop canopies as atmospheric [CO₂] continues to increase. It is less known, however, what the response might be for much larger rain-fed ecosystems such as maize in the Midwestern US. To date, the measurement of ET responses for C₄ crop species to growth in elevated [CO₂] has only been characterized for irrigated sorghum growing in an arid environment (Conley *et al.*, 2001; Triggs *et al.*, 2004). While the response of sorghum ET was relatively similar to that observed for many C₃ species (Kimball & Bernacchi, 2006), photosynthetic and growth characteristics of C₄ species generally do not respond to elevated [CO₂], except during drought conditions (Leakey *et al.*, 2009). Decreased ET could increase soil moisture availability and delay the onset of water stress during dry periods (e.g., Bernacchi *et al.*, 2007; Markelz *et al.*, 2011), however, stomatal closure also decreases transpirational cooling, resulting in warmer canopy temperatures (T_c) and an increased vapor pressure deficit (VPD; Kimball *et al.*, 1999).

Photosynthesis for C₄ species grown in elevated [CO₂] has only been shown to be stimulated under water stressed conditions (Leakey *et al.*, 2006, 2009; de Souza *et al.*, 2013). Therefore, in the absence of drought, reduced g_s in elevated [CO₂] is not likely to be offset by greater canopy leaf area (Leakey *et al.*, 2006) as has been noted for soybean (Dermody *et al.*, 2006; Kimball & Bernacchi, 2006; Bernacchi *et al.*, 2007). As a consequence, reductions in ET as well as changes in water relations have the potential to be greater for maize and other C₄ species than for C₃ species such as soybean (Dermody *et al.*, 2006; Kimball & Bernacchi, 2006; Bernacchi *et al.*, 2007). Data on the interaction of [CO₂] with canopy water fluxes are very limited for rain-fed ecosystems, with only one study showing a 9–16% reduction in ET for soybean grown at elevated [CO₂] over five growing seasons (Bernacchi *et al.*, 2007). As maize comprises more than half of the land area in the expansive US Corn Belt (over 45 million ha, <http://www.nass.usda.gov>) it is a critical component of the overall ecosystem. If elevated [CO₂]-induced decreases in ET for maize are similar to that observed for soybean, then it is likely that these responses will influence

the climate and hydrological cycle of the Midwest region.

The main objectives of this study were to assess the impact of future [CO₂] on maize canopy energy fluxes over diel and seasonal time scales, and to assess the interaction of ET and soil water content. We hypothesize that elevated [CO₂] will reduce ET and increase H and T_c , with the largest changes occurring during mid-day; this will result in less soil water depletion in elevated [CO₂]. We also hypothesize that there will be a greater decrease in ET under elevated [CO₂] for maize than was observed for soybean. This hypothesis is based on the lack of photosynthetic stimulation observed for elevated [CO₂]-grown maize relative to the control (e.g., Leakey *et al.*, 2006), whereas the increased carbon assimilation of soybean can result in greater leaf area (Dermody *et al.*, 2006), and hence more evapotranspiring surfaces that could offset g_s decreases in elevated [CO₂] (Bernacchi *et al.*, 2007). We tested these hypotheses at the Soybean Free Air Concentration Enrichment (SoyFACE) facility located within the Midwestern US Corn Belt in central Illinois, USA. Canopy fluxes were determined using the residual energy balance approach, and soil moisture measurements were collected for maize grown under ambient and elevated [CO₂] during the 2004, 2006 and 2010 growing seasons. This is the first study presenting canopy scale responses to elevated [CO₂] for a C₄ crop under rain-fed, open-air conditions. This study also builds upon the observed responses of soybean ET to growth in elevated [CO₂] at the same research site (Bernacchi *et al.*, 2007), thus completing the investigation of the two major species that are grown as part of the dominant ecosystem in the region.

Materials and methods

Field site, maize cultivation, and FACE setup

The SoyFACE facility is situated in a 32 ha (80 acre) field at the University of Illinois at Urbana-Champaign (40°03'21.3"N; 88°12'3.4"W, 230 m elevation). At SoyFACE, maize and soybean are grown in annual rotation between the eastern and western halves of the field. The soil texture is classified as the Flanagan/Drummer soil series, that can be described as wet, dark-colored 'prairie soils' (fine silty, mixed, mesic Typic Endoaquoll) and organically rich and highly productive, which is typical for northern and central Illinois. The field is tile-drained.

Maize cv 34B43 (Pioneer Hi-Bred International, Inc., IA, USA) was planted on April 29 (day of year 119), April 28 (day of year 118) and April 28 (day of year 118), and emerged on May 9 (day of year 130), May 8 (day of year 128) and May 8 (day of year 128) for 2004, 2006 and 2010, respectively. The agronomic practices were typical of the region, as described previously (Leakey *et al.*, 2004, 2006). Four experimental blocks ($n = 4$) in the maize portion of the site contained two

20-m diameter octagonal plots. One plot in each block was maintained at ambient [CO₂] concentrations that corresponded to roughly global mean concentrations of 376, 382 and 390 $\mu\text{mol mol}^{-1}$ for 2004, 2006, and 2010, respectively (ftp://ftp.cmdl.noaa.gov/ccg/co2/trends/co2_mm_mlo.txt), and the second plot in each block was fumigated during the daylight hours from planting until harvest with elevated [CO₂] using FACE technology. The elevated [CO₂] in 2004 and 2006 was targeted for the year 2050 (550 $\mu\text{mol mol}^{-1}$) according to Intergovernmental Panel on Climate Change (Houghton *et al.*, 2001) and the target concentration in 2010 was 200 $\mu\text{mol mol}^{-1}$ above mean global background concentrations. The average [CO₂] levels in the fumigated plots during the growing seasons in 2004, 2006, and 2010 were 541.5 $\mu\text{mol mol}^{-1}$, 545.8 $\mu\text{mol mol}^{-1}$, and 585.0 $\mu\text{mol mol}^{-1}$, respectively, and values were within $\pm 20\%$ of the target 92–94% of the time. A complete description of the SoyFACE operational procedures has been described in several studies (Leahey *et al.*, 2004, 2006; Markelz *et al.*, 2011).

Climate information

Hourly measurements of precipitation, air temperature, and relative humidity were collected from nearby weather stations as described previously (VanLoocke *et al.*, 2010). Palmer crop moisture index (PCMI) is an estimate of short-term moisture conditions determined from temperature, precipitation, and estimated soil water content (Palmer, 1968). When PCMI is lower than 0, it indicates conditions where crop water demand exceeds supply. The long-term (30 year) PCMI data for East Central Illinois were provided by the Climate Operation Branch of the National Oceanic and Atmospheric Administration (<http://www.usda.gov/oce/waob/jawf/>). The 30-year (1970–2000) mean growing season (May to August) climate data were downloaded from the Midwestern Regional Climate Center (MRCC), at the Illinois State Water Survey (<http://mrcc.isws.illinois.edu/>).

Micrometeorological measurements

The micrometeorological measurements began ca. 40 days after seedling emergence during 2004 and 2006 and 20 days after emergence in 2010. Measurements continued until crop senescence which corresponded to day of year 245 for all years. Maize ET was determined using a residual energy balance approach based on the micrometeorological measurements of H , soil heat flux (G_0) and net radiation (R_n) from individual plots. Evapotranspiration was estimated according to the following energy balance equation:

$$\lambda \text{ET} = R_n - G_0 - H \quad (1)$$

where λ is latent heat of vaporization of water (J kg^{-1}), ET is evapotranspiration ($\text{kg m}^{-2} \text{s}^{-1}$; positive upward), R_n is net radiation (W m^{-2} ; positive downward), G_0 is soil surface heat flux (W m^{-2} ; positive downward), and H is sensible heat flux (W m^{-2} ; positive upward).

The development and validation of the residual energy balance method has been described previously (Huband

& Monteith, 1986; Jackson *et al.*, 1987; Kimball *et al.*, 1994, 1999; Triggs *et al.*, 2004) and has been implemented previously for measurements over soybean (Bernacchi *et al.*, 2007, 2011) at the SoyFACE site and over short and tall grass stands, which are in close proximity to the site (Hickman *et al.*, 2010).

Although the residual energy balance approach does not measure ET directly, it is the only available effective technique for FACE experiments (Kimball *et al.*, 1999). Other techniques such as eddy covariance or flux gradient analysis (Baldocchi *et al.*, 1988) while providing a more direct measure of ET, require a much larger fetch than can be provided using FACE technology. The energy balance approach does not include energy fluxes due to photosynthesis, respiration and heat storage, however, these fluxes represent a very small fraction of incoming solar radiation (Meyers & Hollinger, 2004) and differences in energy partitioned to these components between the control and elevated [CO₂] plots are negligible relative to the overall energy balance of the ecosystem. Each plot was equipped with micrometeorological sensors to measure the three major fluxes in Eqn (1). Each sensor recorded an observation every 10 s and was averaged over 10-min intervals.

Net radiation, R_n

Net radiation in 2004 and 2006 was measured using single channel net radiometers (Models Q*6 or Q*7, Radiation and Energy Balance Systems [REBS], Inc., Seattle, WA, USA) and it was measured using dual channel (long- and short-wave) net radiometer (CNR2, Kipp and Zonen, Delft, Holland) in 2010. The net radiometers in 2004 and 2006 were equipped with ventilators obviating the need for wind corrections and to minimize condensation on the net radiometer domes. Net radiometers were placed 1.0 m above the crop canopy and were raised as the crop canopy grew. A cross-calibration was performed prior to, or immediately after the 2004 and 2006 growing seasons as described previously (Bernacchi *et al.*, 2007, 2011). The net radiometers used in 2010 were factory calibrated immediately prior to installation in the field. In one of the elevated [CO₂] plots during 2006, the net radiometer experienced irreconcilable technical difficulties and thus the values for R_n in remaining three plots in the elevated [CO₂] treatment were averaged and used to replace the data from the missing sensor.

Soil heat flux, G_0

Soil heat flux is the conduction of energy per unit area of soil surface in response to an air/soil temperature gradient and was measured by soil heat flux plates (Model HFT-3, REBS, Inc.) buried at 10 cm. Heat storage in the soil above the heat flux plates was calculated following Kimball *et al.* (1994), which requires the measurement of soil temperature (type-T thermocouple; Omega Engineering, Inc., Stamford, CT USA).

Sensible heat flux, H

Sensible heat is the heat energy transferred between the canopy surface and air when there is a difference in temperature

between them. The determination of H depends on several micrometeorological sensors and was calculated as

$$H = \rho_a c_p \frac{T_c - T_a}{r_a} \quad (2)$$

where ρ_a is the air density (kg m^{-3}), c_p is the heat capacity of the air ($\text{J kg}^{-1} \text{ }^\circ\text{C}^{-1}$), T_c and T_a are the respective canopy and air temperatures ($^\circ\text{C}$), and r_a is the aerodynamic resistance (s/m). Air temperature was measured using a thermistor (Model 107; Campbell Scientific, Inc., Logan UT, USA) mounted in a radiation shield (Model 41303-5A Radiation Shield; Campbell Scientific, Inc.) located at 4.0 m above ground level in each plot. Surface temperatures were measured using infrared thermometers (IRTs) in 2004 and 2006 (IRT, IRT-P; Apogee Instruments, Inc., Logan, UT, USA) and infrared radiometers (IRRs, model IRR-PN; Apogee Instruments, Inc.) in 2010 mounted facing South at an angle 25° from vertical to minimize the influence of exposed soil on the canopy temperature measurement by decreasing the portion of the field of view that is soil. When soil was exposed before canopy closure, canopy surface temperatures included both leaf and soil surface temperatures. Measurements began at or near canopy closure (i.e., between 20 and 40 days after emergence depending on year), thus the soil effect was primarily constrained to the early portions of the measurement period. Furthermore, given the similarity in canopies between treatments, the influence of exposed soil likely had a negligible effect on determining differences in H . The calculation of r_a was based on the wind speed, T_a , T_v , dew point temperature, and canopy height following a previously described method (Jackson *et al.*, 1987; Kimball *et al.*, 1994, 1999; Triggs *et al.*, 2004). Wind speed (Model 12102D; R. M. Young Company, Traverse City, MI, USA) and humidity (Model HMP-45C; Campbell Scientific Inc.) were measured at 4.0 m above ground level in each plot. The canopy height was measured biweekly for each plot, and fitted using a sigmoidal function as described previously (Bernacchi *et al.*, 2007).

Soil moisture data

Soil volumetric water content was measured every 10-cm between depths of 5 and 105 cm using a capacitance probe (Diviner-2000; Sentek Sensor Technologies, Stepney, SA, Australia). Data were collected starting on 30th June at 4 locations within each plot (2 within crop rows, 2 between crop rows) every 4–5 days over the growing season until senescence. Raw data from the probe were calibrated against gravimetric data using the method of Paltineanu & Starr (1997). Data from 2004 were previously published as averages for soil layers of 5–25 and 25–55 cm depth in Leakey *et al.* (2006).

Leaf gas exchange

The diurnal course of gas exchange of the youngest fully expanded leaf in each experimental plot was measured on 5 days in 2004 and 6 days in 2010 using four leaf gas exchange systems (LI-6400, LI-COR, Inc., Lincoln, NE, USA);

measurements were not collected in 2006. The dates of measurements in both years corresponded to a range of vegetative and reproductive crop growth stages. For each date, measurements were performed at 2-h intervals from sunrise to sunset. The schedule of gas exchange measurements from the experimental plots has been described previously (Leakey *et al.*, 2006). For each interval, three plants in each plot were measured for gas exchange parameters. Leaf A and g_s were calculated using the equations of von Caemmerer & Furbank (2003). The VPD was determined from the leaf temperature and the external air humidity.

Data analysis

Diel patterns of micrometeorology. For 2004, the 10 min data were statistically analyzed (SAS v. 9.1; The SAS Institute, Raleigh, NC, USA) using analysis of variance with blocks as random factors, treatment as a main effect and time of day as a repeated measure. This analysis was done for clear (212 DOY in 2004) and overcast (243 DOY in 2004) days that were chosen based on the highest and lowest radiation input available for those periods.

Differences (elevated CO₂ minus control) in the 10-min data over the diel course were statistically analyzed using analysis of variance with time of the day as a repeated measure in such a way that each 10-min record throughout the 24-h time course was averaged across each growing season and this analysis was done for all years.

Seasonal patterns of micrometeorology. The 10-min data between 8:00 hours and 20:00 hours for the four energy fluxes were averaged for each day across several days of measurements and analyzed using analysis of variance with blocks as random factors, treatment as a main effect and day of the year as a repeated measure and this was done separately for each year.

Seasonal crop water use. The 10-min λET (W m^{-2}) flux data were converted to their equivalent water depth in mm using latent heat of water vaporization as described previously (Chavez *et al.*, 2009) and summed to provide the total seasonal crop water use (mm). The daily values of ET (mm) were analyzed using analysis of variance with blocks as random factors, treatment as a main effect and day of the year as a repeated measure and were done separately for each year.

Soil moisture content. Plot means ($n = 4$) were analyzed using the MIXED procedure in SAS (SAS 9.2, SAS Institute, Cary, NC, USA), with the Kenward-Rogers option, to perform a complete block analysis of variance in which [CO₂] treatment was a fixed effect and block was a random factor. Structure in the covariance-variance matrix required day of year (DOY) to be treated as a repeated measure. At each soil depth, saturated H₂O%_{v/v} in each plot at the beginning of the season was treated as a covariate. A probability threshold of 0.10 was used to minimize type II errors, as in prior studies (e.g., Leakey *et al.*, 2006; Markelz *et al.*, 2011).

Results

Climate and meteorological conditions

The daily average temperature between planting and harvest in 2004 was 20.8 °C, which is very similar to the 30-year mean temperature for the same time period. With the exception of 1 day in 2004, the maximum daily high temperatures were rarely above 30 °C. Daily low temperatures seldom fell below 10 °C. The mean temperature over the 2006 growing season was 23.0 °C with a larger number of days when the temperature exceeded 30 °C (Fig. 1). The daily average temperature over 2010 growing period was warmer than the other growing periods and 4.0 °C higher than 30-year long-term average temperature (Fig. 1).

The mean daily total solar radiation was 21.4, 18.6, and 22.5 (MJ d⁻¹), for 2004, 2006, and 2010, respectively. Vapor pressure deficit was slightly higher in 2010 compared with the other 2 years (Fig. 1). The total precipitation recorded during the 2004, 2006, and 2010 growing seasons were 426, 487, and 424 mm, respectively, which were ca. 93%, 106%, and 92% of the long-term climate average (458 mm for 30-year average; MRCC; Fig. 1). The PCMI for the SoyFACE site during the study years was greater than -1 in all years indicating that the water stress was minimal (Fig. 2).

Ecosystem energy fluxes and soil moisture

Two contrasting days in 2004 were selected to illustrate the diel course of ecosystem energy fluxes for relatively clear and overcast conditions (Fig. 3). On both days, the differences over the diel time course between ambient and elevated [CO₂] plots were small for both *R_n* and *G₀*. Both the clear and the overcast day had significantly higher (*P* < 0.001 in both cases) sensible heat flux (*H*),

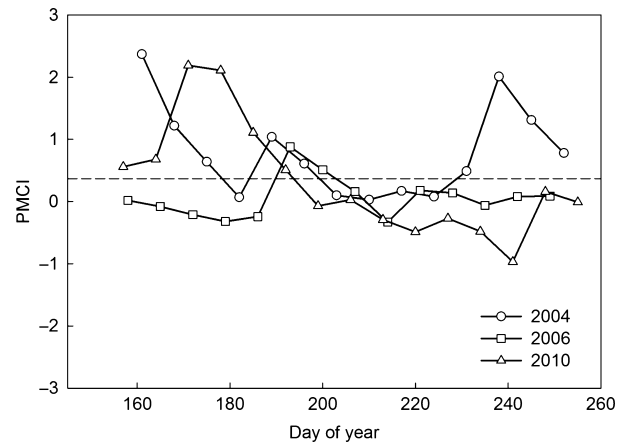


Fig. 2 Weekly mean Palmer Crop Moisture Index (PCMI; Palmer, 1968) and the 30-year long-term average of PCMI value (dotted line) for Illinois climate division 5, which includes SoyFACE.

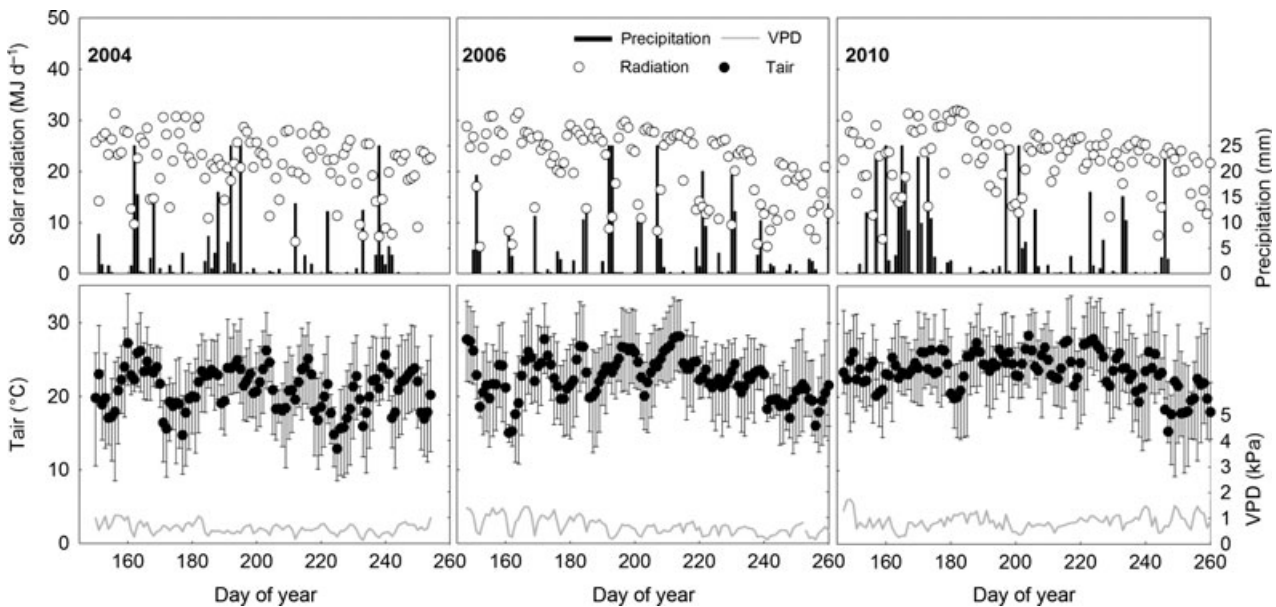


Fig. 1 Daily integrated incoming solar radiation and precipitation (top panel), and daily mean temperatures including temperature range (error bars), and daily average vapor pressure deficit (bottom panel) for the 2004, 2006, and 2010 growing seasons at the SoyFACE facility.

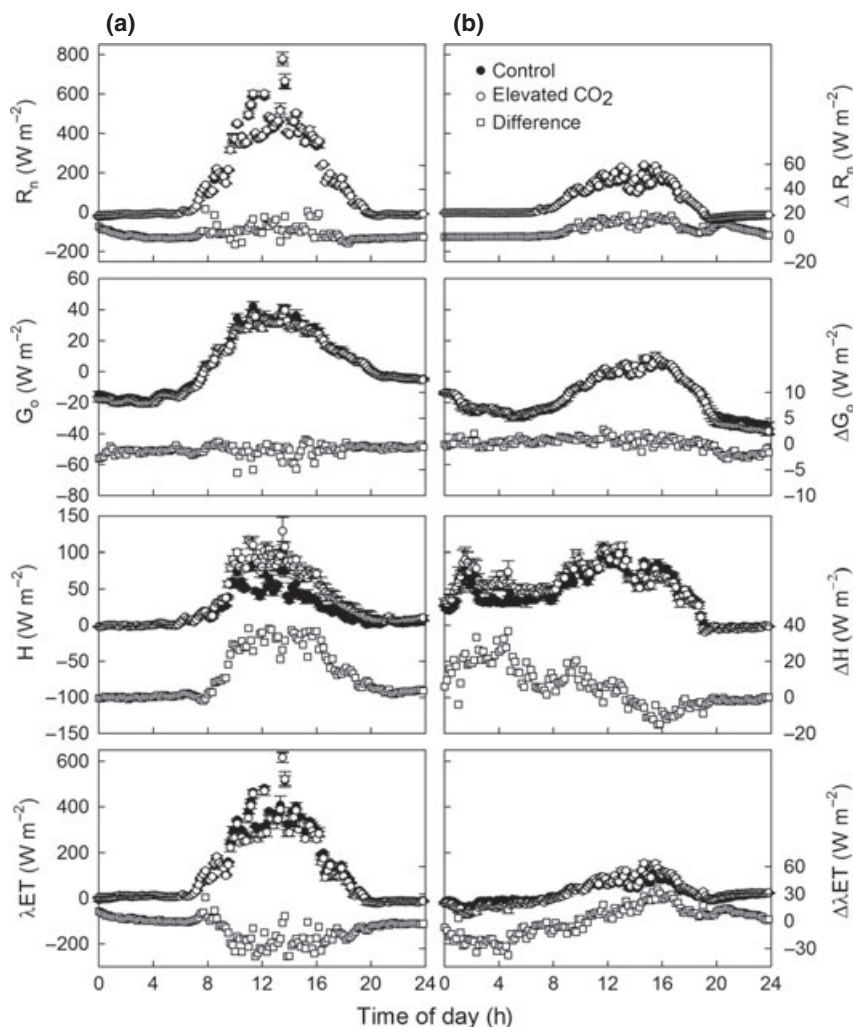


Fig. 3 Ten minute mean net radiation (R_n), soil heat flux (G_o), latent heat flux (λET), and sensible heat flux (H) for an example sunny day (day of year 212, 2004) and cloud cover day (day of year 243, 2004) for the control and elevated [CO_2] and difference (Δ) due to elevated [CO_2]. Bars indicate standard error of mean.

while significantly lower ($P < 0.001$) λET in elevated [CO_2] relative to control.

Over much of the diel period and throughout three growing seasons, λET was lower in the elevated [CO_2] plots relative to the control with the exception of the first ca. 15 days of measurements in 2006 (DOY 170–185) when the control plots had lower λET . The elevated [CO_2] plots also had higher H and T_c relative to control, again with exception of the beginning of the 2006 growing season (Fig. 4). In 2004 and 2010, the observed responses of λET , T_c and H were greatest at the beginning of the measurement period but gradually diminished throughout the growing season (Fig. 4). In 2006, the differences for λET , T_c , and H switched sign ca. 15 days into the measurement period (Fig. 4) and did not diminish as in other years. In 2004 and 2010, the largest differences due to elevated [CO_2] consistently

occurred during midday (10:00 hours to 3:00 hours Central US daylight savings time) while in 2006, the largest differences occurred from midday to early evening after the first ca. 15 days. Overall, the maximum differences in T_c were up to 3 °C, which corresponded to 150 $W m^{-2}$ differences in both H and λET (Fig. 4).

Despite substantial day to day variability in the major fluxes (Fig. 5), daytime mean values of λET were significantly lower and those of T_c and H were significantly higher in the elevated [CO_2] relative to the control plots in all years (Table 1). Sensible heat flux was significantly higher in the elevated [CO_2] relative to ambient, with seasonal mean increase of 25, 30, and 28 $W m^{-2}$ for 2004, 2006, and 2010, respectively (Table 1). Across treatments the majority of energy entering the ecosystem as R_n was partitioned to λET for the majority of growing seasons with an overall seasonal mean of ca.

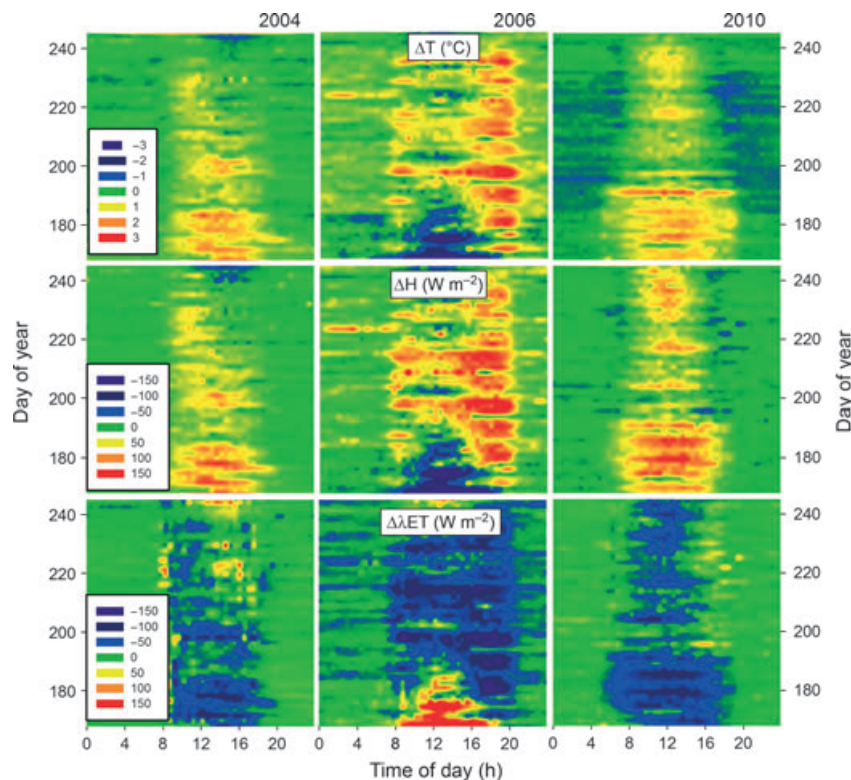


Fig. 4 The difference (elevated $[\text{CO}_2]$ – control) in canopy temperature (ΔT_c ; top row), sensible heat flux (ΔH ; middle row), and latent heat flux ($\Delta \lambda \text{ET}$; bottom row), over the diel time course (X-axes) and throughout the growing season (Y-axes) for 3 years. Standard errors are not graphed here, but range from 0.09 °C to 0.04 °C, 2.58–5.20 W m^{-2} , 3.52–5.43 W m^{-2} for T_c , H , and λET , respectively depending on the year.

Table 1 Seasonal mean energy fluxes (\pm standard errors) over 3 years of measurement of maize grown in control and elevated $[\text{CO}_2]$ at SoyFACE. Each value represents the mean of 10 min data between 08:00 hours and 20:00 hours over the replicated plots ($n = 4$)

Year	Treatment	R_n (W m^{-2})	G_0 (W m^{-2})	H (W m^{-2})	λET (W m^{-2})	T_c ($^{\circ}\text{C}$)	T_c^* ($^{\circ}\text{C}$)
2004	Control	279 ± 0.5	18.1 ± 1.5	55.9 ± 1.7	205 ± 3.3	24.6 ± 0.03	26.7 ± 0.04
	Elevated	285 ± 0.5	18.2 ± 1.5	80.6 ± 1.8	186 ± 3.4	25.1 ± 0.03	27.3 ± 0.04
	<i>P</i> value	<0.0001	<0.002	<0.0001	<0.0001	<0.0001	<0.0001
2006	Control	301 ± 2.5	18.2 ± 1.3	67.0 ± 8.0	216 ± 9.7	27.3 ± 0.2	29.3 ± 0.1
	Elevated	292 ± 2.6	17.2 ± 1.2	97.4 ± 8.1	177 ± 9.7	27.9 ± 0.2	29.5 ± 0.1
	<i>P</i> value	<0.0001	<0.001	<0.003	0.0001	<0.0001	<0.0001
2010	Control	300 ± 3.8	13.5 ± 1.7	19.3 ± 2.8	267 ± 5.8	27.0 ± 0.06	29.2 ± 0.05
	Elevated	304 ± 3.8	14.6 ± 0.5	47.2 ± 2.8	242 ± 5.9	27.5 ± 0.06	29.9 ± 0.06
	<i>P</i> value	<0.0001	<0.004	<0.003	<0.0001	<0.0001	<0.0001
Mean				$\uparrow 25\text{--}30$	$\downarrow 19\text{--}39$	$\uparrow 0.5\text{--}0.6$	$\uparrow 0.2\text{--}0.7$

T_c^* – canopy temperature averaged between midday hours (12:00 hours–16:00 hours).

290 W m^{-2} (Fig. 5; Table 1). The standard deviation of net radiation measurements for the individual plots differed by no more than 1% over the different growing seasons. Differences in daytime mean R_n , while statistically different between control and elevated $[\text{CO}_2]$, were relatively small (Fig. 5; Table 1). Daytime mean H , while variable from day to day (Fig. 5) was

significantly higher in elevated $[\text{CO}_2]$ relative to the control for all years (Table 1). The smallest flux was G_0 which, while statistically different between the treatment and control, showed very small $[\text{CO}_2]$ -induced differences. The overall seasonal mean difference in T_c between ambient and elevated $[\text{CO}_2]$ was small (ca. 0.5 °C) (Table 1), but as expected the biggest

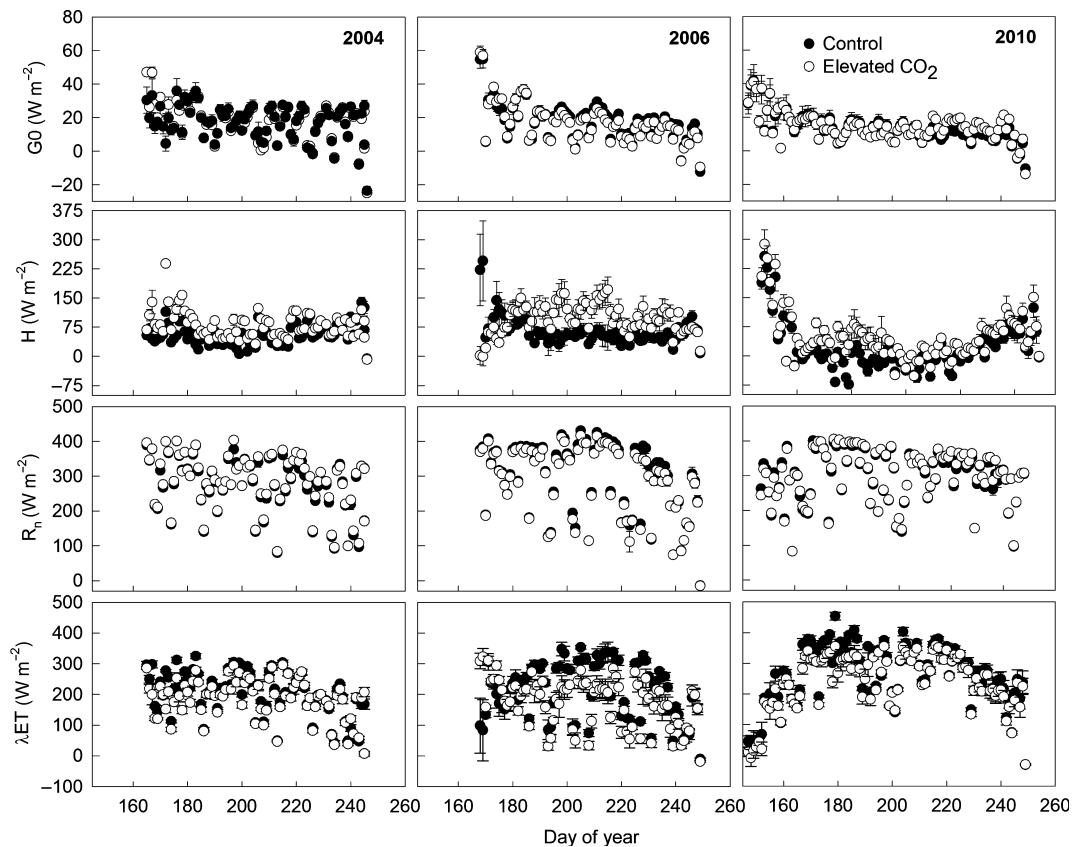


Fig. 5 Seasonal course of daytime mean values of latent heat flux (λ ET), net radiation (R_n), sensible heat flux (H), and soil heat flux (G_0) for control and elevated [CO_2] ($n = 4$) for 2004, 2006, and 2010 growing seasons. Each mean value represents the average 10-min data between 08:00 hours and 20:00 hours. Bars indicate one standard error of mean.

differences during midday were observed in 2004 and 2010 while the midday difference was smallest in 2006 (Table 1). The total reduction in daytime ET for maize grown in elevated [CO_2] was 22, 36 and 47 mm in 2004, 2006, and 2010, respectively, which corresponded to an average decrease of ca. 9% over the 3 years (Table 2).

Soil moisture measurements began 2 weeks prior to the initiation of micrometeorological measurements. There were no differences in volumetric soil water content at the beginning of each growing season (Fig. 6). Overall, the top 50 cm experienced the greatest variability as a result of crop water use during periods of lower rainfall inputs and rewetting after significant rainfall events (Fig. 6; Table 3). Beyond 50-cm depth, there were no large-scale changes in soil volumetric water content over time in either ambient or elevated [CO_2]. In 2004, there was greater volumetric soil water content in elevated [CO_2] compared to ambient [CO_2] from DOY 190 to 243, which corresponded with a prolonged period in which relatively little precipitation fell (Fig. 1). The difference in soil water content between ambient [CO_2] and elevated [CO_2] declined with depth from the surface to about 35–45 cm, depending on date.

Table 2 Comparison of evapotranspiration (mm) in different growing periods. Each value represents the sum of 10 min data over the replicated plots across several days of measurements

Year	Control	Elevated [CO_2]	Difference
2004	316.6 \pm 4.8	294.4 \pm 9.5	–22.2 (7%)
2006	336.9 \pm 2.6	300.7 \pm 10.7	–36.2 (11%)
2010	564.3 \pm 0.03	517.0 \pm 0.01	–47.2 (8%)
Mean			–35.2 (9%)

The difference in soil water content between control and elevated [CO_2] in 2006 was initially restricted to shallow soil layers (5–25 cm), although soil moisture in the elevated [CO_2] plots was about 10% higher than the control to depths of ca. 65 cm during a relatively dry period at the beginning of the season. In 2010, there were consistent periods of drawdown and recharge of soil moisture depending on precipitation input, with greater soil volumetric water content in elevated [CO_2] observed between DOY 220 and 250. An increase of about 10–15% of soil moisture in the elevated [CO_2] plots was apparent in 15–65-cm soil depth (Fig. 6).

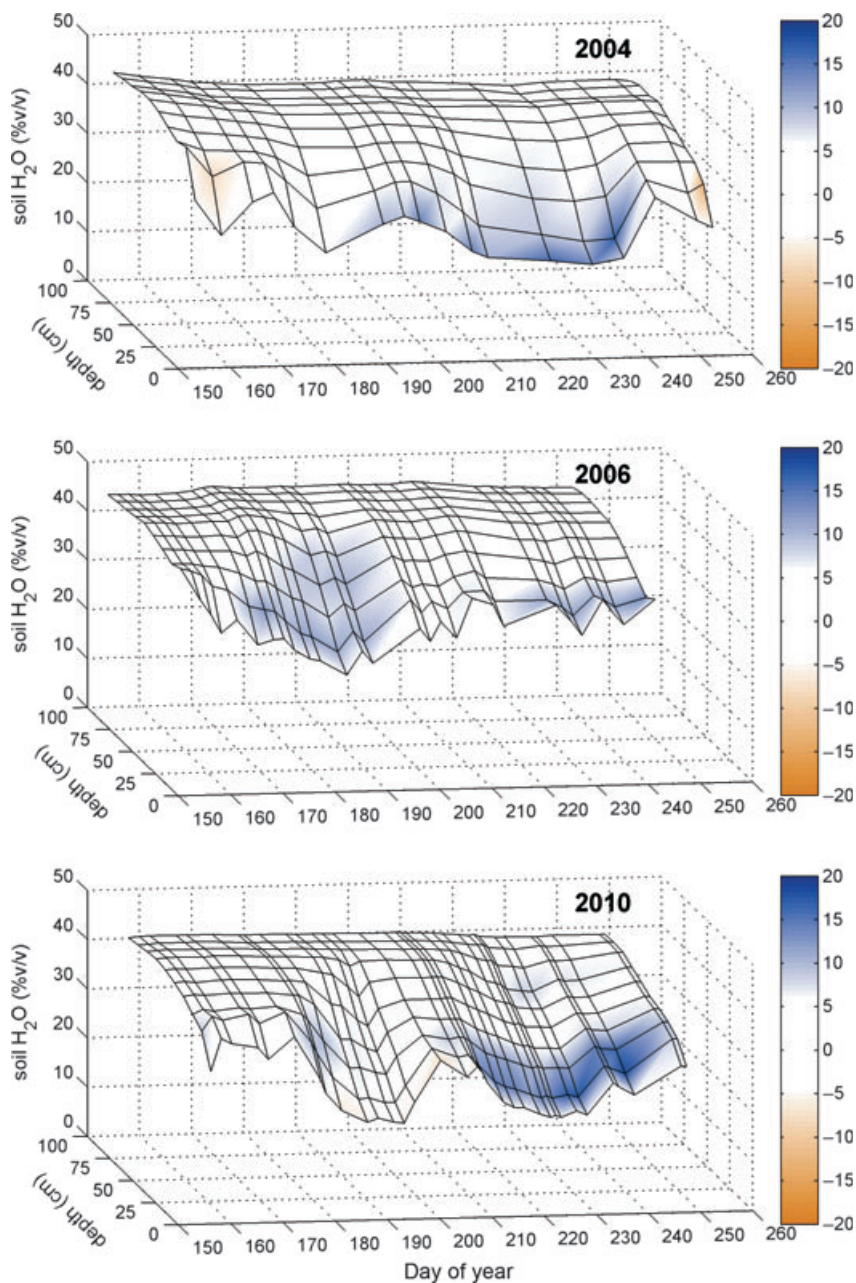


Fig. 6 Soil volumetric moisture content ($\text{H}_2\text{O}\%_{\text{v/v}}$) for three growing seasons. On all three panels, the y -axis represents day of year (DOY), the x -axis soil depth (cm), and the z -axis soil volumetric moisture content ($\text{H}_2\text{O}\%_{\text{v/v}}$). The color scale represents the % change in soil volumetric moisture content in elevated $[\text{CO}_2]$ compared to ambient $[\text{CO}_2]$, with the blue coloring representing greater soil volumetric moisture content in the elevated $[\text{CO}_2]$ treatment.

Comparison of ET response to g_s between maize and soybean

Data for both ET (this study for maize; Bernacchi *et al.*, 2007 for soybean) and g_s (Leakey *et al.*, 2006 for maize; Bernacchi *et al.*, 2007 for soybean) were available for the 2004 growing season. The g_s data of maize and soybean for each plot were averaged across daylight hours and

several days of measurement (ca. biweekly), and plotted against its respective seasonal ET for control and elevated $[\text{CO}_2]$ (Fig. 7). Total growing season ET differed by only ca. 1% between maize and soybean in the ambient plots (Table 4). However, compared to maize, ET was reduced more than twice as much for soybean in elevated $[\text{CO}_2]$ relative to ambient. There was a linear relationship of ET with g_s ($r^2 = 0.59$; Table 4) in both

Table 3 Probabilities associated with treatment effects (day of year = DOY; [CO₂] = CO₂; day of year by [CO₂] interaction = DOY × CO₂) from complete-block repeated measures analysis of variance for soil moisture in 10-cm increments from depths of 5–105 cm in plots of maize during the 2004 and 2006 growing seasons. Significant effects ($P < 0.1$) of CO₂ or DOY × CO₂ are shaded gray

Depth	Effect	2004	2006	2010
5–15 cm	DOY	<0.001	<0.001	<0.001
	CO ₂	0.369	0.695	0.503
	DOY × CO ₂	0.073	0.064	0.988
15–25 cm	DOY	<0.001	<0.001	<0.001
	CO ₂	0.694	0.276	0.081
	DOY × CO ₂	0.006	0.080	0.030
25–35 cm	DOY	<0.001	<0.001	<0.001
	CO ₂	0.322	0.971	0.044
	DOY × CO ₂	0.099	0.531	0.701
35–45 cm	DOY	<0.001	<0.001	<0.001
	CO ₂	0.063	0.247	0.331
	DOY × CO ₂	0.444	0.593	0.999
45–55 cm	DOY	<0.001	<0.001	<0.001
	CO ₂	0.052	0.728	0.567
	DOY × CO ₂	0.382	0.124	0.995
55–65 cm	DOY	<0.001	<0.001	<0.001
	CO ₂	0.454	0.852	0.419
	DOY × CO ₂	0.274	0.622	0.998
65–75 cm	DOY	<0.001	<0.001	<0.001
	CO ₂	0.446	0.814	0.266
	DOY × CO ₂	0.262	0.911	0.007
75–85 cm	DOY	<0.001	<0.001	<0.001
	CO ₂	0.728	0.602	0.195
	DOY × CO ₂	0.493	0.886	0.009
85–95 cm	DOY	<0.001	<0.001	<0.001
	CO ₂	0.862	0.448	0.900
	DOY × CO ₂	0.171	0.440	0.443
95–105 cm	DOY	<0.001	<0.001	<0.001
	CO ₂	0.217	0.877	0.683
	DOY × CO ₂	0.002	0.665	1.000

maize and soybean regardless of [CO₂], with lower values for both ET and g_s in elevated [CO₂] relative to ambient (Fig. 7). In absolute terms, the reduction in g_s in elevated [CO₂] compared to ambient was very similar for maize and soybean, however, on a percentage basis, maize had a larger reduction in g_s than soybean (Table 4). The linear relationship of g_s to ET suggests that for a 20% decrease in g_s , there was 16% decrease in ET in soybean, while 29% g_s decrease had a 7% corresponding decrease in ET in maize (Table 4).

Discussion

The objectives of this study were to evaluate the impact of elevated [CO₂] on ecosystem energy fluxes, and to examine the seasonal changes in maize water use and

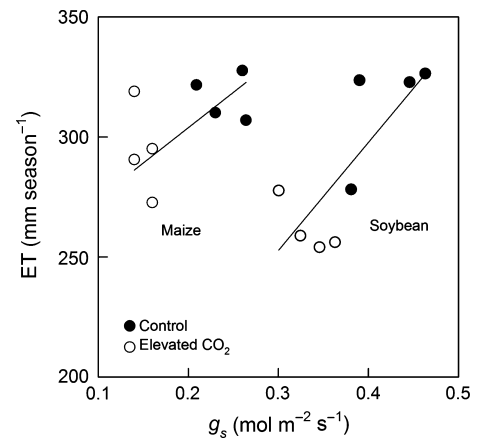


Fig. 7 The linear relationship of ET to g_s based on the several days of measurements in 2004 growing season for soybean and maize. Stomatal conductance of the upper leaves was averaged across the daylight hours and days of measurement for soybean (Bernacchi *et al.*, 2007) and maize (Leakey *et al.*, 2006) and plotted against its corresponding ET for control and elevated CO₂ plots.

Table 4 The parameters of linear regression between ET and g_s (Fig. 7) based on several days of ca. biweekly measurements across 2004 growing season

Parameters	Maize	Soybean
g_s (mol m ⁻² s ⁻¹)		
Control	0.24 ± 0.01	0.41 ± 0.02
Elevated CO ₂	0.17 ± 0.01	0.33 ± 0.01
Difference	0.07 (29%)	0.08 (19.5%)
ET (mm season ⁻¹)		
Control	316 ± 4.9	312 ± 11.6
Elevated CO ₂	294 ± 9.5	261 ± 5.4
Difference	22 (7.2%)	51 (16%)
r^2	0.57	0.60
Intercept	245	117
Slope	294	450

± indicates standard errors of mean.

soil water content under open-air conditions. Our results indicated that elevated [CO₂] reduced maize ET by about 9% over three growing seasons which is smaller than that reported for soybean (Bernacchi *et al.*, 2007), but consistent with the range of values reported for other crops in other FACE studies (e.g., Kimball *et al.*, 1999; Burkart *et al.*, 2011). This is the first study to evaluate the effects of elevated [CO₂] on crop water use for a rain-fed C₄ agro-ecosystem using micrometeorological techniques. While previous experiments show ET reductions under elevated [CO₂] for maize (King & Greer, 1986; Kim *et al.*, 2006; Chun *et al.*, 2011), these

studies were conducted in irrigated systems and cannot be expected to quantitatively represent the rain-fed conditions of the Midwestern US. The $[\text{CO}_2]$ enrichment significantly conserved soil moisture content at shallower soil layers supporting previous findings and discussion in FACE and other studies with maize (Markelz *et al.*, 2011; Manderscheid *et al.*, 2012) and other crops (Kang *et al.*, 2002; Triggs *et al.*, 2004; Bernacchi *et al.*, 2007; Burkart *et al.*, 2011; Manderscheid *et al.*, 2012). The observed response of ET to elevated $[\text{CO}_2]$ coupled with the changes in soil moisture supports the assertion that elevated $[\text{CO}_2]$ can lead to conservation of soil moisture especially in the upper layers. Evidence also shows that increased soil moisture may help in delaying the onset of drought stress during the periods of low rainfall (Samarakoon & Gifford, 1995; Conley *et al.*, 2001; Wall *et al.*, 2001; Bernacchi *et al.*, 2007; Markelz *et al.*, 2011).

The reduction in λET in elevated $[\text{CO}_2]$ is most likely attributed to reduced stomatal conductance. Maize photosynthesis under non-stressed conditions is already saturated at present $[\text{CO}_2]$ due to the CO_2 -concentrating mechanism of the C_4 photosynthetic pathway. Therefore, under non-stressed conditions, the elevated $[\text{CO}_2]$ had no or little change in leaf area, plant biomass or grain yield in maize (Leakey *et al.*, 2006; Chun *et al.*, 2011; Vanaja *et al.*, 2011) and in other C_4 species (Dippery *et al.*, 1995; Owensby *et al.*, 1997; de Souza *et al.*, 2013). As previously shown at the SoyFACE site for 2004 (Leakey *et al.*, 2006) and measured in our experimental plots in 2010 (data not shown), LAI did not differ with $[\text{CO}_2]$ for maize. Because of this, we hypothesized that maize ET would decrease more in elevated $[\text{CO}_2]$ than observed previously for C_3 plants such as soybean (Bernacchi *et al.*, 2007). However, this hypothesis was not supported by the data; the maize response of ET to elevated $[\text{CO}_2]$ (ca. 7%) was less than the average observed for soybean (16%; Table 4). While significant reductions in stomatal conductance at elevated $[\text{CO}_2]$ were observed during the 2004 (Leakey *et al.*, 2006) and 2010 growing seasons from the same experimental plots used in this study (data not shown), other factors may be responsible for maize ET responding less to $[\text{CO}_2]$ than soybean.

One factor that could explain the smaller response for maize could be differences in the size and distribution of the maize rooting system with growth in elevated $[\text{CO}_2]$. So far, little is known about the root characteristics of maize grown in FACE conditions, however, growth chamber studies suggest that maize grown in elevated $[\text{CO}_2]$ can extract more water from deeper layers due to increased root length (Vanaja *et al.*, 2011) and increased root capacity for water absorption (Wall *et al.*, 2001). Our results do not

support these findings, as the largest relative differences in soil moisture between treatments occurred at shallow depths (<55 cm). Another factor could be that the stomata of elevated $[\text{CO}_2]$ -grown maize respond differently to changing environmental conditions such as VPD compared with control plants. Our results show no evidence for a differential response of g_s to VPD across the range of growing season conditions (data not shown); this is consistent with a previous study on maize (Morison & Gifford, 1983).

A factor that does appear to be supported by our data is the possibility that the stomatal control over ET is smaller for maize compared to soybean (Fig. 7; Table 4). While the relative decrease in g_s was greater for maize than soybean, in absolute terms, the response was similar (Table 4). This may be primarily due to the lower inherent rate of g_s for C_4 compared to C_3 plants (Taylor *et al.*, 2010). Approximating the partitioning of ET into the evaporation and transpiration components using LAI data after canopy closure and before the onset of senescence (between DOY 152 and DOY 249; method provided by Kang *et al.*, 2003), our analysis revealed that the seasonal transpiration in maize accounted for ca. 80% of growing season ET (data not shown). A similar analysis on soybean, however, indicates that transpiration accounts for ca. 90% of ET (Sauer *et al.*, 2007). Thus, evaporation could account for a greater portion of total ET for maize than for soybean which could reduce the role of stomata in maize ET responses to elevated $[\text{CO}_2]$.

Our results show a strong dynamic relationship between soil moisture and canopy ET. When soil moisture was similar for the control and elevated $[\text{CO}_2]$ treatment, there was a consistent reduction in λET for elevated $[\text{CO}_2]$. There was no indication of water stress, with PCMI values greater than -1 (Fig. 2), however, as soil moisture was depleted more rapidly in the ambient plots, λET in elevated $[\text{CO}_2]$ approached or even exceeded rates of water use in the control plots (e.g., DOY 170 to 190 in 2006; Figs 4 and 5). Based on the observed differences in volumetric water content for the profile at key dates in each of the growing seasons, the elevated $[\text{CO}_2]$ plots had ca. 13, 15, and 15 mm of additional water available at the time of greatest draw-down of soil moisture in 2004 (DOY 230), 2006 (DOY 223), and 2010 (DOY 184), respectively (Fig. 6). Considering an average water withdrawal rate of ca. 5 mm per day, the elevated $[\text{CO}_2]$ plots would have had enough additional moisture to support approximately 3 days of normal plant growth. During the 2004 and 2010 growing seasons, the differences in ET between the control and elevated $[\text{CO}_2]$ plots were largest during the midday; however, in 2006 there was a shift to much greater differences during the early evening.

While it is not clear what could be driving this response in 2006, a potential explanation could involve the significantly higher overall canopy temperatures in 2006 relative to 2004 and 2010 (Table 1). It is possible that higher heat storage of the canopy in the elevated CO₂ plots results in a slower dissipation of the heat during the evening relative to the control in 2006.

In addition to having significant implications on the hydrologic cycle, reduced ET under elevated [CO₂] could have a large impact on regional climate. The diel differences due to elevated [CO₂] resulted in increased H (up to 150 W m⁻²) and T_c (up to 3 °C) during mid-day (Fig. 4). This finding is in agreement with previous FACE studies in elevated [CO₂], although the magnitude of [CO₂] related canopy temperature increase varies according to the species and experimental conditions (Kimball *et al.*, 1995; Triggs *et al.*, 2004; Bernacchi *et al.*, 2007).

Of particular importance is the lower observed responses of ET for maize in this study to the responses observed for soybean over four growing seasons (Bernacchi *et al.*, 2007). Consequently, the prediction that C₄ species, with a lack of increased growth in elevated [CO₂], would yield greater decreases in ET than C₃ species is not supported by the data. Maize together with soybean forms the single largest continuous ecosystem in the continental United States and vegetation has a strong influence on the climate of continental interiors such as the Midwestern US (Sellers *et al.*, 1997). Therefore, as predicted by regional scale simulations (Sellers *et al.*, 1996; Bounoua *et al.*, 1999), ET reduction from maize/soybean agro-ecosystem at future elevated [CO₂] concentration may result in lower growing season precipitation in the Midwestern US. Because maize ET responses to elevated [CO₂] are less than that for soybean, extrapolating soybean responses to the Midwestern US are potentially misleading. As a result, accurate prediction of the impact of rising [CO₂] on climate and hydrologic processes requires explicit representation of key mechanisms that drive differences between C₄ and C₃ species.

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References

Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosyn-

- thesis, canopy properties and plant production to rising CO₂. *New Phytologist*, **165**, 351–372.
- Ainsworth EA, Davey PA, Bernacchi CJ *et al.* (2002) A meta-analysis of elevated [CO₂] effects on soybean (*Glycine max*) physiology, growth and yield. *Global Change Biology*, **8**, 695–709.
- Arnell NW, Liu C, Compagnucci R *et al.* (2001) Hydrology and water resources. In: *Climate Change 2001: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change* (eds McCarthy JJ, Canziani OF, Leary NA, Dokken DJ, White KS), pp. 191–234. Cambridge University Press, Cambridge, UK and New York, NY, USA.
- Baldocchi DD, Hicks BB, Meyers TP (1988) Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. *Ecology*, **69**, 1331–1340.
- Bernacchi CJ, Kimball BA, Quarles DR, Long SP, Ort DR (2007) Decreases in stomatal conductance of soybean under open-air elevation of [CO₂] is closely coupled with decreases in ecosystem evapotranspiration. *Plant Physiology*, **143**, 134–144.
- Bernacchi CJ, Leakey ADB, Kimball BA, Ort DR (2011) Growth of soybean at future tropospheric ozone concentrations decreases canopy evapotranspiration and soil water depletion. *Environment Pollution*, **159**, 1464–1472.
- Berry JA, Beerling DJ, Franks PJ (2010) Stomata: key players in the earth system, past and present. *Current Opinion in Plant Biology*, **13**, 233–240.
- Bounoua L, Collatz GJ, Sellers PJ *et al.* (1999) Interaction between vegetation and climate: radiative and physiological effects of doubled atmospheric CO₂. *Journal of Climate*, **12**, 309–324.
- Burkart S, Manderscheid R, Weigel HJ (2004) Interactive effects of atmospheric CO₂ concentration and plant available soil water content on canopy evapotranspiration and conductance of spring wheat. *European Journal of Agronomy*, **21**, 401–417.
- Burkart S, Manderscheid R, Wittich KP, Lopmeier FJ, Weigel HJ (2011) Elevated [CO₂] effects on canopy and soil water flux parameters measured using a large chamber in crops grown in free-air CO₂ enrichment. *Plant Biology*, **13**, 258–268.
- von Caemmerer S, Furbank RT (2003) The C-4 pathway: an efficient CO₂ pump. *Photosynthesis Research*, **77**, 191–207.
- Chaudhuri UN, Kirkham MB, Kanemasu ET (1990) Carbon dioxide and water level effects on yield and water use of winter wheat. *Agronomy Journal*, **82**, 637–641.
- Chavez JL, Howell TA, Copeland KS (2009) Evaluating eddy covariance cotton measurements in an advective environment with large weighing lysimeters. *Irrigation Science*, **28**, 35–50.
- Chun JA, Wang Q, Timlin DJ, Fleisher DH, Reddy VR (2011) Effect of elevated carbon dioxide and water stress on gas exchange and water use efficiency in corn. *Agricultural and Forest Meteorology*, **151**, 378–384.
- Conley MM, Kimball BA, Brooks TJ *et al.* (2001) CO₂ enrichment increases water-use efficiency in sorghum. *New Phytologist*, **151**, 407–412.
- Dermod O, Long SP, DeLucia EH (2006) How does elevated CO₂ or ozone affect the leaf-area index of soybean when applied independently? *New Phytologist*, **169**, 145–155.
- Dippery JK, Tissue DT, Thomas RB, Strain BR (1995) Effects of low and elevated CO₂ on C₃ and C₄ annuals. Growth and biomass allocation. *Oecologia*, **101**, 13–20.
- Ellsworth DS (1999) CO₂ enrichment in a maturing pine forest: are CO₂ exchange and water status in the canopy affected? *Plant, Cell and Environment*, **22**, 461–472.
- Hickman GC, Van Loocke A, Dohleman FG, Bernacchi CJ (2010) A comparison of canopy evapotranspiration for maize and two perennial grasses identified as potential bioenergy crops. *Global Change Biology Bioenergy*, **2**, 157–168.
- Hileman DR, Huluka G, Kenjige PK *et al.* (1994) Canopy photosynthesis and transpiration of field-grown cotton exposed to free-air CO₂ enrichment (FACE) and differential irrigation. *Agriculture and Forest Meteorology*, **70**, 189–207.
- Houghton JT, Ding Y, Griggs DJ *et al.* (2001) In: *Climate Change 2001: The Scientific Basis: Contributions of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.
- Huband NDS, Monteith JL (1986) Radiative surface temperature and energy balance of a wheat canopy II: estimating fluxes of sensible and latent heat. *Boundary Layer Meteorology*, **36**, 107–116.
- Hui DF, Luo YQ, Cheng WX, Coleman JS, Johnson DW, Sims DA (2001) Canopy radiation and water use efficiencies as affected by elevated [CO₂]. *Global Change Biology*, **7**, 75–91.
- Jackson RD, Moran MS, Gay LW, Raymond LH (1987) Evaluating evaporation from field crops using airborne radiometry and ground-based meteorological data. *Irrigation Science*, **8**, 81–90.
- Jones P, Allen LH Jr, Jones JW, Valle R (1985) Photosynthesis and transpiration responses of soybean canopies to short- and long-term CO₂ treatments. *Agronomy Journal*, **77**, 119–126.
- Kang S, Zhang F, Hu X, Zhang J (2002) Benefits of CO₂ enrichment on crop plants are modified by soil water status. *Plant and Soil*, **238**, 69–77.

- Kang S, Gu B, Du T, Zhang J (2003) Crop coefficient and ratio of transpiration to evapotranspiration of winter wheat and maize in semi-humid region. *Agricultural Water Management*, **59**, 239–254.
- Kim S-H, Sicher RC, Bae H, Gitz DC, Baker JT, Timlin DJ, Reddy VR (2006) Canopy photosynthesis, evapotranspiration, leaf nitrogen, and transcription profiles of maize in response to CO₂ enrichment. *Global Change Biology*, **12**, 588–600.
- Kimball B, Bernacchi CJ (2006) Evapotranspiration, canopy temperature, and plant water relations. In: *Managed Ecosystems and Rising CO₂: Case Studies, Processes, and Perspectives* (eds Nösberger J, Blum H), pp. 311–324. Springer Verlag, Berlin.
- Kimball BA, LaMorte RL, Seay RS *et al.* (1994) Effects of free-air CO₂ enrichment on energy-balance and evapotranspiration of cotton. *Agricultural and Forest Meteorology*, **70**, 259–278.
- Kimball BA, Pinter PJ Jr, Garcia RL *et al.* (1995) Productivity and water use of wheat under free – air CO₂ enrichment. *Global Change Biology*, **1**, 429–442.
- Kimball BA, LaMorte RL, Pinter PJ Jr *et al.* (1999) Free-air CO₂ enrichment (FACE) and soil nitrogen effects on energy balance and evapotranspiration of wheat. *Water Resources Research*, **35**, 1179–1190.
- King KM, Greer DH (1986) Effects of carbon dioxide enrichment and soil water on maize. *Agronomy Journal*, **78**, 515–521.
- Leakey ADB, Bernacchi CJ, Dohleman FG, Ort DR, Long SP (2004) Will photosynthesis of maize (*Zea mays*) in the US Corn Belt increase in future CO₂ rich atmospheres? An analysis of diurnal courses of CO₂ uptake under free-air concentration enrichment (FACE). *Global Change Biology*, **10**, 951–962.
- Leakey ADB, Uribealarea M, Ainsworth EA, Naidu SL, Rogers A, Ort DR, Long SP (2006) Photosynthesis, productivity, and yield of maize are not affected by open-air elevation of CO₂ concentration in the absence of drought. *Plant Physiology*, **140**, 779–790.
- Leakey ADB, Ainsworth EA, Bernacchi CJ, Rogers A, Long SP, Ort SR (2009) Elevated [CO₂] effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *Journal of Experimental Botany*, **60**, 2859–2876.
- Leipprand A, Gerten D (2006) Global effects of doubled atmospheric CO₂ content on evapotranspiration, soil moisture and runoff under potential natural vegetation. *Hydrology Science Journal*, **51**, 171–185.
- Li FS, Kang SZ, Zhang JH (2004) Interactive effects of elevated CO₂, nitrogen and drought on leaf area, stomatal conductance, and evapotranspiration of wheat. *Agriculture Water Management*, **67**, 221–233.
- Long SP, Ainsworth EA, Rogers A, Ort DR (2004) Rising atmospheric carbon dioxide: plants FACE the future. *Annual Review of Plant Biology*, **55**, 591–628.
- Long SP, Ainsworth EA, Leakey ADB, Nösberger J, Ort DR (2006) Food for thought: lower- than-expected crop yield stimulation with rising CO₂ concentrations. *Science*, **312**, 1918–1921.
- Magliulo V, Bindi M, Rana G (2003) Water use of irrigated potato (*Solanum tuberosum* L.) grown under free air carbon dioxide enrichment in central Italy. *Agriculture Ecosystem and Environment*, **97**, 65–80.
- Manderscheid R, Erbs M, Weigel H-S (2012) Interactive effects of free-air CO₂ enrichment and drought stress on maize growth. *European Journal of Agronomy*, in press. doi: 10.1016/j.eja.2011.12.007
- Markelz RJC, Strellner RS, Leakey ADB (2011) Impairment of C₄ photosynthesis by drought is exacerbated by limiting nitrogen and ameliorated by elevated [CO₂] in maize. *Journal of Experimental Botany*, **62**, 3235–3246.
- Medlyn BE, Barton CVM, Broadmeadow MSJ *et al.* (2001) Stomatal conductance of forest species after long-term exposure to elevated [CO₂] concentration: a synthesis. *New Phytologist*, **149**, 247–264.
- Meehl GA, Stocker TF, Collins WD *et al.* (2007) Global climate projections. In: *Climate change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change* (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL), pp. 10–12. Cambridge University Press, Cambridge.
- Meyers TP, Hollinger SE (2004) An assessment of storage terms in the surface energy balance of maize and soybean. *Agricultural and Forest Meteorology*, **125**, 105–115.
- Morison JIL, Gifford RM (1983) Stomatal sensitivity to carbon dioxide and humidity. A comparison of two C₃ and two C₄ grass species. *Plant physiology*, **71**, 789–796.
- Owensby CE, Ham JM, Knapp AK, Bremer D, Auen LM (1997) Water vapor fluxes and their impact under elevated CO₂ in a C₄-tallgrass prairie. *Global Change Biology*, **3**, 189–195.
- Palmer WC (1968) Keeping track of crop moisture conditions, nationwide: the new Crop Moisture Index. *Weatherwise*, **21**, 156–161.
- Paltineanu IC, Starr JL (1997) Real-time soil water dynamics using multi-sensor capacitance probes: laboratory calibration. *Soil Science Society of American Journal*, **61**, 1576–1585.
- Samarakoon AB, Gifford RM (1995) Soil water content under plants at high CO₂ concentration and interactions with direct CO₂ effects: a species comparison. *Journal of Biogeography*, **22**, 193–202.
- Sauer TJ, Singer JW, Prueger JH, DeSutter TM, Hatfield JL (2007) Radiation balance and evaporation partitioning in a narrow-row soybean canopy. *Agricultural and Forest Meteorology*, **145**, 206–214.
- Sellers PJ, Bounoua L, Collatz GJ *et al.* (1996) Comparison of radiative and physiological effects of doubled atmospheric CO₂ on climate. *Science*, **271**, 1402–1406.
- Sellers PJ, Dickinson RE, Randall DA *et al.* (1997) Modeling the exchanges of energy, water, and carbon between continents and the atmosphere. *Science*, **24**, 502–509.
- de Souza AP, Arundale RA, Dohleman FG, Long SP, Buckeridge MS (2013) Will the exceptional productivity of *Miscanthus × giganteus* increase further under rising atmospheric CO₂? *Agricultural and Forest Meteorology*, **171–172**, 82–92.
- Taylor SH, Hulme SP, Rees M, Ripley BS, Woodward FI, Osborne CP (2010) Ecophysiological traits in C₃ and C₄ grasses: a phylogenetically controlled screening experiment. *New Phytologist*, **185**, 780–791.
- Triggs JM, Kimball BA, Jr P *et al.* (2004) Free-air CO₂ enrichment effects on the energy balance and evapotranspiration of sorghum. *Agricultural and Forest Meteorology*, **124**, 63–79.
- Vanaja M, Yadav SK, Archana G *et al.* (2011) Response of C₄ (Maize) and C₃ (sunflower) crop plants to drought stress and enhanced carbon dioxide concentration. *Plant Soil and Environment*, **57**, 207–215.
- VanLoocke A, Bernacchi CJ, Twine TE (2010) The impacts of *Miscanthus × giganteus* production on the Midwest US hydrologic cycle. *Global Change Biology Bioenergy*, **2**, 180–191.
- Wall GW, Brooks TJ, Adam R *et al.* (2001) Elevated atmospheric CO₂ improved sorghum plant water status by ameliorating the adverse effects of drought. *New Phytologist*, **152**, 231–248.
- Wullschlegel SD, Tschaplinski TJ, Norby RJ (2002) Plant water relations at elevated [CO₂] – implications for water-limited environments. *Plant, Cell and Environment*, **25**, 319–331.
- Yoshimoto M, Oue H, Kobayashi K (2005) Energy balance and water use efficiency of rice canopies under free-air CO₂ enrichment. *Agriculture and Forest Meteorology*, **133**, 226–246.
- Zheng FY, Peng SL (2001) Meta-analysis of the response of plant ecophysiological variables to doubled atmospheric CO₂ concentrations. *Acta Botanica Sinica*, **43**, 1101–1109.