

CO₂ enrichment increases water-use efficiency in sorghum

Matthew M. Conley¹, B. A. Kimball¹, T. J. Brooks⁵, P. J. Pinter Jr.¹, D. J. Hunsaker¹, G. W. Wall¹, N. R. Adam¹, R. L. LaMorte¹, A. D. Matthias³, T. L. Thompson³, S. W. Leavitt⁴, M. J. Ottman², A. B. Cousins⁶ and J. M. Triggs⁵

¹US Water Conservation Laboratory, Agricultural Research Service, USDA, Phoenix AZ, USA; ²Plant Sciences Department, ³Department of Soil, Water and Environmental Science; ⁴Laboratory of Tree Ring Research, University of Arizona, Tucson AZ, USA; ⁵Maricopa Agricultural Center, University of Arizona, Maricopa AZ, USA; ⁶Arizona State University, Department of Plant Biology, Tempe AZ, USA

Summary

Author for correspondence:
Matthew M. Conley
Tel: +1 602 437 1702 x261
Fax: +1 602 437 5291
Email: mconley@uswcl.ars.ag.gov

Received: 6 November 2000
Accepted: 19 February 2001

- Sorghum (*Sorghum bicolor*) was grown for two consecutive seasons at Maricopa, AZ, USA, using the free-air CO₂ enrichment (FACE) approach to investigate evapotranspiration of this C₄ plant at ample and limited water supplies.
- Crop evapotranspiration (ET) was measured using two CO₂ concentrations (control, c. 370 μmol mol⁻¹; FACE, ambient +200 μmol mol⁻¹) and two irrigation treatments (well watered and water-limited). Volumetric soil water content was measured before and after each irrigation using neutron scattering techniques.
- Averaged over both years, elevated CO₂ reduced cumulative ET by 10% when plants were given ample water and by 4% under severe drought stress. Water-use efficiency based on grain yield (WUE-G) increased, due to CO₂ enrichment, by 9% and 19% in wet and dry plots, respectively; based on total biomass, water-use efficiency (WUE-B) increased by 16% and 17% in wet and dry plots, respectively.
- These data suggest that in the future high-CO₂ environment, water requirements for irrigated sorghum will be lower than at present, while dry-land productivity will increase, provided global warming is minimal.

Key words: CO₂, carbon dioxide enrichment, free-air CO₂ enrichment (FACE), *Sorghum bicolor*, evapotranspiration, water-use efficiency, global change.

© *New Phytologist* (2001) **151**: 407–412

Introduction

The Intergovernmental Panel on Climate Change (IPCC, 1996) projects that if 1994 CO₂ emission levels are sustained, the global atmospheric CO₂ concentration will reach 500 μmol mol⁻¹ by the year 2100. An increase in CO₂ concentration causes partial closure of stomata, thereby decreasing leaf conductance to CO₂ and H₂O vapor (Morison, 1985, 1987) and reducing leaf transpiration (Kimball & Idso, 1983) while increasing net carbon assimilation. Reduced leaf conductance reduces evapotranspiration (ET, water evaporated from plants and soil per unit of land area, Allen, 1990). A consequence of decreased conductance is higher leaf temperatures and water vapor pressures, which can negate the expected decreases in ET (Kimball *et al.*, 1992, 1994, 1995). For wheat (C₃), CO₂ enrichment to 550 μmol mol⁻¹ increased yield by 15% (Pinter *et al.*, 2000), canopy temperature by 0.85°C (Kimball *et al.*, 1995, 1999), and reduced ET by 3%. As a consequence, water-use efficiency (WUE) increased by 18% (Hunsaker

et al., 1996). In addition, CO₂ enrichment increased root growth and biomass, especially in inter-row spaces under dry conditions (Wechsung *et al.*, 1995). Wechsung *et al.* (1999) reported 22% more root d. wt due to FACE in wheat. Similarly, Rogers *et al.* (1992) showed a 143% increase in root d. wt of cotton following CO₂ enrichment to 700 μmol mol⁻¹.

C₄ plants utilize a biochemical CO₂ concentrating mechanism and are less reliant than C₃ species upon atmospheric CO₂ (Ca) and conductance to maintain saturation at the active site of carboxylation. In C₄ maize, Samarakoon & Gifford (1995) demonstrated that increased CO₂ caused very small changes in leaf area index, but that it reduced stomatal conductance, which resulted in significant water conservation. In sorghum, shoot and root growth increased when exposed to 795 μmol mol⁻¹ CO₂ while water-use decreased (Chaudhuri *et al.*, 1986). We hypothesized that CO₂ enrichment would have a similar effect on C₄ sorghum. The objective of this study was to determine ET for sorghum grown under open-field conditions and exposed to elevated CO₂ at ample and limited water supplies.

Materials and Methods

Eight 490 m² rings were subjected to two levels of CO₂ and two levels of soil water supply at the University of Arizona, Maricopa Agricultural Center, Maricopa, AZ, USA, as described in detail by Ottman *et al.* (2001).

Carbon dioxide treatments

Using the FACE technique, the air above four 25-m-diameter circular plots (rings) was enriched by 200 µmol mol⁻¹ CO₂ above ambient (FACE treatment, F). An additional four rings with identical air flows, but ambient CO₂, served as experimental controls (control treatment, C). Air enriched with CO₂ was blown into the FACE rings via tri-directional jets near the top of the crop canopy. Wind direction, wind speed, and CO₂ concentration were measured at the centre of each ring. These data were used in a computer-controlled system, which maintained CO₂ concentrations at 200 µmol mol⁻¹ above ambient, 24 h d⁻¹ throughout two successive growing seasons. Control rings were identical in design and air flow to the FACE rings in order to mimic microclimatic perturbances that might be caused by the blowers (Pinter *et al.*, 2000).

Water supply treatments

Level-basin flood irrigation was utilized to create two irrigation regimes. Wet treatments (W) were supplied with adequate water (100% replacement of potential ET) based on predicted soil water depletion, using the irrigation scheduling computer model AZSCHED (Fox *et al.*, 1992). Dry treatments (D) were irrigated only twice each season: the first just before planting and the second at flag leaf emergence. Total irrigation was 1218 and 474 mm in 1998, and 1047 and 491 mm in 1999 for the wet and dry treatments, respectively.

Crop culture

The soil was classified as a Trix clay loam (fine-loamy, mixed calcareous, hyperthermic Typic Torrifuvents) (Post *et al.*, 1988). Pre-planting preparations for each year included laser leveling the field, application of Dual 8E© (metolachlor, CIBA-GEIGY Corporation) herbicide applied at 2.7 kg ha⁻¹ followed by cultivation to control weeds, and a broadcast application of 93 kg ha⁻¹ of urea and 41 kg ha⁻¹ of P. Planting dates were June 15th (day of year (DOY) 166) in 1998, and July 16th (DOY 197) in 1999. In 1998, physiological maturity occurred November 17th (DOY 321) for CW, November 23rd (DOY 327) for FW, December 8th (DOY 342) for CD and after December 8th (DOY > 342) for FD. In 1999, physiological maturity occurred, September 27th (DOY 270) for both FW and CW, October 12th (DOY 285) for CD and October 19th (DOY 292) for FD. The final harvest dates were December 21st (DOY 355)

in 1998 and October 26th (DOY 299) in 1999. Post-emergence weed removal inside experimental plots was achieved by hand. Supplemental applications of N were delivered via the irrigation water. Insecticides were applied as needed in accordance with commercial sorghum production for the area.

Soil water content measurements

Volumetric soil moisture content was determined with neutron probe equipment (Hydroprobe Model 503 DR, Campbell Pacific Co., Martinez, CA, USA). The calibration equation, $\theta = 0.015 + 0.156 * (\text{count}/\text{standard count})$, where θ = volumetric soil water content (θ ; m³ H₂O m⁻³ soil) was based on gravimetric soil water content and bulk density measurements taken in the soil adjacent to the test plots, using a wide range of soil moisture contents. Measurements were taken at 0.3 m intervals to depths of either 1.8 m or 3.0 m during the 1998 and 1999 seasons, respectively. In the 1998 season, the uppermost measurement was taken at 0.46 m, whereas in 1999 it was at 0.23 m. To facilitate year-to-year comparison of data, a model was developed to extrapolate water content for the upper 0.3 m of soil for each dry-down cycle in 1998. This model used a multiple regression of the following independent variables: Normalized Difference Vegetative Index (NDVI) (PJ Pinter Jr, unpublished), which correlates closely with green plant area index or the active portion of the plant with respect to photosynthesis and transpiration; NDVI also correlates with crop coefficients, which are routinely used in irrigation models; Growing Degree Days (GDD), which quantify temperature dependant growth parameters; Arizona Meteorological Network (AZMET) potential grass reference model (modelled ET) (Brown & Yitayew, 1988), which estimates ET from C₄ grass crop coefficients and climatic data; and 0.46 m 1999 data, which incorporate soil water characteristics specific to the field site. This multiple regression model was used to estimate 0.23 m data for 1998.

Active root depth was determined by estimating the expected water extraction front from 0 to 1.76 m (Robertson *et al.*, 1993). Volumetric soil water data was structured in a stair-step model where consecutively deeper depth measurements were incorporated in 0.3 m blocks after expected root penetration had occurred. Thus ET was calculated using the zone of soil containing only roots. ET was calculated during drying periods by using a soil water balance equation (Jensen *et al.*, 1990). By assuming negligible deep percolation, ET was essentially set equal to the temporal changes in water content for the active root zone. ET was estimated by interpolation when irrigation or rain occurred by using the average ET before and after the wetting event.

Potential ET for well-watered sorghum at current CO₂ concentrations was calculated using the Arizona Meteorological Network (AZMET) potential grass reference (modelled ET, Brown & Yitayew, 1988) multiplied by a crop coefficient for sorghum (Allen *et al.*, 1998).

Information about plant harvesting, processing, and measurement techniques are described in detail in Ottman *et al.* (2001). Briefly, total above-ground biomass was determined by summing grain and stover yield d. wts from a nontraffic, final harvest area.

Data were analysed as a strip-split-plot repeated measure experimental design using PROC MIXED (Littell *et al.*, 1996) in SAS (Reference manual version 6.01989) for the ANOVAs.

Results and Discussion

Temporal changes in soil water content

During 1998, volumetric soil water content measurements averaged from 0.0 to 1.8 m of depth (Fig. 1a) and showed two distinct dry-down periods for the dry plots; the first DOY 228–254 and the second DOY 275–330. We observed three dry-down periods in the dry treatment during 1999: DOY 198–218, DOY 228–258, and DOY 268–290. During 1998, periods of plant stress in dry treatments, as inferred from a 30% drop in soil moisture below field capacity, occurred during DOY 247–253 and DOY 290–325 whereas they occurred from DOY 202–218, DOY 244–258, and after DOY 280 until maturity during 1999 (Fig. 1b).

Evapotranspiration

During the first year (1998), differences in cumulative ET between wet and dry treatments were apparent by DOY 273 and were significant over the season (Tables 1, 2). Aside from a divergence during DOY 260–290, when plants were undergoing reproductive growth, FD and CD treatments showed similar patterns in cumulative ET with essentially

no difference. However, clear trend differences between CO₂ treatments were evident in wet plots beginning on DOY 260. FW plots evapotranspired 60 (± 117) mm or 11% ($P=0.40$, $df=11.7$) less than CW over the growing season (Fig. 2a). During 1999, differences in cumulative ET between wet and dry treatments began at DOY 220, became more pronounced after DOY 240, and were significant over the season (Tables 1, 2). Seasonal ET of FD tended to be 25 (± 14) mm or 6% ($P=0.27$, $df=12$) less than CD in 1999; whereas under the wet treatment there was a clearly significant CO₂ effect, where FW evapotranspired 58 (± 34) mm or 9% ($P=0.02$, $df=12$) less water than CW plants (Fig. 2b).

Water-use efficiency

Grain yield and total above-ground biomass were measured in 1998 and 1999 by Ottman *et al.* (2001). Water-use efficiency based on grain yield (WUE-G) was calculated as the ratio of grain yield m⁻² mm⁻¹ ET (Table 1). WUE based on biomass (WUE-B) was calculated as the ratio of shoot biomass m⁻² mm⁻¹ ET (Table 2). In 1998, WUE-G and WUE-B differences between dry and wet treatments were significant (Tables 1, 2). However, the ANOVA result for the two-way interaction effect was nonsignificant. In 1999, significant differences between wet and dry treatments were again evident for WUE-G and WUE-B (Tables 1, 2). Additionally, the interaction effects between CO₂ and irrigation were significant in WUE-G ($P=0.03$, $df=2.84$). WUE-G for FD was 0.11 (± 0.08) g m⁻² mm⁻¹ or 45% significantly greater ($P=0.10$, $df=5.3$) than CD, while FW was not significantly different from CW. The interaction between CO₂ and irrigation was not significant for WUE-B in 1999 ($P=0.28$, $df=6$). Nevertheless, the overall CO₂ effect tended to be larger under dry (26%) than

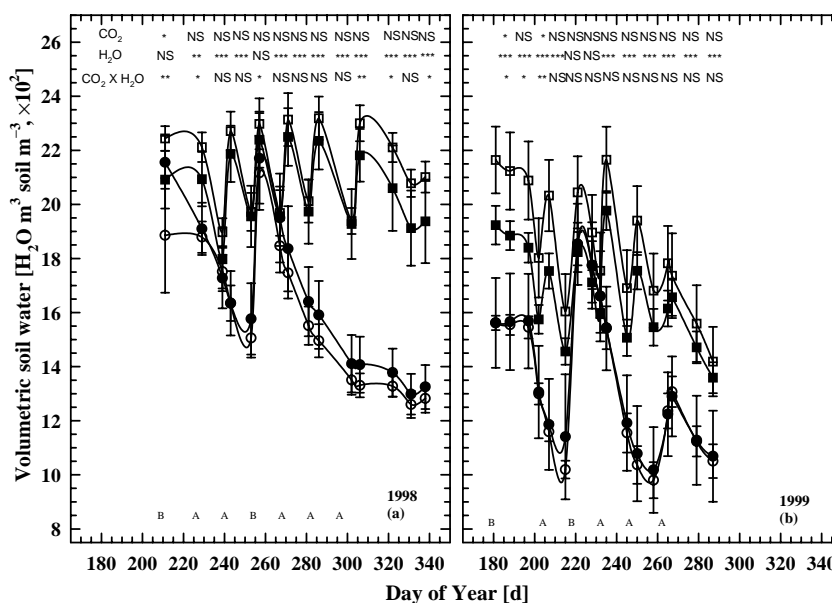


Fig. 1 Mean volumetric soil water contents (0.0–1.8 m depth) in the control-dry (CD; open circles), FACE-dry (FD; closed circles), control-wet (CW, open squares), and FACE-wet (FW, closed squares) plots for the 1998 (a) and 1999 (b) sorghum growing seasons. Bars denote standard errors. Each mean is the average of four replicates. A, when only wet plots were irrigated; B, when both wet and dry plots were irrigated. NS, *, **, *** = not significant at $P > 0.25$ and significant at $P < 0.25$, 0.15, 0.05, respectively.

Table 1 Sorghum grain yield (Ottman *et al.*, 2001), evapotranspiration (ET), water-use efficiency based on grain yield (WUE-G), the percent difference in WUE-G due to FACE enrichment and related ANOVA test *P*-values, ** signifies *P* = 0.10

	1998				1999			
	Yield (g m ⁻²)	ET (mm)	WUE-G (g m ⁻² mm ⁻¹)	WUE-G % diff.	Yield (g m ⁻²)	ET (mm)	WUE-G (g m ⁻² mm ⁻¹)	WUE-G % diff.
FACE-Dry (FD)	553 (± 30)	292 (± 21)	1.93 (± 0.24)	15% (± 24%)	142 (± 33)	404 (± 9)	0.36 (± 0.09)	45%** (± 26%)
Control-Dry (CD)	472 (± 58)	293 (± 22)	1.68 (± 0.32)		106 (± 18)	429 (± 6)	0.25 (± 0.04)	
FACE-Wet (FW)	677 (± 22)	498 (± 72)	1.43 (± 0.24)	15% (± 21%)	424 (± 21)	605 (± 15)	0.70 (± 0.05)	-3% (± 6%)
Control-Wet (CW)	670 (± 11)	559 (± 58)	1.24 (± 0.15)		475 (± 13)	664 (± 25)	0.72 (± 0.05)	
probability (<i>P</i>)								
CO ₂		0.57	0.41			0.02	0.44	
H ₂ O		< 0.01	.03			< 0.01	< 0.01	
H ₂ O × CO ₂		0.55	0.87			0.30	0.03	

Table 2 Sorghum biomass (Ottman *et al.*, 2001), evapotranspiration (ET), water-use efficiency based on biomass (WUE-B), the percent difference in WUE-B due to FACE enrichment and related ANOVA test *P*-values

	1998				1999			
	Yield (g m ⁻²)	ET (mm)	WUE-B (g m ⁻² mm ⁻¹)	WUE-B % diff.	Yield (g m ⁻²)	ET (mm)	WUE-B (g m ⁻² mm ⁻¹)	WUE-B % diff.
FACE-Dry (FD)	1332 (± 80)	292 (± 21)	4.64 (± 0.61)	12% (± 17%)	970 (± 69)	404 (± 9)	2.41 (± 0.22)	26% (± 15%)
Control-Dry (CD)	1176 (± 73)	293 (± 22)	4.13 (± 0.55)		822 (± 58)	429 (± 6)	1.91 (± 0.16)	
FACE-Wet (FW)	1658 (± 43)	498 (± 72)	3.51 (± 0.57)	22% (± 23%)	1551 (± 54)	605 (± 15)	2.56 (± 0.15)	8% (± 3%)
Control-Wet (FW)	1554 (± 5)	559 (± 58)	2.87 (± 0.30)		1566 (± 17)	664 (± 25)	2.37 (± 0.11)	
Probability (<i>P</i>)								
CO ₂		0.57	0.28			0.02	0.04	
H ₂ O		< 0.01	0.02			< 0.01	0.07	
H ₂ O × CO ₂		0.55	0.87			0.30	0.28	

wet (8%) (Tables 1, 2). These data suggest an increasing WUE trend due to CO₂ enrichment exists with increasing drought. Under extreme drought, increases in WUE may become significant, as was the case for WUE-G in 1999. Therefore a yield increase is likely without additional use of water resources at higher than present day ambient CO₂ concentrations.

Increased drought resulting from increased water demand, coupled with a decreased total of applied water can explain the large increase in yield, biomass, and WUE in 1998 relative to 1999. Drought was partially due to an earlier planting date in 1999 (June 15th (DOY 166) in 1999, and July 16th (DOY 197) in 1998). Additionally, the average air temperature over the growing season was 22.5°C in 1998 and 28.8°C in 1999. Therefore 1999 sorghum plants were growing at a hotter time of the year and experienced a greater degree of heat stress. This is consistent with the corresponding lesser (100 mm) modelled ET adjusted for sorghum in 1998 compared with 1999

(Fig. 2a,b). Another factor that may have decreased grain yield and biomass in 1999 is a wind and hail storm, which shredded the sorghum leaves at the time of grain fill on DOY 262 and consequently disrupted carbon translocation to grain.

Large water applications to the dry treatments at the time of flag leaf emergence in 1998 may have prevented late season drought from developing. The only period of substantial drought for the dry treatment in 1998 was around DOY 250 (Fig. 1a). Thus, plant roots in the dry 1998 treatment were able to extend to depths more typical of well-watered plants (1.6 m) after the second irrigation event. These plants were able to utilize water from the second irrigation as well as residual soil water from the first irrigation still stored at lower depths. This use of deeper water, along with decreased late season climatic demand allowed dry plants to complete the season with only moderate drought. Wet plants received adequate water throughout the 1998 season. However, in 1999 a possibility

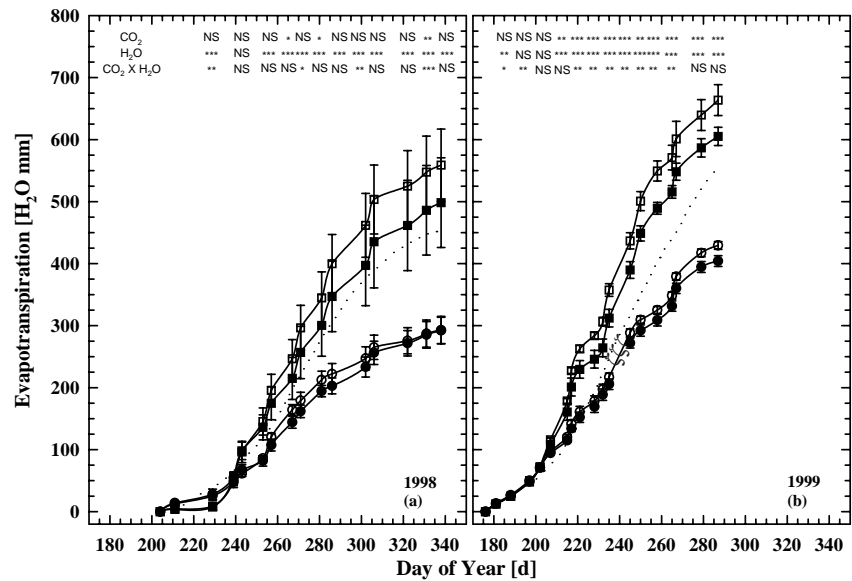


Fig. 2 Mean cumulative evapotranspiration (ET) for the control-dry (CD; open circles), FACE-dry (FD; closed circles), control-wet (CW; open squares), and FACE-wet (FW; closed squares) plots in 1998 (a) and 1999 (b) sorghum growing seasons. Dashed line, modeled ET. Bars denote standard errors. Each mean is the average of four replications. The dotted line represents modelled ET from the Arizona Meteorological Network AZMET (Brown, 1987) adjusted for sorghum. NS, *, **, *** = not significant at $P > 0.25$ and significant at $P < 0.25, 0.15, 0.05,$ respectively.

existed that they did not, due to the extreme summer climate and possible imprecision in application of AZSCHED for irrigation timing. A possible water shortage in wet treatments may have resulted in some degree of drought occurring from DOY 200–220 and again from DOY 244–263 (Fig. 2b). Even a short period of drought in the 1999 wet plants during vegetative growth could have caused decreased yields. Dry plants were substantially droughted in 1999. The only period of recovery for dry plants occurred over DOY 222–240.

Soil substrate properties such as texture and water holding capacity can vary across location and over depth. This was the case at the FACE sorghum field site as evidenced by the consistent difference between the FACE and control soil water contents following re-wetting (Fig. 1a,b). Factors that directly influence root growth include soil strength, soil water, soil temperature and composition of soil atmosphere (McMichael *et al.*, 1993). However, minimal plot substrate variability will not significantly influence the water extraction front velocity (root growth) or the consequent above ground biomass accumulation (Meinke *et al.*, 1993). Therefore relative differences in soil moisture between each treatment should be representative of the treatment ET effect. Differences in ET within the magnitude of 5–90 mm, or 1–20% are difficult to discern with the neutron equipment and soil water balance technique. Consequently, significant statistical differences in ET for CO₂ treatments were not evident over both years at the $P < 0.25$ level. This parallels the results of previous FACE experiments utilizing similar methodology (Hunsaker *et al.*, 1996). Over both years, there was no significance in WUE-G or WUE-B ($P > 0.25$) as a result of CO₂ enrichment. However, there was a significant ($P = 0.09$, $df = 5.28$) WUE-G increase in plants grown in the dry treatment, in 1999, under CO₂ enrichment.

CO₂ enrichment at 200 $\mu\text{mol mol}^{-1}$ above today's ambient mole fraction (*c.* 570 $\mu\text{mol mol}^{-1}$) reduced ET by 13 (± 18)

mm or 4% and 60 (± 151) mm or 10% averaged over both years, for droughted and well-watered sorghum, respectively. CO₂ enrichment also increased WUE-G by 0.18 (± 0.21) $\text{g m}^{-2} \text{mm}^{-1}$ or 19% and 0.08 (± 0.1) $\text{g m}^{-2} \text{mm}^{-1}$ or 9% and WUE-B by 0.50 (± 0.49) $\text{g m}^{-2} \text{mm}^{-1}$ or 17% and 0.42 (± 0.33) $\text{g m}^{-2} \text{mm}^{-1}$ or 16% over both years, for droughted and well-watered sorghum, respectively. Elevated CO₂ caused partial stomatal closure, reduced stomatal conductance, and decreased transpiration per unit of leaf area in both wet and dry plots (Wall *et al.*, 2001). However, the C₄ sorghum did not exhibit an increased leaf area in wet plots (Ottman *et al.*, 2001) consistent with observations on C₄ maize (Samarakoon & Gifford, 1995), so water was conserved in these plots (Fig. 2a,b). In the dry plots, CO₂-enriched plants exhibited reduced stomatal conductance (Wall *et al.*, 2001), which conserved water and enabled them to grow further into a drying cycle. Cumulative ET of FD and CD plants were similar (Fig. 2a,b), however, because FD plants were able to maintain growth longer into a drying cycle than CD plants (Ottman *et al.*, 2001) they had a greater WUE trend (Tables 1, 2). Additionally, FD plants were expected to have greater root length and mass, which would enable them to better mine the soil profile for water and nutrients (Chaudhuri *et al.*, 1986; Wechsung *et al.*, 1999). Therefore, we accept the hypothesis that elevated CO₂ will cause a C₄ crop (sorghum) to decrease ET under well-watered conditions and to increase WUE under both well-watered and droughted conditions.

Averaging over both years and over irrigation treatments, CO₂ enrichment caused a reduction in ET by 36 (± 84) mm or 7%. Both WUE-G and WUE-B, were increased 0.13 (± 0.16) $\text{g m}^{-2} \text{mm}^{-1}$ or 14% and 0.46 (± 0.41) $\text{g m}^{-2} \text{mm}^{-1}$ or 16%, respectively, as a result of CO₂ enrichment. Therefore, our data show that future water requirements for irrigated sorghum should decrease slightly, provided global warming is

minimal. Under rain-fed conditions, where sorghum is more likely to experience drought, elevated CO₂ will likely cause a productivity increase. Moreover, under ample-water or water-limited conditions, increases in CO₂ are likely to cause WUE to increase.

References

- Allen LH Jr. 1990. Effects of increasing carbon dioxide levels and climate change on plant growth, evapotranspiration, and water resources. In: *Managing water resources in the west under conditions of climate uncertainty*. Washington DC, USA: National Academy Press, 101–147.
- Allen RG, Pereira LS, Raes D, Smith M. 1998. Crop Evapotranspiration, Guidelines for computing crop water requirements. *Food and agriculture organization of the United Nations, irrigation and drainage paper 56*. Rome, Italy: Viale delle Terme di Caracalla, 100–111.
- Brown PW. 1987. *User's guide to the Arizona Meteorological Network*. Phoenix, AZ, USA: City of Phoenix, Water Conservation and Research Division and Arizona Cooperative Extension.
- Brown PW, Yitayew M. 1988. Near-real time weather information for irrigation management in Arizona. In: Hay DR, ed. *Planning now for irrigation and drainage in the 21st century: proceedings of a conference: irrigation and drainage division of the American society of civil engineers*. New York, USA: American Society of Civil Engineers (ASCE), 708–715.
- Chaudhuri UN, Burnett RB, Kirkham MB, Kanemasu ET. 1986. Effect of carbon dioxide on sorghum yield, root growth, and water use. *Agricultural and Forest Meteorology* 37: 109–122.
- Fox FA Jr, Scherer T, Slack DC, Clark LC. 1992. *Arizona irrigation scheduling user's manual*. Tucson, AZ, USA: Agriculture and Biosystems Engineering, Cooperative Extension, University of Arizona.
- Hunsaker DJ, Kimball BA, Pinter PJ Jr, LaMorte RL, Wall GW. 1996. Carbon dioxide enrichment and irrigation effects on wheat evapotranspiration and water-use efficiency. *American Society of Agricultural Engineers* 39: 1345–1355.
- IPCC. 1996. *World meteorological organization. United Nations environmental programme*. Cambridge, UK: Cambridge University Press.
- Jensen ME, Burman RD, Allen RG. 1990. Evapotranspiration and Irrigation Water Requirements. *ASCE Manuals and Reports on Engineering Practice*, no. 70, 332.
- Kimball BA, Idso SB. 1983. Increasing atmospheric CO₂: Effects on crop yield, water-use and climate. *Agricultural Water Management* 7: 55–72.
- Kimball BA, LaMorte RL, Pinter PJ Jr, Wall GW, Hunsaker DJ, Adamsen FJ, Leavitt SW, Thompson TL, Matthias AD, Brooks TJ. 1999. Free-air CO₂ enrichment and soil nitrogen effects on energy balance and evapotranspiration of wheat. *Water Resources Research* 35: 1179–1190.
- Kimball BA, Lamorte RL, Seay RS, Pinter PJ Jr, Rokey RR, Hunsaker DJ, Dugas WA, Heuer ML, Mauney JR, Hendrey GR, Lewin KF, Nagy J. 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, LaMorte RL, Wall GW, Hunsaker DJ, Wechsung G, Wechsung F, Kartschall T. 1995. Productivity and water-use of wheat under free-air CO₂ enrichment. *Global Change Biology* 1: 429–442.
- Kimball BA, Pinter PJ Jr, Mauney JR. 1992. Cotton leaf and boll temperatures in the 1989 FACE experiment. *Critical Reviews in Plant Science*. 1: 233–240.
- Littell RC, Milliken GA, Stroup WW, Wolfinger RD. 1996. *SAS system for mixed models*. Cary, NC, USA: SAS Institute, Inc.
- McMichael BL, Quisenberry JE. 1993. The impact of the soil environment on the growth of root systems. *Environmental and Experimental Botany* 33: 53–61.
- Meinke H, Hammer GL, Want PJ. 1993. Potential water extraction by sunflower on a range of soils. *Field Crops Research* 32: 59–81.
- Morison JIL. 1985. Sensitivity of stomata and water-use efficiency to high CO₂. *Plant, Cell & Environment* 8: 467–474.
- Morison JIL. 1987. Intercellular CO₂ concentration and stomatal response to CO₂. In: Zeiger E, Farquhar GD, Cowan IR, eds. *Stomatal function*. Stanford, CA, USA: Stanford University Press, 229–251.
- Ottman MJ, Kimball BA, Pinter PJ Jr, Wall GW, Vanderlip RL, Leavitt SW, LaMorte RL, Matthias AD, Brooks TJ. 2001. Elevated CO₂ increases sorghum biomass under drought conditions. *New Phytologist* 150: 261–273.
- Pinter PJ Jr, Kimball BA, Wall GW, LaMorte RL, Hunsaker DJ, Adamsen FJ, Frumau KFA, Vughts HF, Hendrey GR, Lewin KF, Nagy J, Johnson JB, Wechsung F, Leavitt SW, Thompson TL, Matthias AD, Brooks TJ. 2000. Free-air CO₂ enrichment (FACE): Blower effects on wheat canopy microclimate and plant development. *Agricultural and Forest Meteorology* 103-4: 319–332.
- Post DF, Mack C, Camp PD, Suliman AS. 1988. Mapping and characterization of the soils on the University of Arizona, Maricopa Agricultural Center. In: *Proceedings of Hydrology and Water Resources in Arizona and the Southwest*. Tucson, University of Arizona. 18 (1): 49–60.
- Robertson MJ, Fukai S, Ludlow MM, Hammer GL. 1993. Water extraction by grain sorghum in a sub-humid environment. I. Analysis of the water extraction pattern. *Field Crops Research* 33: 81–97.
- Rogers HH, Peterson CM, McCrimmon JN, Cure JD. 1992. Response of plant roots to elevated atmospheric carbon dioxide. *Plant, Cell & Environment* 15: 749–752.
- 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.
- Wall GW, Brooks TJ, Adam NR, Cousins A, Triggs J, Kimball BA, Pinter PJ Jr, LaMorte RL, Ottman MJ, Leavitt SW, Matthias AD, Williams DG, Webber AN. 2001. Leaf photosynthesis and water relations of grain sorghum grown in free-air CO₂ enrichment (FACE) and water stress. *New Phytologist* (In press.)
- Wechsung G, Wechsung F, Wall GW, Adamsen FJ, Kimball BA, Garcia RL, Pinter PJ Jr, Kartschall TH. 1995. Biomass and growth rate of a spring wheat root system grown in free-air CO₂ enrichment (FACE) and ample soil moisture. *Journal of Biogeography* 22: 623–634.
- Wechsung G, Wechsung F, Wall GW, Adamsen FJ, Kimball BA, Pinter PJ Jr, LaMorte RL, Garcia RL, Kartschall TH. 1999. The effects of free-air CO₂ enrichment and soil water availability on spatial and seasonal patterns of wheat root growth. *Global Change Biology* 5: 519–529.