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Productivity and water use of wheat under free-air CO_2 enrichment

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Abstract

A free-air CO_2 enrichment (FACE) experiment was conducted at Maricopa, Arizona, on wheat from December 1992 through May 1993. The FACE apparatus maintained the CO_2 concentration, [CO_2], at 550 µmol mol^{-1} across four replicate 25-m-diameter circular plots under natural conditions in an open field. Four matching Control plots at ambient [CO_2] (about 370 µmol mol^{-1}) were also installed in the field. In addition to the two levels of [CO_2], there were ample (Wet) and limiting (Dry) levels of water supplied through a subsurface drip irrigation system in a strip, split-plot design.

Measurements were made of net radiation, R_n; soil heat flux, G_o; soil temperature; foliage or surface temperature; air dry and wet bulb temperatures; and wind speed. Sensible heat flux, *H*, was calculated from the wind and temperature measurements. Latent heat flux, λET, and evapotranspiration, *ET*, were determined as the residual in the energy balance. The FACE treatment reduced daily total R_n by an average 4%. Daily FACE sensible heat flux, *H*, was higher in the FACE plots. Daily latent heat flux, λET, and evapotranspiration, *ET*, were consistently lower in the FACE plots than in the Control plots for most of the growing season, about 8% on the average.

Net canopy photosynthesis was stimulated by an average 19 and 44% in the Wet and Dry plots, respectively, by elevated [CO_2] for most of the growing season. No significant acclimation or down regulation was observed. There was little above-ground growth response to elevated [CO_2] early in the season when temperatures were cool. Then, as temperatures warmed into spring, the FACE plants grew about 20% more than the Control plants at ambient [CO_2], as shown by above-ground biomass accumulation. Root biomass accumulation was also stimulated about 20%. In May the FACE plants matured and senesced about a week earlier than the Controls in the Wet plots. The FACE plants averaged 0.6 °C warmer than the Controls from February through April in the well-watered plots, and we speculate that this temperature rise contributed to the earlier maturity. Because of the acceleration of senescence, there was a shortening of the duration of grain filling, and consequently, there was a narrowing of the final biomass and yield differences. The 20% mid-season growth advantage of FACE shrunk to about an 8% yield advantage in the Wet plots, while the yield differences between FACE and Control remained at about 20% in the Dry plots.

Keywords: CO_2, global change, growth, water use, wheat, yield

Introduction

The CO_2 concentration, [CO_2], of the atmosphere is increasing, and climate modellers have predicted a consequent global warming and changes in precipitation patterns. The report of the Intergovernmental Panel on Climate Change edited by Houghton *et al.* (1990) projects [CO_2] increasing from present day concentrations of about 350 µmol mol^{-1} to over 800 µmol mol^{-1} by the end of the next century if no steps are taken to limit emissions. They predict this increase in [CO_2] plus that of other radiatively active 'greenhouse' gases – methane, nitrous oxide, chlorofluorocarbons (CFC's), ozone – would cause an increase in global mean temperature of about 4.2 °C. Some regions might receive increases in precipitation, while others might receive less. However, these projected changes in climate are very uncertain.

As a feedstock for photosynthesis, elevated [CO_2] can accelerate plant growth and could potentially increase agricultural productivity. Doubled CO_2 concentrations have been shown to increase crop yields by 30% or more

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on the average, in experiments conducted mostly under greenhouse and growth chamber conditions (Kimball 1983a,b, 1986; Cure 1985; Poorter 1993; Idso & Idso 1994). However, chambers can affect the growth of plants inside, independent of any [CO_2] effect (Drake *et al.* 1985; Allen *et al.* 1992; Kimball *et al.* 1995), and uncertainty exists as to whether such chamber results adequately represent actual field conditions. Therefore, several cooperating researchers developed the free-air CO_2 enrichment (FACE) technique for exposing plants to elevated [CO_2] (Hendrey 1993; Hendrey & Kimball 1994) in open field plots under realistic natural conditions. Three FACE experiments were conducted on cotton from 1989 to 1991, and the results were reported in Hendrey (1993) and Dugas and Pinter (1994). From December through May in 1992–3, an additional FACE experiment was conducted, this time on wheat at both ample and limiting supplies of water (Fig. 1a). Some of the wheat productivity results are presented in this paper.

In addition to plant photosynthesis and growth, elevated [CO_2] also affects stomatal conductance (Morison 1987), which in turn affects transpirational water loss per unit of leaf area. However, leaf area and canopy temperatures are also affected (Idso *et al.* 1987a), so that the resultant effect of elevated [CO_2] on plant water use per unit of ground area is the net consequence of several factors and is uncertain. Moreover, plant enclosures such as open-top chambers or controlled-environment chambers affect air movement and atmosphere–canopy coupling greatly. Consequently, results from any enclosures can not be expected to represent the evapotranspiration (ET) or water use of an open field. Therefore, the FACE wheat experiment provided an unrivalled opportunity to examine the effects of elevated [CO_2] on the water use of wheat under open field conditions.

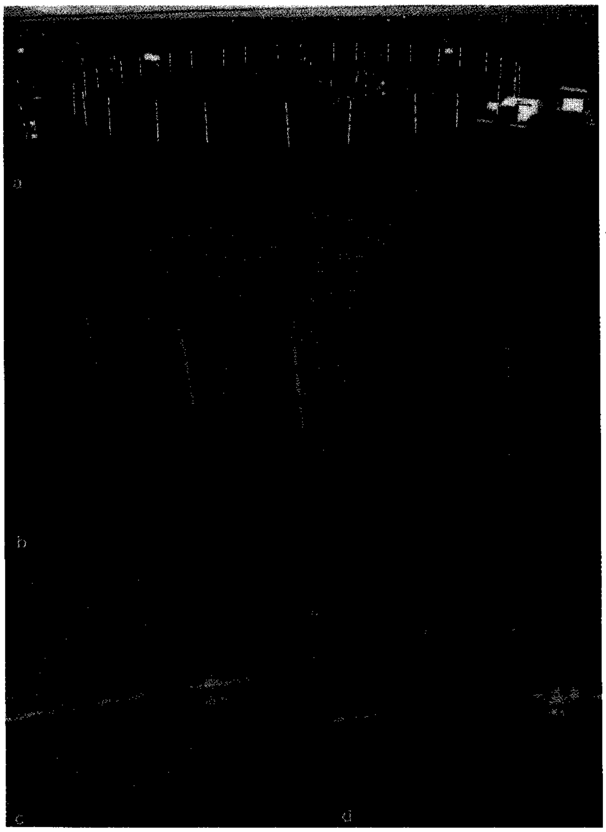


Fig. 1 (a) View of wheat crop on 19 March 1993 with a 25-m-diameter free-air CO_2 enrichment (FACE) array used to elevate the CO_2 concentration in the air across the array from ambient (Control, about 370 mol mol^{-1}) to 550 mmol mol^{-1} (FACE). (b) View of crop on 11 May showing treatment effects on maturity; with Control-Wet in foreground nearly green, FACE-Wet at middle right about 1/2 green, Control-Dry at upper left mostly mature, and FACE-Dry at upper middle fully mature. (c and d) Thermal images of Control and FACE plots, respectively, on 8 April 1993. The top halves were Dry and the bottom halves were Wet. A red circle was artificially added to Fig. 1c to show the outline of the ring, which was barely visible otherwise.

Materials and methods

A crop of wheat (*Triticum aestivum* L. cv Yecora Rojo, a hard red spring semi-dwarf variety) was grown at the University of Arizona, Maricopa Agricultural Centre, Maricopa, Arizona, USA, on Trix clay loam [fine-loamy, mixed (calcareous), hyperthermic Typic Torrifluvent]. Planting was on 15 December 1992 and 50% emergence on 1 January 1993 at a population of 130 plants m^{-2}. Final harvest was on 24 May 1993. The wheat was planted in E–W rows at a spacing of 0.25 m.

Four replicate circular 25-m-diameter vertical vent pipe arrays (Hendrey 1993; Dugas & Pinter 1994) were used to elevate the CO_2 concentration, [CO_2], to 550 μmol mol^{-1} in the air across circular open-field plots (Fig. 1a). Seasonal average concentrations were within 0.5 μmol mol^{-1} of the set point and 93% of the 1-min. averages were within 10% of the set point (Hendrey *et al.* 1993). Enrichment commenced on the day of 50% emergence and continued 24 h d^{-1} until the plants in the FACE plots were mature, except for a two-week period in January 1993 when rainy conditions hampered CO_2 deliveries, so the enrichment period was shortened to 8 h/day centred about solar noon. Four similar Control arrays at ambient [CO_2] (about 370 μmol mol^{-1} during daytime) were also included which had similar piping but no air flow. The array centres were spaced 90 m apart. Plot plans which illustrate the positioning of the 8 arrays in the 20-ha field are shown in Wall and Kimball (1993).

The main [CO_2] plots were split into semi-circular halves that were well-watered (Wet) by replacement of potential evapotranspiration using a sub-surface drip irrigation system (0.5 m tube spacing, 0.3 m emitter spacing, 0.2 m depth) or that were subjected to water

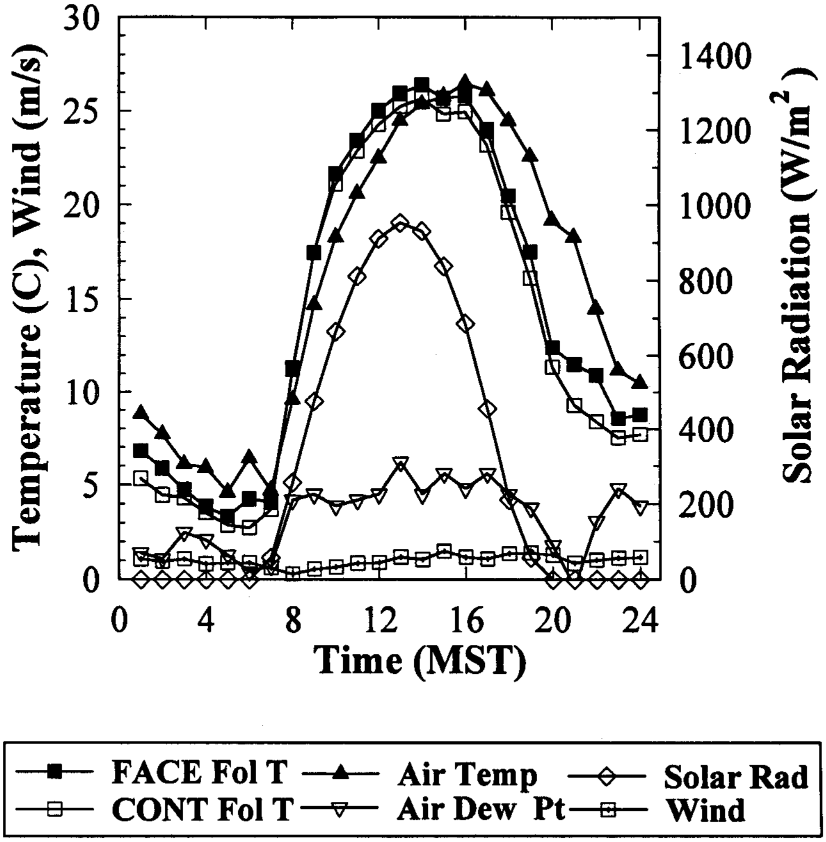


Fig. 2 Hourly average air dry bulb and dew point temperatures, foliage temperatures from FACE and Control plots, wind, and solar radiation for 9 April 1993 (DOY 099). The values are plotted at the end of the corresponding hour.

stress (Dry) by supplying only 1/2 as much water at each irrigation. The Wet plots were irrigated when 30% of the available water in the rooted zone was depleted. The cumulative irrigation totals between emergence and harvest were 600 and 275 mm for Wet and Dry, respectively, and the cumulative rainfall during the same period was 76 mm.

With 4 replicates, 2 [CO_2] levels, and 2 water levels, there were a total of 16 plots. The plots were fertilized by amounts intended to be ample so that nutrients would be non-limiting. A pre-plant application of granular (16–20–0) supplied 54 kg N ha^{-1} and 29 kg P ha^{-1}. On 30 January a superphosphoric acid application supplied an additional 15 kg P ha^{-1}. Nitrogen fertilizer (mostly Uran-32) was applied with the irrigation water at rates of 92, 59, and 72 kg N ha^{-1} on 30 January, 18 March, and 5 April for a total N amount of 277 kg ha^{-1}.

Measurements of whole canopy net photosynthesis, i.e. net carbon exchange rate, A_c, were determined using a transportable steady-state gas exchange system (Garcia *et al.* 1990, 1994). Four 0.75 m^2 chambers were used simultaneously on all treatment combinations of 1 replicate block. They were moved from one set of replicate plots to another at *c.* 10-day intervals.

Plant growth and development were determined from 18 destructive harvests scheduled at 7–10 day intervals from emergence until harvest: *c.* 24 plants were measured in each of the 4 replicates of each [CO_2] and irrigation level (Pinter *et al.* 1995). Plant tissues were partitioned into different biomass components and dried to constant weight at 65–70 °C. The grain was oven-dried for 14 d. The mass per plant was multiplied by the number of plants m^{-2} to obtain the biomass per ground area. Specific leaf area (m^2 g^{-1}) was determined on a subsample of 1–3 plants and multiplied by green leaf biomass to obtain LAI. Root biomass from the surface to 1 m depth was determined on roots washed from 2 soil cores (0.088 m diameter) per plot taken from within plant rows (Wechsung *et al.* 1995).

Evapotranspiration was determined as a residual in the energy balance, similar to the procedure of Kimball *et al.* (1994) for the prior FACE cotton experiments. Briefly, *ET* was calculated as the difference between net radiation, R_n, soil surface heat flux, G_0, and sensible heat flux, H:

$$\lambda ET = R_n - G_0 - H,$$

where λ is the latent heat of vapourization. The *ET* determinations were made only in the Wet plots of replicate blocks 3 and 4 (Wall & Kimball 1993). R_n was measured with duplicate net radiometers (Radiation Energy Balance Systems, Seattle, WA; Model Q6), and G_0 with soil heat flux plates (Radiation Energy Balance Systems; Model HFT-3). H was determined by measuring the temperature difference between the crop surface and

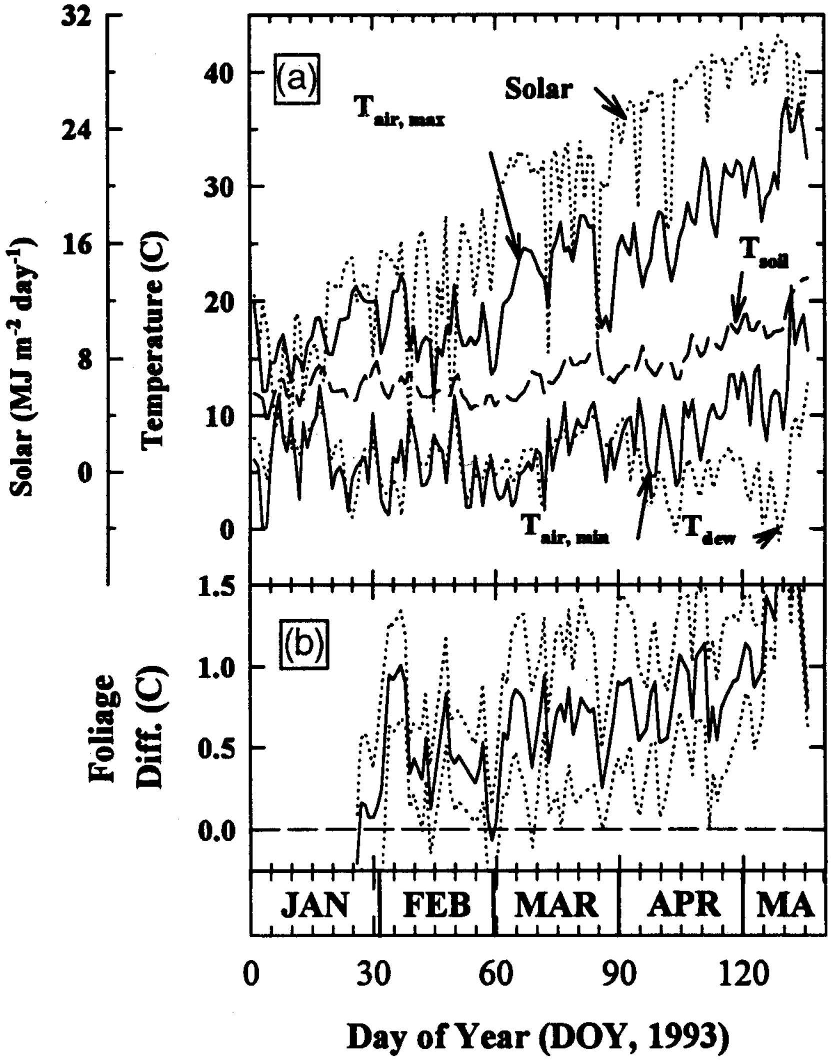


Fig. 3 (a) Weather data for January–May 1993 including: daily total solar radiation, maximum and minimum air temperatures (2 m height), average dew point temperature, and average soil temperature (0.1 m depth). (b) Differences in wheat canopy temperatures between FACE and Control plots and standard errors (dotted lines) for the Wet irrigation treatment (average February through April temperature difference was 0.6 °C).

Table 1 Number of days (post-emergence) required for wheat to reach mid-anthesis and maturity given as mean (SE). Statistical significance of CO_2 and Irrigation treatment means is shown as the probability of obtaining a greater *F*-value based on chance alone.

	Irrigation (% of consumptive seasonal requirement)					
	Dry(50%)		Wet(100%)			
	CO_2 concentration (µmol mol^{-1})				Probability > *F*	
Item	Cont.(370)	FACE(550)	Cont.(370)	FACE(550)	CO_2	Irrigation
Days to mid-anthesis	84.9(0.6)	83.4(0.9)	86.3(0.7)	84.0(1.1)	0.039	0.079
Days to maturity	130.3(0.3)	129.5(0.3)	137.0(0.4)	130.6(0.5)	< 0.01*	< 0.01*

*The CO_2 by Irrigation interaction was significant ($P < 0.01$) for this parameter. Least significant differences computed from pooled mean square errors and 't' values (d.f. obtained using Satterwaite's approximation) indicate significant differences ($P < 0.01$) between CO_2 levels in the Wet Irrigation treatment and between Irrigation levels in the 370 µmmol mol^{-1} CO_2 treatment.

the air and then dividing the temperature difference by an aerodynamic resistance calculated from a measurement of wind speed (R.M. Young Co., Traverse City, MI; Model 12170C 3-cup anemometer with photochopper) at the 2.0-m height at one position in the field (about 10 m east of Rep.3, Control-Wet). The air temperature was measured at the 2-m height in each plot with an aspirated psychrometer, and the crop surface temperature was measured

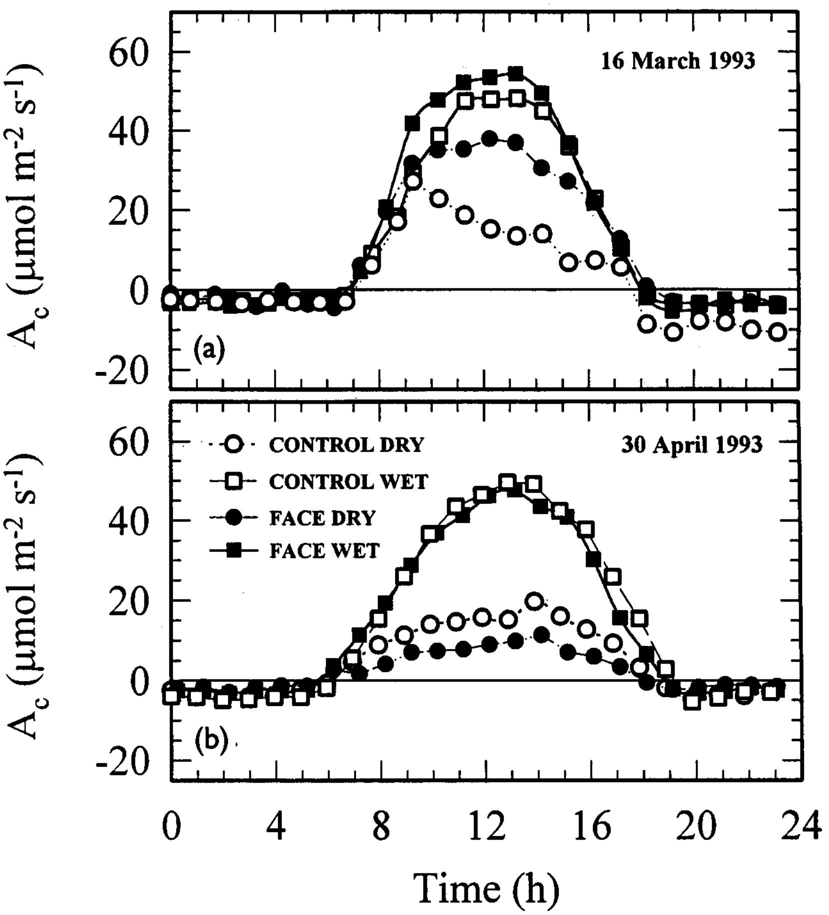


Fig. 4 Net wheat canopy carbon exchange rates (A_c; per m^2 of ground area basis) vs. time of day on 16 March 1993 (a) and on 30 April 1993 (b) for the FACE-Wet (550 mmol mol^{-1} CO_2, 100% irrigation), FACE-Dry (550 mmol mol^{-1} CO_2, 50% irrigation), Control-Wet (ambient CO_2, 100% irrigation) and Control-Dry (ambient CO_2, 50% irrigation) treatments.

with duplicate infrared thermometers (IRT's; Everest Interscience, Fullerton, CA; Model 4000AL, 15° field-of-view) mounted above each plot to view the canopy toward the north at an angle of 20° below horizonal. The IRT's were calibrated over a wide range of target and ambient temperatures before and after each experiment. The net radiometers were also calibrated before and after the season using the shadow technique with an Eppley pyranometer (Eppley Laboratory, Newport, RI; Model 15) as the standard. Also before and after, the anemometers were calibrated by mounting them on a horizonatal bar at 2 m and regressing their output over a wide range of wind speeds observed in a 3-day period against a nearly new anemometer reserved for calibrations, relying on the factory calibration for the standard. An improvement over the methodology of Kimball *et al.* (1994) with the cotton is that nearly new duplicate net radiometers and IRTs were used, and they were switched weekly between the FACE and Control plots. Also, the IRT temperatures were corrected for canopy emittance (assumed = 0.98) and reflected sky radiation, and the same stability correction was used during day and night whenever the canopy temperature was below air temperature.

Thermal images of FACE and Control plots were also obtained on one day during the season (8 April 1993) using a thermal scanner (Model 760, Inframetrics) flown at 150 m above ground level. Like the fixed-mount IRTs, the imager was calibrated over a wide range of head and black-body target temperatures before and after the experiment.

Results

Weather

A typical daily weather pattern for spring is illustrated in Fig. 2 for 9 April 1993. Wheat canopy temperatures are also plotted which were about 3 °C cooler than the 2-m air temperature, except for a period from about dawn until shortly after noon when they rose above air temperature. The FACE canopy temperatures were slightly warmer than those of the Controls. The seasonal weather pattern for 1993 is illustrated in Fig. 3A, with air temperatures ranging from a lowest daily minimum of –1.1 °C in January to the highest daily maximum of 37.7 °C in May.

Canopy temperatures

Elevated [CO_2] caused increases in canopy temperature, as illustrated by the clearly defined circle of influence in the thermal image of a FACE plot acquired on 8 April 1993 (Fig. 1d), compared to that from a Control plot (Fig. 1c). Averaging the temperature over the area in these plots and their corresponding replicates, the mean ($\pm$ SE) temperatures were $21.7 \pm 0.3, 21.5 \pm 0.1, 23.4 \pm 0.2$, and 22.7 ± 0.2 °C for Control-Dry, Control-Wet, FACE-Dry, and FACE-Wet, respectively. The Dry-minus-Wet (top half minus bottom half in Fig. 1c and 1d) temperature differences were 0.2 and 0.7 °C for Control and FACE, respectively. However, on this particular day, which was 3 days following irrigations, elevated [CO_2] was causing even larger temperature differences than the irrigation treatments. The FACE-minus-Control (Fig. 1d minus 1c) differences amounted to 1.2 and 1.7 °C for Wet and Dry, respectively. Although point-to-point observations of foliage temperature increases due to elevated [CO_2] have been reported previously (Idso *et al.* 1987a; Kimball *et al.* 1992), this first thermal image shows that the entire canopy was consistently warmed by the elevated [CO_2].

The elevated-[CO_2]-caused increases in canopy temperature continued day after day throughout most of the growing season, as shown in Fig. 3b, for the Wet plots. Averaged from February through April, the mean increase in canopy temperature was 0.6 °C. These increases in canopy temperature were associated with the direct effects of [CO_2] on reducing leaf stomatal conductance and transpiration (Garcia *et al.* 1995).

Plant development and senescence

Elevated [CO_2] accelerated plant development by 2.3 and 1.5 days to mid-anthesis (Zadoks growth stage 65) for Wet and Dry, respectively, and shortened time to maturity by 6.4 and 0.8 days (Table 1). The differences in maturity times were clearly visible as gradations in greenness on 11 May, when the Control-Wet plants were mostly green, the Control-Dry and and FACE-Wet plants were partially green, and the FACE-Dry plants were a mature yellow (Fig. 1b). The accelerated rates of development were associated with higher plant canopy temperatures under elevated [CO_2] (Figs 1d, 3b)

Canopy photosynthesis

During most of the season, the diurnal behaviour of net canopy photosynthesis, A_c, was similar to that shown in Fig. 4a for 16 March 1993. At midday on 16 March, rates of A_c of the FACE plants were 12 and 38% greater than those of the Control plants for the Wet and Dry treatments, respectively. When integrated over whole (24 h) days

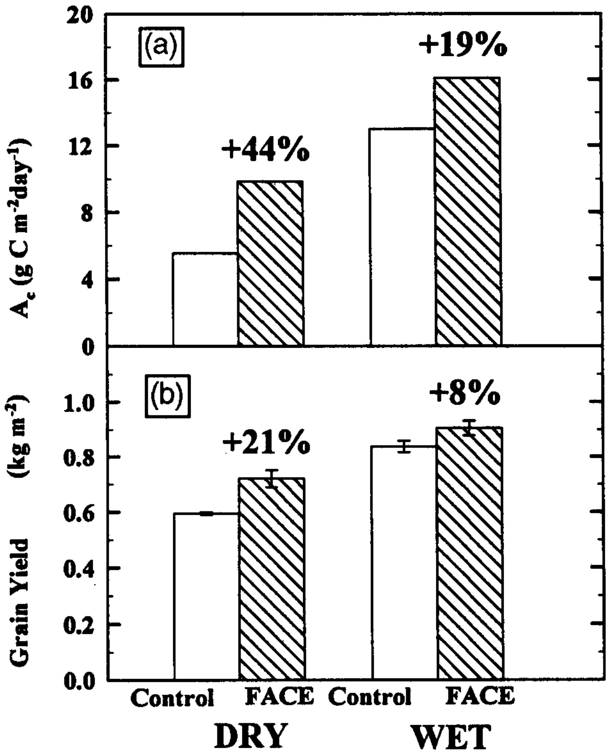


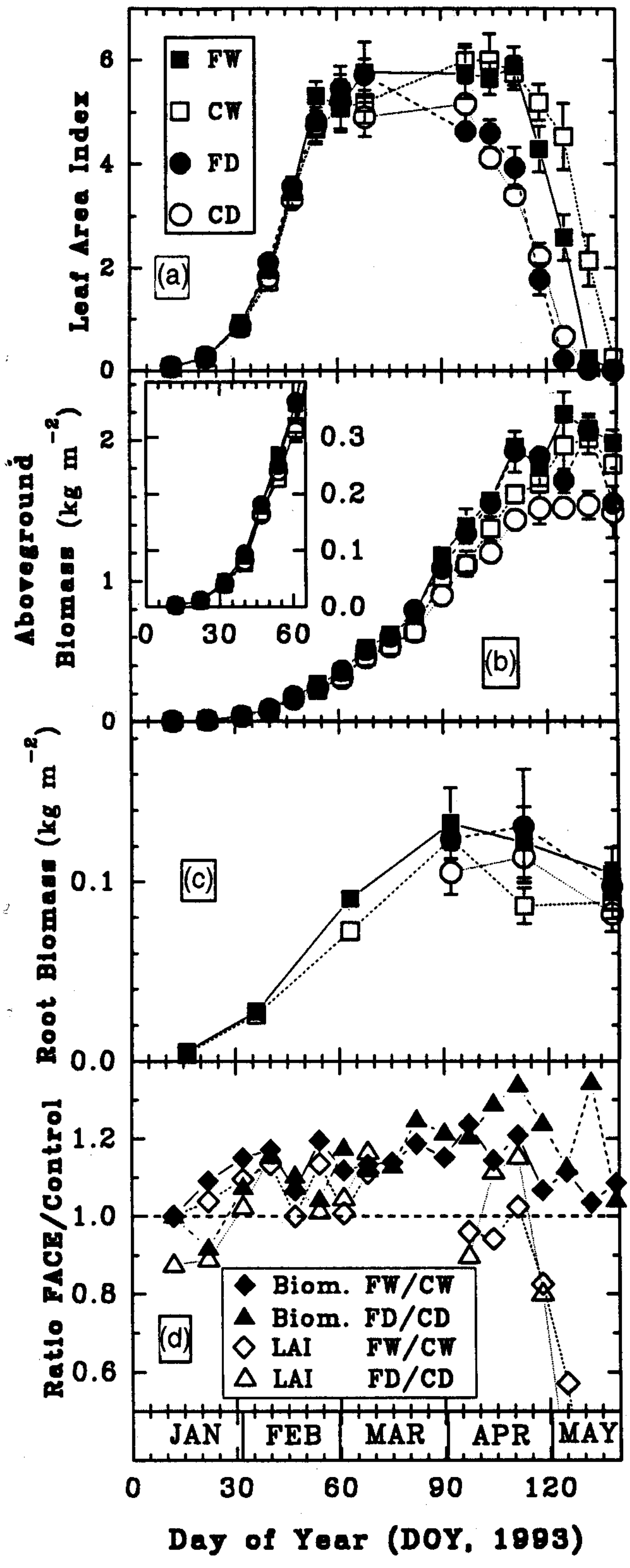
Fig. 5 (a) Average daily integrated values of net canopy carbon exchange rates, A_c, for 17 selected days in 1993 between tillering and maturity for the Control (ambient CO_2) and FACE (550 mol mol^{-1}) CO_2 treatments under Wet (well-watered) and Dry (water-stressed) conditions. (b) Grain yield (dry weight) obtained at final harvest of 20.8 m^{-2} area in each plot.

and averaged over several days through the course of the 1992–3 growing season, the degrees of stimulation were 19% and 44% (Fig. 5a; $P < 0.01$, paired *t*-test).

The acceleration of senescence by elevated [CO_2] affected canopy photosynthesis toward the end of the growing season, as illustrated by Fig. 4b for 30 April 1993. FACE-Dry plants were nearly mature and had lower rates than Control-Dry plants. By this date, the FACE-Wet plants had just started to senesce, and their photosynthetic rates had dropped below those of the Control-Wet plants, whose leaves were still fully green.

Leaf area

Early in the growing season, elevated [CO_2] tended to gradually increase leaf area index (LAI) to a maximum of about 15% above the Control plants by the end of February (Fig. 6a, d). Then, for the next two months, the differences in LAI due to the [CO_2] treatments gradually disappeared. However, as the crop senesced, starting in mid-April for the Dry plots, there was a dramatic decline in green leaf area, with the Dry plots declining first, then FACE-Wet, followed by Control-Wet (Fig. 1b). The ratios



of the leaf areas in the FACE plots to those in the Control plots (Fig. 6d) were slightly above 1.0 for the Wet plots and tended to be about 1.1 for the Dry, until the latter part of April when the accelerated senescence of the FACE plants caused the ratios to plunge to zero.

Biomass accumulation

Total above-ground biomass accumulation showed highly significant ($P < 0.01$) effects of [CO_2] on plant growth during the season (Pinter *et al.* 1995), as shown in Fig. 6b. For both Wet and Dry treatments, the relative increase in biomass resulting from elevated [CO_2] showed a progressive increase with time during the season until mid-April (Fig. 6d), reaching values of about 17 and 21% for the Wet and Dry treatments, respectively, for the 8-week period before maturation (Figs 6d, 7). Then there were declines in the ratios starting in late April, especially for the Wet treatment, due to the accelerated development and senescence of the plants growing at elevated [CO_2] (Figs 1b, 6d).

The effects of elevated [CO_2] on the patterns of root biomass accumulation were similar to those on above-ground biomass (Fig. 6b, c). However, there was significantly greater root growth between the plant rows due to FACE early in the season (Wechsung *et al.* 1995), which suggests that elevated [CO_2] enabled the plants to explore a greater volume of soil, as well as greater ramification within the same volume.

Averaging the ratios of the FACE to Control above-ground and root biomass data from samples taken between day-of-year (DOY) 61 and DOY 113 in 1993, i.e. before the onset of senescence, the relative effects of elevated [CO_2] on the mid-season root biomass were somewhat larger than on the above-ground biomass for the Wet treatment (Fig. 7 17% for above-ground vs. 25% for roots), but for the Dry treatment, the effects were larger for above-ground than for roots (21% for above-ground and 17% for roots). Overall, the mid-season pre-senescent increase in growth due to FACE amounted to about 20%.

Fig. 6 Seasonal course by day of year (DOY) in 1993 of: (a) green leaf area index (LAI) for FACE-Wet (FW), Control-Wet (CW), FACE-Dry (FD), and Control-Dry plots; (b) above-ground biomass accumulation for the FW, CW, FD, and CD plots, with an insert with expanded scale for Jan. and Feb.; (c) root biomass accumulation from 1-m-deep soil cores taken from within the plant rows; and (d) ratios of above-ground biomass and LAI in the FACE plots to those from the corresponding Control plots. Bars for LAI, above-ground biomass, and root biomass indicate SE based on 4 replicate plots. For many of the points, the error bars are narrower than the plotted symbol and are not visible.

Grain yield

Final grain yields were high (Fig. 5b). The yields from the Control-Wet treatment, i.e. the normal present-day irrigated field condition, were 12% higher than the yield potential listed for developmental lines of the cultivar (Hanson *et al.* 1982) and 41% higher than average county wheat yields reported for 1993 (Arizona Agricultural Statistical Service 1994). Under this well-watered regime, elevated [CO_2] caused a modest but statistically significant average increase in grain yield of 8% (Pinter *et al.* 1995). On the other hand, under the Dry treatment, elevated [CO_2] caused a highly significant 21% average increase in final grain yield. Elevated [CO_2] also caused a small but significant ($P < 0.001$) increase in harvest index (ratio of grain biomass to total above-ground biomass) of 0.02 from about 0.45 to 0.47 for both Wet and Dry conditions.

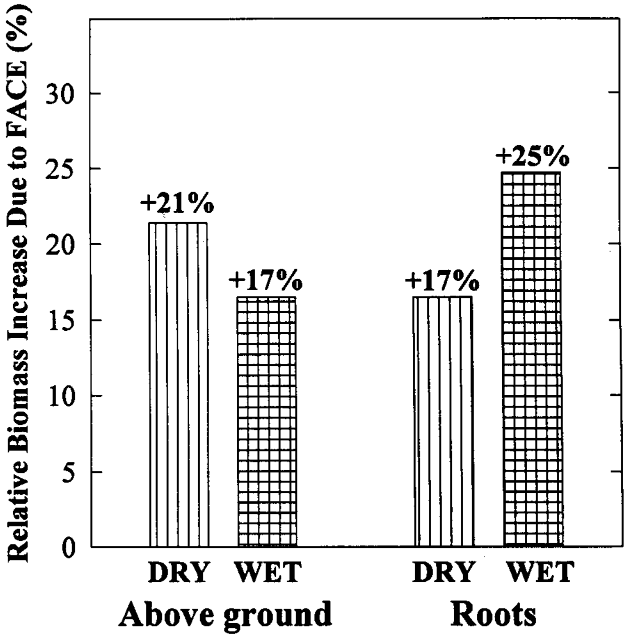


Fig. 7 Mid-season responses of above-ground and root biomass to the FACE treatment relatiave to the ambient Control treatment averaged over sampling dates between 2 March (DOY 61) and 23 April (DOY 133) 1993. For the above-ground values, there were 8 samplings, while for the roots, there were 2 and 3 samplings for Wet and Dry, respectively.

Daily energy budget

Net radiation, R_n (Fig. 8a) was the largest component of the energy budget, generally much larger in magnitude than surface soil heat flux, G_o (Fig. 8b), or sensible heat flux, H (Fig. 8c) for 9 April 1993, which was a typical day. Consequently, the latent heat flux, λET (Fig. 8d), tended to follow R_n. The differences in R_n between FACE and Control were small (Fig. 8a), but the error bands on R_n were narrow, and FACE R_n was consistently less than Control R_n – by 16 W m^{-2} or 2.5% at mid-day for 9 April. Theoretically, a 0.6 °C increase in canopy temperature under FACE (Figs 2,3b) would increase the upgoing thermal radiation by only about 4 W m^{-2}, so there must have also been changes in the short-wave radiation balance. Because the crop was warmer than the air from about dawn until mid-afternoon (Fig. 2), H was positive for this portion of the day and negative otherwise (Fig. 8c). At about 10.00 hours on 9 April, H in the FACE plots exceeded that of the Controls by 51 W m^{-2}, which was 48% more than Control H but only 8% of the maximum R_n. The effects of FACE on λET were also small, but consistently the λET of the FACE plots was lower than that of the Controls, amounting to 47 W m^{-2} or 9% less, near noon on this particular day.

Seasonal energy budget

On a seasonal basis, most components of the surface energy balance showed small yet consistent differences between the FACE-Wet and Control-Wet treatments (Fig. 9). It is important to note that we were unable to detect any systematic bias in the data when our carefully calibrated infrared radiometers and infrared thermometers were switched weekly between the FACE and Control plots. The FACE data from Fig. 9 are plotted against the corresponding Control values in Fig. 10, and regressions were run in order to detect the [CO_2] treatment differences. At the beginning of the season in January, the instruments viewed much soil, and at the end of the season in May, the [CO_2] effects on senescence (Table 1, Fig. 1b) caused the FACE plants to be much warmer than the Control plants (Figs 1d, 3b). Therefore, in all of the regressions in Fig. 10, the January and May data were excluded, so that the results pertain only to the actively growing crop.

Daily R_n in the FACE plots averaged 4% (± 1%) less than that in the Control plots from February through April (Figs 9a, 10a). The daily (24 h) totals of G_o were very small (generally < 1 MJ m^{-2} d^{-1}), as expected (not shown). Daily H in the FACE plots tended to be larger than that in the Control plots (Figs 9b, 10c). For many of the days, especially toward the end of the season in April (Fig. 9b), 'larger' means less negative. This tendency resulted from the slightly warmer canopies in the FACE plots relative to those of the Control plots most of the time (Figs 2, 3b) even though both FACE and Control canopies were cooler than the air, except from about dawn until mid-after noon (Figs 2, 8c).

Daily λET in the FACE plots was less than that of the Control plots on most days (Figs 9c, 10b). At the end of

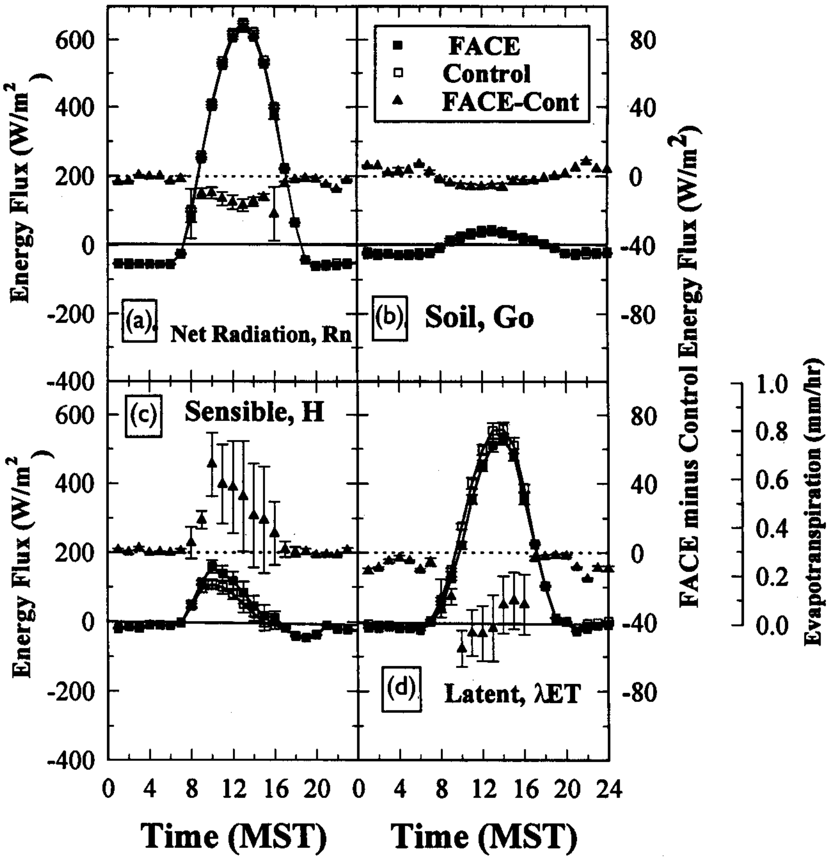


Fig. 8 (a) Net radiation, R_n (b) soil heat flux, G_o (c) sensible heat flux, *H*, and (d) latent heat flux, λET, in CONTROL and FACE plots vs. time of day on 9 April 1993 (DOY 099). Standard error bars are included, but often they were narrower than the symbol width and therefore not visible.

the season in May, the FACE plants matured earlier leading to decreased transpiration from the FACE plots compared to the Control plots. Excluding these May data, as well as the January data when the instruments viewed more soil, the regression of FACE on CONTROL λET from February through April indicates that the FACE treatment decreased λET by an average of about 7.9% (± 1.5%).

Discussion

In these free-air CO_2 enrichment experiments with unrestricted rooting volumes, there was no evidence of any significant acclimation or down-regulation of photosynthesis at the biochemical level in the Wet plots (Nie *et al.* 1995a, b), in contrast to many previous studies (Sage 1994). The indication from the biochemical data that there should be stimulation of photosynthesis by elevated $[CO_2]$ throughout the growing season was borne out by the actual measurements of whole canopy net photosynthesis, i.e. net carbon exchange rate, A_c, in both Wet and Dry plots (Figs 4a, 5a), which showed an average increase of 19% in the Wet plots and a substantial 44% in the Dry plots (Fig. 5a). Although FACE did not stimulate photosynthesis as much as the Dry treatment decreased it, nevertheless, under the Dry conditions, the FACE treatment stimulated photosynthesis, in relative terms, much more than under the Wet treatment.

The infrared themometer and imager measurements showed that crop temperatures can increase with rising CO_2 concentration (Figs 1d, 3b), which implies that the climate ranges over which particular crops can be grown could shift even in the absence of any increase in global air temperature. Accelerated rates of development were associated with the higher plant canopy temperatures under elevated $[CO_2]$ (Table 1, Figs 1b, 6a, d).

The trend for the growth stimulation in elevated $[CO_2]$ to increase through the season (Fig. 6d) parallels the seasonal increase in air temperature (Fig. 3a). This suggestion of a strong positive $[CO_2]$ by temperature interaction is consistent with observations we have made previously with other crops (Idso *et al.* 1987b) and with predictions that Long (1991) has set forth for photosynthetic response. It is also consistent with the observations of Oechel *et al.* (1994) who found significant acclimation of photosynthesis of Arctic tundra to elevated $[CO_2]$ under cool conditions but only slight acclimation under warmer conditions.

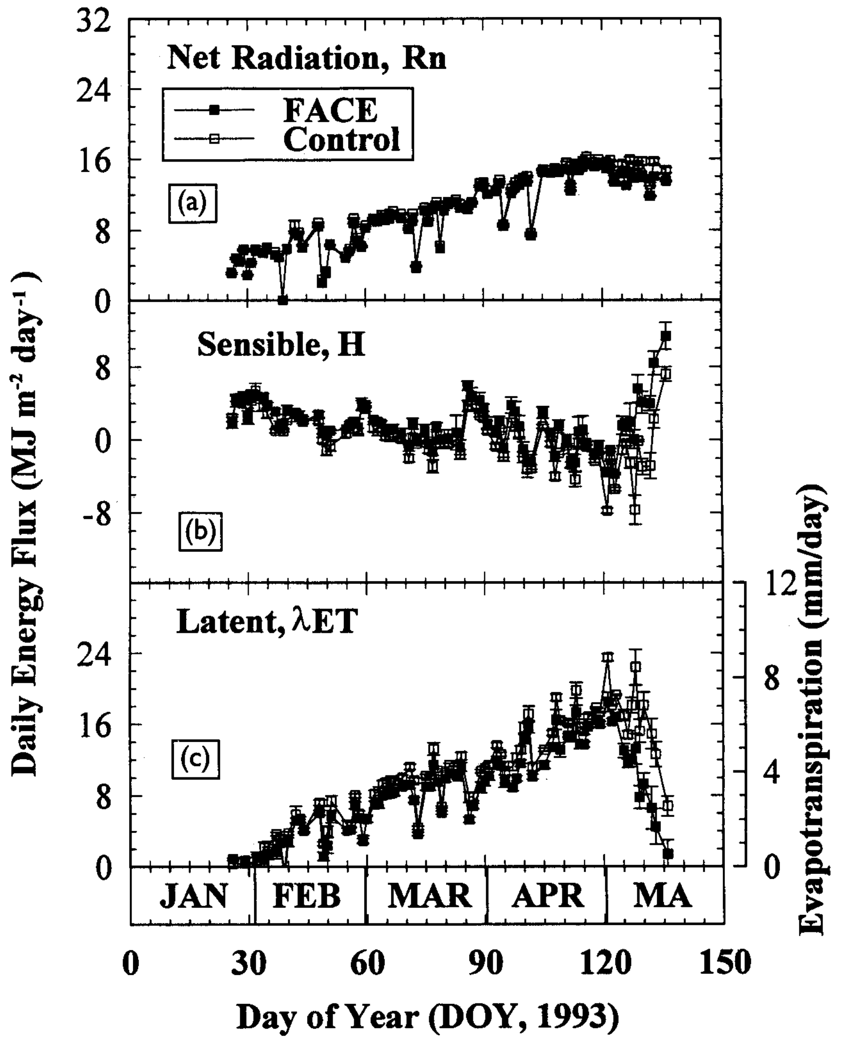


Fig. 9 (a) Daily total net radiation, R_n (b) daily total sensible heat flux, H, and (c) daily total latent heat flux, λET, for CONTROL and FACE plots vs. day of year in 1993. Standard error bars are included, but often they were narrower than the symbol width and therefore not visible.

An analysis of the effects of elevated [CO_2] on wheat yield in prior chamber studies has suggested that wheat yield could increase about 38% (95% confidence interval for these studies ranged from 15 to 74%) with a doubling (to *c.* 700 mol mol^{-1}) of CO_2 concentration (Kimball 1986). These previous chamber studies are consistent with our midseason [CO_2] growth responses for both Wet and Dry treatments (Figs 6, 7) and also with the final [CO_2] yield response for the Dry treatment (Fig. 5B) of about 20% for enrichment to 550 mol mol^{-1}, assuming a roughly linear response between 350 and 700 mol mol^{-1}. However, the lower final yield response of only about 8% for the Wet treatment (Fig. 5b), associated with the effects of [CO_2] on accelerating senescence, was a surprise that was not anticipated on the basis of the prior chamber work. Nevertheless, even an 8% increase in grain yield under well-watered conditions at 550 μmol mol^{-1} [CO_2] would be important for feeding future populations, and a 21% increase under water-stress would help compensate for possible future decreases in precipitation.

These stimulations of wheat growth of about 20% maximum due to the 550 μmol mol^{-1} FACE treatment (Figs 6B,7) are strikingly smaller than the 40% increases we observed previously with cotton, both in FACE (Mauney *et al.* 1994; Pinter *et al.* 1995) and open-top chamber (Kimball & Mauney 1993) experiments. We speculate that one reason for such a difference is because wheat is a cool weather crop (winter crop in Arizona), whereas cotton is a warm weather crop (summer crop in Arizona). Such a seasonal differences in [CO_2] growth response between cool and warm season crops are consistent with a strong positive [CO_2] by temperature interaction, as discussed above. Another reason for a smaller [CO_2] response in wheat compared to cotton is that wheat is an herbaceous determinate plant, whereas cotton is woody and indeterminate. Thus, cotton almost always has sinks in the form of newly added fruits or wood to accommodate any additional photosynthate resulting from additional photosynthesis in elevated [CO_2]. Moreover, because cotton is grown in summer, the photosyn-

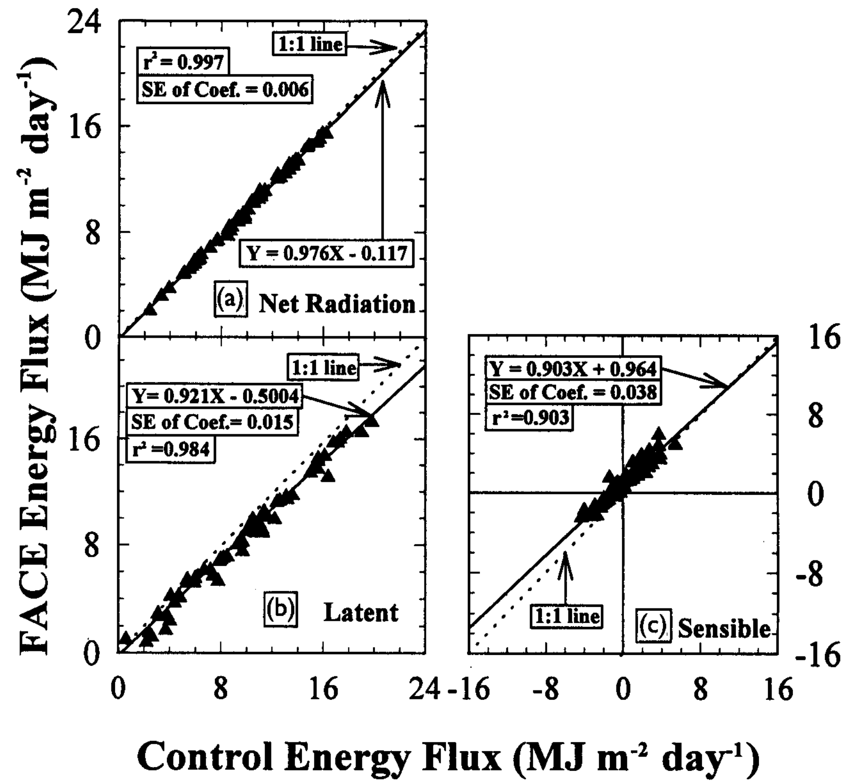


Fig. 10 (a) Daily total FACE net radiation, R_n (b) daily total FACE latent heat flux, λET, and (c) daily total FACE sensible heat flux, H, vs. the corresponding Control values from February through April 1993.

thesis and biochemical growth processes are less restricted by cool temperatures. In contrast, wheat withstands freezing temperatures, but it grows slowly in winter with little [CO_2] response (Fig. 6). The number of tillers is set during this cold (Fig. 3a) slow-growth time, which restricts the number of sinks for photosynthate. Then, when temperatures warm in the spring (Fig. 3a), the fact that it has already fixed the number of tillers and can not add more flowers makes it sink-limited and unable to respond as much as cotton to elevated [CO_2].

Increasing CO_2 concentration has been shown to cause partial stomatal closure which reduces the conductance of water vapour from inside the leaf stomatal cavities to the outside air (Morison 1987). The decrease in conductance reduces transpiration per unit of leaf area, as has been observed many times (Kimball & Idso 1983) and was observed also in these FACE wheat experiments (Garcia *et al.* 1995). Such a decrease in the rate of leaf water loss suggests the possibility that reductions in evapotranspiration (*ET*) and plant water requirements per unit of land area may be forthcoming in the future high-CO_2 world (Kimball & Idso 1983; Rosenberg *et al.* 1990), and that there might be an improvement in streamflow and future water resources (Idso & Brazel 1985), provided that the climate does not change too adversely (Revelle & Waggoner 1983).

On the other hand, as the elevated [CO_2] causes partial stomatal closure, the resultant decrease in transpirational cooling increases the foliage temperature, as we observed previously with cotton (Idso *et al.* 1987a; Kimball *et al.* 1992) and found again with the wheat (Figs 1b, 3b). The increased foliage temperature increases water vapour pressure inside the leaves and increases leaf transpiration, thereby counteracting the CO_2-induced stomatal closure. At the same time, the CO_2 stimulation of growth can result in larger plants (e.g. Kimball 1986) with larger leaf areas, which would also tend to increase whole-plant transpiration (Rosenberg *et al.* 1990). Thus, there are also reasons why *ET* and plant water requirements might instead be expected to increase as the [CO_2] level rises.

In the prior FACE cotton experiments (Dugas & Pinter 1994), there was no detectable effect of FACE at 550 μmol mol^{-1} (same concentration as this FACE wheat experiment) on *ET* (Dugas *et al.* 1994; Hunsaker *et al.* 1994; Kimball *et al.* 1994), so the increased leaf area of the cotton (Mauney *et al.* 1994) and leaf temperatures (Kimball *et al.* 1992) apparently compensated for the reduced transpiration per unit of leaf area. In contrast, the effects of FACE on leaf area in the Wet plots in this wheat experiment were minor until the onset of senescence (Fig. 6a), and consequently, the reductions in transpiration per unit of leaf area apparently caused a reduction of about 8% in *ET* (Fig. 10b). This result suggests that future water requirements for wheat may be slightly lower in the future high-CO_2 world (provided any global warming is small).

Extensive modelling studies have already been conducted to assess the impact of global environmental change, especially climate change, on future world production of wheat and other crops (Parry *et al.* 1988; Smith & Tirpak 1989; Wolf 1993; Rosenzweig & Parry 1994). These studies have either ignored the direct effect of $[CO_2]$ or chosen to use simple constant multiplication factors. For example, Rosenzweig & Parry (1994) assumed a 17% increase in photosynthetic rate for wheat exposed to an elevated CO_2 concentration similar to that of this study. Their assumption agrees with the 19% increase we found for the average of several days during the growing season for the Wet treatment (Fig. 5a). However, it does not agree with the 44% increase we found for Dry conditions (Fig. 5a). Indeed, generally these models do not agree with the observations we have made under actual field conditions of (a) the distinct interaction of $[CO_2]$ with water supply (b) seasonal changes in $[CO_2]$ response suggestive of a strong temperature interaction with $[CO_2]$, and (c) the effects of elevated $[CO_2]$ on foliage temperature and plant senescence. Fortunately, the development of more sophisticated models which can account for many of the interactive effects of elevated $[CO_2]$ with other environmental variables appears to be proceeding nicely [Grant *et al.* 1995a (this issue), b; Grossman *et al.* 1995; Kartschall *et al.* 1995]. The deficiencies in the simple models underscore the need for field scale experiments to allow testing and development of the more sophisticated models which can account for the interactive effects of elevated $[CO_2]$ with other environmental variables. Development of these more accurate models appears crucial to avoid misleading the planning for the security of future food supplies under global environmental change.

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