

Free-Air CO₂ Enrichment: Responses of Cotton and Wheat Crops

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I. Introduction

Net photosynthetic rates for many C₃ food and fiber crops are limited by present concentrations of atmospheric carbon dioxide (CO₂) (Percy and Björkman, 1983). As a result, anticipated increases in CO₂ during the next century are likely to have important consequences for agricultural systems. In fact, a projected doubling of CO₂ could boost biomass production and marketable yields of agricultural crops by one-third (Kimball, 1983) or even more if other constraints to productivity are limiting (Idso and Idso, 1994). Until only recently, these projections have been based solely on results obtained from controlled-environment enclosures, glass-houses, and open-top field chambers, where restricted soil rooting volumes and/or microclimatic changes caused by the chambers themselves may have influenced the outcome (Lawlor and Mitchell, 1991; Arp, 1991; Kimball *et al.*, in press). Despite a preponderance of evidence that shows a positive effect of CO₂ on plant growth under enclosed conditions, justifiable concern has focused on possible artifacts caused by the test environments themselves (Allen *et al.*, 1992). Would the results have been the same if an entire community of plants was exposed to high CO₂ levels under more natural field conditions?

Responding to the need for appropriate experimental methodology to answer this question, scientists and engineers from Brookhaven National Laboratory (BNL) developed an innovative system in the mid- to late-1980s

to fumigate plants with CO₂ in an open-field setting (Allen, 1992). The experimental facility they created was given the acronym FACE, which stands for free air carbon dioxide enrichment. FACE was found to be free of most of the microclimatic artifacts that had plagued earlier studies in chambers and, thus, was expected to provide more realistic information on plant responses to CO₂ conditions that might be encountered in the future. Furthermore, since FACE enabled large areas (~500 m²) to be fumigated as a single unit, plants were also expected to function as a complex community, with natural competitive interactions for environmental resources. The large number of plants treated by FACE also implied that many different types of studies could be carried out on the same community and that destructive sampling could be accommodated without affecting the response of remaining plants.

The first FACE field trials took place in 1987 and 1988 in a cotton field near Yazoo City, MS, where the enrichment system was operated for varying numbers of weeks during the season (Allen, 1992). In 1989, the FACE facility was moved to The Maricopa Agricultural Center (MAC), about 40 km south of Phoenix, AZ. Since then, the system has been used to evaluate the effects of elevated CO₂ on cotton (three seasons from 1989 until 1991) and wheat (two seasons, 1992–1993 and 1993–1994) within an agricultural production environment. Many of the biological investigations have been conducted by USDA Agricultural Research Service (ARS) personnel. However, more than 100 scientists and graduate students from 43 different research locations and 8 countries have participated in FACE experiments, which examine the effects of increased CO₂ on the dynamics of carbon and water cycling of plants growing in realistic, open-field conditions (see Appendix).

Results from our cotton FACE experiments have been summarized and published in special dedicated issues of *Critical Reviews in Plant Sciences* (Vol. 11; Hendrey, 1992) and *Agricultural and Forest Meteorology* (Vol. 70; Dugas and Pinter, 1994). Discussion in this chapter will review the effects of CO₂ on photosynthesis, conductance, growth, and yield of cotton from those FACE experiments in Arizona. Analyses of data from wheat grown in the FACE facility are underway. Nevertheless, enough of the preliminary findings is presented here to provide interesting comparisons and contrasts with cotton.

In addition to the studies we will present here, open-air field systems have been used for a number of years to test the effects of gaseous pollutants on vegetation (McLeod *et al.*, 1985). FACE facilities have been operational for several growing seasons in Switzerland, where investigations include growth responses of ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) (Blum, 1993). A prototype FACE system for forests has been tested in an experimental plantation of loblolly pine (*Pinus taeda*) at Duke

University in Durham, NC (Hendrey and Kimball, 1994). Plans are also underway to use FACE and FACE-like systems for evaluating the effect of CO₂ on production and animal utilization of pasture forage in New Zealand, of forests and crops in Europe, and of chaparral and desert shrubs in the western United States.

A. The Maricopa Agricultural Center (MAC)

MAC is a research and demonstration farm administered by The University of Arizona. It is located in the midst of an extensive agricultural region in central Arizona (33.07° N latitude, 111.98° W longitude, 358-m elevation). Primary crops in the area are cotton, alfalfa, barley, spring wheat, and pecans; all must be irrigated by surface, subsurface (drip), or sprinkler irrigation to realize an economic yield. The experimental FACE site was located in two adjacent 4.5-ha fields at MAC, where soil was classified as a reclaimed Trix clay loam [fine loamy, mixed (calcareous), hyperthermic Typic Torrifluvents].

B. FACE Facility at MAC

The FACE system used in the Arizona experiments was designed by BNL and operated jointly by BNL and ARS personnel. The apparatus consisted of four circular plenums, each connected to an array of 32 vertical vent pipes, encompassing an area about 25 m in diameter. Pure gaseous CO₂ (from a 48-Mg liquid storage vessel) was metered into the intake of a high volume fan attached to the plenum, mixed with ambient air, and injected from emitter ports of vent pipes on the upwind side of the array. An algorithm based on wind speed, wind direction, and CO₂ concentration in the center of each array was used to maintain CO₂ treatments at desired levels. Each FACE plot was paired with a similarly sized control plot located 90–100 m away in the same field (Wall and Kimball, 1993). During the 1990 and 1991 cotton experiments and both wheat experiments, controls were equipped with a plenum and vent pipe construction similar to that of the FACE arrays, but without fans for air injection. Additional information on FACE design, construction, and control algorithms can be found in Lewin *et al.* (1994) and Nagy *et al.* (1994).

C. FACE Performance and Reliability

FACE technology depends on atmospheric dispersion for the uniform distribution of injected CO₂ across the experimental area (Lipfert *et al.*, 1991, and 1992). During our experiments, it was possible to control CO₂ at the center of FACE arrays at the desired set point ($550 \pm 20\%$ $\mu\text{mol mol}^{-1}$) for 99% of the time, thus meeting or exceeding original system design criteria (Hendrey *et al.*, 1993a; Nagy *et al.*, 1994). Three-dimensional analyses of gas concentrations showed that CO₂ had a tendency to build

up beneath dense cotton canopies on calm days late in the season (Hileman *et al.*, 1992), and concentrations were slightly higher on the upwind side of the array (Hendrey *et al.*, 1993b). Nevertheless, on a spatial basis, most CO₂ concentrations also fell within the original design criteria. Analyses of the starch content of leaves (Hendrix, 1992), yield parameters (Mauney *et al.*, 1994), and stable carbon isotopes of lint ($\delta^{13}\text{C}$; Leavitt *et al.*, 1994) were sufficiently uniform across the FACE array to indicate that the cotton plant integrated most of the shorter term fluctuations in CO₂. When comparing FACE performance characteristics to other CO₂-controlled apparatus, it is relevant to note that temporal and spatial concentrations of CO₂ can be quite variable under natural field conditions. Standard deviations of CO₂ ranging from 30 to 100 $\mu\text{mol mol}^{-1}$ have been reported in open-top chambers (Leadley and Drake, 1993).

II. Materials and Methods

A. Experimental Crops and Treatments

1. Cotton and Wheat Test Crops An early goal of the FACE program was to examine the effects of supraambient CO₂ on the response of simple agricultural monocultures before applying FACE technology to more complex natural vegetation communities. Accordingly, we selected two C₃ crop species that are important to world agriculture and that also represent contrasts in patterns of growth and development. A short-staple cotton (*Gossypium hirsutum*, L., cv. Deltapine 77) was chosen because it was a warm-season, perennial, woody plant that had an indeterminate fruiting pattern. A hard, red, spring wheat (*Triticum aestivum*, L., cv. Yecora Rojo) was selected as being representative of cool-season annual grasses with determinate grain-filling characteristics. The cultivars chosen for our experiments were well-adapted to central Arizona climatic conditions and grown commercially by local farmers.

Culture practices (cultivation, insect and weed control, soil nutrient levels, etc.) were managed according to the recommendations of Arizona State Extension Service and University of Arizona research and farm support staff. Cotton was seeded during mid- to late-April on raised soil beds spaced 1.02 m apart. After emergence, the population was thinned to about 10 plants m⁻². Cotton was supplied with an average of 142 kg ha⁻¹ N during each year. Irrigation was terminated and seed cotton harvested in mid-September.

Wheat has been studied for two complete growing seasons in the FACE facility. It was sown in December (1992 and 1993) and harvested during late May in 1993 and June in 1994. Plants were grown on a flat, unbedded

soil surface in rows spaced 0.25 m apart; density at the time of harvest was 109 and 153 plants m⁻² in 1993 and 1994, respectively. Wheat received 277 kg N ha⁻¹ and 44 kg P ha⁻¹ in 1992–1993 and 261 kg N ha⁻¹ and 29 kg P ha⁻¹ in 1993–1994.

2. Carbon Dioxide Treatments Wheat and cotton crops were exposed to ambient (control, ~370 μmol mol⁻¹) and enriched (FACE, ~550 μmol mol⁻¹) levels of CO₂; paired treatment plots were replicated four times. In the FACE plots, CO₂ enrichment began shortly after emergence and continued until shortly before harvest. During the cotton experiments, CO₂ was injected into FACE plots during daylight hours. At night, FACE and control plots were exposed to similar ambient CO₂ concentrations, which often exceeded 400 μmol mol⁻¹ (Nagy *et al.*, 1994). In the wheat experiments, treatments continued 24 hr a day except for the last 2 weeks of January 1993, when heavy rains prevented regular CO₂ delivery and enrichment was shortened to daylight hours to conserve supplies.

Irrigation Treatments Cotton plants were irrigated using microirrigation (drip) tubing that was buried at a 0.18- to 0.25-m depth and spaced 1.02 m apart. In the first year of the experiment (1989), all plots were well-watered (WET treatment). Irrigation timing and amounts were based on full-season consumptive use requirements of cotton as determined from estimates of potential evapotranspiration (PET) obtained from an on-farm meteorological station. In 1990 and 1991, main CO₂ treatment plots were split to test the interactive effects of deficit irrigation (DRY treatment) and elevated CO₂ on cotton. WET treatments received irrigation amounts equivalent to that evaporated from a class A pan (1990) and PET (1991). DRY plots were irrigated on the same days as WET plots, but received only 75 and 67% of that supplied to the WET plots during 1990 and 1991, respectively. The differential irrigations were initiated on July 3, 1990, and on May 20, 1991. The combined amounts of irrigation and rainfall from planting to harvest averaged 1232 mm across all years for the WET treatment, while DRY treatments received 1185 mm in 1990 and 833 mm in 1991 (Mauney *et al.*, 1994; Hunsaker *et al.*, 1994a).

In the FACE wheat project, similar to the preceding cotton experiments, each of the main plots was split in half to provide two irrigation levels as subplots in strips within replications. Microirrigation tubing was spaced 0.51 m apart (parallel to plant rows) and buried 0.18–0.25 m deep. An irrigation scheduling program based on a soil water balance approach was used to determine irrigation of the WET treatment when ~30% of the available soil moisture in the root zone had been depleted. Amounts given to the WET subplots were based on estimates of daily PET multiplied by an appropriate crop coefficient. In 1992–1993, plants in the DRY treatment were irrigated on the same day as those in the WET treatment, but received

only 50% of the amount. During 1993–1994, plants in the DRY subplots received the same amount as the WET subplots, but only on every other irrigation. Irrigation totals from emergence to harvest averaged 600 mm for the WET treatment during both years. Dry treatments received 275 mm in 1992–1993 and 257 mm the following season. Rainfall over the same periods was 76 and 61 mm, respectively, for the 2 years.

B. Experimental Measurements

1. Cotton Plant Sampling Protocol Cotton biomass was measured by destructive plant sampling at 1- to 2-week intervals during the growing season (Mauney *et al.*, 1994). Sampling consisted of pulling every third cotton plant (with as much of the lateral and tap root structures as possible) from three separate, 1-m-long segments of plant row in all replicates of each CO₂-irrigation treatment combination (subplot). This was equivalent to sampling all the plants in a contiguous 1.02-m² area, but did not leave large gaps in the canopy that might have adversely affected the response of remaining plants or the aerodynamics of CO₂ flow. Leaf area was obtained by using an optical planimeter. Dried biomass was measured separately for root, stem, leaf, and fruiting structures.

2. Wheat Plant Sampling Protocol Wheat was sampled at 7- to 10-day intervals during the 1992–1993 and 1993–1994 seasons (18 and 22 sampling periods, respectively). A minimum of six plants was obtained from four sampling zones in each subplot (24 plants total). Plant phenology (according to both the Zadoks and Haun development scales; Bauer *et al.*, 1983), number of stems (tillers), green stem area, and green leaf area were determined on a subsample of 12 median-sized plants per subplot. Heads were counted when awns first became visible above the ligule. Dried biomass was determined for crown, stem, green leaf, non-green leaf, and head components of all 24 plants after oven-drying at 65–70°C. Leaf area index was computed from specific leaf weight of the subsample, green leaf biomass of all plants, and plant density. Beginning 1 week after anthesis, developing grains were separated from the chaff by a combination of hand and machine threshing of the heads and oven-dried for a total of 14 days at 65–70°C. Final grain yields were determined by machine harvest of ~20 m⁻² of each subplot on May 25–27, 1993 and on June 1, 1994.

3. Measurements of Photosynthesis and Transpiration Carbon assimilation was measured by using several different techniques during the FACE experiments. At the individual leaf level, we used portable LI-COR Model 6200¹

¹Names are necessary to report factually on available data; however, the USDA neither guarantees nor warrants the standard of the product, and the use of the name by the USDA implies no approval of the product to the exclusion of others that may also be suitable.

photosynthesis systems (LI-COR, Inc., Lincoln, NE) that were equipped with either 0.25 or 1.0-l cuvettes and moved between subplots from dawn until dusk (Hileman *et al.*, 1992, 1994; Idso *et al.*, 1994). At the canopy level, two types of chamber systems were used. The closed chamber systems used during the first 2 years of cotton experimentation have been described by Hileman *et al.* (1994).

During the third year of cotton and both FACE wheat experiments, continuous-flow, gas exchange chambers were used to measure canopy gas exchange rates within the perimeter of FACE and control arrays. These systems were engineered similar to those described by Garcia *et al.* (1994). They consisted of an aluminum frame covered with Propafilm C¹ (ICI Americas, Inc., Wilmington, DE), a material having a high transmittance of thermal infrared radiation that minimized temperature increases when chambers were exposed to direct sunlight. Differences in CO₂ and H₂O vapor concentrations between inlets and outlets of the chamber were measured with a LI-COR Model LI-6262¹ infrared gas analyzer (IRGA). In FACE arrays, absolute CO₂ was controlled at 550 $\mu\text{mol mol}^{-1}$ by injecting CO₂ into the inlet stream and monitoring it via a second IRGA. A calibrated infrared thermometer (IRT) and quantum sensor were positioned inside the chamber to measure foliage temperatures and incident photosynthetic photon flux density (PPFD), respectively. Chamber ventilation afforded four complete air exchanges per minute and a slight positive pressure, which reduced the potential contribution of soil CO₂ flux to the overall net measurement. Gas exchange (CO₂ and H₂O) was measured continuously (10- to 15-min averages) for 7–14 days, after which systems were moved to a different treatment replicate and plant material was harvested for the determination of biomass and leaf area index. Chambers used in the cotton experiments measured 1.15 \times 1.0 m wide and stood 2 m tall, enclosing one row of cotton plants that was 1 m in length; in wheat, the chambers were 0.75 \times 0.75 m wide by 1.3 m high, enclosing three adjacent rows of plants, each 0.75 m in length.

III. Results and Discussion

A. Net Photosynthesis

1. Leaf Photosynthesis Effects of elevated CO₂ on net photosynthesis (P_n) at the individual leaf level provided comparative data for cotton and wheat. In well-watered cotton, for example, there was about a 30% increase in midday P_n associated with a change in CO₂ from control to FACE conditions (Hileman *et al.*, 1992, 1994; Idso *et al.*, 1994). Significant differences related to CO₂ treatments were also found in light response functions (Idso *et al.*,

1994). Elevated levels of CO₂ increased the asymptotic limit of P_n by 22%, increased initial light conversion efficiency by 28%, and decreased the light compensation point from 63 to 10 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ compared with controls. The latter factors implied greater stimulation of P_n by CO₂ at lower light intensities found at levels deep within the canopy, although this was not explicitly tested with leaves from the lower levels.

Analysis of P_n data from upper canopy leaves during the 1992–1993 wheat study showed similar results. Under well-watered conditions, FACE increased midday P_n values by 28% compared with control values (Garcia *et al.*, 1995), without any evidence of acclimation in the photosynthetic process (Nie *et al.*, 1995 and the FACE Team, unpublished data in press). The CO₂ effect was even larger (>50%) for the DRY irrigation treatments (G. Wall *et al.*, personal communication). The stimulatory effect of CO₂ was also much greater for leaves in the middle and lower levels of the canopy, where they were exposed to lesser intensities of photosynthetically active radiation (PAR) (Osborne *et al.*, 1995). Unlike cotton, however, CO₂ stimulation of single leaf P_n disappeared toward the end of the grain filling period in wheat (Garcia *et al.*, 1995). These observations were consistent with accelerated developmental rates and senescence of leaves in FACE and decreased synthesis of major proteins involved in the photosynthetic process (Nie *et al.*, in press).

2. Canopy Photosynthesis Canopy-level measurements revealed increases in the rates of carbon assimilation that mirrored CO₂ enhancement effects observed on a single leaf basis and were similar to studies reported in the literature for other species (Drake and Leadley, 1991). Hileman *et al.* (1994), using closed chambers in the 1989 and 1990 experiments, reported a midday P_n for well-watered cotton canopies in the FACE treatment that was approximately 30% higher than control values. The P_n enhancement caused by CO₂ was greatest during the middle part of the season when plants in the FACE treatments were larger and intercepted more light (Pinter *et al.*, 1994).

Representative data from flow-through chamber systems operated during the 1991 cotton and 1992–1993 wheat FACE experiments showed CO₂ exchange rates that varied with treatment and time of year (Figs. 1 and 2). During early August 1991, when cotton canopy cover was 100% and plants had a moderately heavy boll load, P_n in the control WET canopy rose to 60–70 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ during midmorning and remained constant for about 5 hr (Fig. 1a). Assimilation rates in the FACE WET treatment on the same day were 35–40% higher, a difference that remained fairly consistent each day during this period of canopy development. As the season progressed, however, absolute P_n values declined. By early September (Fig. 1b), the P_n of control WET was only 30 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, a reduction

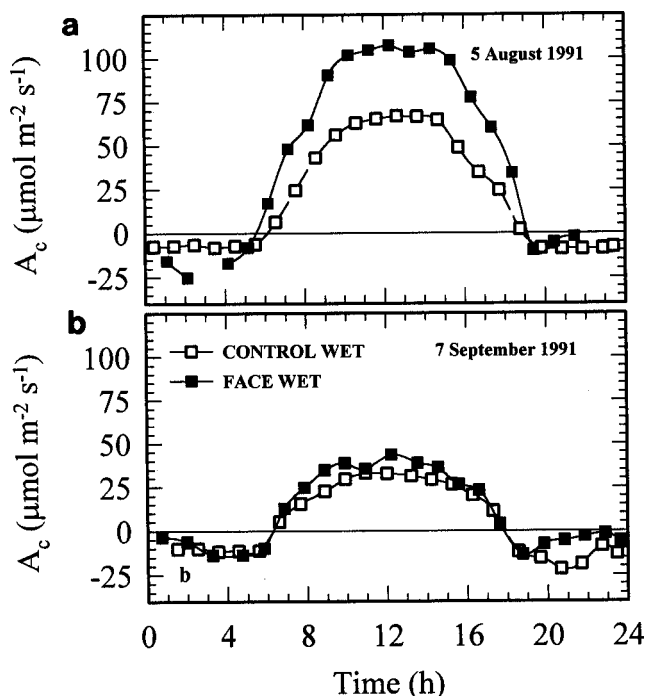


Figure 1 Diurnal trajectories of net canopy assimilation (A_c , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of cotton exposed to FACE ($\sim 550 \mu\text{mol mol}^{-1}$) and control CO₂ ($\sim 370 \mu\text{mol mol}^{-1}$) treatments. Data were measured under clear sky conditions using continuous-flow chambers on representative days during early-August (a) and early-September (b) 1991. Measurements were made only in the WET irrigation treatment.

of 50% from values measured a month earlier. Despite this decline, the enhancement due to extra CO₂ was still evident during midday, with FACE showing an approximate 20% increase over control. Nighttime gas exchange data indicated that dark respiration of cotton was reduced by elevated CO₂, but the results were inconclusive.

Daily values of net canopy photosynthesis were measured with similar continuous-flow chambers during both years of our wheat experiments. Typical trends in these data are shown for mid- and late-season crops in 1993 (Fig. 2). During mid-March, wheat plants in all of the treatments were just beginning to flower, canopy cover was nearly 100%, and the green leaf area index (GLAI) was approaching seasonal maximum values of 5 or 6. The FACE WET canopy had P_n rates on that day that remained above 50 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for more than 4 hr (Fig. 2a). Compared with the control WET canopy, this represented a P_n enhancement of about 20%. Above-average winter precipitation prevented the development of measurable

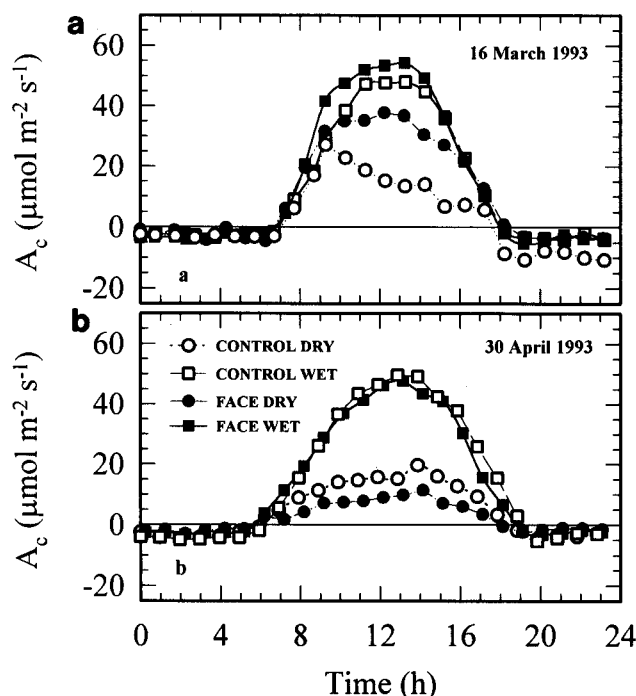


Figure 2 Diurnal trajectories of net canopy assimilation (A_c , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of wheat exposed to FACE ($\sim 550 \mu\text{mol mol}^{-1}$) and control CO_2 ($\sim 370 \mu\text{mol mol}^{-1}$) treatments. Data were measured under clear sky conditions using continuous-flow chambers during mid-March (a) and late-April (b) 1993. Measurements were made in the WET and DRY irrigation treatments.

differences in biomass or GLAI between our WET and DRY treatments until about 1 week later in the season, but the effects of water stress were expressed clearly in reduced canopy P_n (Fig. 2a). The interaction between water stress and CO_2 was also evident in these data; the CO_2 stimulation of P_n in the DRY treatment was considerably larger than the effect measured in the WET treatment.

Stimulation of canopy P_n by elevated CO_2 continued from anthesis through the milk and early dough stages of grain development (from March through the middle of April). During this period, plants also continued to respond more favorably to elevated CO_2 under deficit irrigation regimes than they did in the WET treatments. This presumably was because the larger root systems of FACE DRY (Wechsung and Wechsung, personal communication) enabled plants to extract soil moisture more efficiently. By April 30, however, CO_2 enhancement of P_n had disappeared from the

WET treatment and reversed itself in the DRY treatment (Fig. 2b). This phenomenon was similar to the response seen in individual leaf P_n data and was caused by different rates of canopy and leaf senescence that will be presented later. The gas exchange methodology was not sufficiently sensitive to resolve differences in respiration between CO₂ treatments.

B. Water Relations

Effects of CO₂ on water relations and latent energy exchange processes of cotton and wheat were examined at the leaf, whole-plant, and canopy levels by using a number of diverse experimental techniques.

1. Leaf Water Potentials Total leaf water potentials (ψ_1) were measured on a diurnal basis on numerous occasions during our FACE experiments by using a pressure chamber. At midday there was a tendency for both species in the WET treatment to have a slightly less negative total leaf water potential in the FACE than in the control. However, these differences generally were small and disappeared altogether earlier and later in the day [for cotton, see Bhattacharya *et al.* (1994); for wheat, see Wall *et al.* (1995)]. Toward the end of the season in cotton and for much of the season in wheat, ψ_1 in the FACE DRY irrigation treatments was often significantly less negative than that in control DRY. We suspect that this interaction between CO₂ and irrigation treatment was a compounded result of two phenomena in the FACE treatment: (1) improvement in internal leaf water status caused by partial stomatal closure and (2) the larger volume of soil being exploited by roots (Prior *et al.*, 1994; Wechsung and Wechsung, personal communication).

2. Stomatal Numbers and Conductance No direct effects of CO₂ exposure were observed in the stomatal density (number of stomata per unit area) or the stomatal index (number per epidermal cell) in either the cotton (S. Malone, personal communication) or wheat plants grown in the FACE facility (Estiarte *et al.*, 1994). Single leaf conductances (g) obtained during the cotton experiments by using a LI-COR Model LI-1600¹ steady state porometer and during the wheat experiments by using a LI-COR Model LI-6200¹ closed, gas exchange system revealed a consistent closure response of leaf stomata to elevated CO₂. During the 1990 cotton experiment, Hileman *et al.* (1994) reported that average midday g values of leaves exposed to 550 $\mu\text{mol mol}^{-1}$ in the WET treatment were 22% lower than those in controls. Bhattacharya *et al.* (1994) showed similar g differences in cotton toward the end of the 1991 FACE season and found an even larger g closure in response to CO₂ in the DRY irrigation regime. Midday g values of wheat leaves in the FACE WET treatment were 38% lower than in control WET throughout the 1992–1993 wheat experiment (Garcia *et al.*, 1995). Reductions in g were also accompanied by small, but consistent increases

in canopy temperatures (T_c) measured with infrared thermometers. Compared with the control WET treatment, midday T_c values of plants in the FACE WET treatment were about 0.8°C warmer for cotton (Kimball *et al.*, 1992) and 0.6°C warmer for wheat (Kimball *et al.*, 1994b).

3. Sap Flow Transpiration Estimates Constant power sap flow gauges were used to quantify the effect of elevated CO_2 on the transpiration of whole cotton plants and individual wheat tillers. On a ground area basis, mean transpiration rates of cotton in the well-watered treatments varied between 4.4 and 9.5 mm day⁻¹ (Dugas *et al.*, 1994). No consistent differences in sap flow were found between FACE and control wheat on either a diurnal or a seasonal basis. When calculated over 2-week intervals, integrated cotton sap flows were similar to cumulative evapotranspiration obtained via soil water depletion data (Hunsaker *et al.*, 1994a).

The effects of elevated CO_2 on sap flow transpiration estimates of individual wheat tillers were variable and confounded by spatial variation of soil water distribution from the buried microirrigation line (Senock *et al.*, in press). Daily differences in transpiration between CO_2 treatments were small and often nonsignificant. However, the cumulative water use (on a ground area basis) by well-watered FACE plants was 7–23% less than that by control plants during heading and early grain fill.

4. Evapotranspiration Estimates from Soil Moisture Depletion Cumulative evapotranspiration (ET_c) was estimated from temporal changes in soil water contents within the rooting zone of the plants (Hunsaker *et al.*, 1994a,b). The effect of CO_2 on ET_c was not statistically significant for any year of our study for either cotton or wheat. However, when ET_c of the WET treatment was averaged over both years of the wheat experiments, it was 4.5% less in FACE than in controls. In the DRY treatment the CO_2 effect was reversed, with the ET_c of FACE averaging 3% higher than that of control (most likely because the larger plants in the FACE DRY treatment were able to exploit a larger volume of soil than control DRY plants).

5. Evapotranspiration Estimates from the Canopy Energy Balance The effects of CO_2 on ET_c of crops under well-watered conditions were also investigated by calculating the latent energy exchange of the canopy as a residual in the surface energy balance. Kimball *et al.* (1994a) concluded that ET_c differences between CO_2 treatments in the FACE cotton study were within the uncertainties associated with measuring net radiation (R_n). By using improved R_n measurement techniques during the wheat experiments, daily totals of latent heat flux and ET_c of plants in the elevated CO_2 treatment were shown to be 8% lower than in controls in 1992–1993 and 11% lower in 1993–1994 (Kimball *et al.*, 1994b).

6. Ecosys-Modeled Evapotranspiration in Wheat Energy exchange between the atmosphere and wheat canopy in the FACE experiments was also exam-

ined by using a mathematical model, ecosys, which predicts the hourly growth and consumption of water by a wheat crop (Grant *et al.*, 1995). The overall net effect of increasing CO₂ to 550 from 370 $\mu\text{mol mol}^{-1}$ was to reduce simulated, season-long transpiration under well-watered conditions by 7%. This value is comparable to the 5% reduction in seasonal evapotranspiration using soil water balance (Hunsaker *et al.*, 1994b), the 10% average reduction estimated from daily measurements of latent energy exchange (Kimball *et al.*, 1994b), and the 7–23% average reduction in transpiration measured during peak leaf area with sap flow gauges (Senock *et al.*, in press). However, these observations and predictions for the canopy contrast sharply with the 38% reduction in conductance measured using single leaf cuvette systems (Garcia *et al.*, 1995). In the ecosys simulation and processes measured on the community scale, CO₂-mediated rises in canopy temperature and early season increases in GLAI with elevated CO₂ appear to eliminate or moderate the transpiration effects observed at the leaf surface.

C. Growth and Yield Responses

1. Cotton Biomass, Leaf Area, and Fruit Production Deficit irrigation and elevated CO₂ had significant effects on the growth of cotton during each year of our study (Mauney *et al.*, 1992, 1994). Destructive plant samples obtained at intervals throughout the season showed that water stress significantly reduced total biomass and GLAI in the DRY treatments compared with the WET treatments (Fig. 3). Although cotton fruit production was also lower in the DRY treatments, harvest indices (defined here as the ratio of flower plus boll biomass to total biomass) were larger.

Exposure of cotton plants to higher CO₂ levels increased total biomass significantly compared to the ambient CO₂ treatment. It also increased the dry weight density and weight per unit length of cotton roots over the whole soil profile during the early vegetative and midreproductive developmental stages of growth (Rogers *et al.*, 1992; Prior *et al.*, 1994). The overall effects of elevated CO₂ on photosynthetically active components of the canopy were more varied and depended upon the degree of water stress to which the crops were subjected. In the DRY treatments, elevated CO₂ conferred a modest advantage on GLAI and light interception during most of the season (Pinter *et al.*, 1994). An advantage was also present during the first part of the growing season in the WET treatments. We believe that these early differences in GLAI had cumulative effects on productivity that were important in developing a bigger plant having a larger photosynthetic apparatus and higher fruiting potential under the elevated CO₂ conditions.

Resource partitioning by the cotton plants during 1991 is shown in Fig. 4. In early July, when the plants were just starting to flower profusely, stem tissue composed about 50% of the total plant biomass in the FACE treatment compared with about 45% for controls. At the same time, the

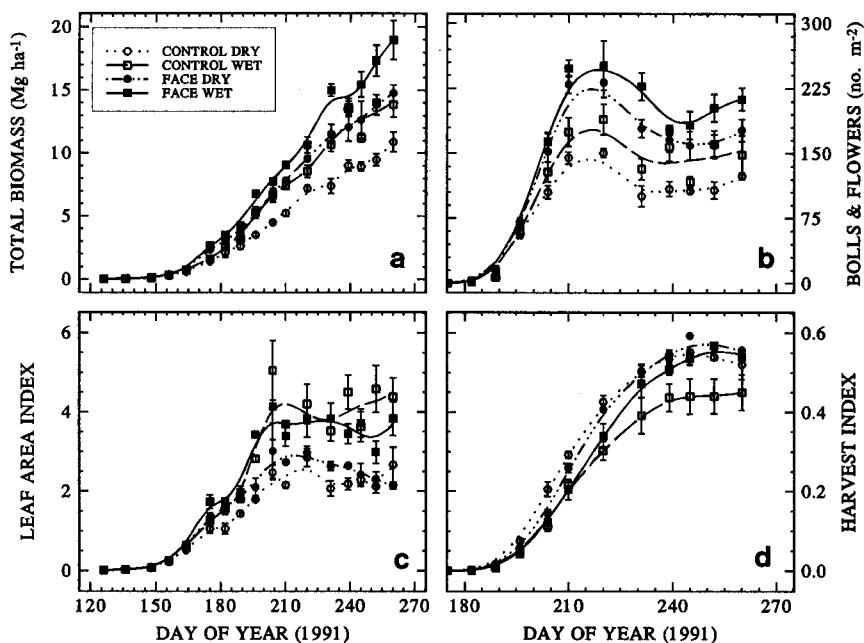


Figure 3 Treatment comparisons of total cotton biomass (Mg ha^{-1} , includes most tap roots but not small lateral and fine roots), boll and flower density (no. m^{-2}), green leaf area index ($\text{m}^2 \text{m}^{-2}$), and harvest index (boll biomass divided by total biomass) obtained from 17 weekly samples of cotton in the 1991 FACE experiment. Data are the means of four replicates per treatment combination. Bars show ± 1 standard error.

green leaf component in FACE was ca. 37% of the total versus 40% in controls. From that point until the end of August, plants in all treatments translocated a proportionately larger share of photosynthate into maturing fruit, and the relative allocation of resources to stem and leaf tissues declined markedly. Stem and leaf biomass (on an absolute basis) continued to increase slightly during July and then leveled off for the remainder of the season. Despite similar sizes in the photosynthetically active biomass of their canopies, plants exposed to elevated CO_2 had a 25% higher light utilization efficiency than controls (Pinter *et al.*, 1994). We believe that this enabled FACE plants to initiate and sustain significantly more fruit (Fig. 3b) prior to cutout (a source-limited hiatus in flowering that normally occurs during August). Large differences between the harvest indices of FACE and control WET (Fig. 3d) may likewise be explained by a larger plant with increased sinks (fruit) that could benefit more from the fertilization effect of extra CO_2 late in the season. At the end of the season, the ratio between green and mature bolls rapidly declined in the DRY treatments because the recruitment of new fruit was limited by water stress.

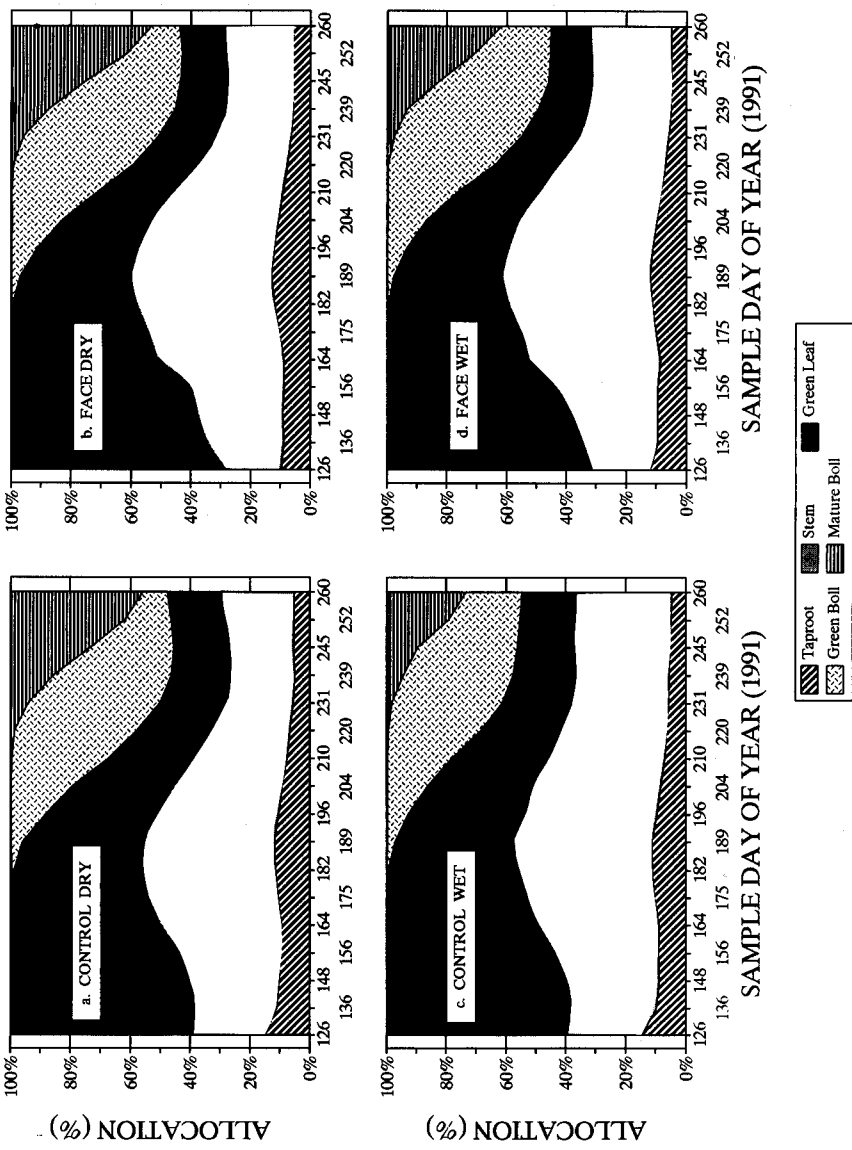


Figure 4 Allocation of biomass (expressed as a percentage of the total dry weight) to different cotton plant compartments in the 1991 FACE experiment. Data are shown for tap roots obtained when plants were pulled from soil, stems, green leaves, green fruit (bolls), and mature bolls (burr, seed, plus lint). Data are the means of four replicates per treatment combination that have been smoothed with three-term running average.

Although treatment-related differences in biomass allocation were not particularly evident in the partial tap root component of plants sampled at frequent intervals during the season (Fig. 4), Mauney *et al.* (1994) show a trend toward higher root to shoot ratios during boll development that was associated with FACE. The more precise root core studies of Rogers *et al.* (1992) and Prior *et al.* (1994) revealed that the cotton plant's belowground investment in total roots was increased significantly by elevated CO_2 .

2. Wheat Biomass, Leaf Area, and Head Production Seasonal trajectories of total biomass accumulation revealed relatively small CO_2 and irrigation effects and slow growth rates during the winter when temperatures were cool (Fig. 5). As temperatures warmed and PAR intensity and duration increased, biomass increased exponentially and the effects of elevated CO_2 and deficit irrigation became more noticeable. During this period, FACE plants grew at a faster rate than controls, with much of the difference attributed to increases in the biomass of stems and nascent reproductive

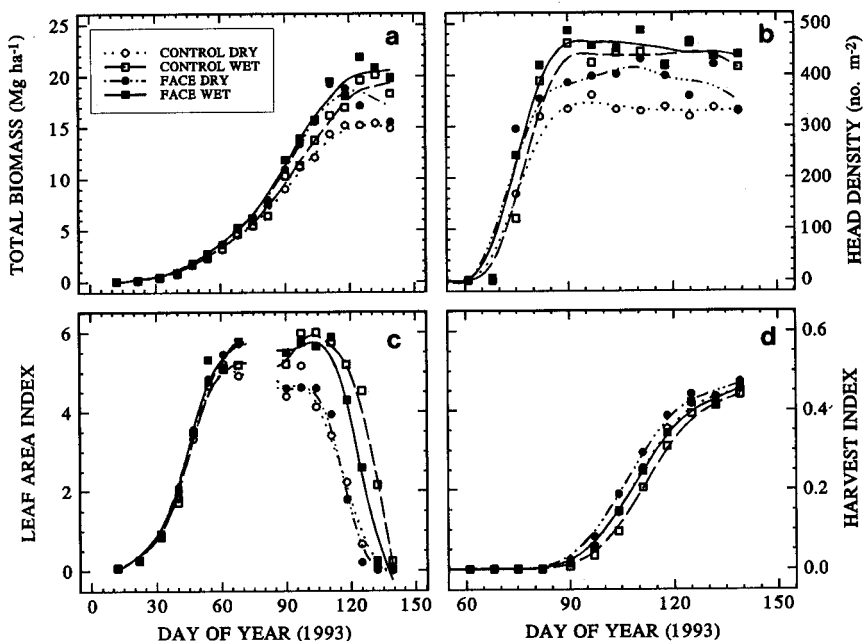


Figure 5 Treatment comparisons of total wheat biomass (Mg ha^{-1} , includes crown tissue but not roots), head density (no. m^{-2}), green leaf area index (GLAI, $\text{m}^2 \text{m}^{-2}$), and harvest index (grain biomass divided by total biomass) obtained from 18 weekly samples of wheat in the 1993 FACE experiment. GLAI data were not obtained for plants on sample days 75 and 82. Data are means of four replicates per treatment combination.

tissues (Fig 6). The accelerated rate of development with elevated CO₂ was a biologically significant finding. We observed, for example, that plants exposed to elevated CO₂ reached anthesis about 2 days sooner than controls, regardless of irrigation treatment. Furthermore, wheat plants in the FACE WET treatment matured 1 week earlier than plants in the control WET treatment. In the DRY treatment, grain matured at about the same time in FACE and control plants. The effect of CO₂ on developmental rate during grain fill may have been suppressed by the improved water status of FACE DRY plants compared with controls.

The processing protocol for the weekly destructive samples provided wheat head numbers and biomass values as soon as awns were visible above the ligule of the flag leaf. These data show that the heads appeared ca. 5 days earlier under FACE (Fig. 5b). After about 2 weeks, most of the heads had emerged in all of the treatments, and numbers stabilized during the grain filling period. Elevated CO₂ appeared to ameliorate the effects of water stress on final head density in the DRY irrigation treatment, but did not affect final head density under well-watered conditions.

GLAI expanded rapidly during February 1993, attaining 2.5 by the end of tillering and reaching maximum levels of more than 5 prior to the booting stage in early-March (Fig 5c). Processing delays spoiled our GLAI data during the 2-week period in March when plants were just beginning to show symptoms of water stress. However, treatment effects were very evident during the second half of the season. Water stress during early grain fill reduced GLAI in the DRY treatment to about 80% of levels observed in the WET treatment. Later in the season, differences among treatments in the senescence of leaves paralleled the pattern of grain maturity and provided a partial explanation for changes in canopy photosynthesis that were discussed earlier. Leaf senescence occurred 2–3 weeks sooner in the DRY treatments than it did under well-watered conditions. Wheat canopies exposed to elevated CO₂ senesced about 1 week earlier than controls.

The evolution of harvest index (HI) (Fig. 5d) and changes in the allocation of biomass to chaff and grain (Fig. 6) show a close correspondence with temporal patterns of head emergence, grain fill, and phenology. Giuntoli and the FACE Team (unpublished data) found that the HI increase rate was independent of CO₂ and irrigation treatment effects during its linear phase. Similar to our findings in cotton, the end of season HI of wheat was greater with water stress and elevated CO₂.

3. Cotton Lint Yields Final marketable yields from the control WET cotton plots (Fig. 7a) met or exceeded statewide averages during each year of our FACE experiments (Mauney *et al.*, 1992, 1994). Lint production was not significantly affected by irrigation treatment in either 1990 or 1991, a result that was partly due to compensatory increases in the harvest index of plants

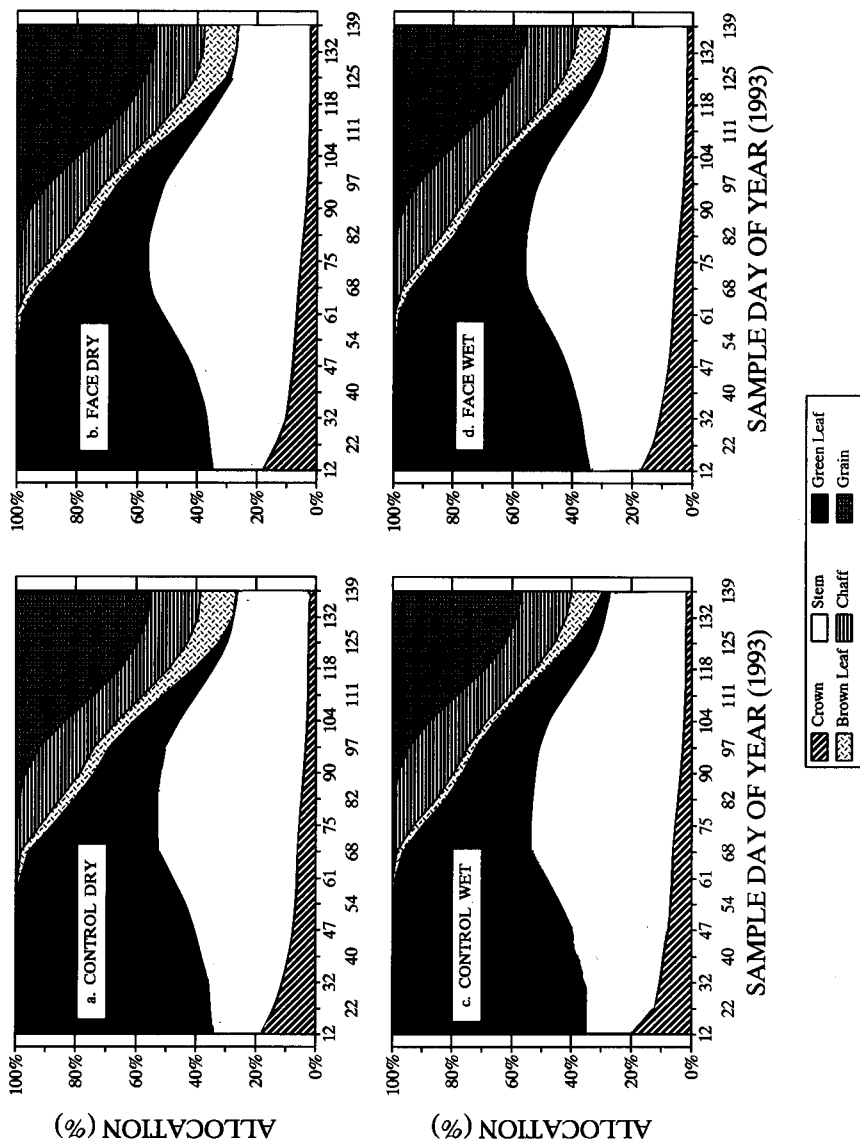


Figure 6 Allocation of biomass (expressed as a percentage of total dry weight) to different wheat plant compartments in the 1992–1993 FACE experiment. Data are shown for crowns (belowground stem and crown tissue without roots), aboveground stems, green leaves, brown or yellow leaves, chaff (nongrain portion of the head), and grain. Data are the means of four replicates per treatment combination that have been smoothed with a three-term running average.

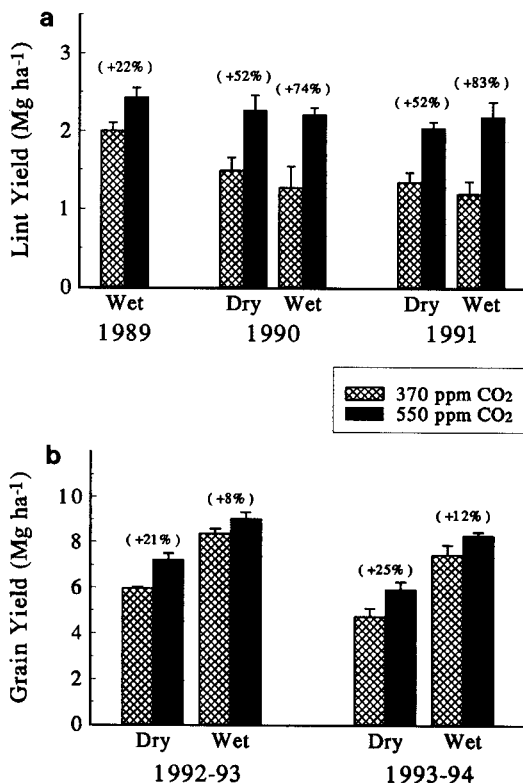


Figure 7 Final marketable yields of cotton lint (a) and wheat grain (b) on a dry weight basis (Mg ha⁻¹) grown in the FACE facility at MAC. [For reference: 1 Mg lint ha⁻¹ = 1.86 standard (480 lb.) cotton bales acre⁻¹, and 1 Mg dry grain ha⁻¹ = 16.7, 60-lb. bushels acre⁻¹ at 12% moisture content.] Hats on bars show 1 standard error above the mean of four replicates. Enhancement effects of the 550 $\mu\text{mol mol}^{-1}$ CO₂ (FACE) treatment compared to ambient CO₂ (controls) are shown in parentheses.

in the DRY treatment and partly due to the relatively minor water stress to which the plants were actually exposed. Elevated CO₂ caused significant increases in lint yield that were proportionately greater than end of season biomass differentials [see the chapter in this volume by Amthor and Koch (1996)]. The CO₂-related yield enhancement in the WET irrigation treatment was 60% when averaged over the 3 years of the study. Elevated CO₂ stimulated lint yields from the DRY irrigation treatment by 52% in 1990 and 1991.

4. Wheat Grain Yields. Final yields of spring wheat in our FACE studies were obtained from relatively large (~20 m²) undisturbed areas within each of

the subplots. Yields measured for plants grown under well-watered conditions were very high (Fig. 7b). In fact, plants in the control WET treatment during the 1992–1993 season produced 40% more grain than the county average for spring wheat and 10% more than the potential yields for the same cultivar. The effects of treatments on yield were very consistent during both seasons. Grain yields in the DRY treatment were 24 and 32% lower than the well-watered treatments during the first and second years, respectively. After our experiences with cotton, the modest effect ($\sim 10\%$) of CO_2 on final grain yield in the WET treatment was somewhat unexpected. However, when yields were reduced by deficit irrigation, the stimulatory effect of CO_2 doubled. Analyses of variance revealed that the differences between CO_2 treatment means were statistically significant at $p = 0.037$ in 1992–1993 and $p = 0.062$ in 1993–1994.

The CO_2 -related stimulation of growth that we observed using FACE technology compared favorably with results from open-top chamber studies conducted in the same field as our FACE experiment in 1992–1993 [A. Frumau and H. Vugts as cited by Kimball *et al.* (in press)]. However, our findings for a non-water-stressed, wheat agrosystem in an open-field experiment showed a smaller CO_2 response than has been reported for wheat grown in chamber experiments [see the chapter in this volume by Dijkstra *et al.* (1996) and reviews by Kimball (1983), Poorter (1993), and Idso and Idso (1994)].

Accelerated rates of phenology and postanthesis canopy senescence were surprising phenomena that occurred with elevated CO_2 during both years of our wheat study. Plants in the FACE WET treatment had grain ready for harvest about 1 week before their control counterparts. One possible factor influencing the rates of development may have been related to temperature. For example, Wiegand and Cuellar (1981) showed that the duration of grain filling in wheat was reduced by about 3 days for every 1°C increase in ambient air temperature above 15°C . In our study, however, elevated levels of CO_2 increased average canopy temperatures by an observed 0.6°C over the entire season (Kimball *et al.*, 1994b), probably because of the reduction in g in the FACE treatment. Thus, it appeared that tissue temperature by itself did not completely account for the shortened grain filling period. Furthermore, higher ambient temperatures were usually associated with decreased kernel weights (Wardlaw *et al.*, 1980; Wiegand and Cuellar, 1981). Yet in both FACE wheat experiments, kernels from the FACE WET treatment averaged ca. 6% larger than those from control WET. At present we are unable to explain these results, but expect that accelerated developmental rates will provide important clues explaining wheat plant response to elevated CO_2 . Regardless of the cause for the decreased grain filling period, the highly deterministic growth patterns in wheat permitted ambient CO_2 treatments to play catch-up at the end of the season, narrowing

the differential between the CO₂ treatments in final yields, especially in the WET treatments.

5. Comparison of CO₂ Effects on Cotton and Wheat A crop's response to elevated CO₂ is mediated by ambient temperature (Idso *et al.*, 1987; Long, 1991) and by its ability to develop additional sinks for the accumulation of greater photosynthetic products (Mauney *et al.*, 1978; Stitt, 1991). We thus expected cotton and wheat to be good plant models for our FACE research because they are grown during different seasons of the year and represent extremes in potential sink capacity. Our indeterminate example, cotton, is a warm-season, woody shrub that continues to increase in size and produce fruit as long as growing conditions remain favorable. Although a perennial crop, it is normally cultivated as an annual to minimize problems from overwintering insects. By comparison, wheat is strongly determinate. It is an annual plant with rigid genetic constraints on the rate and extent of sink growth. It also is adapted to grow during cooler temperatures than cotton. Our results showed that the net photosynthesis of both of these crops responded similarly to supraambient CO₂ concentrations as provided by FACE. However, the seasonal trends in biomass and GLAI and the end of season yields revealed important distinctions between the two.

The most important difference between the two crops was related to the effects of CO₂ on the development and persistence of GLAI during the season. CO₂ enhancement of GLAI was greatest for DRY cotton (Fig. 8a), where water stress prevented plants from attaining 100% canopy cover and plants were not source-limited by incident light. The large GLAI coupled with greater light use efficiency explained the greater CO₂-related stimulation of biomass and final lint yield in cotton growing in the DRY treatment. In WET cotton (Fig. 8c), CO₂ effects on GLAI and biomass were more variable. Even though CO₂ enrichment was associated with small (10–20%) reductions in GLAI during the second half of the season, the canopy remained green and CO₂ stimulation of biomass continued until harvest in mid-September.

In wheat, however, the patterns were significantly different (Figs. 8b and 8d). CO₂ caused a small, yet consistent advantage in GLAI during the first part of the season. This disappeared during midseason as the final leaf emerged and expanded. Then, midway into the grain filling period, the wheat leaves in the FACE treatment began to senesce at a much faster rate than controls. The final result was that, during grain filling, the green leaf area duration in FACE was much reduced compared with controls. The CO₂ enhancement factor for biomass gradually increased during the season, reaching a peak around day of year 104 in the WET treatment and about 1 week later in the DRY. Then, as leaf senescence was accelerated in CO₂

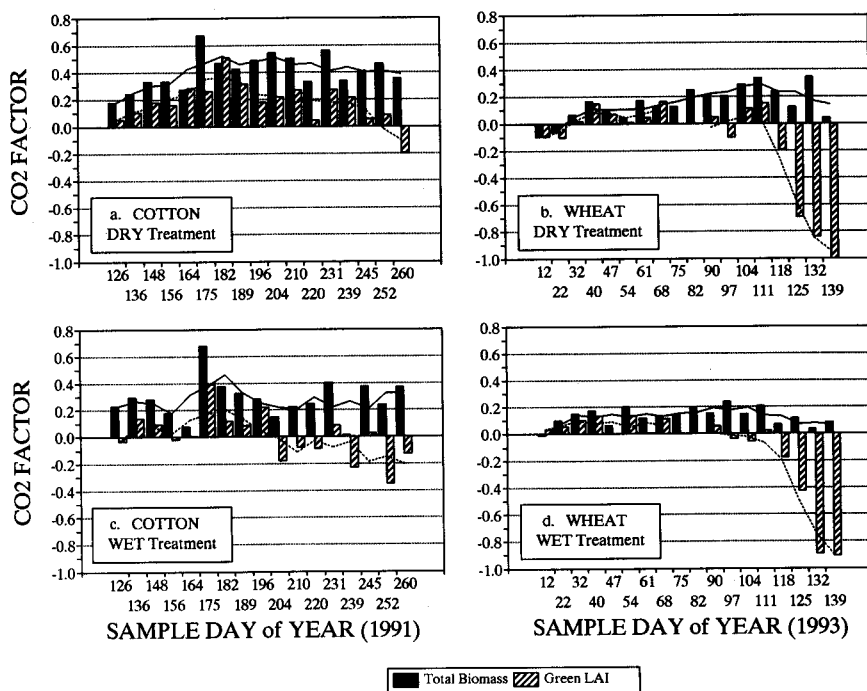


Figure 8 CO₂-related enhancement [(FACE - control)/control] of biomass and green leaf area index (GLAI) for cotton in the 1991 FACE experiment (Figs. 8a and 8c) and wheat in the 1992–1993 FACE experiment (Figs. 8b and 8d). Bars show CO₂ enhancement on the indicated sample day; lines show a three-term running average.

enriched canopies, biomass in control treatments increased relative to the FACE treatments. This caused the CO₂ enhancement factor for biomass to decline in both water treatments. These data support a hypothesis that the determinate growth patterns of wheat render it sink-limited when exposed to supraambient CO₂ levels. They also offer a plausible explanation for the minimal effects of CO₂ on final grain yield under well-watered conditions.

D. Light and Water Utilization Efficiencies

Cotton developed a larger leaf canopy earlier in the season when grown under supraambient CO₂ conditions. This resulted in 15–40% higher absorption of PAR (APAR, MJ m⁻² day⁻¹) during the first half of the season (Pinter *et al.*, 1994), an important factor affecting potential yield in a crop with indeterminate fruiting behavior. Light use efficiency (LUE) was used to quantify season-long responses of the cotton canopy to CO₂ and irrigation

treatments. Defined as dry biomass ($\text{g m}^{-2} \text{ day}^{-1}$) produced per unit of APAR, LUE was computed for each plant sampling interval and then averaged across the season (Pinter *et al.*, 1994). Results showed that this parameter varied significantly from year to year and reflected the effects of CO₂ and irrigation (Fig. 9a). Elevated CO₂ resulted in an average 26% increase in LUE for the WET irrigation treatment and a 21% increase for the DRY treatment.

Soil water depletion studies showed very similar seasonal ET_c from FACE and control cotton canopies, although marketable yields were increased by elevated levels of CO₂. As a consequence, water use efficiencies [WUE, defined here as kilograms of lint produced per cubic meter of water used

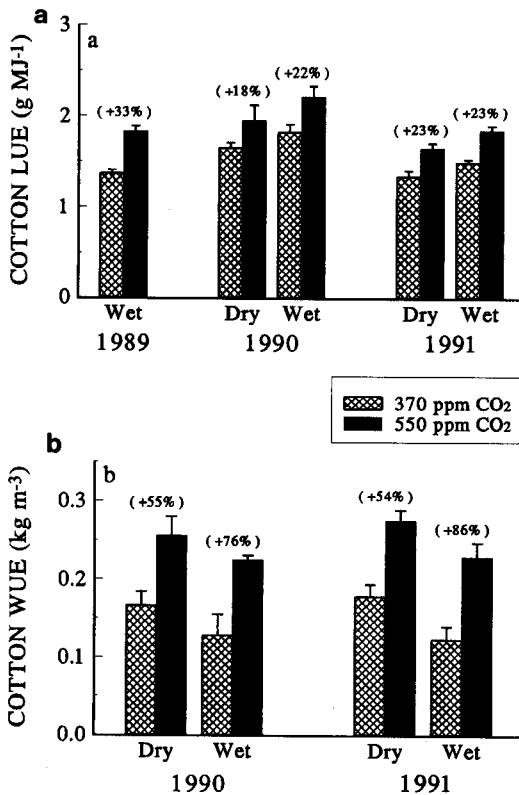


Figure 9 Cotton light use efficiency (panel a, g dry biomass per MJ absorbed PAR) and water use efficiency (panel b, kg lint per m³ water) measured during the FACE experiments. Cumulative water use was not measured in 1989. Hats on bars show 1 standard error above the mean of four replicates. Enhancement effects of the 550 $\mu\text{mol mol}^{-1}$ CO₂ (FACE) treatment compared to ambient CO₂ (controls) are shown in parentheses.

by the crop (ET_c) during the season] followed the trends in yield and were significantly higher for FACE cotton than for controls (Fig. 9b).

Light and water use efficiencies of wheat grown in FACE are currently being analyzed for comparison with cotton data.

E. Soil Carbon Budget and Sequestration

A rigorous budget of soil carbon has not yet been attempted for our experiments. However, analyses of soil and root samples are continuing, and a few preliminary results are available. First of all, CO_2 -related stimulation of total root growth was consistent with observed increases in aboveground biomass [for cotton, see Fig. 3 and also Mauney *et al.* (1994); for wheat, see Fig. 5]. Elevated CO_2 caused about a 40% increase in cotton roots (Prior *et al.*, 1994) and about a 20% increase in wheat roots (Wechsung and Wechsung, personal communication). Such increases represent greater net input of organic carbon to the soil and, thus, would be expected to influence the rates of many different soil processes.

This indeed seems to be the case. In the cotton experiments, for example, Runion *et al.* (1994) observed higher microbial activities with elevated CO_2 . Supraambient CO_2 also increased soil respiration by an average of 12% during the 1990 and 1991 cotton seasons (Nakayama *et al.*, 1994) and by 19% during the 1992–1993 wheat experiment (Nakayama, 1993). Since these fluxes of CO_2 at the soil surface were averages of measurements obtained during and shortly after the growing season, they do not account for carbon losses that may have occurred between seasons. Notwithstanding, the soil respiration data from cotton imply a net gain in soil C under FACE, while the preliminary data from wheat suggest that soil C inputs and outputs were more balanced.

Support for this hypothesis in cotton comes from two independent studies that were conducted after cotton had been grown under the FACE treatment for several consecutive seasons. In the first study, Wood *et al.* (1994) observed an overall tendency for soil cores taken from the FACE treatment to have higher total C contents than controls, but the differences were statistically significant only for the 0.1–0.2-m depth increment. In the second study, Leavitt *et al.* (1994) used a sensitive carbon isotope technique that was possible because the petrochemically derived CO_2 used for FACE enrichment had different $^{13}C/^{12}C$ and $^{14}C/^{12}C$ ratios than current ambient air. Their analyses showed that about 10% of the organic carbon in the FACE soil in 1991 had been derived from the previous 3 years of FACE treatment of the cotton. Moreover, much of this increased C in the soil was in a recalcitrant 6 N HCl resistant fraction, suggesting that elevated CO_2 can indeed increase the sequestration of C in the soil and may mitigate some of the projected rise in atmospheric CO_2 concentration.

IV. Summary and Future Investigations

Growth and yield responses of plants to elevated levels of atmospheric CO₂ have complex interactions with temperature, water, and nutrients that are difficult to quantify by using conventional approaches with closed or open-top chambers. As a result, these responses have not yet been adequately accounted for in simplistic models predicting world food production in the future (viz., Rosenzweig and Parry, 1994). Our series of FACE studies has provided the first interdisciplinary insight into the full-season responses of several important agricultural crops to elevated CO₂ under natural, open-air, field-scale conditions. We believe that our research results will provide unique validation opportunities for simulation models that will be capable of extrapolating the potential impacts of global change in a more realistic fashion [Wall *et al.*, 1994; see the chapter in this volume by Amthor and Loomis (1996)].

Several important conclusions regarding the effects of elevated CO₂ on plants can be drawn from the observations of photosynthesis, transpiration, growth, and yield for cotton and wheat in the FACE experiments.

- In the absence of nutrient limitations, enrichment to 550 $\mu\text{mol mol}^{-1}$ CO₂ caused 20–30% increases in net photosynthesis at individual leaf and canopy levels.
- Midseason accumulation of biomass under the FACE treatment increased from about 20% in wheat to about 40% in cotton.
- CO₂ stimulation of final yields and end of season biomass appears to depend on temperature and the availability of expanding sinks for extra photosynthate.
- Indeterminate crops such as cotton respond more favorably to increased levels of CO₂ than determinate crops such as wheat.
- Photosynthesis, growth, and final grain yields of spring wheat were all stimulated more by elevated CO₂ under water stress conditions than under well-watered conditions.
- Despite significant decreases in stomatal conductance at elevated CO₂, compensatory increases in GLAI resulted in no differences in transpiration per unit ground area in cotton, but there was a slight decrease in wheat.

Although water is perhaps the most important limiting factor affecting the productivity of crops in intensively managed lands, agriculture in less developed regions and plants in most natural ecosystems are additionally restricted by nutrient availability. The consensus of participants in the San Miniato GCTE Workshop in Italy (October, 1993) was that reduced nutrients were important in controlling plant response to CO₂ and probably explained some of the differences that have been observed between man-

aged agricultural systems and more complex, N-limited natural ecosystems. FACE appears to be the most appropriate technology for probing this hypothesis on the ecosystem scale (McLeod, 1993; Schulze and Mooney, 1993). It also confers an "economy of scale" compared with controlled-environment or open-top chambers that makes the cost per unit of scientific opportunity attractive for large, multidisciplinary research projects (Kimball, 1992; Hendrey *et al.*, 1993b).

The logical extension of the research reported here will be to use FACE to determine the CO₂ response of wheat when nutrients are limiting. Beginning in December 1995, wheat will be exposed to ambient and elevated CO₂ and to two levels of soil fertility. Research emphasis will be placed on biogeochemical soil processes, but work will continue on wheat physiology, development, biomass partitioning, and water use. Another area that needs urgent attention is the interaction between CO₂ and atmospheric pollutants such as ozone, which threaten grain productivity in northern, midlatitude agricultural regions (Allen, 1989; Chameides *et al.*, 1994).

Results from such studies are expected to provide meaningful data on the strength of the "CO₂ fertilization effect" on natural terrestrial ecosystems. They will also offer realistic insight into the adequacy of future world food production.

Appendix

Measurements and participants in the FACE experiments with cotton and wheat at the Maricopa Agricultural Center between 1989 and 1994. Acronyms identifying the affiliations of scientists are listed alphabetically at the end of the table.^a

Experimental parameters	Cotton (1989, 1990, 1991)	Wheat (1992–1993, 1993–1994)
SOIL PROPERTIES		
Carbon isotope analysis	S. Leavitt (TRL); E. Paul (MSU)	S. Leavitt (TRL)
Chemistry	G. Huluka (TU); R. Rauschkolb, H. Cho (MAC); C. W. Wood, H. Rogers, G. Runion, S. Prior (NSDL)	R. Rauschkolb, H. Cho (MAC)
Concentration and fluxes of CO ₂ (soil respiration)	F. Nakayama (WCL)	F. Nakayama (WCL)
Decomposition of plant residue	—	D. Akin (RRC); A. Ball (UE); H. W. Hunt, S. Smith (GSU)
Fluxes of CH ₄ and N ₂ O	—	F. Nakayama (WCL); A. Mosier (SPNR)
Hydraulic conductivity, water retention curve, texture, bulk density	B. Kimball, B. Alexander (WCL); D. Post, A. Warrick (UA); F. Whisler (MISS)	G. Wechsung (HU); F. Adamsen, G. Wall, D. Hunsaker, B. Kimball (WCL)
Mineralization	C. W. Wood, H. Rogers, G. Runion, S. Prior (NSDL)	H. Rogers, S. Prior (NSDL)
Rhizosphere microbes	G. Huluka, R. Ankuma (TU); G. Runion, E. Curl, H. Rogers (NSDL)	—
Volumetric water content	D. Hunsaker (WCL)	D. Hunsaker (WCL)
AGRONOMY		
Population density, biomass components, leaf area, organ counts, heights, yield	J. Mauney (WCRL)	P. Pinter (WCL); A. Giuntoli, F. Miglietta (IATA)
Root biomass and density	H. Rogers, S. Prior (NSDL)	G. Wechsung (HU); F. Wechsung (PIK); G. Wall (WCL)
ANATOMY		
Biomechanical properties of straw	—	H. Rogers, S. Prior (NSDL)
Leaf anatomy	—	D. Akin (RRC)
Stomatal density	S. Malone (GSU)	M. Estiarte, J. Peñuelas (IRTA); A. Giuntoli, F. Miglietta (IATA)

Experimental parameters	Cotton (1989, 1990, 1991)	Wheat (1992–1993, 1993–1994)
BIOCHEMISTRY		
Carbohydrate storage	D. Hendrix (WCRL)	D. Hendrix (WCRL)
C, N in tissues	G. Huluka, D. Hileman, P. Biswas (TU)	F. Wechsung (PIK); G. Wechsung (HU); F. Adamsen (WCL); D. Akin (RRC); T. Sinclair (APL)
Digestibility	D. Akin (of sudangrass planted among cotton, RRC)	D. Akin (RRC)
Lint or grain quality	J. Mauney (WCRL)	C. Morris (WWQL)
Phenolics, antioxidants, secondary compounds	—	M. Estiarte, J. Peñuelas (IRTA); L. Jahnke (UNH); S. Long (UE); M. Badiani, A. Paolacci (UT); D. Clark (ASU)
EVAPOTRANSPIRATION (ET)		
Eddy correlation	—	A. Fruman, M. Groen, H. Vugts (FUA); Y. Harazono (NIAS)
ET (energy balance and Bowen ratio)	B. Kimball (WCL); D. Fangmeier, M. Vitayew, A. Matthias (UA)	B. Kimball (WCL); A. Fruman, M. Groen, H. Vugts (FUA)
Plant transpiration (stem flow)	W. Dugas, M. Heuer (BRC)	R. Senock, J. Ham (ETL)
Soil evaporation	B. Kimball, M. Johnson (WCL)	B. Kimball, M. Johnson (WCL)
Soil water balance	D. Hunsaker (WCL)	D. Hunsaker (WCL)
MORPHOLOGY		
Organ development, phenology	J. Mauney (WCRL)	G. Wall (WCL); A. Li, A. Trent (UI); M. Bauer, J. Gräfe, P. Michaelis, E. Blum, F. Wechsung (PIK)
PHYSIOLOGY		
Canopy CO ₂ flux (eddy diffusivity)	—	Y. Harazono (NIAS)
Canopy photosynthesis and resistance	D. Hileman, G. Huluka (TU); N. Bhattacharya (WCRL); R. Garcia (WCL)	R. Garcia (WCL)
Chlorophyll concentration	P. Pinter, S. Idso (WCL)	P. Pinter (WCL); F. Wechsung (PIK)
Head and awn photosynthesis	—	F. Wechsung (PIK); R. Garcia (WCL)

Intrinsic water use efficiency	H. Johnson (GSWR); E. Paul (MSU)	H. Johnson (GSWR); E. Paul (MSU)
Leaf fluorescence	J. Burke (PSWC); S. Long (BNL, UE)	S. Long (BNL, UE); A. Giuntoli (IATA)
Leaf photosynthesis, respiration, CO ₂ response, and stomatal conductance	D. Hileman (TU); L. Evans (MC); R. Garcia, S. Idso, G. Wall (WCL); N. Bhattacharya, D. Hendrix, J. Radin (WCRL)	R. Garcia, G. Wall (WCL); C. Osborne, S. Long (BNL, UE); M. Badiani, A. Paolacci (UT)
Leaf water potential, osmotic potential	N. Bhattacharya, J. Radin (WCRL); B. Kimball (WCL)	G. Wall, B. Kimball (WCL)
PAR interception and conversion efficiencies	P. Pinter (WCL)	P. Pinter (WCL); A. Frumau (FUA)
Photosynthetic acclimatization, leaf proteins, rubisco activity	—	G. Nie, S. Long (BNL, UE); A. Webber (CEEP); D. Hendrix (WCRL); J. Vu, L. H. Allen (PSP)
ENTOMOLOGY		
Arthropod populations	D. Akey, J. Mauney (WCRL); B. Miller, D. Byrne (UA)	D. Akey (WCRL); P. Pinter (WCL)
COMPARISONS WITH OTHER SYSTEMS		
Open-top chambers	—	A. Frumau, P. Jak, N. de Jong, H. Bleeksma, J. Rozema (FUA)
OTHER SPECIES		
FACE effects on barley growth, development, photosynthesis	—	M. Bauer, J. Grafe, F. Wechsung (PIK); G. Wall (WCL)
MICROMETEOROLOGY AND REMOTE SENSING		
Leaf, canopy, and soil spectral properties	P. Pinter (WCL)	P. Pinter, T. Clarke (WCL)
Leaf, canopy, and soil temperatures	P. Pinter, B. Kimball (WCL); D. Fangmeier (UA)	P. Pinter, B. Kimball, T. Clarke (WCL); A. Frumau, M. Groen, H. Vugs (FUA)
Solar, PAR, net radiation, soil heat flux, air and soil temperature profiles, vapor pressure, wind speed, precipitation	B. Kimball (WCL); P. Brown (UA)	B. Kimball (WCL); A. Frumau, M. Groen, H. Vugs, J. Worm (FUA); P. Brown (UA)
CULTURAL PRACTICES		
Cultivation, planting	J. Mauney (WCRL)	G. Wall, R. Garcia, P. Pinter, B. Kimball, R. LaMorte, B. Alexander (WCL)
Fertilization	J. Mauney (WCRL)	G. Wall, R. Garcia, R. LaMorte (WCL)
Irrigation timing and amounts	K. Lewin (BNL); J. Mauney (WCRL)	D. Hunsaker, R. LaMorte, P. Pinter (WCL)

Experimental parameters	Cotton (1989, 1990, 1991)	Wheat (1992–1993, 1993–1994)
FACE SYSTEM PERFORMANCE		
CO ₂ concentrations	K. Lewin, J. Nagy, G. Hendrey (BNL)	R. LaMorte (WCL); K. Lewin, J. Nagy, G. Hendrey (BNL)
CO ₂ flow dynamics	F. Lipfert, G. Alexander (BNL); L. H. Allen (PSP)	—
COMPUTER SIMULATIONS AND MODELING		
CO ₂ concentrations and fluxes	—	D. Suarez (SL)
Energy balance	J. Anthor (WCL, WHRC, LLNL); G. Wall, B. Kimball (WCL)	R. Grant (UAL); J. Anthor (WCL, WHRC, LLNL); T. Kartschall, S. Grossman (PIK)
Plant growth	J. Anthor (WCL, WHRC, LLNL); G. Wall, B. Kimball (WCL); S. Maas (CRS)	J. Anthor (WCL, UCD, WHRC, LLNL); R. Grant (UAL); L. A. Hunt (UG); T. Kartschall, S. Grossman, F. Wechsung (PIK); K. Kobayashi (NIAS); J. Müller (AAQ); N. Nikolov, W. Massmann (RMF); T. Sinclair (APL); A. Trent (UI); G. Wall, B. Kimball (WCL)

* Research group acronyms: AAQ, Abtelling Agro-ökosystemforschung Quedlinburg, Quedlinburg, Germany; APL, USDA, ARS, Agronomy and Physiology Laboratory, Gainesville, FL; ASU, Arizona State University, Department of Botany, Tempe, AZ; BNL, Brookhaven National Laboratory, Upton, Long Island, NY; BRC, Blackland Research Center, Texas Agricultural Experiment Station, Temple, TX; CEEP, Center for Early Events in Photosynthesis, Arizona, State University, Tempe, AZ; CRS, USDA, ARS, Cotton Research Station, Shafter, CA; CSU, Colorado State University, Natural Resource Ecology Laboratory, Boulder, CO; ETL, Evapotranspiration Laboratory, Kansas State University, Manhattan, KS; FUA, Free University of Amsterdam, Amsterdam, Netherlands; GSWR, USDA, ARS, Grassland Soil and Water Research Laboratory, Temple, TX; GSU, Georgia Southern University, Department of Biology, Statesboro, GA; HU, Humboldt University Berlin, Faculty of Agriculture and Horticulture, Berlin, Germany; IATA, Institute of Environmental Analysis and Remote Sensing for Agriculture, CNR, Firenze, Italy; IRTA, Institut de Recerca i Tecnologia Agroalimentaries, Barcelona, Spain; LLNL, Global Climate Research Division, Lawrence Livermore National Laboratory, Livermore, CA; MAC, University of Arizona, Maricopa Agricultural Center, Maricopa, AZ; MC, Manhattan College, Laboratory of Plant Morphogenesis, The Bronx, NY; MISS, Agronomy Department, Mississippi State University, Mississippi State, MS; MSU, Michigan State University, Department of Crop and Soil Sciences, East Lansing, MI; NIAS, National Institute of Agro-Environmental Sciences, Kannondai, Tsukuba, Japan; NSDL, USDA, ARS, National Soil Dynamics Laboratory, Auburn, AL; PIK, Potsdam Institute for Climate Impact Research, Potsdam, Germany; PSP, USDA, ARS, Plant Stress and Protection, Gainesville, FL; PSWC, USDA, ARS, Plant Stress and Water Conservation Research, Lubbock, TX; RMF, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO; RRC, USDA, ARS, Russell Research Center, Athens, GA; SL, USDA, ARS, U.S. Salinity Laboratory, Riverside, CA; SPNR, USDA, ARS, Soil and Plant Nutrition Research, Ft. Collins, CO; TRL, University of Arizona, Tree Ring Laboratory, Tucson, AZ; TU, Tuskegee University, Tuskegee, AL; UA, University of Arizona, Tucson, AZ; UAL, University of Alberta, Department of Soil Science, Edmonton, Alberta, Canada; UE, University of Essex, Department of Biology, Colchester, United Kingdom; UCD, University of California, Department of Agronomy and Range Science, Davis, CA; UG, University of Guelph, Crop Science Department, Guelph, Ontario, Canada; UI, University of Idaho, Plant, Soil and Entomological Sciences, Moscow, ID; UNH, University of New Hampshire, Department of Plant Biology, Durham, NH; UT, Università della Tuscia, Department of Biochemistry and Agrochemistry, Viterbo, Italy; WCL, USDA, ARS, U.S. Water Conservation Laboratory, Phoenix, AZ; WCRL, USDA, ARS, Western Cotton Research Laboratory, Phoenix, AZ; WHRC, Woods Hole Research Center, Woods Hole, MA; WWQL, USDA, ARS, Western Wheat Quality Laboratory, Pullman, WA.

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