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Sap flow measurements of transpiration from cotton grown under ambient and enriched CO_2 concentrations

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Abstract

Increasing atmospheric CO_2 concentration has many implications for agriculture and forestry, one of which is the effect it will have on transpiration (T). The objective of this work was to quantify T of cotton (*Gossypium hirsutum* L.) grown in the field under ambient (370 μmol mol^{-1}) and enriched (550 μmol mol^{-1}) CO_2 concentrations. Measurements were made in 1990 and 1991 at the Maricopa Agricultural Center, Arizona. Constant-power sap flow gauges were used to measure T. In 1990, three plants and in 1991, 10 plants were simultaneously instrumented with gauges in each of the CO_2 treatments. Leaf area of plants with gauges was measured. T measured by sap flow was compared with evapotranspiration (ET) calculated by water balance in 1990 and with T calculated by water balance in 1991. Soil evaporation was measured using microlysimeters in 1991, and was found to be essentially equal (approximately 0.8 mm day^{-1}, or about 10% of T) in the two CO_2 treatments. There were no consistent differences in leaf area of plants with gauges between the two CO_2 treatments. Sap flow, for periods from 15 min to 2 weeks, was not significantly different between the two CO_2 treatments in either year, except for a few days in 1990. In 1991, the coefficient of variation of daily sap flow across plants was the same (about 30%) for both CO_2 treatments throughout the year. The water balance ET (1990) and T (1991) were similar to sap flow in both years, and also showed no effect of CO_2 treatment. These results show that for this crop, grown under well-watered and high-fertility conditions, there was no effect of CO_2 on T, on a per unit ground area or per plant basis. These results are relevant for assessing the effects of increasing atmospheric CO_2 concentrations on transpiration by cotton.

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1. Introduction

Increases in atmospheric CO_2 concentration during the past 125 years (Keeling et al., 1982) and increases projected for the next 50 years (Trabalka et al., 1986) have had and will have many implications for agriculture and forestry. One important consequence is the effect increasing atmospheric CO_2 concentrations will have on transpiration (T).

Decreases in leaf T per unit leaf area (Kimball and Idso, 1983; Goudriaan and Unsworth, 1990) or leaf stomatal conductance (Morison, 1985, 1987; Nederhoff, 1992; Harley et al., 1992; Nederhoff et al., 1992) caused by increasing CO_2 concentrations are well documented. There are substantial complications, however, when one tries to scale up from these leaf-level responses, generally measured on potted plants in growth chambers or greenhouses, to the response of plants in a field grown under enriched CO_2 concentrations for an entire growing season (Morison, 1993; De Bruin and Jacobs, 1993). For example, there may be large effects in the field associated with increased leaf area (Kimball, 1983; Mauney et al., 1994) or plant temperatures (Idso et al., 1987; Kimball et al., 1992; Nederhoff et al., 1992) under higher CO_2 concentrations, or effects associated with the possible non-representative response of plants in pots (Bazzaz and McConnaughay, 1992; McConnaughay et al., 1993).

Data on the consequences of increasing atmospheric CO_2 concentration on T are needed to evaluate accurately the direct effects on plants (e.g. plant water use efficiency (Kimball and Idso, 1983)) and to validate models that simulate plant response to increasing CO_2 concentrations (e.g. Wall et al., 1994). Much of the experimental field-work on the effects of increasing CO_2 concentration on evapotranspiration (ET) has shown the effects to have been small (e.g. Jones et al., 1985; Chaudhuri et al., 1986, 1990; Baker et al., 1990), especially relative to effects on growth (Allen, 1990).

An experiment was conducted in Arizona using a free-air CO_2 enrichment (FACE) facility conceived to evaluate the effects of increasing CO_2 on plants in a typical field setting, and to evaluate the terrestrial plant feedback regulation on the rate of change of atmospheric CO_2 (Hendrey and Kimball, 1994). The current work centered on the first of these objectives. The specific objective of this work was to quantify T of cotton grown in the field under ambient and enriched atmospheric CO_2 concentrations.

2. Methods

Measurements were made in 1990 and 1991 at the Maricopa Agricultural Center (33.07°N,111.98°W), near Maricopa, Arizona. Annual precipitation averages 200 mm. The soil is a reclaimed Trix clay loam (fine-loamy, mixed (calcareous), hyperthermic Typic Torrifluvents).

2.1. Experimental design and crop management

Details on the experimental design and crop management were presented by

Mauney et al. (1994). Briefly, cotton (*Gossypium hirsutum* L. cv. 'Deltapine 77') was sown on 23 April 1990 and 16 April 1991 in east–west rows of 1.0 m width. Plant population was established at 10 plants m^{-2} by thinning and transplanting. Crops were harvested in September in both years. Four replicates were established of a full-season, daytime exposure to two CO_2 concentrations (ambient at 370 μmol mol^{-1} (Nagy et al., 1994), termed control, and enriched at about 550 μmol mol^{-1}, termed FACE). Each replicate was contained in a ring of 23 m (1990) or 25 m (1991) diameter. Replicates 1 and 2 were used in this study. Details on the procedures for CO_2 enrichment and control of CO_2 concentration have been presented by Lewin et al. (1994) and Nagy et al. (1994), respectively.

Sap flow measurements were made on cotton plants grown under full irrigation (the 'wet' treatment; Mauney et al., 1994). A total of approximately 1300 mm and 1000 mm of irrigation and precipitation was applied in 1990 and 1991, respectively. In 1990, total growing season precipitation was 125 mm, whereas in 1991 it was 41 mm.

2.2. Sap flow gauges

Given the number and size of replicates, the use of lysimeters or micrometeorological methods for measurement of ET in both CO_2 treatments was inappropriate because of the cost and fetch requirements, respectively. Constant-power sap flow gauges (Baker and Van Bavel, 1987), which measure the mass flow rate of water in an individual plant, were, however, an appropriate method. The mass flow can be considered equal to T for plants of the size used in the experiment, especially for periods of more than 1 h. The method has been shown to be accurate for several economically important plants (Sakuratani, 1981, 1984; Ham and Heilman, 1990), including cotton (Baker and Van Bavel, 1987; Dugas, 1990b; Ham et al., 1990). It has the advantages of providing an accurate, integrated measurement for the whole plant, having a low cost and a simple yet theoretically sound basis, and being appropriate for measurements in small plots (Dugas, 1990a). For field-scale estimates of T (e.g. Sakuratani, 1987), however, the possible large plant-to-plant variability of T (Dugas, 1990b) may require many plants to be instrumented to obtain a representative value.

The mass flow of water for individual cotton plants was calculated from the heat balance of a stem to which a known, constant heat input was applied. Sap flow gauges for stems of 10–19 mm in diameter were used (Models SGA10, SGA13, SGB13, SGA16, SGB16, and SGB19; Dynamax, Inc., Houston, TX). T was calculated from the following equation:

$$\mathrm{T} = \frac{P - K_{st} A[(\Delta T_b + \Delta T_a)/\Delta x] - K_g E}{C \Delta T_{ba}} \quad (1)$$

where P is measured input power (W), K_{st} is stem thermal conductivity (W m^{-1} K^{-1}), A is stem area (m^2), ΔT_a and ΔT_b are vertical temperature differences (K) above and below the heater, respectively, Δx is distance (m) between the two junctions above and below the heater, K_g is a gauge factor (W V^{-1}) representing the radial power loss, per volt, through the gauge when T = 0, E is voltage (V) of a thermopile mounted on the outside of a heater which encircles the stem, C is specific heat capacity (J g^{-1} K^{-1})

of the xylem sap, and ΔT_{ba} is temperature difference (K) across the heater. The second and third terms in the numerator of Eq. (1) are losses associated with vertical heat conduction along the stem and radial heat conduction outward through the gauge, respectively. After attachment to a stem, gauges were covered with 'cling film' for waterproofing and with aluminum foil and foam, around both the gauge and stem sections above and below the gauge, to reduce externally induced temperature gradients.

P was varied from 0.2 to 0.4 W, depending upon gauge size, and K_{st} was assumed to be 0.42 W m^{-1} K^{-1} (Sakuratani, 1984). Under moderate to high flow rates, sap flow calculations are relatively insensitive to the value of K_{st} (Ishida et al., 1991). K_g was set to one value for the entire period of measurements on a plant in a replicate. Similar to the method of Steinberg et al. (1989) and Dugas et al. (1993), K_g was determined from the apparent K_g calculated by solving Eq. (1) for T = 0 for each day from 00:00 to 05:30 h Mountain Standard Time (MST). The daily K_g varied by less than 5% over the days when a gauge was on a plant.

Gravimetric measurements of a potted cotton plant on the edge of the experimental field which had the soil surface covered were used to verify the assumption that T = 0 from 00:00 to 05:30 h MST and to validate the accuracy of the technique for cotton. Total measured mass loss from the potted plant from 00:00 to 05:30 h on 29 and 30 August 1991 was 7 g and 3 g, respectively, as compared with daily sap flow totals of 400–1000 g. On these 2 days, cumulative T from both the sap flow gauge and gravimetric measurements was 2.3 kg, and the root mean square difference (RMSD; $RMSD = [\sum(T_{sapflow} - T_{grav})^2/(n-1)]^{0.5}$) for the 15 min values was 15 g h^{-1} per plant, or approximately 15% of measured midday T (see below).

Gauge signals (dT_a, dT_b, E, and dT_{ba}) and P were averaged for 15 min periods. A software filter was used to eliminate spurious flow calculations during low flow conditions (Van Bavel and Van Bavel, 1990). Occasionally, calculated sap flow was substantially overestimated during periods of high sap flow (Sakuratani, 1990; Ham and Heilman, 1990). These data were deleted from the analyses for that day.

In 1990, three plants were simultaneously instrumented with gauges in each of the control and FACE CO_2 treatments from 28 June to 6 August in Replicate 1 and from 8 August to 16 September in Replicate 2. In 1991, 10 plants were simultaneously instrumented with sap flow gauges in both CO_2 treatments from 28 June to 16 July, and from 8 to 27 August in Replicate 1 and from 19 July to 6 August and from 30 August to 17 September in Replicate 2. Plants were selected to give a representative sample of stem diameters. Gauges malfunctioned occasionally. In 1990, the small number of plants with gauges (fewer than four in each treatment) resulted in a small sample size.

Leaf area of each plant with a gauge was measured at the time of gauge removal by passing all leaves through a leaf area meter (Li-Cor Model 3100; Li-Cor, Lincoln, NE, USA). Daily T was compared for the two CO_2 concentrations using a t-test. Transpiration (per plant) was converted to per unit land area using a population of 10 plants m^{-2}.

2.3. Water balance components and meteorology

T measured by sap flow was compared with ET in 1990 and with T in 1991, both of which were calculated (Hunsaker et al., 1994) as a residual from a water balance (Tanner, 1967) using irrigation, precipitation, soil water content, and, in 1991, soil evaporation measurements.

In 1991, soil evaporation was measured using microlysimeters (Boast and Robertson, 1982). Acrylic sleeves (of 76 mm i.d., 152 mm length, and 3.3 mm wall thickness) were used to extract soil cores. Soil core masses were measured approximately daily from 1 July to 15 September using eight microlysimeters each in two replicates of the FACE and control treatments (two in the row and two each at 0.25, 0.5, and 0.75 m north of the row). Cores were used for a minimum of 3 days and an average of 5 days, after which new cores were used. Average soil evaporation of all cores in a replicate was used to calculate T. If mass measurements were not made daily, the soil core mass change was averaged for the number of days since the previous mass measurement.

Air temperature, global radiation, precipitation, relative humidity, and wind speed were measured about 1 km northeast of the cotton field (Brown, 1989). Daily reference crop (short grass) potential ET was calculated from these measurements (Brown, 1989). During the time of sap flow measurements, reference crop potential ET decreased from about 10 to 6 mm day^{-1} in both years.

3. Results and discussion

3.1. Leaf area

Leaf area of plants with gauges attached to them (Fig. 1) was similar to the leaf area for a larger sample of plants in the replicate (Mauney et al., 1994). Thus, plants with sap flow gauges (and therefore T from these plants) were representative for the replicate. There were no consistent differences in leaf area of plants with sap flow gauges in the two CO_2 treatments (Fig. 1). At these high leaf area indices (ranging from 2.6 to 10.3, assuming a plant density of 10 plants m^{-2}), T is insensitive to leaf area (Ritchie, 1972). Therefore, analyses were made on a per plant basis (e.g. g day^{-1} per plant) as opposed to a per leaf area basis (e.g. g day^{-1} m^{-2} leaf).

3.2. Sap flow

Average daily sap flow for the period of measurements in a replicate varied from 442 to 950 g day^{-1} per plant (Fig. 2). Given a plant density of 10 plants m^{-2}, this translates to evaporation equivalents of 4.4–9.5 mm day^{-1}. The high average for the control CO_2 treatment for measurements beginning on 6 August 1990 (Replicate 2) was caused by a small and, perhaps, unrepresentative sample of plants (i.e. one or two plants) which had a high sap flow. Sap flow from these plants appears suspect because potential ET was decreasing at the time of these measurements in 1990. Regardless of

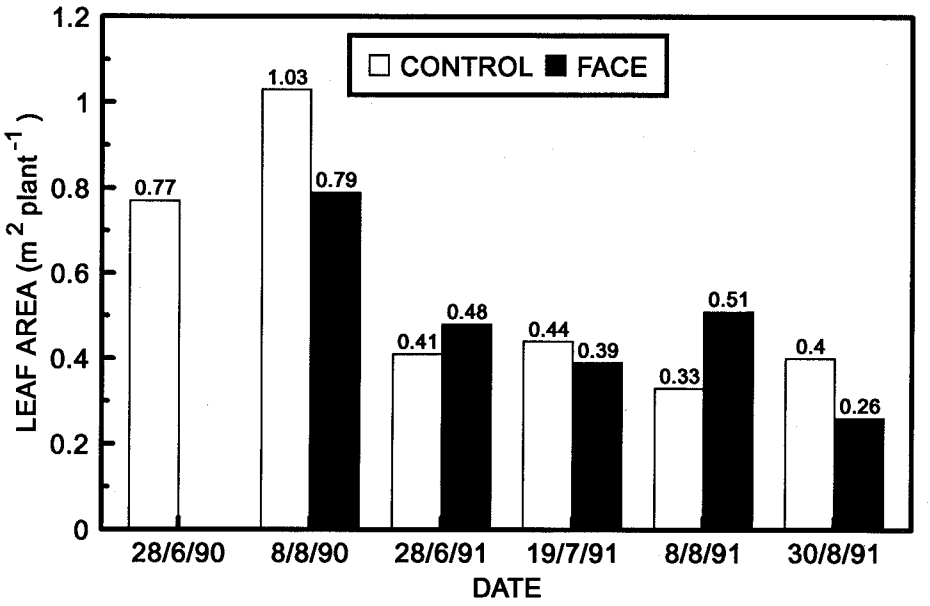

Fig. 1. Average leaf area of plants with sap flow gauges in control and FACE CO_2 treatments in 1990 and 1991. The date is the first date of sap flow measurements in a replicate.

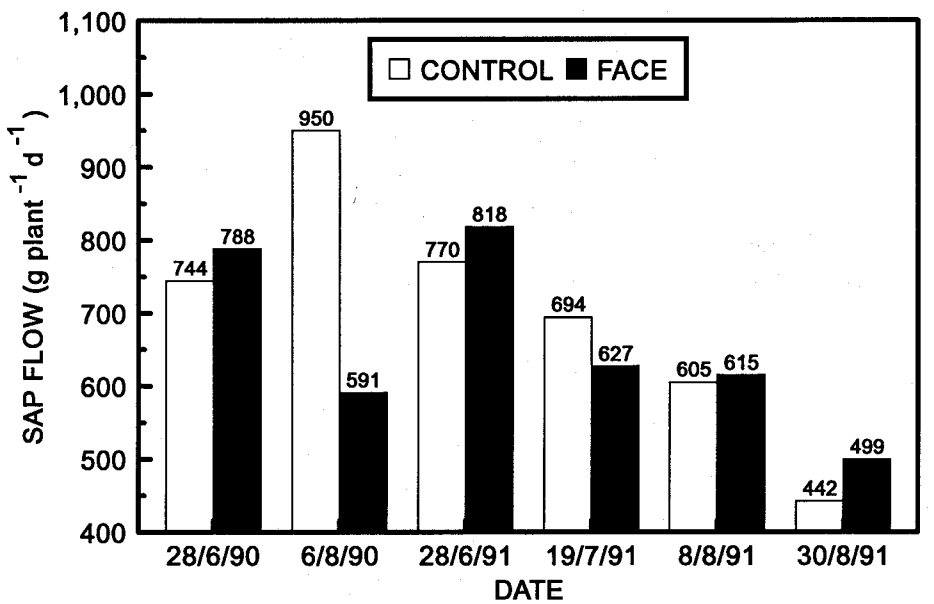

Fig. 2. Average daily sap flow of plants with sap flow gauges in control and FACE CO_2 treatments in 1990 and 1991. The date is the first date of sap flow measurements in a replicate (N.B.: 1000 g day^{-1} per plant $\approx$ 10 mm day^{-1}).

this result, there was no consistent difference in sap flow between the two CO_2 treatments for measurements in both years and replicates. The greater leaf area in 1990 (Fig. 1) did not cause a consistent increase in sap flow in 1990 over that in 1991 (Fig. 2).

The lack of difference in sap flow between the two CO_2 treatments was also shown by the ratio of daily sap flow from the control and FACE CO_2 treatments (Fig. 3). The sap flow ratio was generally greater than 1.0 in 1990 (i.e. the control values were greater) and was about equal to 1.0 in 1991. The variability was greater in 1990 because of the small number of plants with gauges. For example, there was a large shift in the ratio from 15 to 19 July 1990 (Fig. 3), when there was a change of gauges used and of plants measured. In 1991, there were no large shifts in the ratio when gauges (approximately 10 of which were used per treatment) were moved between replicates. In 1990, there were 8 days, concentrated at the beginning of measurements in Replicate 1, which had a statistically significant difference in sap flow ($P < 0.05$). There were no significant differences in 1991. Kimball et al. (1994) also showed little difference in ET, derived as a residual from the energy balance, between the two CO_2 treatments.

On first approximation, these results are somewhat in conflict with previous work (Morison, 1985, 1987) showing a decrease in stomatal conductance under elevated CO_2 conditions. Two related studies in this experiment (Bhattacharya et al., 1994; Hileman et al., 1994) also showed a decrease in stomatal conductance for plants in the

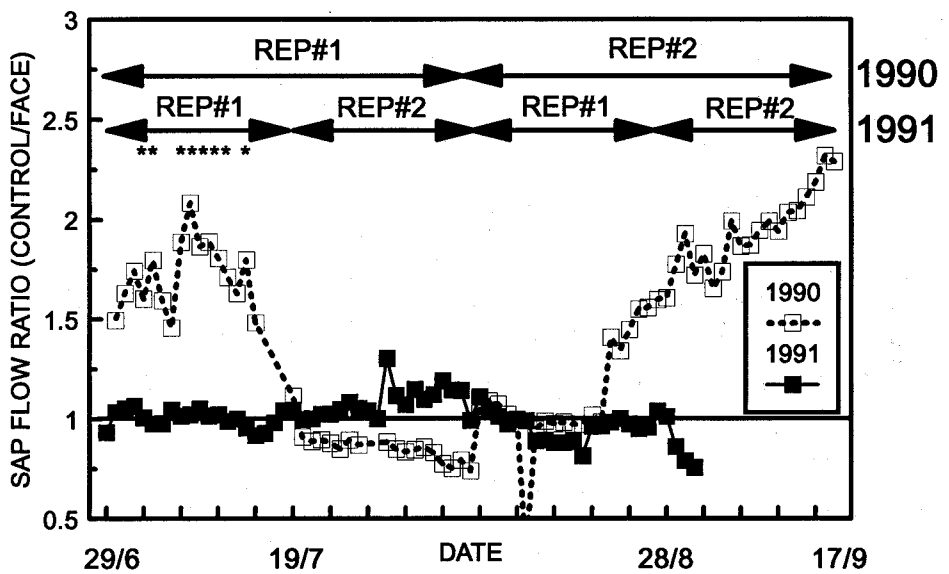

Fig. 3. Ratio of average daily sap flow from plants in control and FACE CO_2 treatments in 1990 and 1991. Period of sap flow measurements in Replicates 1 and 2 in each year is shown by arrows. Asterisks denote days, in 1990, when there was a significant difference ($P < 0.05$) between the sap flow in the two treatments. There were no significant differences in 1991. Sap flow measurements were not made in the control CO_2 treatment after 2 September 1991.

FACE CO_2 treatment at various times in the season. This study and the results of Hunsaker et al. (1994) and Kimball et al. (1994), however, did not show a consistent effect on whole-plant T throughout the year. Again, the translation of differences in leaf stomatal conductance (usually measured on fully exposed, sunlit leaves) to whole-plant T is complicated by the lack of representativeness of leaf conductance measurements for the entire plant, and by differences in plant size and leaf temperature (Kimball et al., 1992).

Daily sap flow was consistently less than or equal to daily potential ET in both CO_2 treatments in 1991 (Fig. 4). Owing to the smaller sample size in 1990, the variability of the sap flow/potential ET ratio was greater in 1990 than in 1991 (results not shown). The low values of this ratio in early July and in mid-August were probably due to mild water stress, whereas the low values in September were probably due to declining leaf areas (Fig. 1) and stomatal conductance (Bhattacharya et al., 1994; Hileman et al., 1994).

Diurnal patterns of sap flow from plants in the two CO_2 treatments were also similar (Fig. 5). Maximum midday values from this study are about 40% greater than those shown by Dugas (1990b) for cotton, probably as a result of higher atmospheric demand in the current study. However, the variation of sap flow values between plants is similar in both studies. Total T for the control and FACE CO_2 treatments on the day shown in Fig. 5 was 864 g day^{-1} per plant and 820 g day^{-1} per plant, respectively.

On 21 August 1990, there was no CO_2 enrichment in the FACE treatment from about 14:00 h MST until the end of the day, owing to equipment malfunction. There

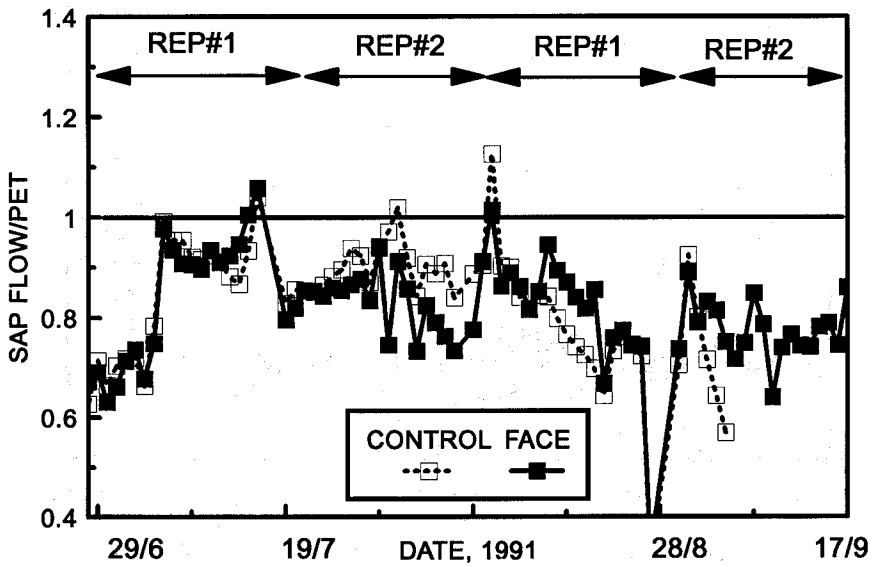

Fig. 4. Ratio of average daily sap flow from plants in control and FACE CO_2 treatments to potential evapotranspiration (PET) in 1991. Period of sap flow measurements in Replicates 1 and 2 is shown by arrows.

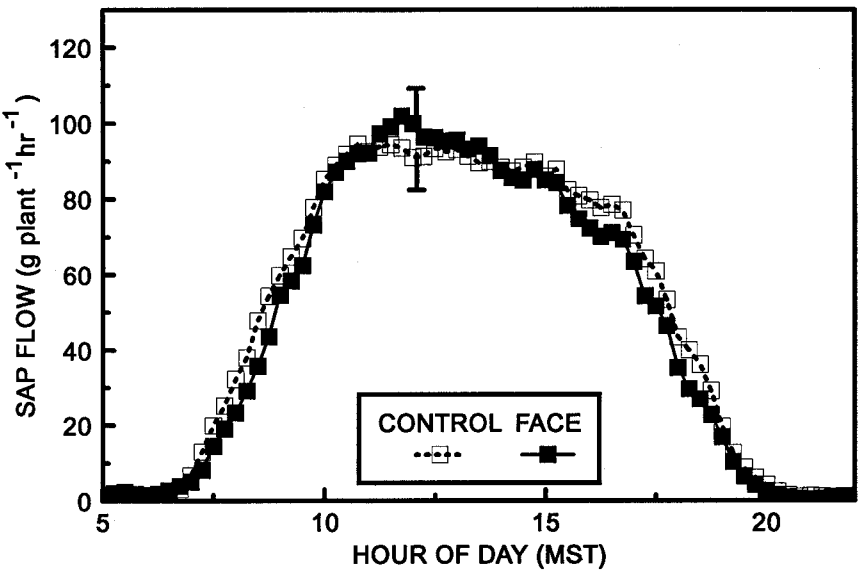

Fig. 5. Fifteen minute average sap flow from plants in control and FACE CO_2 treatments on 17 July 1991. The standard error of mean sap flow at 12:00 h MST in each treatment is denoted by a vertical line.

was no change in sap flow in the FACE treatment as a result of this short-term elimination of CO_2 enrichment (results not shown). There were no significant periods of CO_2 enrichment failure in Replicates 1 and 2 in 1991.

In 1991, the CV of daily sap flow across plants was about 30% throughout the year, and was similar in both CO_2 treatments (Fig. 6). The CV of daily sap flow was greater in 1990 than in 1991 (results not shown), owing to the small sample size used in 1990. The CV of sap flow, when expressed per unit leaf area and not per plant, was similar to that shown in Fig. 6 (results not shown). This variability, similar to that shown by Dugas (1990b), underscores the need to have a large sample of instrumented plants, to allow a representative value to be be obtained.

3.3. Sap flow vs water balance evaporation

Soil evaporation was slightly, but consistently higher in the control than in the FACE treatment (Fig. 7). The seasonal average of daily soil evaporation was 0.85 mm day^{-1} and 0.70 mm day^{-1} in the control and FACE treatments, respectively. The reason for this difference in soil evaporation is unknown. The low soil evaporation rates reflect the dry soil surface owing to the subsurface trickle irrigation system and the small number of days with precipitation (Fig. 7). Soil evaporation was typically 0.5 mm day^{-1}, except immediately after precipitation, and was greatest late in the season when precipitation was more frequent.

For periods defined by dates of soil water content measurements (7–14 days, depending upon dates of soil water content measurements; see Hunsaker et al., 1994), cumulative ET (1990) and T (1991), both calculated as a residual from the

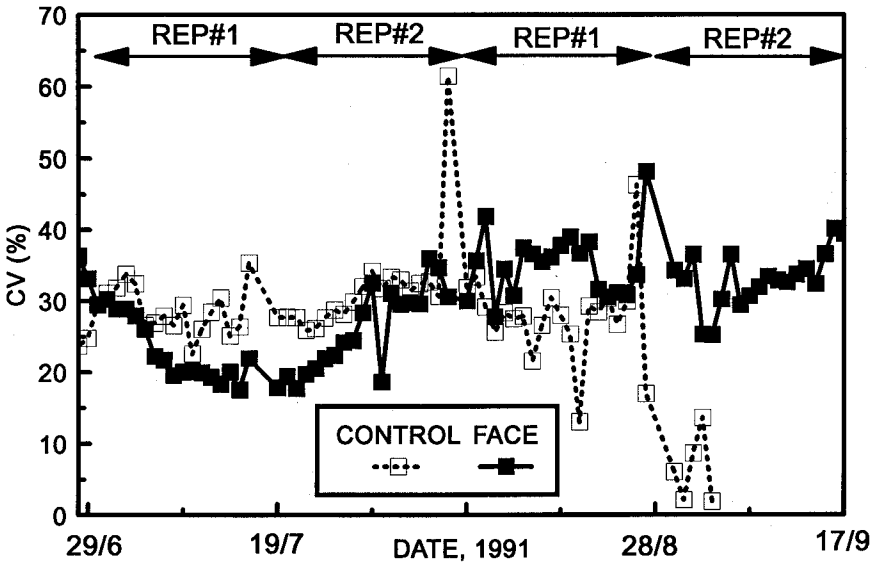

Fig. 6. Coefficient of variation (CV) of daily sap flow from plants in control and FACE CO_2 treatments in 1991. Period of sap flow measurements in Replicates 1 and 2 is shown by arrows. Sap flow measurements were not made in the control CO_2 treatment after 2 September 1991.

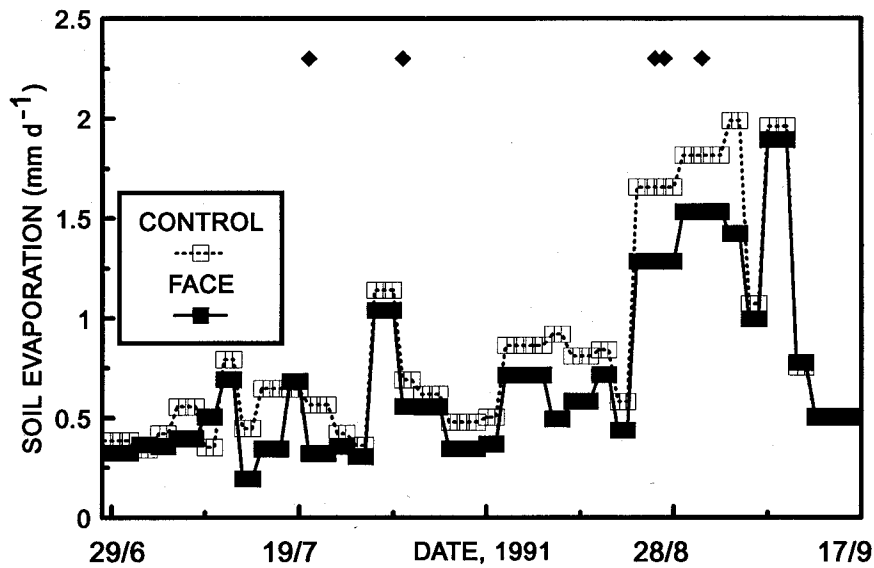

Fig. 7. Daily soil evaporation in control and FACE CO_2 treatments in 1991. ♦, Days with precipitation of 1 mm or more. The average daily standard error of soil evaporation measurements was 0.05 mm day^{-1}.

water balance, were similar to cumulative sap flow for the same period in both years and replicates (Fig. 8). Similar to the comparison of sap flow results from the CO_2 treatments (Fig. 3), water balance ET and T differences between CO_2 treatments were too small to be detected significantly at the 0.05 probability level (Hunsaker et al., 1994). Water balance ET in 1990 should have been slightly higher than sap flow because the latter does not include soil evaporation. Using a typical period length for comparison of 14 days, the cumulative soil evaporation would have been about 10 mm.

Pooled across years, replicates, and treatments, the RMSD between daily sap flow and evaporation was 22 mm, or approximately 1.5 mm day^{-1} for a 14 day period, whereas daily T was about 7 mm day^{-1} (Fig. 2). This is good agreement between these two independent methods. These results, in conjunction with the finding of Hunsaker

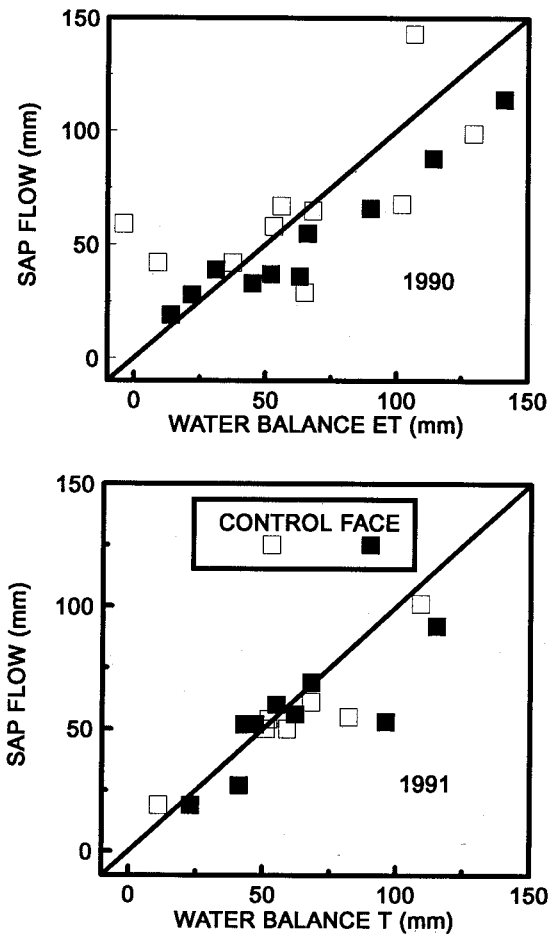

Fig. 8. Cumulative sap flow vs cumulative water balance evapotranspiration (ET) in 1990 or cumulative water balance transpiration (T) in 1991 in control and FACE CO_2 treatments.

et al. (1994) that seasonal ET differed by less than 2% in both years, support the conclusion there was no effect of CO_2 on T.

4. Conclusions

The following can be concluded concerning the effects of increasing atmospheric CO_2 concentration on cotton sap flow (transpiration, T) in plants growing in a field at ambient (370 μmol mol^{-1}) and enriched (550 μmol mol^{-1}) CO_2 concentrations: (1) sap flow from individual plants, for periods from 15 min to 2 weeks, was not significantly different under the two concentrations, except for a few days in 1990; (2) cumulative sap flow for 14 day periods was similar to cumulative evapotranspiration or T calculated from a water balance. Neither method showed an effect of CO_2.

These results show that for this C_3 crop, which had a high stomatal conductance (Bhattacharya et al., 1994; Hileman et al., 1994) and was grown under well-watered and high-fertility conditions in Arizona (Mauney et al., 1994), there was no effect of CO_2 on T that could be measured using sap flow gauges. This result, in conjunction with the increases in above-ground (Mauney et al., 1994) and root (Prior et al., 1994) biomass measured under enriched CO_2 concentrations, supports the premise of Goudriaan and Unsworth (1990) that improvement in water use efficiency of C_3 plants is a more robust measurement of plant response to the effect of CO_2 than is T alone. Our T results, because of the variation in our measurements, cannot be considered different from the modeling results of Goudriaan and Unsworth (1990), who showed an approximate 10% decrease in whole-canopy T for C_3 plants as a result of a doubling in atmospheric CO_2 concentration. These are some of the first data on T responses to increasing atmospheric CO_2 concentrations for plants grown in a typical field environment. Although our results may not translate to other species or environments, these results have direct relevance for assessing the direct and indirect effects of increasing CO_2 on agricultural plants.

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