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Transpiration from sorghum and soybean growing under ambient and elevated CO_2 concentrations

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Abstract

The increasing concentration of carbon dioxide in the atmosphere ($[CO_2]$) has several direct effects on plants and these effects may be different for C_3 and C_4 plants. Our objective was to measure hourly and daily whole-plant transpiration rates from the C_4 plant grain sorghum (*Sorghum bicolor* (L.) Moench) and the C_3 plant soybean (*Glycine max* (L.) Merr.) grown under ambient (359 μmol CO_2 mol^{-1} dry atmospheric air) and elevated (705 μmol mol^{-1}) $[CO_2]$ values. Transpiration measurements were made for 22 days in August 1994 at Auburn, Alabama, USA, using stem flow gauges on plants growing in open top chambers, $n = 8$ for each $[CO_2]$ and species. Leaf area averaged slightly more than 0.1 m^2 per plant for sorghum and about 0.2 m^2 per plant for soybean. Averages (15 min and daily) of transpiration, per unit leaf area, were consistently greater from plants growing under the ambient $[CO_2]$ for both sorghum and soybean. Average daily transpiration from plants growing under the elevated $[CO_2]$ was significantly smaller ($P = 0.05$) on all but 2 days for soybean and on 9 of the 22 days of measurements for sorghum. Average daily sorghum transpiration was 1128 g m^{-2} day^{-1} and 772 g m^{-2} day^{-1} from plants growing under an ambient and elevated $[CO_2]$, respectively. Corresponding soybean averages were 731 g m^{-2} day^{-1} and 416 g m^{-2} day^{-1}. The transpiration reduction under elevated $[CO_2]$ was greater for the C_3 plant soybean than for the C_4 plant sorghum. These results support previous studies showing that transpiration, per unit leaf area, from sorghum and soybean will both be reduced if atmospheric $[CO_2]$ continues to increase, although the reduction may be greater for C_3 plants.

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1. Introduction

The concentration of carbon dioxide in the atmosphere ([CO_2]) has increased 30% from the preindustrial level of about 280 μmol CO_2 mol^{-1} dry atmospheric air (Raynaud and Barnola, 1985; Neftel et al., 1985) and may rise to twice the current level during the next century (Houghton et al., 1990). Elevated atmospheric [CO_2] often reduces stomatal conductance of plants (Morison, 1985; Morison, 1987; Nederhoff, 1992; Nederhoff et al., 1992; Rodaglou et al., 1992) and also may reduce transpiration per unit leaf area (Kimball and Idso, 1983; Goudriaan and Unsworth, 1990). However, elevated atmospheric [CO_2] may not decrease whole-plant or canopy transpiration (Eamus, 1991; Morison, 1993; De Bruin and Jacobs, 1993) because of other compensating effects under elevated atmospheric [CO_2] such as increased leaf area (Mauney et al., 1994) or elevated leaf temperature (Idso et al., 1987; Kimball et al., 1992; Nederhoff et al., 1992), which may cause increased leaf–air vapor pressure deficits (Jones et al., 1984). In addition, effects of elevated atmospheric [CO_2] on transpiration may be different for C_3 vs. C_4 species (e.g. Nie et al., 1992) owing to the greater photosynthetic efficiency of C_4 species (Devlin, 1975).

Several researchers have investigated the effect of elevated [CO_2] on soybean water use. Valle et al. (1985) showed that diurnal transpiration from soybean leaves, per unit leaf area, was about equal at 330 and 660 μmol mol^{-1} because the small reduction in stomatal conductance at elevated [CO_2] was compensated for by an increase in leaf temperature. Jones et al. (1984; Jones et al., 1985) showed there was little difference in transpiration, per unit ground area, from plants growing at 330 and 800 μmol mol^{-1} because the reduced bulk canopy conductance at the greater [CO_2] was offset by increased leaf area and vapor pressure deficits for plants growing under a [CO_2] of 800 μmol mol^{-1}. However, there were reductions in soybean transpiration, per unit leaf area, from plants grown at a [CO_2] of 800 μmol mol^{-1} in the studies of Jones et al. (1984; Jones et al., 1985). Prior et al. (1991) also showed a consistent reduction in soybean transpiration, per unit leaf area, as [CO_2] increased above ambient.

There has been less research on the effects of elevated [CO_2] on transpiration from the C_4 plant sorghum. Van Bavel (1974) showed that sorghum transpiration decreased, both per unit leaf area and per unit ground area, as [CO_2] increased from 100 to 1800 μmol mol^{-1}. Chaudhuri et al. (1986) showed 'no definite trend for evapotranspiration rate' from lysimeters planted with sorghum grown at [CO_2]s of 330, 485, 660, and 795 μmol mol^{-1}. There was, however, an increase in leaf area with increasing [CO_2] and, therefore, there was, assuming soil evaporation was equal in all treatments, a decrease in transpiration, per unit leaf area, with increasing [CO_2]. In both studies, leaf temperatures increased with increasing [CO_2]. Owensby et al. (1993) showed through simulation analyses that evapotranspiration from a tallgrass prairie made up of C_4 species would be reduced by 15% when plants were grown in an open-top chamber at 700 μmol mol^{-1} vs. those grown in a chamber at 350 μmol mol^{-1}.

Several investigators have used stem flow gauges similar to the ones used in this study for soybean transpiration measurements (e.g. Sakuratani, 1987, Sakuratani, 1991; Inoue et al., 1994). Senock and Ham (1993) showed that transpiration from soybean plants measured using a similarly designed gauge was within 5% of gravimetrically-measured transpiration. Cohen et al. (1993) showed that transpiration measured by stem flow gauges for soybeans averaged within 10% of gravimetrically-measured transpiration. Gerdes et al. (1994), however, did find that gauge-measured soybean transpiration was too large relative to water-balance transpiration estimates, possibly because gauges of this design (i.e. heaters too narrow relative to stem diameter) may be in error at large transpiration rates (Ham and Heilman, 1990). Transpiration rates in the current study were about one-fifth of those measured by Gerdes et al. (1994) and, thus, erroneous transpiration measurements were probably not a problem in the current study.

For sorghum, Tolk et al. (1989) found that this type of stem flow gauge provided reasonably accurate transpiration measurements. Accuracy improved as the averaging time was lengthened. Tolk et al. (1991) showed that gauge measurements of sorghum transpiration, when scaled up to a population of plants in a lysimeter, compared favorably with gravimetric transpiration measurements, depending upon the scaling procedure. Zhang and Kirkham (1995) found that stem flow gauge and gravimetric measurements of sorghum transpiration were very similar as long as flow rates were at least 20 g per plant h^{-1}.

There have been few field studies measuring whole-plant transpiration simultaneously from C_3 and C_4 plants growing under ambient and elevated [CO_2]. The objective of this study was to measure transpiration from sorghum and soybean grown under ambient and elevated [CO_2] in open-top chambers (OTCs).

2. Methods

2.1. Open-top chambers

Transpiration measurements were made from 6 to 27 August (Day 218–Day 239) 1994 at the National Soil Dynamics Laboratory (32.6°N, 85.5°W), Auburn, AL, USA. The soil at the study site is a Blanton loamy sand topsoil (loamy, siliceous, thermic Grossarenic Paleudult). Plants were continuously exposed to ambient or elevated [CO_2] in OTCs. Prior et al. (1991) and Reeves et al. (1994) have provided details on the OTCs.

The [CO_2] in these OTCs can be controlled precisely (Prior et al., 1991; Reeves et al., 1994). In the 1994 growing season, for example, the average daytime [CO_2] in the ambient OTCs was 359 μmol mol^{-1}, whereas that in the elevated OTCs was 705 μmol mol^{-1}. The standard error of the mean of these daytime averages was always less than 0.5 μmol mol^{-1}. Variation of [CO_2] during the daytime also was small. The level of control and the concentrations were similar to these during the period of transpiration measurements.

Hourly averages of dry bulb and dewpoint temperature and global radiation were measured by the National Weather Service at a location about 1000 m from the OTCs. We did not measure microclimatic conditions (e.g. radiation, vapor pressure, wind speed, and temperature) inside the OTCs. Daily precipitation was measured at the OTCs using a non-recording raingauge.

2.2. Cultural practices

Sorghum ('Savanna 5') was sown on 18 June 1994 and soybean ('Stonewall') was sown on 5 May 1994. The sorghum planting date was later because the first sorghum planting on 5 May failed owing to root rot caused by moist and cool soil. Plant densities were 26 plants m^{-2} and 30 plants m^{-2} for sorghum and soybean, respectively. The east–west rows were 0.76 m wide. Harvest dates were 30 September for sorghum and 14 September for soybean.

Plants were well watered throughout the experiment. During the period of stem flow measurements, 6.4 mm of irrigation was applied about every 3 days. All plants had adequate fertility. At the time of stem flow measurements, sorghum plants had about eight leaves and soybean plants were in the pod fill stage.

2.3. Stem flow gauges

Constant-power stem flow gauges (Baker and Van Bavel, 1987) were used to measure whole-plant transpiration from individual sorghum and soybean plants. Measurements were made in eight OTCs, four for each species (two ambient and two elevated). Each OTC had one species. Thirty-two plants were instrumented with gauges (Models SGA5, SGA10, and SGA13, Dynamax, Inc., Houston, TX, USA), four in each OTC. After attachment to a stem, gauges were covered with cling film for waterproofing and with aluminum foil to reduce externally induced temperature gradients.

Gauge signals and heater voltage were sampled every 15 s and averaged for 15 min. A software filter (Van Bavel and Van Bavel, 1990) was used to eliminate spurious flow calculations during low flow conditions. Daily transpiration totals were calculated for the period from 06:00 to 20:00 h Central Daylight Time (CDT).

Several investigators have demonstrated the accuracy of these types of gauges for soybean (Sakuratani, 1987; Senock and Ham, 1993; Cohen et al., 1993). We therefore did not perform a separate validation of transpiration measurements using these gauges for soybeans.

We did, however, measure gravimetric transpiration from a potted sorghum plant and transpiration using stem flow gauges in a glasshouse in Temple in September 1988. Daylight transpiration totals varied from about 30 to 370 g over the 12 days of measurements. Average daily transpiration was 138 g from the stem flow gauge and was 164 g from the gravimetric measurements. The root mean square difference of daily transpiration was 65 g or about 40% of the gravimetric measurement. This error is higher than that shown for other plants (e.g. Dugas, 1990), probably because measurement of transpiration on monocots using stem flow gauges is more difficult (Baker and Nieber, 1989), although Zhang and Kirkham (1995) suggested that stem flow rates are more important than stem anatomy in determining gauge accuracy.

2.4. Leaf area

To account for leaf area differences, transpiration of plants with stem flow gauges was expressed on a per unit leaf area basis (one-sided, e.g. $g\,m^{-2}\,h^{-1}$) using the whole-plant, green leaf area measured at harvest with a leaf area meter. The increase of leaf area between the time of stem flow measurements and harvest (about 0.04 m^2 per plant) was estimated from leaf length (sorghum) and leaf number (soybean) measurements and was about equal for both species and CO_2 treatments. Therefore, using the harvest leaf area to normalize transpiration did not affect comparisons between CO_2 treatments. It did, however, bias our transpiration rates low by about 10% for soybean and 30% for sorghum.

2.5. Analytical procedures

Measurements from plants in the two OTCs at a given $[CO_2]$ for a species were pooled. For both sorghum and soybean, 15 min and daily transpiration averages from plants in ambient and elevated OTCs were compared using the ANOVA procedure in a general linear model procedure (SAS Institute, Inc., 1988) with $[CO_2]$ as the main effect and plants as replicates. Slopes of daily transpiration from ambient and elevated OTCs were compared for both species. Transpiration data were analyzed for a normal distribution, equality of variances, and, for regression analyses, independence of residuals. Transpiration data were normally distributed (Shapiro–Wilk statistic greater than 0.83), had equal variances, and had no residuals with a significant effect on the regression.

3. Results and discussion

3.1. Weather

During the 22 days of stem flow measurements, 36 mm of precipitation were measured (on 6 days) and 31.8 mm of irrigation was applied. Daily total global radiation varied from 5 to 26 MJ m^{-2} day^{-1}. On most days, it was greater than 18 MJ m^{-2} day^{-1}. Average daily dry bulb and dewpoint temperatures ranged from 25 to 28°C and from 23 to 20°C, respectively.

3.2. Leaf area

Leaf area of sorghum plants with stem flow gauges averaged slightly greater than 0.1 m^2 per plant, whereas it was about 0.2 m^2 per plant for soybean (Fig. 1). For both species, leaf area differences between the two $[CO_2]$ values were small and not significantly different. The smaller sorghum leaf area was primarily a result of the later planting date.

These average leaf areas translate into leaf area indices of about 2.6 for sorghum and six for soybean. According to Ritchie (1972), row crop transpiration is most sensitive to leaf area at leaf area indices greater than three. Therefore soybean transpiration rates, per unit leaf area, from this study may be biased low because all of the soybean leaf area may not have been equally effective in transpiring water.

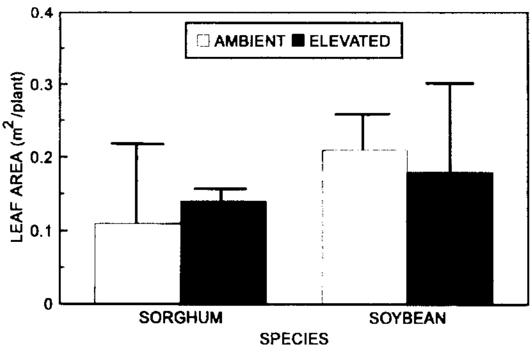

Fig. 1. Average leaf area measured at harvest for sorghum and soybean plants growing under ambient and elevated carbon dioxide concentrations (359 and 705 μmol mol^{-1}). Vertical bars denote one standard error of the mean.

3.3. Transpiration

The 15 min averages of transpiration were greater from plants growing under the ambient [CO_2] for both sorghum and soybean for almost the entire daylight period for each of the 3 days shown in Fig. 2. Results from other days were similar (data not shown). Daily total global radiation was about 24 MJ m^{-2} day^{-1} on each of these 3 days. During each day, transpiration fluctuated similarly in all treatments (e.g. 12:00 and 12:30 h CDT on Day 222). We could not find a close relationship between hourly average radiation and 15 min transpiration averages, probably because of the different averaging periods and the distance between OTCs and radiation sensor (about 1000 m).

In most instances on these 3 days, 15 min transpiration averages for the two [CO_2]s were significantly different ($P = 0.05$) for both sorghum and soybean from about 10:00 to 16:00 h CDT. To illustrate the variability between plants in a [CO_2] treatment, the standard error of the mean transpiration at 13:00 h CDT on each of these 3 days was about 15 g m^{-2} h^{-1} for sorghum and 8 g m^{-2} h^{-1} for soybean. Midday transpiration rates (per unit ground area) in Fig. 2 are about equal to 0.6 mm h^{-1} for both species, and, for sorghum, about equal to 30 g per plant h^{-1}, which is greater than the threshold for accurate sorghum transpiration measurements suggested by Zhang and Kirkham (1995). The greater variation of sorghum transpiration is related to the larger transpiration rates and, possibly, the more rapid response of stomata to light for C_4 plants (Rogers, 1975).

Average daily transpiration totals (Fig. 2) were significantly different ($P = 0.05$) for the two [CO_2] values on each of these 3 days for both sorghum and soybean. The greater daily totals on Day 223 were probably a result of irrigation applied late in the afternoon on Day 222.

These midday soybean transpiration rates (Fig. 2), about 100 g m^{-2} h^{-1} for ambient [CO_2] and about 50 g m^{-2} h^{-1} for elevated [CO_2], are about one-third of midday soybean canopy evapotranspiration measured by Jones et al. (1985) and are about one-fourth of midday transpiration measured on mature, upper-canopy, sunlit soybean leaves by Valle et al. (1985) and Allen et al. (1994). Midday transpiration rates from this

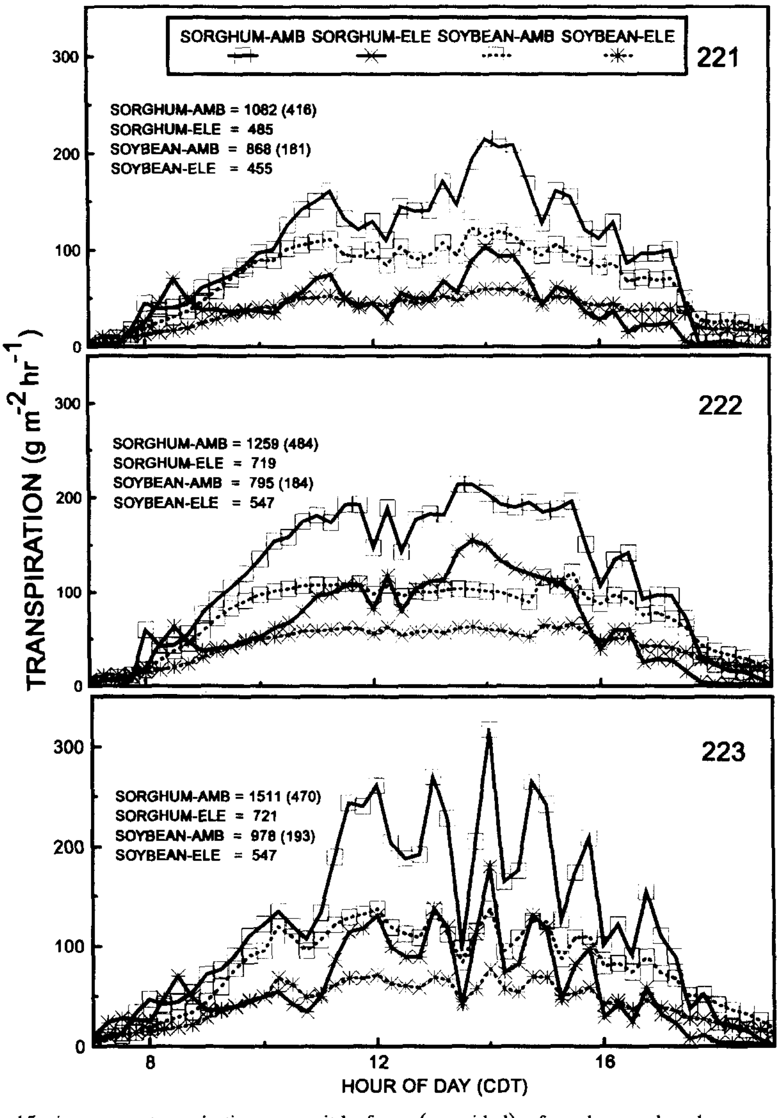

Fig. 2. The 15 min average transpiration, per unit leaf area (one sided), of sorghum and soybean growing under ambient and elevated carbon dioxide concentrations (359 and 705 μmol mol^{-1}) on Days 221, 222, and 223 (9-11 August 1994). Daily totals (g m^{-2} day^{-1}) of transpiration and least significant difference between transpiration from plants growing under ambient and elevated concentration ($n = 8$) are shown for each species and day. CDT, Central Daylight Time.

study, relative to those from Jones et al. (1985), are probably smaller because the measurements by Jones et al. included soil evaporation, plant density was greater in the current study, and, perhaps, different environmental conditions existed in the chambers.

Similar to 15 min averages, average daily transpiration from both sorghum and soybean was consistently greater from plants growing under ambient [CO_2] (Fig. 3). For

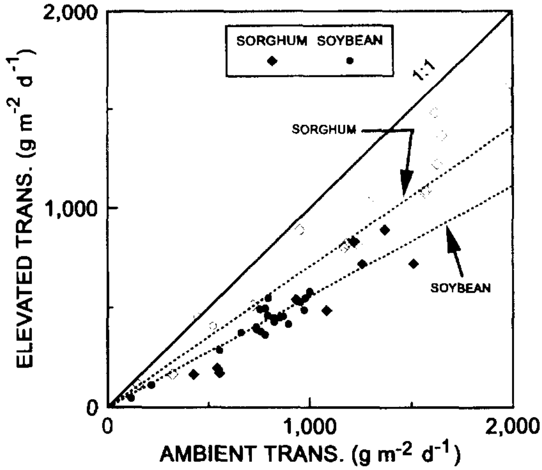

Fig. 3. Average daily transpiration, per unit leaf area (one sided), of sorghum and soybean growing under ambient and elevated carbon dioxide concentrations (359 and 705 μmol mol^{-1}). Filled symbols represent daily totals that were significantly different between the two concentrations ($P = 0.05$). Open symbols were not significantly different. The 1:1 line and the least-squares linear regression lines for each species are shown.

all days, the average daily sorghum transpiration was 1128 g m^{-2} day^{-1} and 772 g m^{-2} day^{-1} from plants growing under ambient and elevated [CO_2], respectively. (Equivalent rates per unit ground area are 2.9 mm day^{-1} and 2.0 mm day^{-1}.) This is a 32% reduction in transpiration owing to increasing [CO_2]. Corresponding soybean averages were 731 g m^{-2} day^{-1} and 416 g m^{-2} day^{-1} (4.4 mm day^{-1} and 2.5 mm day^{-1}), equivalent to a 43% reduction. Thus, the reduction of transpiration under elevated [CO_2] was greater for the C_3 plant soybean. The slopes of regression lines for sorghum and soybean (Fig. 3) were significantly different ($P = 0.006$). Neither intercept was significantly different from 0.0 ($P = 0.05$). The soybean ET rates measured by the stem flow gauges in this study are only about 25% of those measured by Gerdes et al. (1994).

Daily soybean transpiration averages for the two [CO_2] values were significantly different from each other ($P = 0.05$) on all but two of the days (Fig. 3), whereas sorghum daily averages were significantly different on 9 of the 22 days. Again, this suggests that the effect of [CO_2] on transpiration was greater for the C_3 plant soybean.

Results from Jones et al. (1985; Table 2), Prior et al. (1991; Fig. 4), and the current study all showed large reductions (about 45%) in soybean transpiration, per unit leaf area, when the [CO_2] was increased from ambient (330–350 μmol mol^{-1}) to about 700 μmol mol^{-1} (Fig. 4). Results from Pallas (1965) and Prior et al. (1991) suggest that the relationship between transpiration reduction and increasing [CO_2] is nonlinear. The midday, upper-canopy leaf measurements of both Valle et al. (1985; Table 1) and Allen et al. (1994; Fig. 2) showed a smaller reduction of leaf transpiration at a comparable elevated [CO_2] (Fig. 4). It is possible that midday transpiration measurements on upper-canopy, mature leaves are not representative of daily whole-plant or canopy transpiration rates. Jones et al. (1984; Fig. 2) showed a smaller reduction of midday whole-canopy soybean transpiration at a [CO_2] of 800 μmol mol^{-1} than measured in the

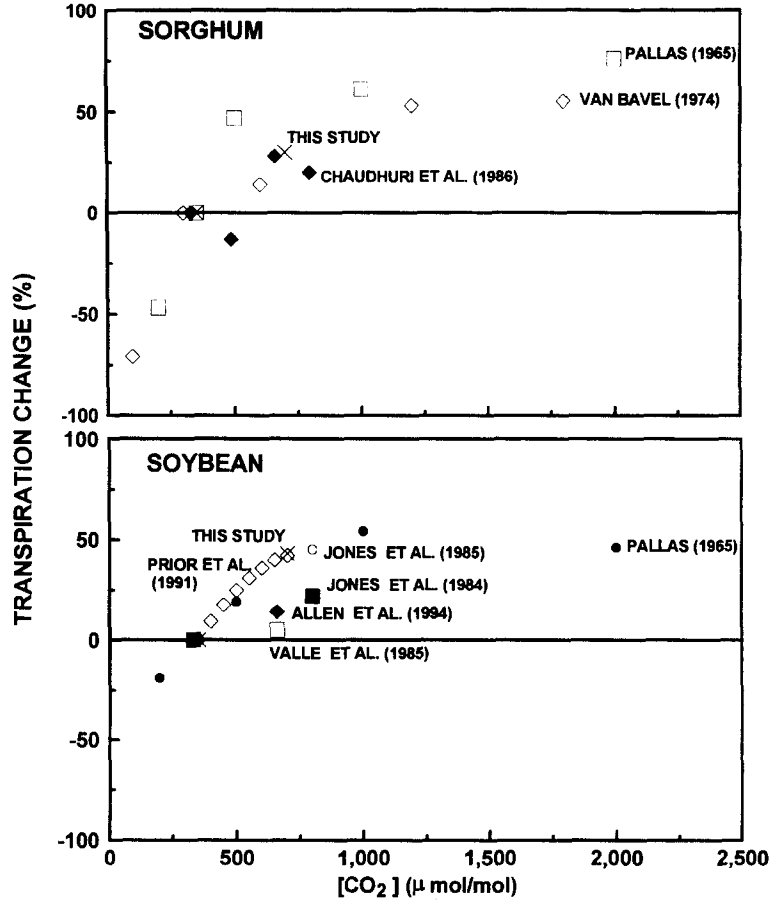

Fig. 4. Summary of results from this study and previous studies showing percentage change (positive indicates reduction) in transpiration, per unit leaf area, for sorghum (upper) and soybean (lower) grown at different carbon dioxide concentrations ($[CO_2]$). Transpiration change for each study was calculated relative to transpiration measured at a $[CO_2]$ near ambient (ranging from 300 to 350 $\mu mol \, mol^{-1}$). Chaudhuri et al. (1986) results are for evapotranspiration, i.e. they include soil evaporation.

current study (Fig. 4), perhaps because the large leaf area indices (greater than seven) in their study confounded the calculated per unit leaf area transpiration rates.

The reduction of sorghum transpiration under elevated $[CO_2]$ measured in the current study was similar to that measured by Van Bavel (1974; Table 3) and Chaudhuri et al. (1986; Table 2 and Fig. 4). Again, the results from Pallas (1965) and Van Bavel (1974) imply a nonlinear relationship.

4. Conclusions

Hourly and daily whole-plant transpiration, normalized for leaf area, from the C_4 plant sorghum and the C_3 plant soybean were greater for plants grown at an ambient carbon dioxide concentration ([CO_2]) of 359 μmol mol^{-1} than for plants grown at an elevated [CO_2] of 705 μmol mol^{-1}. The transpiration reduction at elevated [CO_2] was greater for soybean. Because leaf area differences were small between plants grown at the two [CO_2] values in this study, results of transpiration reduction owing to elevated [CO_2] would be similar on a per plant (grams per plant per day) and a per unit ground area (mm day^{-1}) basis.

Therefore, part of the hypothesized larger increase of water use efficiency for C_3 plants vs. C_4 plants with increasing [CO_2] (Morison, 1993) may be due to a larger decrease of transpiration for C_3 plants as well as increased biomass production. These results support previous studies showing that transpiration, per unit leaf area, from both the C_4 plant sorghum and the C_3 plant soybean will be reduced if atmospheric [CO_2] continues to increase.

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