

Atmospheric Carbon Dioxide Enrichment Effects on Cotton Midday Foliage Temperature: Implications for Plant Water Use and Crop Yield¹

S. B. Idso, B. A. Kimball, and J. R. Mauney²

ABSTRACT

In an experiment designed to determine the likely consequences of the steadily rising carbon dioxide (CO₂) concentration of Earth's atmosphere for the foliage temperature, water use, and yield of cotton (*Gossypium hirsutum* L. var. Deltapine-61) plants, cotton was grown out-of-doors at Phoenix, AZ, in open-top, clear-polyethylene-wall, CO₂-enrichment chambers for three summers under mean daylight CO₂ concentrations of 340, 500 and 640 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air on an Avondale clay loam soil [fine-loamy, mixed (calcareous), hyperthermic Anthropic Torrifluvent]. Infrared thermometer measurements of the cotton foliage temperature (T_f) indicated that a 330 to 660 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air doubling of the atmospheric CO₂ content results in a midday T_f increase of 1.1°C for well-watered cotton at Phoenix in the summer. This temperature increase was predicted to produce a 9% reduction in per-unit-leaf-area plant transpiration rate and an 84% increase in crop biomass production, which compared favorably with the measured crop biomass increase of 82% for such a doubling of the air's CO₂ content. These findings, together with similar findings for a second plant species—water hyacinth [*Eichhornia crassipes* (Mart.) Solms]—allowed us to develop a technique for assessing the effects of a 330 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air CO₂ concentration increase on the percentage yield increase (Y) of a crop via infrared thermometry by means of the equation $Y = 7.6\% \times (\text{IJ})^{-1}$, where IJ represents the Idso-Jackson plant water stress index. If this equation holds up under further scrutiny, it could provide a rapid and efficient means for assessing the yield response of crops to atmospheric CO₂ enrichment.

Additional index words: Plant productivity, Transpiration, Water use efficiency, *Gossypium hirsutum* L.

INCREASING the atmospheric concentration of carbon dioxide (CO₂) tends to induce partial stomatal closure in most plants. In a recent review of this subject, for instance, Kimball and Idso (1983) found that an approximate 330 to 660 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air doubling of the atmospheric CO₂ concentration reduced transpiration by an average of 34% in 18 different plant species. One consequence of this phenomenon should

be higher foliage temperatures, because the excess heat load on the plant leaves resulting from the decreased efficiency of latent heat removal under these conditions can only be dissipated by increases in the magnitudes of convective and radiant heat transfer processes, which are primarily brought about by an increase in foliage temperature. Thus, the primary purpose of this study was to document and evaluate the magnitude of this phenomenon in cotton (*Gossypium hirsutum* L. var. Deltapine-61).

Two secondary objectives were to determine the implications of CO₂-induced foliage temperature change for plant water use and crop biomass production through a new application of the Idso-Jackson (IJ) plant water stress index (Idso et al., 1981; Jackson et al., 1981), which O'Toole et al. (1984) have recently concluded to be the preferred technique for the rapid, accurate, and efficient assessment of the water status of both crops and natural plant communities in a comparison of many different approaches to this problem.

To briefly recapitulate, the IJ index is based, first of all, on the concept of a "non-water-stressed-baseline," which is a plot of foliage-air temperature differential ($T_f - T_a$) vs. air vapor pressure deficit (VPD) under conditions of minimal water stress when transpiration is occurring at the potential rate. Although Idso (1982)

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² Research physicist and soil scientist, U.S. Water Conservation Lab., 4331 E. Broadway, Phoenix, AZ 85040; and research plant physiologist, Western Cotton Res. Lab., 4135 E. Broadway, Phoenix, AZ 85040.

demonstrated by actual measurement that the non-water-stressed-baselines of 26 different plant species appeared to be linear functions over the air VPD range generally experienced in nature. Idso et al. (1986a) have recently shown that there is a slight curvature to the baseline and that it can be determined directly from the equation

$$T_F - T_A = \frac{r_A R_N}{\rho c_p} - \frac{e_F^* - e_A}{\gamma(1 + r_{FP}/r_A)}, \quad [1]$$

where T_F is foliage temperature ($^{\circ}\text{C}$), T_A is air temperature ($^{\circ}\text{C}$), R_N is net radiation (W m^{-2}), e_F^* is the saturated vapor pressure (kPa) at the temperature of the foliage, e_A is the actual vapor pressure of the air (kPa), ρ is the density of air (kg m^{-3}), c_p is the heat capacity of air ($\text{J kg}^{-1} \text{ }^{\circ}\text{C}^{-1}$), γ is the psychrometric constant ($\text{kPa } ^{\circ}\text{C}^{-1}$), r_A is the aerodynamic resistance of the plants to sensible heat transfer (s m^{-1}), and r_{FP} is the plant foliage resistance to water vapor transport under conditions of potential transpiration (s m^{-1}).

The second requirement for computing the IJ index is a knowledge of how high the foliage-air temperature differential of a plant canopy will rise in the absence of any transpirational water loss. Again, the approach used in this study to calculate this parameter is the most recent elucidation of the technique described by Idso et al. (1986a). For any given $T_F - T_A$ determination, then, the IJ index is given by the expression

$$IJ = \frac{(T_F - T_A) - (T_F - T_A)_L}{(T_F - T_A)_U - (T_F - T_A)_L}, \quad [2]$$

where the subscripts L and U refer to the lower and upper baseline values of $T_F - T_A$, respectively. However, since T_A is identical in all the terms of Eq. [2], the IJ index may be more compactly written as

$$IJ = \frac{T_F - T_{FL}}{T_{FU} - T_{FL}}, \quad [3]$$

where T_{FL} and T_{FU} are the lower and upper limiting (baseline) foliage temperatures, respectively, under identical air temperature and vapor pressure conditions.

MATERIALS AND METHODS

Experimental work was conducted over three summer growing seasons—comprising the months of June, July, and August in 1983, 1984, and 1985—at Phoenix, AZ, detailed descriptions of which are provided by Kimball et al. (1983–1985). In brief, cotton was grown out-of-doors in square, open-top, clear-polyethylene-wall, CO_2 -enrichment chambers measuring 3 m on a side and 2 m in height. Two replications of three treatments were maintained in each year: an ambient CO_2 treatment that had a mean daylight CO_2 concentration of $340 \mu\text{mol CO}_2 \text{ mol}^{-1}$ air over the 3 yr, a $500 \mu\text{mol CO}_2 \text{ mol}^{-1}$ air treatment, and a $640 \mu\text{mol CO}_2 \text{ mol}^{-1}$ air treatment. In all years the plants were irrigated so as to maintain plant transpiration at the maximum potential rate.

Foliage temperatures were measured on most cloudless days of all years over a 4-h midday time period centered at about 1330 h MST, with an Everest Interscience (Tustin, CA) Model No. 110 infrared thermometer.³ In 1983, each data point acquired represented the mean of 20 separate measurements taken with the infrared thermometer looking

straight down over the center of each chamber's middle row. Data acquisition in 1984 and 1985 was similar, but with 10 observations taken from each of the east and west sides of the middle row. In all cases, the infrared thermometer had a tilt of about 5° from the vertical, which, according to the study of Huband and Monteith (1986), would produce a change in radiant canopy temperature almost imperceptible from that measured from the vertical. In each year a different person collected the data. Maximum standard deviations of the individual data points from the mean foliage temperatures thus acquired were typically no greater than 0.4°C . Air wet- and dry-bulb temperatures were measured at hourly intervals with shielded aspirated psychrometers located about 0.5 m above the tops of the plants in each chamber.

Throughout the 1984 and 1985 growing seasons, leaf diffusion resistance was measured periodically as described by Kimball et al. (1983–1985) with a LI-COR (Lincoln, NE) 1600 steady state porometer³ in 1984, and a LI-COR 6000 portable photosynthesis system³ in 1985. When using the LI-COR 1600 instrument, three adaxial and three abaxial leaf surfaces at the top of the plant canopy were measured near the center of each chamber's middle row. From each pair of adaxial/abaxial measurements, a leaf stomatal diffusion resistance was calculated by summing the parallel resistances of both surfaces. Results for the three leaves were then averaged to yield a mean leaf diffusion resistance for each chamber. In the case of the LI-COR 6000 instrument, an average leaf resistance was obtained directly. Again, three measurements were pooled to produce each mean value. Due to various instrument problems, weather conditions, and lengths of time from irrigation, only 12 days of good data were available from the 1984 experiment, and 7 days from the 1985 study.

RESULTS AND DISCUSSION

Foliage Temperatures

Figure 1 shows the results obtained in 1985. The solid lines (which are identical on all three data-containing sections of the figure) represent the non-water-stressed baseline for cotton growing under ambient CO_2 conditions ($340 \mu\text{mol CO}_2 \text{ mol}^{-1}$ air), derived from Eq. [1] with R_N set equal to 525 W m^{-2} , which was typical (to within $\pm 100 \text{ W m}^{-2}$) of the season (June–August) and time period (centered at 1330 h MST) over which T_F , T_A , and VPD data were collected; r_A set equal to 15.0 s m^{-1} , the value determined to be appropriate for cotton by Idso et al. (1986a); and r_{FP} set equal to 25.0 s m^{-1} , the mean value found to pertain to ambient CO_2 conditions by Idso et al. (1986a), where both of these latter numbers were determined by fitting Eq. [1] to an independent ($T_F - T_A$) vs. VPD data set for well-watered cotton. For comparison, Fig. 1d also depicts non-water-stressed baselines for r_{FP} values of 29.6 and 35.8 s m^{-1} , which we determined to be the appropriately elevated values for the 500 and $640 \mu\text{mol CO}_2 \text{ mol}^{-1}$ air treatments from our 1984 and 1985 stomatal diffusion resistance measurements, which—although few in number—were the only basis we had for arriving at independent estimates of r_{FP} under CO_2 -enriched conditions. In the case of the r_A value used, the standard deviation of the data about the mean was $\pm 25\%$, while in the case

³ Trade names and company names are included for the benefit of the reader and imply no endorsement of the products listed by the U.S. Department of Agriculture.

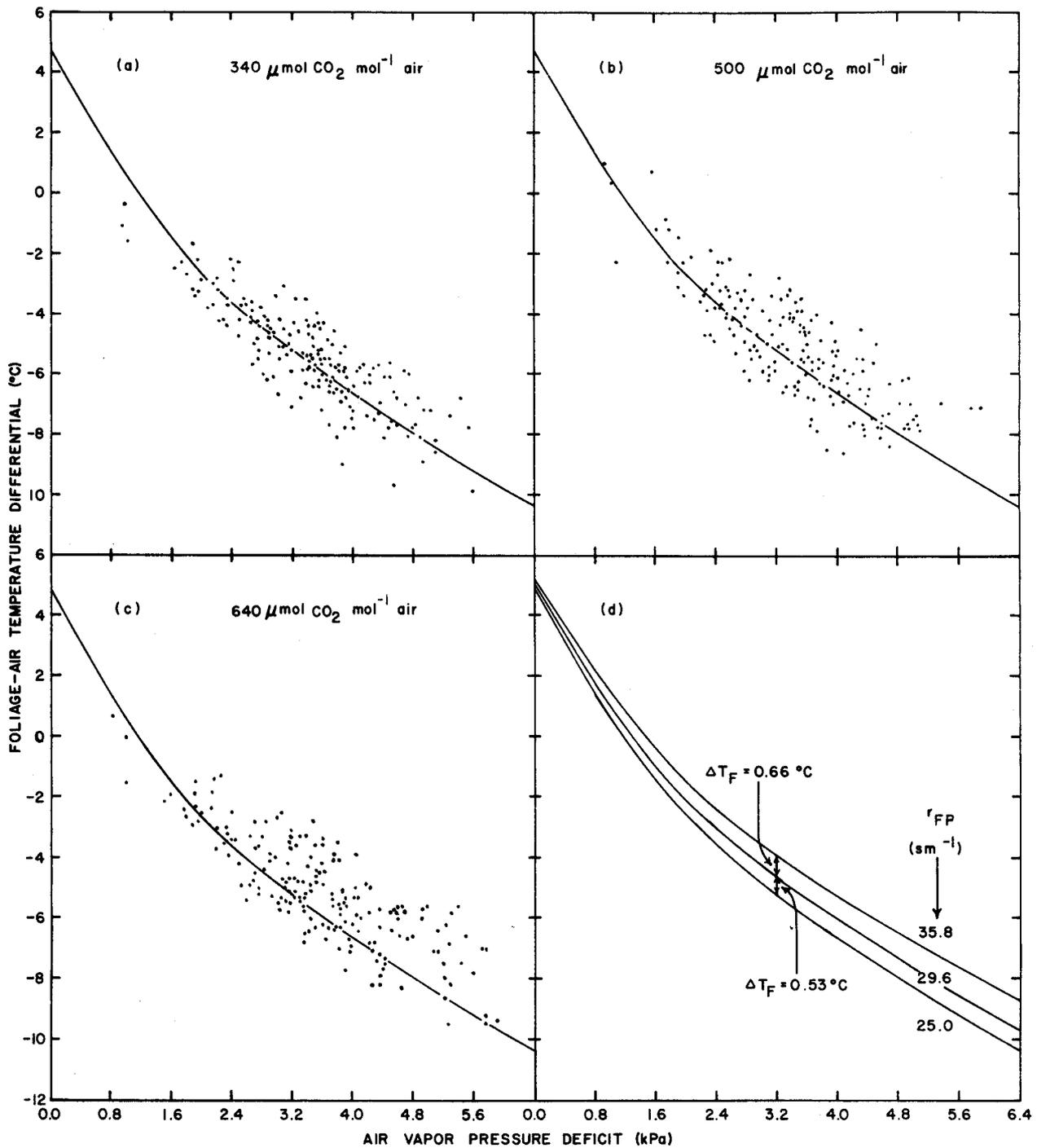


Fig. 1. Approximate 1330 h MST foliage-air temperature differential ($T_F - T_A$) vs. air vapor pressure deficit (VPD) for cotton growing under three different atmospheric CO₂ concentrations and transpiring at the potential rates for those conditions during June, July, and August at Phoenix, AZ. The solid dots are the data obtained during 1985. The solid lines passing through the three data sets are identical to each other and to the $r_{FP} = 25.0 \text{ s m}^{-1}$ non-water-stressed baseline of section (d). The three baselines of this section are calculated from Eq. [1] for a representative R_N value of 525 W m^{-2} , an r_A value of 15 s m^{-1} (as determined by Idso et al., 1986a), and the listed r_{FP} values determined in this study to prevail under the three different atmospheric CO₂ concentrations maintained in the chambers. The specified foliage temperature differentials (ΔT_F) between the 340 and 500 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air baselines and the 500 and 640 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air baselines are mean results for the entire air VPD range of 0.0 to 6.4 kPa.

of the r_{FP} values, standard deviations were about $\pm 15\%$.

Concentrating first on Fig. 1d, it can be seen that the vertical separation of the three CO₂-treatment baselines is small. Averaged over the air VPD range of 0.0 to 6.4 kPa (e.g., 3.2 kPa), a mean foliage tem-

perature increase (ΔT_F) of only 0.53°C is predicted for the 340 to 500 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air transition, while a further T_F increase of only 0.66°C is predicted for the subsequent 500 to 640 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air transition. Consequently, it can be appreciated from viewing the rest of the figure that we are looking for a CO₂-

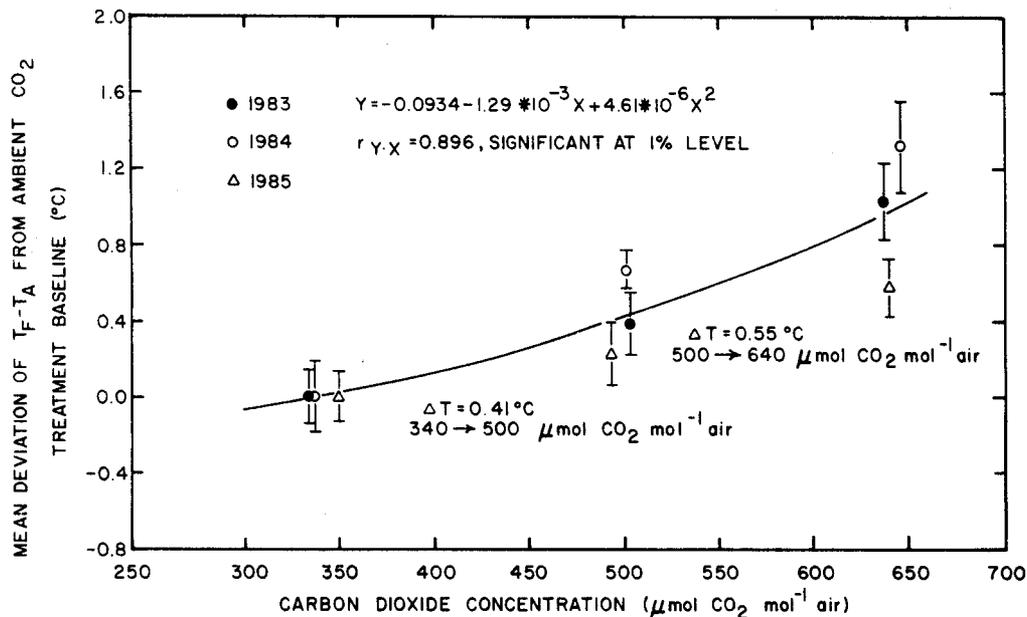


Fig. 2. Cotton foliage-air temperature differential increases caused by atmospheric CO_2 enrichment in the 3 yr of the study. Error bars represent 95% confidence intervals about the means for each year. The equation and r value were calculated by second order regression analysis of the nine mean temperature differentials plotted on the graph.

induced foliage temperature response that is much smaller than the magnitude of variability in the primary T_F , T_A , and VPD data. Nevertheless, in observing the changing relationship between the $r_{FP} = 25.0 \text{ s m}^{-1}$ non-water-stressed baseline and the $(T_F - T_A)$ vs. VPD data as the atmospheric CO_2 concentration increases from 340 to 500 to 640 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air, it appears that an antitranspirant effect of this magnitude is indeed present.

In order to determine the functional form of the $T_F - T_A$ dependency of cotton on the atmospheric CO_2 concentration, we calculated the mean deviation of all data points in each CO_2 treatment from the $r_{FP} = 25.0 \text{ s m}^{-1}$ baseline and plotted the result as a function of each treatment's atmospheric CO_2 content, as shown in Fig. 2. As can be seen in Fig. 2, all 3 yr show monotonically increasing foliage-air temperature differentials with increasing atmospheric CO_2 . In addition, the mean T_F/CO_2 response—as determined by the specified polynomial that provided the best fit to the data—is very close to that predicted by Eq. [1], utilizing our measured values of r_{FP} under CO_2 -enriched conditions: a measured ΔT_F of 0.41°C vs. a calculated value of 0.53°C for the 340 to 500 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air transition, and a measured ΔT_F of 0.55°C vs. a calculated value of 0.66°C for the 500 to 640 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air transition. Consequently, we conclude that a 330 to 660 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air doubling of the atmospheric CO_2 content produces about a 1.1°C increase in cotton foliage temperature under summer conditions at Phoenix, AZ, due to the effect of CO_2 on the parameter, r_{FP} .

Further support for this conclusion is provided by Fig. 3, where we have plotted calculated CO_2 -induced foliage temperature increases vs. measured CO_2 -induced foliage temperature increases for cotton, as determined from our study, and for water hyacinth [*Eichhornia crassipes* (Mart.) Solms]—the only other

plant so studied to date—as determined, in the case of the measured values, by the study of Idso et al. (1986b), and in the case of the calculated values, by the study of Idso et al. (1984a), which produced the appropriate r_{FP} values for the enriched CO_2 treatments, and the study of Idso et al. (1986a), which produced the appropriate r_A value. In all five comparisons there depicted, there is good agreement between calculated and measured results.

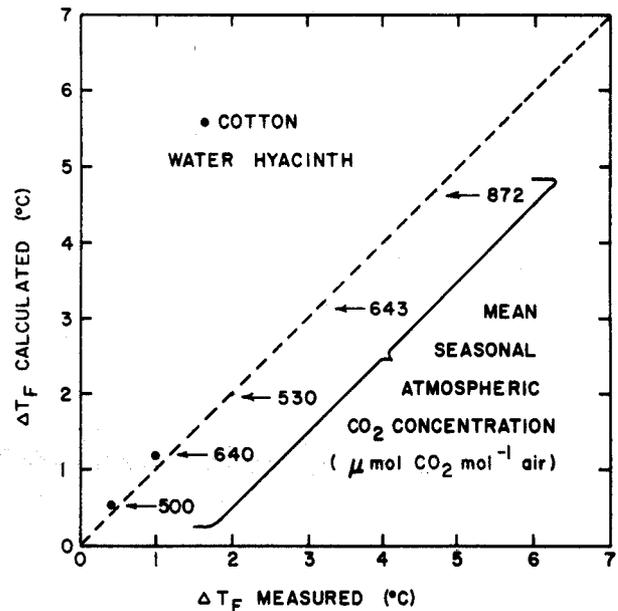


Fig. 3. Calculated vs. measured foliage temperature increases caused by atmospheric CO_2 enrichment. The solid dots are the mean results for the 3-yr cotton study, while the open circles are the results of a similar 1-yr study of water hyacinths performed by Idso et al. (1986b). The dashed 1:1 line represents the locus of perfect agreement between calculations and measurements. The mean ambient atmospheric CO_2 concentration for both studies was $340 \mu\text{mol CO}_2 \text{ mol}^{-1}$ air.

Plant Water Use

In the course of its theoretical development, Jackson et al. (1981) showed, by derivation from basic principles, that per-unit-leaf-area plant transpiration rate is an inverse linear function of the IJ index, which prediction has subsequently been experimentally confirmed by Idso et al. (1984a) in an open-field, free-air, CO₂-enrichment study of water hyacinths. A second test of the IJ technique for plant transpiration assessment is provided by Idso et al. (1985, 1986b), wherein a 330 to 660 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air doubling of the atmospheric CO₂ content resulted in a $3.0 \pm 0.1^\circ\text{C}$ increase in water hyacinth's midday foliage temperature and a $20.1 \pm 2.2\%$ reduction in water hyacinth's 24-h per-unit-leaf-area plant transpiration rate. In arriving at a prediction of this reduction in plant water use, we employ the most recent approach to calculating the IJ index provided by Idso et al. (1986a) and use as input parameters the same R_N value employed in our cotton study, 525 W m^{-2} , the mean air VPD value determined from Fig. 1 of Idso et al. (1986b), 4.4 kPa, the corresponding mean air temperature for this air VPD value determined from Fig. 3 of Idso et al. (1986a), 36.3°C , and the relationships for the upper and lower limiting values of $T_F - T_A$ provided by Fig. 1 and Fig. 4 of Idso et al. (1986a). By doing so, we calculate an IJ index of 0.197 ± 0.007 , and, noting that this index would apply throughout the entire daylight period for continuous CO₂ enrichment, this calculation thus implies a CO₂-induced decrease in water hyacinth's 24-h per-unit-leaf-area plant transpiration rate of $19.7 \pm 0.7\%$, which is in good agreement with the $20.1 \pm 2.2\%$ measured reduction.

With the confidence provided by this finding and the one previous validation of the IJ technique for estimating plant transpiration reduction (Idso et al., 1984a), we now calculate the per-unit-leaf-area plant transpiration rate reduction in cotton for a 330 to 660 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air doubling of the atmospheric CO₂ content under the mean conditions of the 3 yr of our experiment. Again, the appropriate value for R_N is 525 W m^{-2} ; however, for the air VPD, a mean value of 3.6 kPa is seen to prevail when all data are considered. For this air VPD value, Fig. 3 of Idso et al. (1986a) yields a mean T_A of 32.0°C , and, following the above procedure with these input parameters and our value of 1.1°C for the foliage temperature increase in cotton caused by a 330 to 660 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air doubling of the atmospheric CO₂ content, we calculate an IJ index of 0.09, which implies a CO₂-induced decrease in per-unit-leaf-area plant transpiration rate in cotton of 9%.

In the case of this prediction, it is more difficult to get a good comparison with measurements than it was with the water hyacinths. In all 3 yr of our experiment, for instance, soil water depletion measurements with a Campbell (Campbell Pacific Nuclear, Pacheco, CA) nuclear hydroprobe neutron soil moisture probe³ indicated a mean 5% increase in plant water use for a 330 to 660 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air doubling of the atmospheric CO₂ concentration (Kimball et al., 1983–1985). This seemingly contradictory finding could be due to an observed increase in leaf area with increasing CO₂, which would tend to offset the small per-unit-

leaf-area plant transpiration reduction predicted above, or it could be due to various problems associated with the hydroprobe method of crop water use assessment (Kimball et al., 1983–1985). In 1 yr (1983) of the study, for example, plant water use was additionally measured by lysimetry. In this year the lysimeter data indicated a 5% decrease in plant transpirational water loss rate with a 330 to 660 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air doubling of the air's CO₂ concentration. Thus, about all we can say is that our predicted per-unit-leaf-area crop water-use reduction (9%) is not inconsistent with the measurements of total crop water use we have acquired over 3 yr of experimentation.

Crop Yield

Net photosynthetic rates of plant leaves (Idso et al., 1982, 1984a, 1984b) and final yields of several crops (Idso et al., 1981; Diaz et al., 1983; Pinter et al., 1983; Reginato, 1983; Nakayama and Bucks, 1984) have been shown to be inverse linear functions of the IJ index. This relationship does not carry over directly to the situation we are investigating here, however, because the yield-reducing impact of closing plant stomata is more than compensated for by the stimulatory effect of higher atmospheric CO₂ concentrations on the photosynthetic process itself. Nevertheless, it would seem logical that a plant that does not close its stomata as much as does another, in response to an increase in atmospheric CO₂ content, will probably have a greater photosynthetic or yield response to that atmospheric CO₂ enrichment than does the other plant. Furthermore, since reductions in yield correlate linearly with the IJ index (i.e., since yield is an inverse linear function of the IJ index) (Idso et al., 1986a), it is also logical to assume that such relative increases would likewise correlate linearly with the relative IJ index responses of the two crops in question. That is, we feel it is a logical consequence of prior IJ index/crop yield studies to expect the yields of two crops (Y_1 , Y_2) to be related to their CO₂-induced IJ index values (IJ_1 , IJ_2) in the following way, as a result of an increase in atmospheric CO₂ concentration:

$$\frac{Y_1}{Y_2} = \frac{IJ_2}{IJ_1} \quad [4]$$

As a test of this hypothesis, we predict the biomass increase of cotton (Y_c) caused by a 330 to 660 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air doubling of the atmospheric CO₂ concentration, to be $Y_c = Y_{WH} \times (0.20/0.09)$, where Y_{WH} is the percentage biomass increase of water hyacinths caused by such a CO₂ concentration doubling, which Idso et al. (1985) have experimentally determined to be 38% (from their Fig. 1). Our predicted CO₂-induced biomass increase for cotton then is 84% ($Y_c = 38\% \times 0.20/0.09$), which is in good agreement with the mean 82% measured biomass increase of cotton for such a CO₂ concentration doubling obtained over the 3 yr of our experiment (Kimball et al., 1983–1985). It is also in good agreement with the corresponding 87% increase in the actual seed yield of cotton measured over this period. Consequently, we take these good correspondences between calculated and measured growth responses to provide support for the general

validity of Eq. [4]. It should be pointed out, however, that results for each individual year of the study do not correlate nearly as well with each other (i.e., calculated vs. measured biomass and yield) as do the 3-yr mean results.

CONCLUSIONS

On the basis of our experimental observations and their use in conjunction with other published findings, we conclude that: (i) A 330 to 660 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air doubling of the atmospheric CO_2 concentration leads to a midday foliage temperature increase in well-watered cotton of about 1.1°C when the mean air VPD is about 3.6 kPa. (ii) The per-unit-leaf-area plant transpiration reduction responsible for this foliage temperature increase is approximately 9%. (iii) The biomass or yield increase in well-watered cotton caused by a 330 to 660 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air doubling of the air's CO_2 content under these conditions is about 84% [(82 + 87)/2]. (iv) As a result of Conclusions (ii) and (iii), the per-unit-leaf-area water use efficiency of well-watered cotton grown at Phoenix, AZ, under summertime conditions rises by about 92% for such a CO_2 concentration doubling.

Another implication of our work is that foliage temperature measurements under ambient and CO_2 -enriched conditions may possibly be used to infer the transpiration and yield responses of many other crops with relative ease—the transpiration response directly from the crop's IJ index value, and its yield response (for a 330–660 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air doubling of the air's CO_2 content) from the equation

$$Y = 7.6\% (\text{IJ})^{-1}, \quad [5]$$

which comes directly from Eq. [4], and where the numerical coefficient 7.6 is the mean value of $Y_2 \cdot \text{IJ}_2$ for cotton ($84\% \times 0.09 = 7.6\%$) and for water hyacinth ($38\% \times 0.20 = 7.6\%$). More work of this nature should thus be conducted on other crops to determine the generality of Eq. [5], because, if it is universally valid for C_3 plants, it provides a rapid and efficient means for assessing the yield response of such crops to atmospheric CO_2 enrichment.

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