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Carbon dioxide enrichment and temperature effects on cotton canopy photosynthesis, transpiration, and water-use efficiency [1]

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Abstract

The objectives of this study were to evaluate effects of ambient and double ambient [CO_2] at a range of growing temperatures on photosynthesis, respiration, transpiration, water-use efficiency and dry matter accumulation of cotton plants (*Gossypium hirsutum* L., cv. DPL 50). In Experiment I, plants were grown outdoors until first bloom, then transferred into naturally lit growth chambers and grown for 22 days at 30/18°C with five CO_2 concentrations varying from 350 to 900 $\mu l\, l^{-1}$. In Experiment II, air temperatures were maintained at 20/12, 25/17, 30/22, and 35/27°C day/night during a 70-day experimental period with [CO_2] of 350 and 700 $\mu l\, l^{-1}$ at each temperature. Photosynthesis increased with [CO_2] from 350 to 700 $\mu l\, l^{-1}$ and with temperature. Plants grown at 35/27°C produced fewer bolls due to abscission compared with plants grown at optimum temperatures (30/20°C). At higher [CO_2], water-use efficiency increased at all temperatures due mainly to increased canopy photosynthesis but also to more limited extent to reduced canopy transpiration. Increased photosynthesis at higher [CO_2] resulted in greater dry matter accumulation at all temperatures except at 20/12°C. Respiration increased as dry matter and temperature increased. Plants grown at higher [CO_2] had less respiration per unit dry matter but more per unit area. These results indicate that future increases in [CO_2] are likely to benefit cotton production by increasing carbon assimilation under temperatures favorable for cotton growth. Reduced fruit weights at higher temperatures indicate potential negative effects on production if air temperatures increase as projected in a high-CO_2 world.

Keywords: Atmospheric CO_2; *Gossypium*; Photosynthesis; Temperature; Transpiration; Water-use efficiency

1. Introduction

The global atmospheric carbon dioxide concentration [CO_2] has increased by 30% since the industrial revolution, and the continuous measurement of [CO_2] at Mauna Loa, Hawaii, during a recent 32-y period indicated a 12% increase in the average annual concentration (Keeling and Whort, 1991). Currently, atmospheric [CO_2] is above 352 $\mu l\, l^{-1}$ and further increases are expected to result in 600 $\mu l\, l^{-1}$ CO_2 sometime between 2030 and 2070 (Schneider, 1989). Continuing increases in [CO_2] and other 'greenhouse' gases may cause as much as 3 to 6°C rise in average global atmospheric temperature due to doubling of present day [CO_2] (Grotch, 1988; Adams et al., 1990).

The primary effect of elevated [CO_2] on well-watered plants is an increase in net photosynthesis

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(Jones et al., 1984; Baker et al., 1990). Increased [CO_2] also causes partial stomatal closure, and increased stomatal resistance resulting in reduced transpiration per unit leaf area (Jones et al., 1985) which may increase leaf temperature (Idso et al., 1987). This indirect effect of [CO_2] on canopy temperature, in addition to any general rise in air temperature (Grotch, 1988; Adams et al., 1990), will have significant effects on productivity of agricultural crops (Reddy et al., 1992b; Hodges et al., 1993).

The positive short-term effects of CO_2 on growth and productivity of crops have been well documented by the reviews of Kimball (1983), Cure and Acock (1986), and Newton (1991); however, several aspects of effects of elevated CO_2 and temperature on productivity of crop plants are not yet clear (Gifford, 1992). Socias et al. (1993) reported that long-term exposure to high [CO_2] caused *Phaseolus vulgaris* L. plants to have lower rates of photosynthesis than control plants. Plants grown in high [CO_2] were less sensitive to low oxygen concentrations and, although they had similar amounts of ribulose-1,5-biphosphate carboxylase/oxygenase, some of it remained uncarbamylated and thus idle. Idso and Kimball (1993) on the other hand, reported that doubling the [CO_2] from 360 to 720 $\mu l\ l^{-1}$ increased net photosynthesis by a factor of two and decreased respiration by 50% in two tree species grown for 2 and 4 y. Cure and Acock (1986) failed to find reports about interacting effects of temperature and CO_2 on seed yield in their survey of eight major crops and they found only three studies of CO_2–temperature interactions on biomass production. More recently, Baker and Allen (1994) also pointed out the lack of information on the interactive effects of [CO_2] and temperature while noting that existing knowledge indicates that responses are species dependent. They suggested that more research is needed to determine plant responses to interactive effects of [CO_2] and other environmental variables.

In recent studies, growth and developmental rates of cotton were characterized at a range of temperatures under ambient [CO_2] (Reddy et al., 1991b, 1992a). They found that fruiting of well-watered cotton plants is sensitive to 35 and 40°C (daytime) temperatures. Plants grown at 35°C produced only 4% as much fruit as plants grown at 30°C, and plants grown at 40°C produced no fruit. They also found that temperature sensitivity of fruiting was similar among several upland cotton (*Gossypium hirsutum* L.) cultivars while pima cotton (*G. barbadense* L.) was even more sensitive to high temperature than upland cultivars (Reddy et al., 1992a). Thus, the effects of exposure to CO_2 and temperature are interactive, but literature showing plant responses to elevated atmospheric [CO_2] at different temperatures is limited. It is important to quantify the effects of [CO_2] and temperatures on plants because these variables can have a large impact on growth, development and yield.

The objective of this study was to evaluate the interactive effects of temperature and CO_2 on photosynthesis, transpiration, water-use efficiency, and dry matter accumulation by cotton.

2. Materials and methods

2.1. Plant culture

In Experiment I, upland cotton (cv. DPL 50) was sown 8 July 1989 into sand–vermiculite (3:1 v/v) in polyvinyl-chloride pots (0.15 m diameter, 0.67 m deep) as described by Reddy et al. (1991a). The plants were grown in the natural environment until first bloom and then moved into naturally lit plant growth chambers in three rows with a population of nine plants m^{-2}. These chambers were described in detail by Acock et al. (1985) and Reddy et al. (1991a). The plants were irrigated three times per day with half-strength Hoagland's nutrient solution (Hewitt, 1952) via a drip irrigation system. The chambers were set at 30/18°C (± 0.1°C, day/night) and maintained at 350, 450, 600, 750, and 900 $\mu l\ CO_2\ l^{-1}$ air ($\pm 10\ \mu l\ l^{-1}$) during the daylight. Plants were grown in the temperature- and CO_2-controlled conditions for 22 days. These plants achieved complete canopy closure, 98% solar radiation intercepted as measured by continuous monitoring with a model LI 191SB radiation sensor (LI-COR, Inc., Lincoln, NE) located at the bottom of the canopy, after only 2 days in the growth chamber. Graded shade cloths were adjusted around the plants to simulate shading effects found in a field crop. Gas-exchange data were summarized and photosynthesis calculated daily as described below. Photosynthesis at 1600 $\mu mol\ m^{-2}\ s^{-1}$ was averaged over 14 days in which peak PPFD exceeded 1600 $\mu mol\ m^{-2}\ s^{-1}$.

In Experiment II, DPL 50 plants were grown from seed in the controlled-environment chambers. Seed were germinated in moistened paper towels at 28/23°C day/night temperatures for 48 h. The germinated seed, with radicals emerging, were selected for uniformity and planted on 3 March 1989 into chamber soil bins filled with a mixture of sand and vermiculite (3:1 v/v). Plants were spaced 10 cm apart in three 0.66-m rows (15 plants m^{-2}). The plants were irrigated with a drip-irrigation system with one emitter per plant, three times a day with half-strength Hoagland's solution (Hewitt, 1952). Amount of water and thus nutrients supplied depended on the previous day's transpiration. To avoid plant damage, insects were controlled by spraying appropriate insecticides.

The temperature- and CO_2-controlled chambers were maintained at 28/23°C ($\pm$0.1°C, day/night) for 14 days after emergence (DAE). At that time, the cotyledons of the cotton plants were fully expanded and the plants were 30 mm in height. Temperature and CO_2 treatments were imposed 15 DAE. Thereafter, air temperatures in the chambers were maintained at 20/12, 25/17, 30/22, 35/27°C ($\pm$0.1°C) until the plants were harvested, 70 DAE. Dewpoint temperatures were not controlled, but measured at 10-s intervals with gold mirror hygrometers installed inside the return air line. The average daytime and nighttime dewpoint temperatures were 18.1°C $\pm$ 0.38 and 15.5°C $\pm$ 0.39 during the first 14 days (prior to temperature treatment). Vapor pressure deficits, calculated between dew point and chamber temperatures, varied little during daytime hours while increasing from near 1.2 kPa at 20°C to near 3.0 kPa at 35°C. There were no differences between CO_2 levels maintained at the same air temperatures. Daytime temperatures were initiated at sunrise and returned to nighttime temperature 1 h after sunset. The CO_2 concentrations were maintained at 350 and 700 $\mu l\ l^{-1}$ air ($\pm$10 $\mu l\ l^{-1}$) for each temperature utilizing eight controlled-environment cabinets. Graded shades surrounded the plants to simulate border plants. All the plants were dissected at harvest into leaves, stem, roots, and fruiting structures, dried, and the parts weighed. When the plants were grown at near optimum temperature (30/22°C), they produced about 15 bolls per plant.

2.2. Carbon dioxide and temperature control

Carbon dioxide concentration, air temperature, and irrigation in the chambers were controlled by a computer and a data acquisition system that monitored environmental and gas-exchange variables. Continuous circulation of air maintained uniform temperatures throughout the chambers and low leaf boundary-layer resistance. The chambers were sealed, and the CO_2 concentration was monitored at 10-s intervals and averaged over 900-s periods (Acock et al., 1985). Carbon dioxide was injected automatically from a gas cylinder into the chambers as necessary to maintain the desired set points + 10 $\mu l\ l^{-1}$.

2.3. Measurement of photosynthesis and transpiration

Solar radiation was measured with a model 200 SB pyranometer (LI-COR, Inc., Lincoln, NE) at a weather station about 50 m from the site and summarized with a data acquisition system at 900-s intervals.

Data for canopy net CO_2 exchange rates (P_n) were summarized over the same time intervals. Gross photosynthesis (P_g) was calculated by adding dark respiration (R_d) to observed net photosynthesis (P_n).

$$P_g = P_n + R_d \quad (1)$$

Dark respiration used in Eq. 1 was the average rate for the first hour of each night while air temperature was still that maintained during the day. Curves of P_g vs. I (photosynthetic photon flux density, PPFD) were fitted with a rectangular hyperbola (Acock et al., 1976):

$$P_g = \alpha I \tau C / (\alpha I + \tau C) \quad (2)$$

where α is canopy light-utilization efficiency, τ is canopy conductance to CO_2 transfer, and C is external CO_2 concentration. The initial slope of the curve is α and the asymptotic value of P_g when the light is no longer limiting is τC. Daily data for P_g and I were fitted with Eq. 2 using the Gauss–Newton nonlinear least-squares interactive method as interpreted by the SAS Institute (1990) in their NLIN procedure. This allowed interpolation of standard P_g rates at 1600 μmol photons $m^{-2}\ s^{-1}$.

Condensate water was collected from the cooling coils and weighed automatically each 900-s period (McKinion and Hodges, 1985). This condensate rep-

resented whole-canopy transpiration as a vapor barrier was placed over the soil surface and sealed around the plant stems to prevent evaporation from the soil. Excess irrigation escaped via a small opening in the soil bin.

2.4. Statistical procedures

Statistical analyses to test differences between treatments were performed using dummy-variable regression analysis of SAS GLM procedures (SAS Institute, 1990). Differences between treatments over time were determined using tests for heterogeneity of slopes and comparison of intercepts for canopy photosynthesis, canopy transpiration and water-use efficiency. Standard error of each mean was calculated and presented in the figures. Environmental control was maintained throughout both experiments as documented by 900-s monitoring logs. The chambers were designed to avoid hot or cold spots, and with uniform water and nutrient applications, variance among plants within each chamber was small. Previous replicated experiments demonstrated that there was more variance within than between chambers.

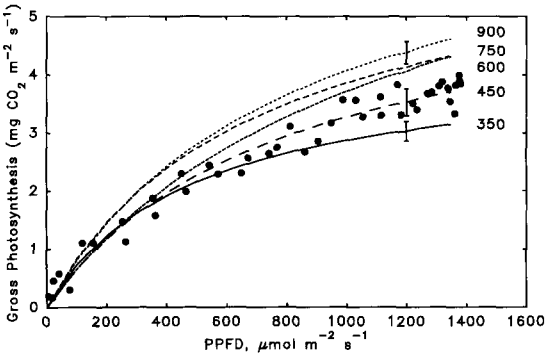

Fig. 1. Canopy gross photosynthesis (P_g) as a function of photosynthetic photon flux density (PPFD) 16 days after beginning CO_2 treatment for fruiting cotton plants grown in 30/18°C day/night temperatures (Experiment I). The regression lines were estimated by a least-squares fit of the 900-s data points collected throughout the day for each treatment. For clarity, individual points are presented only for the 450 μl CO_2 l^{-1} air treatment. Vertical bars represent 95% confidence intervals for three CO_2 concentrations at 1200 μmol m^{-2} s^{-1}.

3. Results

3.1. Canopy photosynthesis and respiration

In Experiment I, photosynthesis of fruiting cotton plants increased as CO_2 and PPFD increased (Fig. 1). There were differences in canopy light-utilization efficiency (initial slopes of curves when PPFD was limiting) but the responses did not increase linearly with additional CO_2. Also, the differences were not consistent from day to day (Table 1). There were increases in P_g throughout the boll-filling period with the increases being greater with elevated [CO_2] (data not shown). The response to additional PPFD decreased as radiation increased particularly for canopies grown in lower CO_2 concentrations. Average P_g rates at 1600 μmol m^{-2} s^{-1} PPFD observed during a 14-d period for plants in Experiment I are illustrated in Fig. 2. The P_g of plant canopies averaged 34% more when grown

Table 1
Canopy light utilization efficiency (α) and canopy conductance to CO_2 transfer (τ) for cotton canopies grown in 350 and 700 μl CO_2 l^{-1} air at various temperatures (Experiment II). Standard errors of the mean are given

Days after emergence	Temp. (°C)	α (μmol CO_2 μmol^{-1} photons)		τ (mm s^{-1})	
		350 μl CO_2 l^{-1} air	700 μl CO_2 l^{-1} air	350 μl CO_2 l^{-1} air	700 μl CO_2 l^{-1} air
64	20/12	0.014 ± 0.002	0.011 ± 0.001	1.2 ± 0.09	0.3 ± 0.05
	25/17	0.052 ± 0.004	0.045 ± 0.003	7.5 ± 0.39	4.9 ± 0.36
	30/22	0.055 ± 0.004	0.084 ± 0.005	9.1 ± 0.55	6.7 ± 0.29
	35/27	0.057 ± 0.005	0.068 ± 0.003	10.3 ± 0.68	8.1 ± 0.31
70	20/12	0.018 ± 0.003	0.027 ± 0.002	1.8 ± 0.19	0.5 ± 0.29
	25/17	0.066 ± 0.003	0.064 ± 0.003	9.0 ± 0.35	7.0 ± 0.46
	30/22	0.061 ± 0.003	0.077 ± 0.003	11.8 ± 0.68	9.6 ± 0.42
	35/27	0.057 ± 0.003	0.077 ± 0.003	14.7 ± 0.97	11.4 ± 0.61

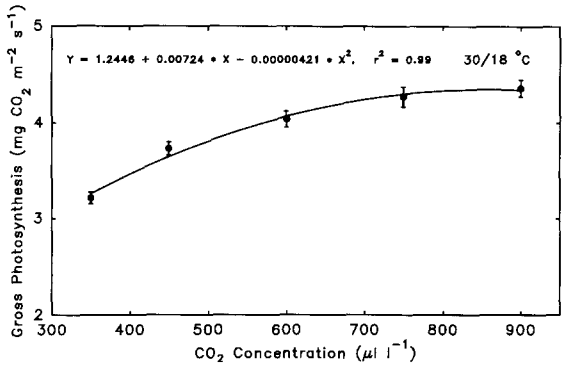

Fig. 2. Canopy gross photosynthesis of fruiting cotton canopies to different atmospheric CO_2 concentrations at a photon flux density of 1600 μmol m^{-2} s^{-1} (Experiment I). Rates at 1600 μmol m^{-2} s^{-1} were estimated from a least-squares fit of the 900-s data points collected throughout each day for each treatment when photosynthetic flux density exceeded 1600 μmol m^{-2} s^{-1}, and those values averaged for the 14 days ± standard error of the mean.

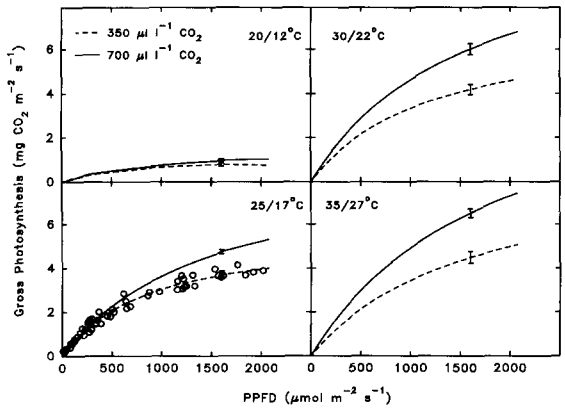

Fig. 3. Responses of canopy gross photosynthetic rate (P_g) to photosynthetic photon flux density (PPFD) 64 DAE for cotton grown in various temperatures at 350 and 700 μl CO_2 l^{-1} air (Experiment II). For simplicity, individual points are provided only for the 350 μl l^{-1} at 25/17°C. Vertical bars represent 95% confidence intervals at 1600 μmol m^{-2} s^{-1}.

in 900 μl CO_2 l^{-1} air than when grown in 350 μl l^{-1}. Canopy photosynthetic capacity of fruiting plants reached maximum values at 700 μl l^{-1} CO_2 and followed by a leveling response from 700 to 900 μl l^{-1}.

In Experiment II, canopy photosynthesis of plants grown from seed, expressed on a ground-area basis, was greater at 700 μl CO_2 l^{-1} air than that of plants grown in 350 μl l^{-1} at all four temperatures (Fig. 3). Photosynthesis increased as temperature increased to 30/22°C in both CO_2 concentrations. Canopy photosynthesis at 1600 PPFD μmol m^{-2} s^{-1} increased

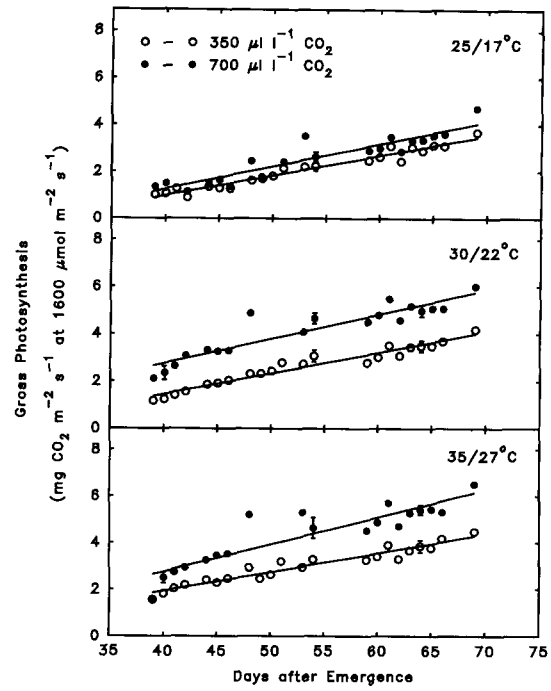

Fig. 4. Effects of temperature and CO_2 concentration on cotton canopy gross photosynthetic rate (P_g) at a photon flux density of 1600 μmol m^{-2} s^{-1} (Experiment II). The vertical bars represent 95% confidence intervals from the regression equation fit to each day's data at 40, 54 and 64 DAE. Regression parameters are presented Table 2.

Table 2
Parameters for linear equations regressing canopy photosynthesis (y, mg CO_2 m^{-2} s^{-1}) as a function of days after emergence (x) where $y = b_0 + b_1 x$ (Experiment II)

Temperature (day/night) (°C)	CO_2 (μl l^{-1})	Regression parameters		r^2
		b_0^a	b_1^b	
25/17	350	−2.443	0.0854	0.98
	700	−2.591	0.0962	0.93
30/22	350	−2.059	0.0878	0.97
	700	−1.390	0.1036	0.93
35/27	350	−1.309	0.081	0.97
	700	−1.901	0.117	0.90

[a]The intercepts are significantly different ($P = 0.05$) between CO_2 levels within temperatures at 25/17 and 30/22°C and between temperatures within CO_2 level.
[b]The slopes differ significantly ($P = 0.05$) between CO_2 levels at 35/27°C.

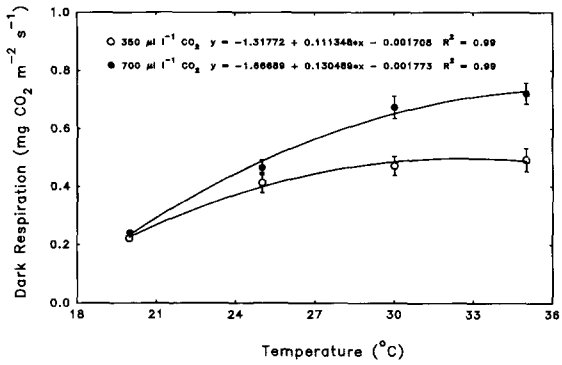

Fig. 5. Respiration rates of cotton canopies grown at various temperatures and CO_2 concentrations of 350 and 700 μl l^{-1} air (Experiment II). The data were averaged from 35 to 69 DAE and standard errors of the means are shown where they are larger than the symbols. The data are expressed on a ground area basis.

continuously from 40 to 70 DAE in both CO_2 concentrations at all temperatures (Fig. 4, Table 2). Photosynthetic rates of plants in 350 μl l^{-1} at 70 DAE were more than double the rates of the same plants 40 DAE; and plants growing in 700 μl l^{-1} were fixing carbon three times more rapidly at 70 DAE than at 40 DAE. Photosynthetic rates of plants growing at 700 μl l^{-1} and in 35/27°C increased significantly faster than for plants growing in 350 μl l^{-1} at the same high temperatures. This difference was probably due to the more rapid addition of new leaves by plants growing in high CO_2 and high temperature. Rapid addition of new leaves provides the canopy with a population of younger leaves that more effectively respond to the high CO_2 (Reddy et al., 1994). Photosynthetic rates of plants growing in 700 μl CO_2 l^{-1} air at 25/17°C and 30/22°C were greater than plants growing in 350 μl l^{-1}, but the changes in rates with age of the plants were not different between CO_2 levels.

The changes in respiration reflected changes in temperature and accumulated dry matter. Canopy respiration of plants grown in 700 μl CO_2 l^{-1} air increased as temperature increased (Fig. 5). Respiration rates of plants in ambient CO_2 were greatest at 30°C. The increase in respiration with elevated CO_2 and increased photosynthesis probably was due mostly to the greater amount of biomass present (leading to more maintenance) and to the faster growth rate (leading to more respiration associated with biosynthesis).

3.2. *Canopy light-utilization efficiency and canopy conductance to carbon dioxide transfer*

Canopy light-utilization efficiency (α) was greater in plants grown in higher [CO_2] (Table 1). The α values tended to increase as temperature increased to 30°C (day) but were inconsistent at 35°C. Large α values were generally associated with treatments having high growth rates. Canopy conductance to CO_2 transfer (τ) for canopies in 350 and 700 μl CO_2 l^{-1}

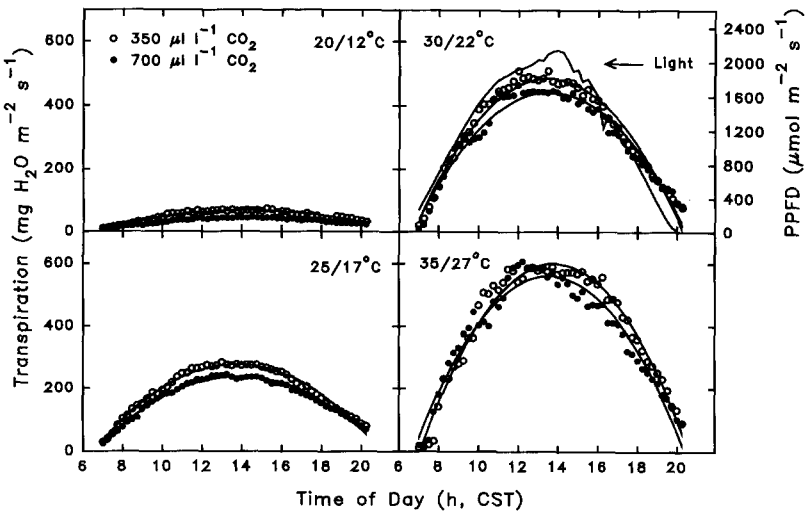

Fig. 6. Diurnal trends in canopy transpiration rates and photosynthetic photon flux density 62 DAE for cotton canopies grown at various temperatures in 350 and 700 μl CO_2 l^{-1} air (Experiment II). The data points are 900-s measured values. Regression parameters are presented Table 3.

Table 3
Parameters for quadratic equations regressing canopy transpiration (y, mg H_2O m^{-2} s^{-1}) as a function of hours of the day (x) where $y = b_0 + b_1x + b_2x^2$[a] (Experiment II)

Temperature (day/night) (°C)	CO_2 ($\mu l\ l^{-1}$)	Regression parameters[a]			r^2
		b_0	b_1	b_2	
20/12	350	−163	32	−1.13	0.98
	700	−91	19	−0.65	0.98
25/17	350	−728	146	−5.30	0.99
	700	−625	124	−4.48	0.99
30/22	350	−1437	285	−10.53	0.99
	700	−128	254	−9.36	0.98
35/27	350	−908	363	−13.14	0.99
	700	−1653	327	−12.06	0.98

[a]Regression lines are significantly different ($P = 0.05$) between CO_2 levels within the temperatures and between temperatures within the CO_2 level.

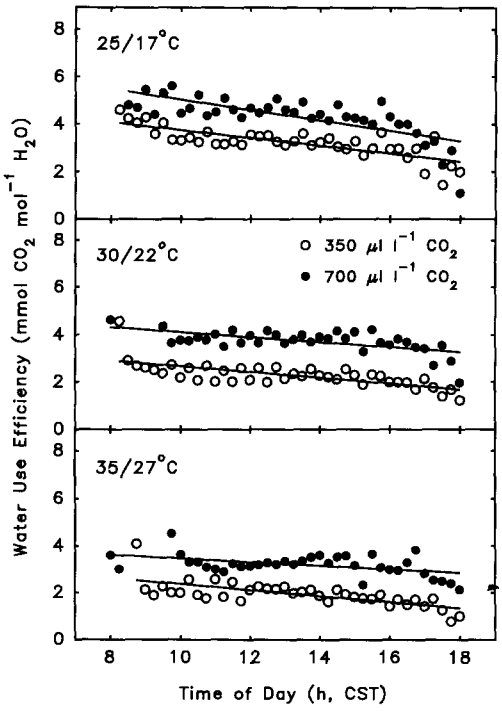

Fig. 7. Diurnal trends in water-use efficiency 62 DAE of cotton canopies grown at 25/17°C, 30/22°C, or 35/27°C and in 350 or 700 μl CO_2 l^{-1} air (Experiment II). Leaf areas of plants grown in 700 $\mu l\ l^{-1}$ CO_2 were 51, 35 and 49% more than those of similar plants grown in 350 $\mu l\ l^{-1}$ at the respective temperatures. Regression parameters are presented Table 4.

air 64 and 70 DAE in various temperatures are presented in Table 1. Plants grown in 350 $\mu l\ l^{-1}$ had significantly larger τ values than plants grown in 700 $\mu l\ l^{-1}$ on all days and at all growing temperatures. Canopy conductance increased with increased growing temperatures in both CO_2 levels.

3.3. Transpiration and water-use efficiency

The diurnal trends of canopy transpiration rates of plants grown in 350 and 700 $\mu l\ l^{-1}$ at four temperatures (Experiment II), and the diurnal trend in photosynthetic photon flux density (PPFD) are presented for a fairly cloud-free day (DAE 62) in Fig. 6 and Table 3. Transpiration rates closely tracked PPFD at both CO_2 levels and in all temperatures. Transpiration increased significantly with increasing temperature, while CO_2 enrichment reduced transpiration a smaller, but significant, amount at all temperatures.

The larger photosynthetic rates and the slightly lower transpiration rates of plants grown in high CO_2 resulted in greater water-use efficiency (Fig. 7 and Table 4). Average water-use efficiency increased about 41% at 25/17°C, 57% at 30/22°C, and 52% at 35/27°C by 100% increase in CO_2 concentration.

3.4. Dry matter accumulation

Dry matter accumulation reflected treatment differences in canopy photosynthesis caused by temperature

Table 4
Parameters for linear equations regressing water-use efficiency (y, mmol CO_2 mol^{-1} H_2O) as a function of hours of the day (x) where $y = b_0 + b_1x$ (Experiment II)

Temperature (day/night) (°C)	CO_2 ($\mu l\ l^{-1}$)	Regression parameters		r^2
		b_0^a	b_1^b	
25/17	350	5.386	−0.00273	0.77
	700	7.239	−0.00367	0.73
30/22	350	3.893	−0.00204	0.69
	700	5.162	−0.00175	0.68
35/27	350	3.640	−0.00213	0.59
	700	4.223	−0.00129	0.47

[a]The intercepts are significantly different ($P = 0.05$) between CO_2 levels within temperatures, and between temperatures at the 350 $\mu l\ l^{-1}$ level.

[b]The slopes differ significantly ($P = 0.05$) between temperatures at 700 μl CO_2 l^{-1} air.

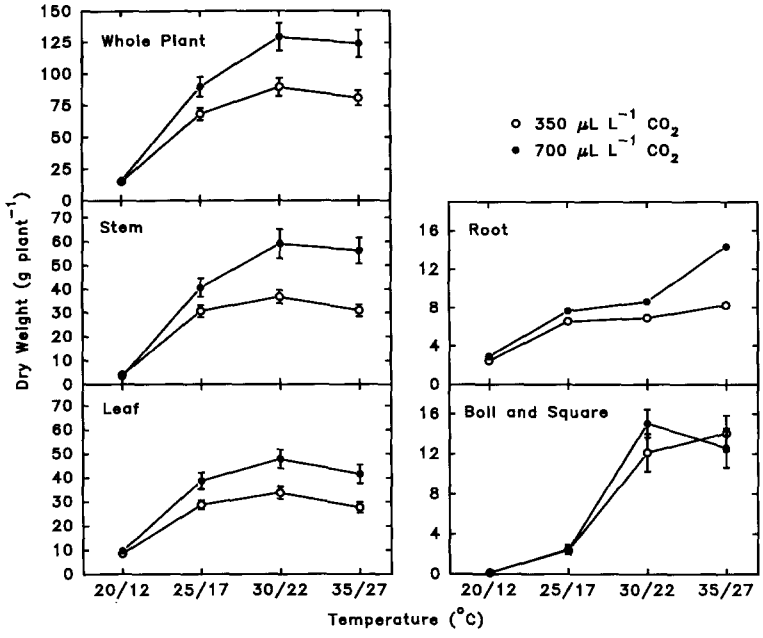

Fig. 8. Dry matter accumulation in cotton plant parts as affected by temperature and CO_2 concentrations at 70 DAE (Experiment II). Standard errors of the means of nine plants are shown where they are larger than the symbols.

and CO_2 concentrations of Experiment II (Fig. 8). Maximum dry matter accumulation occurred in plants grown at 30/22°C at both [CO_2], even though gross photosynthesis rates were slightly greater on most days for plants grown at 35/27°C. Respiration rates were also greater in plants grown at 35/27°C compared to 30/22°C, resulting in more dry matter accumulation at 30/22°C. Dry matter accumulation was greater in plants grown in all temperatures at 700 μl CO_2 l^{-1} air compared to 350 μl l^{-1}.

4. Discussion

4.1. Canopy photosynthesis and respiration

Photosynthesis increased rapidly with increases in PPFD and small differences due to atmospheric CO_2 were detected very quickly. Idso and Kimball (1993) found that eucalyptus and Australian bottle trees increased photosynthetic rates considerably more when exposed to high CO_2 environments for a 4-y period than when similar trees were grown in ambient CO_2 environments, or exposed to high concentrations of CO_2 for only short periods.

Plants placed in varying CO_2 environments at flowering appeared to saturate in response to CO_2 between 700 and 900 μl CO_2 l^{-1} air (Fig. 2). This response is in contrast to the linear increases in P_n found in eucalyptus between 400 and 1000 μl l^{-1} (Idso and Kimball, 1993). It was similar, however, to rice canopies grown at a range of [CO_2] (Baker et al., 1990). The low [CO_2] at which these cotton plants appeared to saturate may have been due to the limitations in sink activity. The plants had just begun flowering when placed in the controlled environments and they had only a few young bolls at the time of these measurements.

Photosynthesis at 20/12°C was less than 1 mg CO_2 m^{-2} s^{-1} at both CO_2 concentrations. Temperature at 20/12°C was much more limiting to photosynthesis than CO_2 at these concentrations.

Canopy photosynthesis at 1600 μmol m^{-2} s^{-1} PPFD was about 50% more for young cotton plants grown for 70 d in the high CO_2 environment (Figs. 3, 4) than in fruiting cotton transferred into high CO_2 at first flower (Fig. 2). This is not surprising as plants grown from seedlings to 70 d had the opportunity to develop additional sinks compared to plants grown outside and moved into the chambers at flowering.

The leaf area index of plants grown in Experiment II more than doubled between 40 and 70 DAE (Reddy

et al., 1994). The P_g rates were thus enhanced by greater light capture as well as greater photosynthetic capacity and rapid growth (Fig. 4). Day-to-day variation observed at all temperatures did not appear to be treatment-related. Similar day-to-day variation in canopy photosynthesis was reported for cotton (Reddy et al., 1991a), for soybean (Dreger et al., 1969; Acock et al., 1985), and for rice (Baker et al., 1990), but the cause of the variation is unknown.

Respiration rates are strongly influenced by carbohydrate supply (Baker et al., 1972; Coggeshall and Hodges, 1980; Mullen and Koller, 1988; Reddy et al., 1991a). Specific respiration rates of plants grown in high CO_2 were reported to decrease (Wullschleger et al., 1992; Idso and Kimball, 1993). In this experiment biomass was measured only at the end. If one makes an assumption that the ratios of biomass found in the CO_2 treatments at the end of the study represented the ratios when respiration measurements were taken throughout the experiment, then the plants grown in 700 μl CO_2 l^{-1} air were respiring 16% less per unit aboveground biomass than those in 350 μl l^{-1} CO_2. Amthor (1991) proposed several alternative mechanisms that might cause altered levels of respiration at elevated [CO_2]. A more likely situation in this experiment may be that plants grown in high CO_2 for longer periods accumulated more biomass. Most of that tissue is probably structural parts or storage material that has only a small respiratory requirement.

4.2. Transpiration and water-use efficiency

Transpiration rates of plants grown in high [CO_2] were significantly lower in all temperatures than plants grown in ambient CO_2. Total daily transpiration was 18, 6, and 5% less in the 700 μl CO_2 l^{-1} air compared at 350 μl l^{-1} at 25/17°C, 30/22°C, and 35/27°C, respectively (Fig. 6). These decreases in canopy transpiration occurred in spite of 10 to 15% more leaf area of plant canopies grown in high-CO_2 (Reddy et al., 1994). The exact amount depended on temperature. This indicates greater canopy resistance to water vapor flux in high-CO_2 grown canopies. Canopy water-use efficiency declined with increased temperature due to increased water loss. Doubling [CO_2] enhanced water-use efficiency mainly due to increased photosynthesis. Similar reductions in canopy transpiration were reported for rice (Baker et al., 1990) and soybean (Jones et al., 1985) with increasing [CO_2]. Using simulation models, under a climate-change scenario of increased temperature and doubled [CO_2], Curry et al. (1990) predicted increased water-use rather than decreased water requirements (reciprocal of water-use efficiency) as observed in our studies and others (Jones et al., 1985; Baker et al., 1990).

4.3. Dry matter accumulation

Total dry matter increased by 6% at 20/12°C, 30% at 25/17°C, 45% at 30/22°C, and 53% at 35/27°C plants grown with high CO_2 compared plants grown with ambient CO_2 (Fig. 8). Dry matter accumulation increased in all plant parts except fruiting structures as temperature increased at both [CO_2] levels. The response to [CO_2] was greater with favorable growing temperatures. Plants grown in high [CO_2] increased stem weight compared to ambient CO_2 environments by 19, 32, 61, and 81% at 20/12, 25/17, 30/22 and 35/27°C, respectively. A similar response to increased [CO_2] was observed in leaf weight. The increases in root dry matter with high atmospheric CO_2 were 20, 16, 25 and 74% at 20/12, 25/17, 30/22 and 35/27°C, respectively. The relatively large increase in root weight (74%) at 35/27°C was probably caused in part by more readily available carbohydrates due to high-temperature-induced fruit abortion. It was reported that high temperature inhibits production of pollen in cotton (Meyer, 1969) and enhances square and fruit abortion (Reddy et al., 1992b). Canopy temperature was not measured in these experiments, but other studies have shown only small midday differences between air and canopy temperatures in these chambers. Differences in root growth due to [CO_2] did not result in any shift in root/shoot ratio of plants in any of the temperature treatments.

In earlier field studies where cotton plants were exposed to various temperatures for short periods, it was concluded that photosynthesis rates were not responsive to temperature (Baker, 1965; Baker et al., 1972). By contrast, in this study, the plants were grown at several well-controlled temperatures throughout most of the growth cycle, resulting in large differences in growth rates and demand for carbon. Higher photosynthetic rates also occurred in plants grown at the two higher temperatures than occurred at the two lower

temperatures. It is not feasible to separate cause and effect from these data.

5. Conclusions

This study evaluated cotton plants exposed to different atmospheric [CO_2] and temperatures. The greatest effect of high CO_2 atmospheres was at temperatures near optimum for growth. Large increases in photosynthesis and small decreases in transpiration due to doubling the ambient [CO_2] resulted in large increases in water-use efficiency. Leaf areas of plants grown in high CO_2 increase more rapidly than leaf areas of plants grown in ambient CO_2 and the two effects of elevated CO_2 are somewhat compensating until the ground is shaded with leaves. However, after a full canopy is developed one would expect the effect of decreased transpiration due to increased stomatal resistance of plants grown in high CO_2 to deplete soil moisture more slowly. The processes sensitive to leaf or soil-water status will be less effected by elevated CO_2. Plants grown in 700 μl CO_2 l^{-1} air had large increases in plant weight.

Plants grown at 35/27°C were above optimum temperature for fruit retention. Doubling CO_2 did not increase mass in fruiting structures compared to increases in vegetative structures at these higher temperatures. Temperatures of 35/27°C and higher are common during the flowering periods in many cotton growing areas even in present-day CO_2 environments. The anticipated 3 to 6°C rise in average summer temperatures in the U.S. cotton belt will be very detrimental for cotton fruit production, as CO_2 enrichment did not ameliorate fruit retention at high temperatures. Our results demonstrate prospects for improved plant growth and yield at elevated CO_2, but the responses are highly temperature dependent. Heat tolerant cultivars are needed, will be more productive, and have fewer delays due to abscised fruit, in the present-day CO_2 world. They will surely be more essential in a warmer global climate.

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