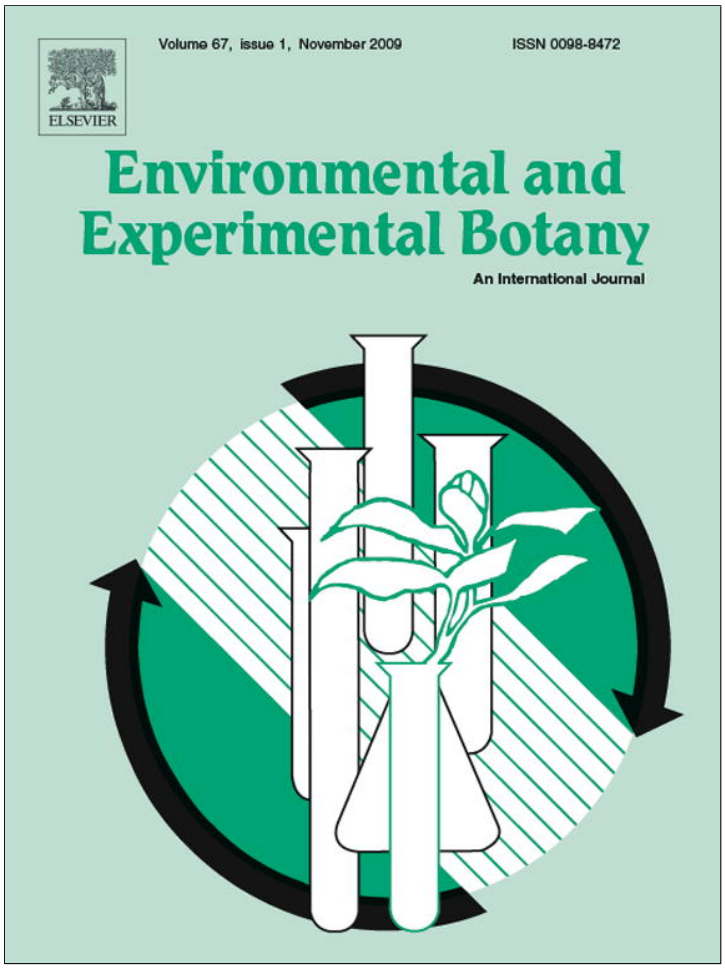

Environmental and Experimental Botany 67 (2009) 178–187

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Growth and development of cotton (*Gossypium hirsutum* L.) in response to CO_2 enrichment under two different temperature regimes

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ARTICLE INFO

Article history:
Received 13 January 2009
Received in revised form 18 June 2009
Accepted 29 June 2009

Keywords:
Global climate change
CO_2 × temperature interaction
Gossypium hirsutum L.
Elevated CO_2
Biomass and partitioning

ABSTRACT

An increase in atmospheric CO_2 concentration ($[CO_2]$) together with other climate change factors could greatly affect agricultural productivity. Understanding the impact of the change in atmospheric $[CO_2]$ in conjunction with the ongoing global change is crucial to prepare for mitigation and any adaptation for future agricultural production. The main goal of this project was to study the time-course pattern of cotton plant growth in response to $[CO_2]$ and temperature to investigate the hypothesis that whether response to elevated $[CO_2]$ would change at different temperatures. An experiment was conducted in the controlled-environment chambers of the Georgia Envirotron with two different day/night temperatures levels, e.g., 25/15 °C and 35/25 °C, and three CO_2 concentrations, e.g., 400, 600 and 800 μmol l^{-1}. The experimental design was completely randomized with four replicates (plastic containers) per treatment. Growth analysis was conducted at bi-weekly intervals during the growing season. In addition, leaf area, leaf dry mass, root dry mass, square dry mass, boll dry mass and total above dry mass per plant were also measured at each sampling. Plant traits, including plant height, number of leaves, number of squares and number of bolls were recorded weekly. The number of days to emergence, squaring, flowering and maturity were also observed. The results showed that by increasing $[CO_2]$ to 600 μmol l^{-1} total biomass increased at both temperature levels, but a further increase of $[CO_2]$ up to 800 μmol l^{-1} increased total biomass only at the temperature of 35/25 °C. Throughout the growing season, there was no significant effect of $[CO_2]$ levels on LAI. Increasing temperature from 25/15 °C to 35/25 °C had a positive impact on LAI across all CO_2 levels ($P < 0.05$). Increasing CO_2 from 400 to 600 μmol l^{-1} significantly increased the number of squares by 31.4%, but a further increase to 800 μmol l^{-1} caused a 6.6% decrease (non-significant) in the number of squares. The interactive effects of $[CO_2]$ and temperature indicated that at a higher temperature, CO_2 would be more beneficial as we proceed towards the end of the growing season. However, further studies are needed to really understand the interaction between higher $[CO_2]$ and temperature levels and cultivar characteristics.

1. Introduction

It is well known that the carbon dioxide (CO_2) concentration of the global atmosphere has increased during the last few decades and continues to increase, mainly due to energy consumption from fossil fuels. It is expected that it might reach a concentration of 600–1000 μmol l^{-1} by the end of this century (Cox et al., 2000). Elevated $[CO_2]$ is expected to enhance the productivity of C3 plants because of its stimulatory effect on photosynthesis and inhibiting effect on photorespiration (Lawlor and Mitchel, 2000). Along with an increase in $[CO_2]$, climate projections indicate changes in other climate factors such as temperature. Interactive effects of climate factors on plants significantly contribute to and increase the uncertainty of crop performance under potential climate change (Kimball et al., 2002; Bannayan et al., 2005; Bloom, 2006). Understanding the linear and non-linear response of crop growth and development to CO_2 under either low or high temperatures is very crucial for accurate prediction of crop performance under future climate change. Elevated $[CO_2]$ could enhance cotton production for areas where, due to low temperature, production of cotton is now limited. On the other hand, a temperature rise above the cotton required optimum range (Bednarz and van Iersel, 2001) and along with elevated $[CO_2]$ (Reddy et al., 1995a) could potentially result in a serious reduction in crop productivity. Cheng et al. (2009) found that high night temperature during the reproductive growth stage reduced the stimulatory effect of elevated $[CO_2]$ on brown rice yield.

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doi:10.1016/j.envexpbot.2009.06.015

There are still many uncertainties about the interactive effects of increasing temperature and [CO_2] on plant growth and development. The quantification and analysis of the interactive effects of temperature and [CO_2] is very important in order to understand the plant's carbon balance. Idso et al. (1987), Baker et al. (1989), Delgado et al. (1994) and Newman et al. (2001), working with a range of crops including aquatic floating plants, soybean, winter wheat and forages, reported that CO_2 effects generally increase with increasing temperatures, whereas, rice studies by Allen et al. (1995), soybean studies by Tremmel and Patterson (1993) and *Abutilon theophrasti* and *Amaranthos retrofletus* studies by Coleman and Bazzaz (1992) showed that CO_2 effects were greater at ambient temperature (28/22 °C) than at high temperature (38/31 °C).

Reddy et al. (2005) indicated that, similar to other C3 crops, the leaf-level photosynthetic rates of cotton were 9% and 22% greater for plants grown at 450 and 700 μl CO_2 l^{-1} when compared to those grown at 350 μl CO_2 l^{-1} at 26 °C. They also stated that individual cotton leaf photosynthesis response to atmospheric [CO_2] would be greater at higher temperature, and showed that at 700 μl CO_2 l^{-1} photosynthesis increased by 22% at 26 °C, 22% at 31 °C and 54% at 36 °C. Reddy et al. (2005) monitored the response of the cotton canopy to elevated [CO_2] at 34 °C and found that either a further decrease or increase in temperatures would lead to a lower canopy response. However, there was no effect of elevated [CO_2] on timing of phenological development stages, i.e., days required from emergence to first square, square to flower, and from flower to open boll (Reddy et al., 2005). Elevated [CO_2] also showed a positive effect on cotton dry matter production and final yield (Kimball and Mauney, 1993; Mauney et al., 1994; Reddy et al., 1995b). The positive response of fruit yield was related to a greater number of bolls under CO_2 enrichment, which in turn was due to an increase in branching and more fruiting sites for each branch.

During the growing season, many environmental factors have a significant effect on the morphological structure and physiological functioning of plants. It is clear that, depending on the development stage, the plant's response might be different (Rawson, 1992; Hacour et al., 2002). Quantification of the interactive effects of CO_2 and temperature would be more reliable when the isolated effect of either factor could be studied, not only at a specific growth stage or at maturity, but especially during the growing season with frequent plant sampling and growth analyses. Certainly, the magnitude and direction of the response to each environmental factor can vary with the developmental stage. Considering this fact, a growth analysis sampling procedure within the growing season would fulfill the detailed required information of the plant's response to CO_2 and temperature. However, most studies that have been conducted so far for cotton did not analyze plant growth and partitioning over time. The response of any crop to different combinations of CO_2 and temperature is a critical research issue in order to be able to predict cotton production under possible future climate change. The hypothesis of this study was that the responses to elevated [CO_2] may differ at different temperature levels and that a potential reduction in yield due to high temperatures very relevant when studying the effect of elevated [CO_2] on crop performance under future climate change (Baker et al., 1989). The objective of this study, therefore, was to monitor the response of cotton to CO_2 and temperature and their interaction on the various facets of plant growth and development as the growth proceeds from emergence towards maturity.

2. Materials and methods

2.1. Environment

The experiment was conducted in the controlled-environment chambers of the Georgia Envirotron, located at the University of Georgia Griffin Campus (Ingram et al., 1998). Six Conviron growth chambers (model CG72), with a floor space of 8.64 m^2 and a height of 2.20 m, were used in this experiment. Each chamber was individually controlled with a touch screen that included alarm condition information, programming, diagnostics, and data logging features. A central personal computer allowed for programming of the desired climate conditions in the chambers and storing the environmental data for each chamber. Lighting levels were adjustable at five different intensity levels and were provided by banks of twenty high-pressure sodium lamps and twenty metal halide lamps. Photosynthetic active radiation (PAR) was 753.7 μmol m^{-2} s^{-1} during the course of the experiment. An external refrigeration unit controlled temperature over a range of 4.0 ± 0.5 to 40 ± 0.5 °C. Carbon dioxide was automatically injected into the chambers and the level was controlled using a CO_2 delivery system and chamber vents. An individual LICOR infrared gas analyzer (LI-800 GasHound CO_2 Analyzer, LI-COR, NE, USA) was used to monitor CO_2 levels for each chamber independently; the accuracy of the analyzer was 2% at a level of 700 μmol l^{-1}. All chambers also included a drip irrigation system.

There were six treatments, consisting of all combinations of 2 day/night temperatures (25/15 °C and 35/25 °C) and three CO_2 concentrations (400, 600 and 800 μmol l^{-1}). The experimental design was completely randomized, with four replicates (plastic containers) per treatment. The experimental unit was a container with one plant per container; there were a total of 28 containers in each chamber. The containers were filled with washed sand; the weight of the sand in each container was 22 kg. Five seeds of the cotton cultivar DP 448B were sown in each container and thinned to one plant per container after germination. The containers were watered with a modified half-strength of Hoagland's solution (Downs & Hellmers, 1975) three or four times per week in order to avoid water and nutrient stresses. The containers were rotated biweekly until flowering to minimize any borders effects. The distance between containers was maintained at 35 cm × 30 cm (9.5 plants m^{-2}) and was similar to the plant spacing found in farmers' fields.

2.2. Measurements

Growth analysis was conducted six times during the growing season. For each growth analysis sampling, four containers, containing one plant each, were randomly selected from each growth chamber to determine the individual plant components. At each sampling, above ground components, root weight, plant height, number of leaves, number of squares and bolls were measured. For sampling, each plant was cut at the base and the individual plant components were separated into leaves, stems, petioles, squares (greater than 3 mm) and bolls. They were then dried at 65 °C for a minimum of 72 h. Total aboveground dry biomass for each container was obtained by adding all plant aboveground components. The leaf area was determined with a leaf area meter (LI 3000, LI-COR, NE, USA). Following each sample, the total leaf area, leaf dry mass, root dry mass, petiole dry mass, square dry mass, boll dry mass, total above dry mass and root dry mass per plant were determined.

The roots were carefully washed in water to remove all soil particles and were dried at 65 °C for a minimum of 72 h and total root biomass was obtained. For each growth analysis sample, the root:shoot ratio (R:S) and average root biomass per plant, the specific leaf area (SLA) as the ratio of leaf area to leaf biomass, leaf area ratio (LAR) as leaf area to aboveground biomass, leaf mass ratio (LMR) as leaf biomass to total plant aboveground biomass were also calculated. The number of days to 50% emergence, squaring and flowering were also recorded.

Table 1
Days from planting to emergence and from emergence to start of squaring, start of flowering and harvest maturity under CO_2 enrichment and two different temperature regimes.

Temperature (°C) (day/night)	CO_2 level (μmol l^{-1})	DDE[a]	Emergence (DAP)[b]	Squaring (DAE)[c]	Flowering (DAE)	Maturity (DAE)
	400	730.3	5	59	81	150
25/15	600	716.9	5	67	90	148
	800	643.2	4	72	78	146
	400	1135.6	3	47	62	146
35/25	600	1102.2	3	46	61	144
	800	1068.8	2	46	59	142

[a] DDE: degree days after emergence.
[b] DAP: days after planting.
[c] DAE: days after emergence.

2.3. Statistical analysis

An analysis of variance was conducted to evaluate the effects of CO_2 and temperature on several growth characteristics using the ANOVA Procedure of SAS System, Version 8.1 (SAS Ins., 2001). Growth characteristics included in the analysis of variance (ANOVA) consisted of plant height, leaf number, leaf area, root, leaf, stem and reproductive organs weight for each week during the treatment period. [CO_2] and temperature were main-plot factors, and days after emergence was a split-plot factor. A two way ANOVA of the dry weight of each organ and whole plants, boll weight and seed and lint yield at harvest for effects of [CO_2], temperature and [CO_2] × temperature.

The individual plant data were converted to unit ground area by considering the plant population of the experiment.

3. Results and discussion

3.1. Development

3.1.1. Temperature

Most cotton cultivars are insensitive to photoperiod and it is generally expected that temperature is the main environmental factor that controls development. Increasing the temperature from 25/15 °C to 35/25 °C decreased the number of days from seeding to emergence by 2 days across all CO_2 levels (Table 1). Increasing the temperature also prominently reduced the number of days from emergence to squaring (Table 1). On average, the number of days from emergence to squaring at 35/25 °C was almost 46 days, which was 20 days less than the number of days from emergence to squaring at 25/15 °C. These results were consistent with Reddy et al. (1995a). Similar to squaring, increasing the temperature from 25/15 °C to 35/25 °C also reduced the number of days from emergence to flowering. The mean number of days from emergence to flowering for 35/25 °C was 61, compared to 83 days for 25/15 °C across all [CO_2] levels. Increasing the temperature to 35/25 °C also decreased the maturity date by 4 days at each [CO_2] level.

3.1.2. Carbon dioxide

At a [CO_2] of 800 μmol l^{-1}, emergence was 1 day faster for both temperature regimes. At 25/15 °C, increasing [CO_2] from 400 to 600 μmol l^{-1} increased the number of days to squaring by 8 days, and a further increase of CO_2 to 800 μmol l^{-1} decreased the number of days to squaring by 13 days, compared to 400 μmol l^{-1}. At both temperature levels, the number of days from emergence to flowering decreased by 2 days when CO_2 increased from 400 to 600 μmol l^{-1}. Increasing [CO_2] further from 600 to 800 μmol l^{-1} decreased the number of days from emergence to flowering by 13 days, compared to 400 μmol l^{-1}. At the higher temperature (35/25 °C), increasing [CO_2] shortened the time from emergence to flowering (Table 1). The time to flowering decreased by 2 days as [CO_2] increased from 400 to 600 μmol l^{-1} and from 600 to 800 μmol l^{-1}. The comparison between the temperature of 35/25 °C and 25/15 °C showed that [CO_2] had less effect on the duration from emergence to flowering at the higher temperature (Table 1). At both temperature levels, each increment increase in [CO_2] by 200 μmol l^{-1} decreased the number of days from emergence to maturity by 2 days (Table 1). However, these results are in contrast to Reddy et al. (1999), who did not find any [CO_2] effect on phenology when CO_2 was increased from 360 to 720 μmol l^{-1}. Higher [CO_2] might affect reproductive development either directly or indirectly by an increase in canopy temperature due to lower transpiration rates of the cotton plants. Further research is needed to determine the exact mechanism of the effect of CO_2 on phenology. However, there is no indication that a reduction in transpiration due to higher [CO_2] would sufficiently increase the canopy temperature to affect vegetative and reproductive development (Yoshimoto et al., 2005).

Both the direct and indirect effect of CO_2 on phenology is still in discussion, and different crops have shown different responses (Allen et al., 1989; Bhattacharya et al., 1985; Hesketh and Hellmers, 1973; Chaudhuri et al., 1986; Garbutt et al., 1990). Li et al. (1997) reported that CO_2 enrichment significantly increased spikelet primordium initiation and decreased the duration of the spikelet development phase for spring wheat grown under free-air CO_2 enrichment (FACE). However, little or no effect of CO_2 on wheat development was reported in earlier studies (Krenzer and Moss, 1975; Schonfeld et al., 1989). Acceleration of the development rate due to CO_2 enrichment was also reported for rice (Imai et al., 1985). In a review, Rawson (1992) concluded that carbon availability can modify the development rate. He also mentioned that a change in the development rate due to CO_2 enrichment is associated with source limiting conditions. Such a condition is most likely also associated with a high temperature, which increases the sink demand. It is clear that a high temperature impacts cotton phenology, but that the effect of CO_2 due to contrasting results of various experiments requires further study.

3.2. Vegetative growth

3.2.1. Canopy height and leaf number

Increasing the [CO_2] compared to ambient [CO_2] had little effect on plant height. At final sampling, plant height was 25% higher at 600 μmol l^{-1} and 30% higher at 800 μmol l^{-1} compared to ambient [CO_2] for the 25/15 °C treatments. At the higher temperature level (35/25 °C), plant height was not changed at both higher [CO_2] (600 and 800 μmol l^{-1}). Reddy et al. (1995a) found that plants at 700 μl CO_2 l^{-1} were taller than those grown at 350 μl CO_2 l^{-1}. For the entire growing season, plant height at 35/25 °C was 2.8 times higher compared to 25/15 °C at 400 μmol l^{-1}, 2.7 times at 600 μmol l^{-1} and 2.2 times at 800 μmol l^{-1}. Similar to Reddy et al. (1995a), we also found that canopy height was more sensitive to temperature than to CO_2.

Table 2
Final leaf number, RGRL (relative growth rate of leaves), SLA (specific leaf area) and root:shoot ratio, averaged over the entire growing season based on growth analysis samples in response to CO_2 and temperature.

Thermal environment	CO_2 (μmol l^{-1})		
	400	600	800
Final leaf number (per plant)			
25/15 °C^{b}	20.7^{a}	15.2^{c}	19.2^{b}
35/25 °C^{a}	37.7^{b}	32.7^{c}	38.0^{a}
RGRL			
25/15 °C^{a}	0.87^{a}	0.88^{a}	0.99^{a}
35/25 °C^{a}	1.04^{a}	1.05^{a}	1.04^{a}
SLA (cm^2 g^{-1})			
25/15 °C^{b}	118.03^{a}	101.66^{b}	87.81^{c}
35/25 °C^{a}	147.36^{a}	150.75^{a}	106.85^{b}
Root:shoot ratio			
25/15 °C^{b}	0.18^{a}	0.15^{a}	0.19^{a}
35/25 °C^{a}	0.20^{a}	0.22^{a}	0.22^{a}

Mean values followed by the same letter are not significant different at $P \leq 0.05$. Effects of CO_2 should be valued for each temperature separately. Letters on left side of temperature regime signify only temperature effect.

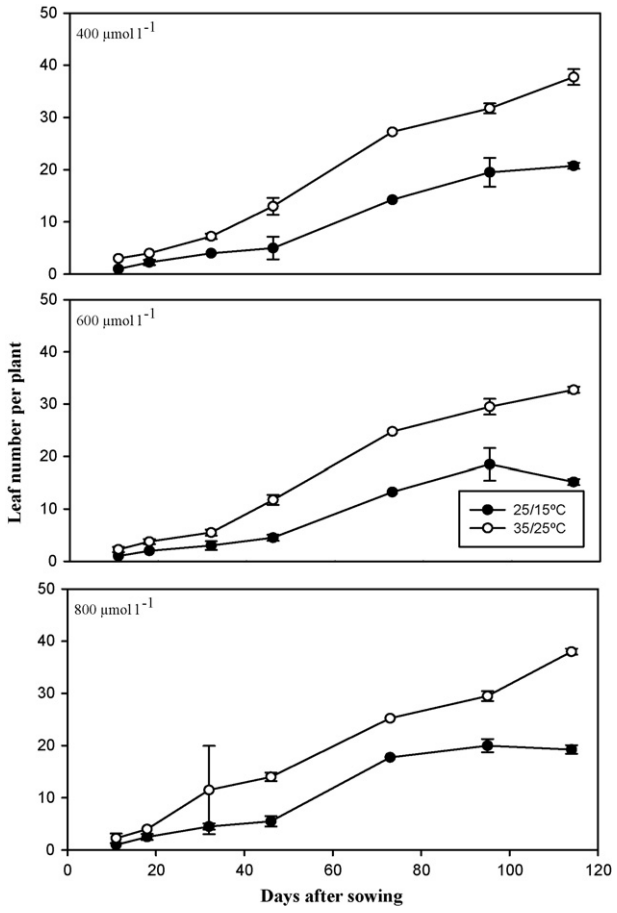

Fig. 1. The number of leaves per plant as a function of days after planting for two temperature regimes and three [CO_2] levels.

In comparison to ambient, elevated [CO_2] at 600 μmol l^{-1} did not change the number of leaves significantly ($P > 0.05$) for the entire growing season. However, a further increase to 800 μmol l^{-1} increased the number of leaves at both temperature levels (Table 2), but it was not significant. For all three [CO_2], levels, the increase in the number of leaves due to temperature was significant ($P < 0.05$) (Table 2, Fig. 1).

3.2.2. Biomass accumulation and partitioning

The time course of above ground biomass was different among the three [CO_2] levels (Fig. 2a). At 25/15 °C, there was not much difference among the effects of the [CO_2] levels on biomass accumulation up to 67 days after sowing, which almost coincided with the beginning of canopy closure. For the remainder of the season, however, [CO_2] had a strong effect on above ground biomass accumulation (Fig. 2a) and there was a difference among [CO_2] levels and their impact on biomass. The ANOVA analysis of the growth data showed that the interaction of CO_2 × temperature up to four weeks after emergence was not significant. Starting around six weeks after emergence, which coincided with the linear or constant growth rate, this interaction was significant until final harvest. At final harvest, total biomass was 2.2 times higher at 600 μmol l^{-1} compared to 400 μmol l^{-1}, while a further increase to [CO_2] 800 μmol l^{-1} resulted in an almost 10% higher total biomass compared to 600 μmol l^{-1} at 25/15 °C. At the higher temperature (35/25 °C), total biomass decreased by 23% when [CO_2] increased from 400 to 600 μmol l^{-1}, but it increased by 6% at 800 μmol l^{-1} compared to ambient [CO_2]. Data analysis revealed a significant different effects of both CO_2 and temperature and their interaction on total biomass ($P < 0.05$) at final harvest. Reddy et al. (1995b) reported that doubling CO_2 caused cotton plants to produce 40% more leaf, stem and root mass than when grown in ambient [CO_2]. Kimball and Mauney (1993) reported a 63% increase of cotton above ground biomass by increasing [CO_2] from 350 to 650 μmol l^{-1} for a 5 year study conducted in open top chambers. Similar results were obtained for cotton plants grown under FACE conditions of 370 vmol mol^{-1} vs 550 vmol mol^{-1} [CO_2] (Prior et al., 1994).

In our study, the increase in total biomass with elevated [CO_2] at both temperatures was higher, but not proportional to the change of LAI in response to CO_2. This may indicate higher resource use efficiency per absorbing unit leaf area than increasing the area for capturing of resources (Fig. 2b). It is obvious that plants with more or less the same LAI produced more biomass at elevated [CO_2], which reflects the limiting CO_2 effect at ambient levels (Fig. 2b). Reddy et al. (2005) stated that a higher total production in response to elevated [CO_2] was due to higher photosynthetic rates. In their study, temperature showed a higher impact on biomass than CO_2. We found that at final harvest, an increase in temperature from 25/15 °C to 35/25 °C increased total biomass by 69% at 400 μmol l^{-1}, 41% at 600 μmol l^{-1}, and 54% at 800 μmol l^{-1} of [CO_2].

At the lower temperature (25/15 °C), an increase in CO_2 from 400 to 600 μmol l^{-1} showed a relative decrease in root weight over the entire growing season compared to the lower CO_2 level. However, at 800 μmol l^{-1} root weight responded positively and starting at six weeks after emergence until final harvest it was significantly higher than the two lower [CO_2] levels. Root weight at a temperature of 35/25 °C compared to 25/15 °C, was significantly higher for all [CO_2] levels. In comparison to 400 μmol l^{-1}, root weight at 35/25 °C increased by 41.4% and 6.2% in response to 600 and 800 μmol l^{-1} of CO_2, respectively. An increase in root dry weight under elevated [CO_2] conditions has been found for various crops, including wheat (Chaudhuri et al., 1990), sorghum (Chaudhuri et al., 1986), and soybean (Del Castillo et al., 1989). Prior et al. (1994) applied 370 and 550 μmol l^{-1} CO_2 and found 60% more root weight in cotton plants exposed to elevated [CO_2].

Regardless of the change in production capacity, indices such as LAI or NAR, environmental factors may modify carbon partitioning among different organs during the growing season. Increasing temperature increased the root to shoot ratio (R:S), at final harvest but the change was not significant ($P = 0.77$). An increase in [CO_2] from 400 to 600 μmol l^{-1} at 25/15 °C, decreased the R:S ratio, but a further increase in [CO_2] to 800 μmol l^{-1} increased the R:S ratio again (Fig. 3). It seemed that at 25/15 °C and at elevated [CO_2] (600 μmol l^{-1}), most of the carbon was partitioned to the shoot

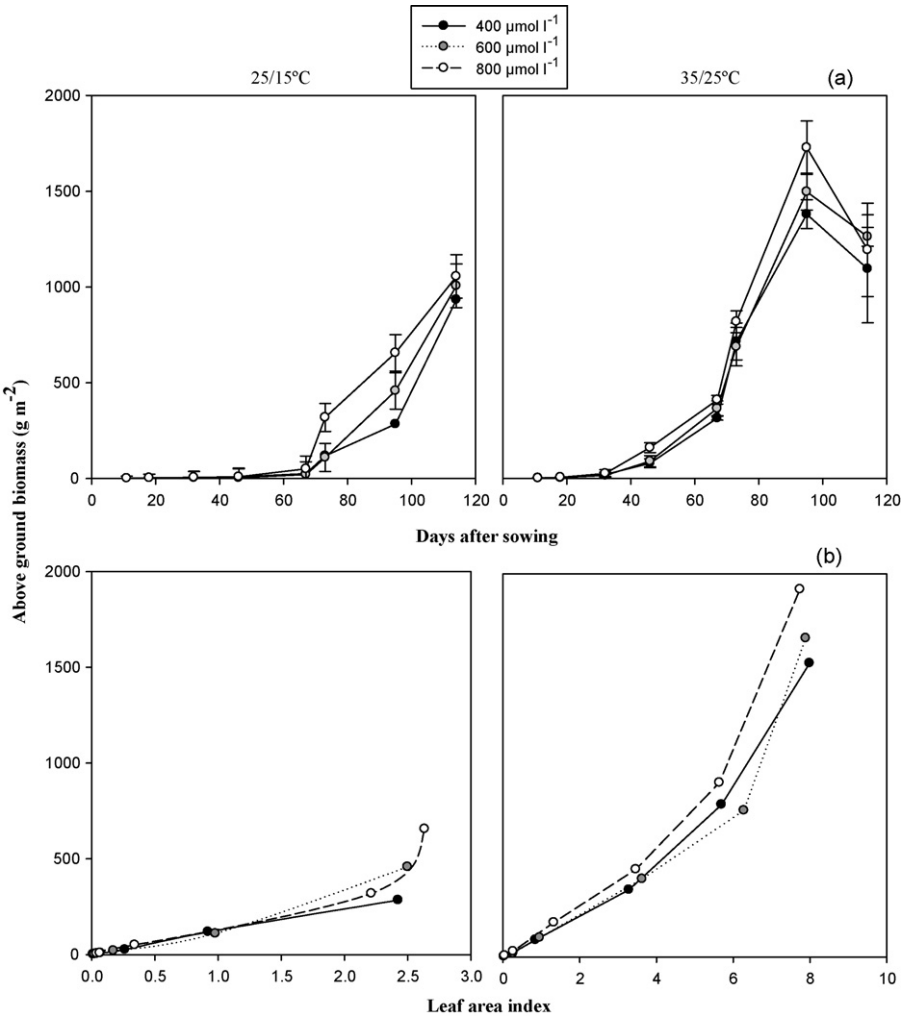

Fig. 2. Total biomass production in response to [CO_2] and temperature (a), relationship between leaf area and biomass (b), for plants exposed to two temperature regimes and three [CO_2] levels.

(Fig. 3). At 35/25 °C both 400 and 600 µmol l^{-1} levels of [CO_2] increased the R:S ratio.

Partitioning biomass to leaves showed a similar response to partitioning to roots throughout the growing season at the two temperature and three [CO_2] levels (Fig. 3). However, partitioning to leaves was higher for the two elevated [CO_2] treatments compared to ambient [CO_2], mainly prior to canopy closure (67 days after planting). Partitioning to stems (Fig. 3) showed an opposite response to CO_2 and temperature compared to partitioning to leaves. Overall, [CO_2] did not show a significant effect on biomass partitioning to stems. However, partitioning was slightly lower at both elevated [CO_2] compared to ambient [CO_2] throughout the growing season. For the higher temperature treatment (35/25 °C), plants partitioned more biomass to stems compared to the lower temperature treatment 25/15 °C ($P < 0.05$) for all three [CO_2] levels. It seemed that higher CO_2 was more beneficial to leaves than to stems, but when the temperature increased, more biomass was partitioned into the stems as structural organs.

3.2.3. Leaf area

Our results showed that there was no significant effect ($P = 0.19$) of [CO_2] levels on LAI throughout the growing season, although LAI was slightly higher at both 600 and 800 µmol l^{-1} compared to ambient [CO_2] (Fig. 4). This was consistent with Rufty et al. (1994), who found that leaf area of cotton was only slightly higher under elevated [CO_2] compared to ambient for different light conditions. Reddy et al. (1995a) found a positive response of LAI to elevated [CO_2] for cotton plants. In contrast to CO_2, temperature showed a significant effect ($P < 0.0001$) on LAI and the increase in temperature increased LAI (Fig. 4). Plants exposed to higher temperature (35/25 °C) showed an earlier start of the linear increase in LAI when compared to the lower temperature (25/15 °C) (Fig. 4). Maximum LAI obtained at 95 DAS at 35/25 °C compared to 25/15 °C, was higher by 3.3% at 400 µmol l^{-1}, 3.2% at 600 µmol l^{-1} and 3.0% at 800 µmol l^{-1} CO_2. A similar effect of temperature on leaf area was reported by Reddy et al. (1995a).

The relative growth rate of LAI (RGRL), which is the slope of the natural logarithm of LAI against days after sowing (DAS), showed an increase by increasing CO_2 at the lower temperature (25/15 °C) (Table 2), while for 35/25 °C, all [CO_2] levels showed similar effect on RGRL. This result indicated a higher canopy closure rate at elevated [CO_2] at the lower temperature, although there was no significant difference in final LAI in comparison with ambient [CO_2].

Leaf area development of different crops responds differently to CO_2. Ziska et al. (1996) found that the leaf of rice increased with an increase in N fertilizer rates, but did not find any effect of CO_2 on leaf area or LAI. However, the LAI of perennial ryegrass (Nijs et al., 1998), soybean (Heinemann et al., 2005) and peanut

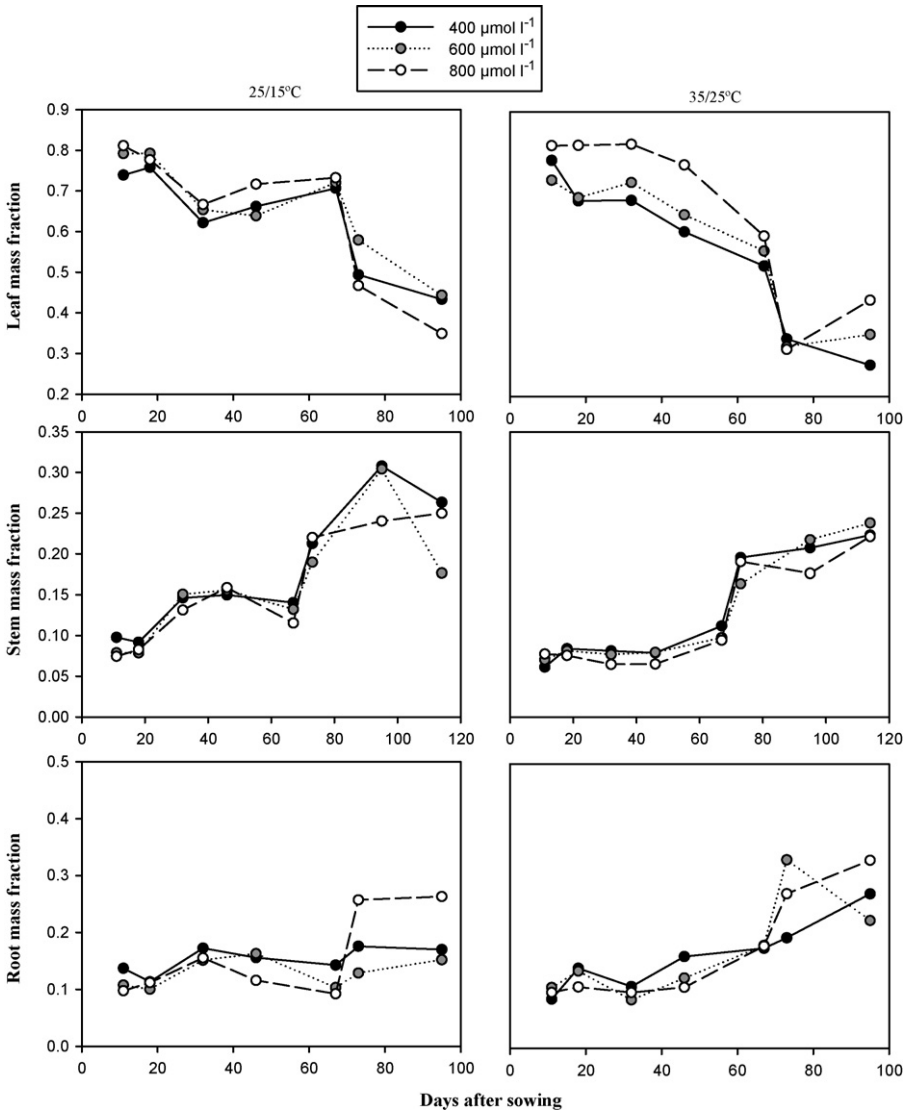

Fig. 3. Partitioning of biomass to leaves, stems, and roots as a function of days after planting for plants exposed to two temperature regimes and three [CO_2] levels.

(Bannayan et al., 2009) increased with an increase in CO_2. However, an analysis of LAI and related indices might reveal information to justify these results. In contrast to LAI, the specific leaf area at the lower temperature (25/15 °C) decreased by increasing [CO_2] to 600 and also to 800 μmol l^{-1} (Table 2, Fig. 5). At the higher temperature (35/25 °C), an increase in [CO_2] to 600 μmol l^{-1} caused a slight increase of SLA, but it decreased with a further increase of CO_2 to 800 μmol l^{-1} (Fig. 5). Although the SLA was reduced, leaf biomass showed a positive response to CO_2 at both temperature levels (Fig. 5). For the final growth analysis at 95 DAS, increasing [CO_2] from 400 to 600 μmol l^{-1} at a temperature of 25/15 °C resulted in a 61.4% increase in leaf biomass. For a further increase of [CO_2] to 800 μmol l^{-1} compared to 400 μmol l^{-1}, leaf biomass increased by 109.7%. At a temperature of 35/25 °C, increasing [CO_2] from 400 to 600 μmol l^{-1} resulted in a 29.6% increase in leaf biomass, while a further increase to 800 μmol l^{-1} resulted in a 61.2% increase in leaf biomass.

The leaf area ratio, i.e., the ratio of leaf area to total biomass, showed a decreasing trend in response to CO_2 for both temperature levels (Fig. 5), although there was no significant difference ($P > 0.05$) between 400 and 600 μmol l^{-1} of CO_2. The larger amount of total biomass in response to CO_2 could not be due to a slightly higher LAI, as LAR showed a decreasing trend and was lower at elevated [CO_2] compared to ambient. Rufty et al. (1994) also found a difference in LAI and growth of cotton plants in response to CO_2 and concluded that the higher biomass production was associated with a higher net assimilation rate (NAR) under elevated [CO_2]. NAR was calculated as the ratio of RGR to (SLA × leaf mass) (Poorter, 1993). In our study, NAR at 35/25 °C was lower at 600 μmol l^{-1} compared to 400 μmol l^{-1} up to 67 DAS, but it was higher for the remainder of the growing season. However at 800 μmol l^{-1} compared to 400 μmol l^{-1}, NAR was higher starting at 18 DAS until the end of the growing season.

3.3. Reproductive growth

For the final growth sampling at 95 DAS, increasing [CO_2] from 400 to 600 μmol l^{-1} at a temperature of 25/15 °C resulted in a 13.1% increase in the number of squares and increased by 62.3% at 800 μmol l^{-1} compared to 400 μmol l^{-1} (Fig. 6). At a temperature of 35/25 °C, the number of squares decreased by 0.7% for 600 and 4.1% for 800 μmol l^{-1} compared to 400 μmol l^{-1} [CO_2]. Although at the higher temperature an increase in [CO_2] decreased the number of squares compared to 25/15 °C, the actual num-

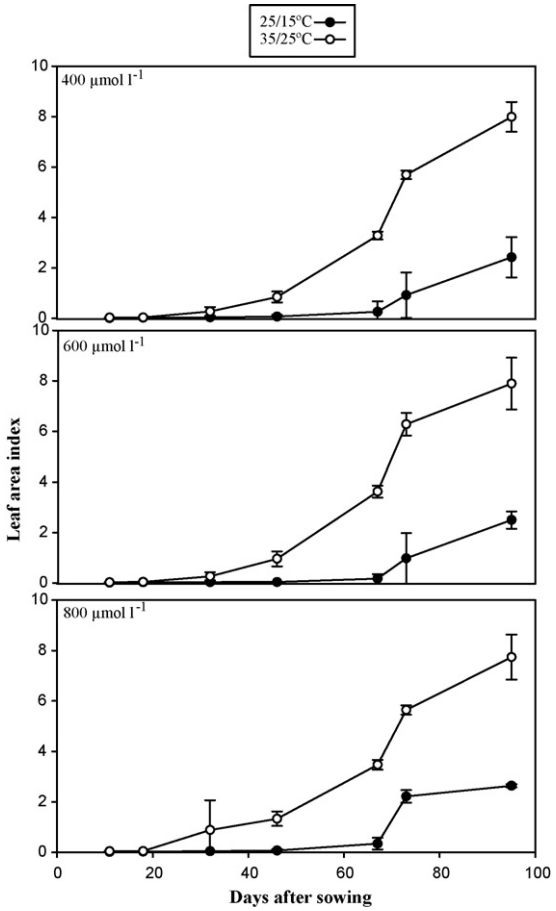

Fig. 4. Leaf area index (LAI) as a function of days after planting for two temperature regimes and three [CO_2] levels.

ber of squares numbers were significantly higher at each level of [CO_2] (Fig. 6). At 35/25 °C compared to 25/15 °C, the number of squares increased by 6.8% for 400 μmol l^{-1}, 6.0% for 600 μmol l^{-1}, and 4.0% for 600 μmol l^{-1}. The smaller number of squares at the lower temperature combination might be due to a slower development rate (Reddy et al., 2005). Our growth analysis data showed a significant positive response ($P < 0.05$) of the number of bolls to elevated [CO_2] in comparison to ambient [CO_2] (Fig. 6). At 25/15 °C, the number of bolls increased by 25.4% at 600 μmol l^{-1} and 14.3% at 800 μmol l^{-1} compared to 400 μmol l^{-1}. At 35/25 °C, the number of bolls increased by 413.3% at 600 μmol l^{-1} and 233.3% at 800 μmol l^{-1}. An increase in the number of squares per individual cotton plant under elevated [CO_2] was also reported by Zhao et al. (2003). Reddy et al. (2005) reported that the higher number of fruiting sites in response to [CO_2] was mainly due to a larger number of secondary branches and more fruiting sites per branch. Morgan et al. (2005) found that the number of reproductive sites for soybean was stimulated by elevated [CO_2]. The higher number of bolls and squares in response to elevated [CO_2] is similar to the findings of Reddy et al. (2005). However, the response of the number of bolls was different than the number of squares to temperature. The increase in temperature significantly increased the number of squares starting at 73 DAP up to final harvest across all [CO_2] levels (Fig. 6). In contrast to the number of squares, the number of bolls decreased due to the increase in temperature. It was reduced by 76.2% at 400 μmol l^{-1}, 2.5% at 600 μmol l^{-1} and 30.6% at 800 μmol l^{-1} at 35/25 °C compared to the 25/15 °C at final harvest (Table 3). This is consistent with the results of Reddy et al. (1999) who employed a range of temperatures from

Table 3
Number of squares, bolls and boll weight and seed + lint yield (at harvest) in response to CO_2 and temperature.

Thermal environment	CO_2 (μmol l^{-1})		
	400	600	800
Number of squares (m^{-2})			
25/15 °C	144.9[c]	163.9[b]	235.1[a]
35/25 °C	990.4[a]	983.3[b]	950.0[c]
Number of bolls (m^{-2})			
25/15 °C	9.5[c]	19.0[b]	38.0[a]
35/25 °C	26.1[c]	116.4[b]	118.8[a]
Boll weight (g m^{-2})			
25/15 °C	6.0[c]	9.5[b]	37.6[a]
35/25 °C	6.1[c]	208.7[a]	143.0[b]
Seed + lint yield (g m^{-2})			
25/15 °C	620.3[b]	620.8[b]	715.0[a]
35/25 °C	44.2[c]	282.7[a]	79.2[b]

Mean values followed by the same letter are not significant different at $P \leq 0.05$. Effects of CO_2 should be valued for each temperature separately. Letters on left side of temperature regime signify only temperature effect.

Table 4
Interactive effect of CO_2 and temperature on above ground biomass, boll weight (at harvest), and the maximum leaf area index (LAI).

Thermal environment	CO_2 level (μmol l^{-1})			Elevated/ambient ratio	
	400	600	800	600/400	800/400
Final above ground biomass (g m^{-2})					
25/15 °C	933.8	1006.3	1055.4	1.08	1.13
35/25 °C	1095.2	1262.4	1194.0	1.15	1.09
LAI_{max}					
25/15 °C	2.42	2.50	2.63	1.03	1.09
35/25 °C	7.99	7.89	7.74	0.99	0.97
Maximum boll weight (g m^{-2})					
25/15 °C	0.16	0.25	3.96	1.59	6.29
35/25 °C	0.65	21.97	15.06	34.07	23.34

22 °C to 30 °C. The reduction in the number of bolls due to temperature might be due to the high sensitivity of boll retention to temperature.

The two elevated [CO_2] levels increased total boll weight when compared to 400 μmol l^{-1}. Overall, an increase in temperature increased the total boll weight, except for the temperature of 35/25 °C and 800 μmol l^{-1}, which showed a slight reduction (Table 3). The final boll weight at harvest was 1.59 times (at 600 μmol l^{-1}) and 6.3 times (at 800 μmol l^{-1}) higher compared to ambient [CO_2]. Increasing the temperature increased this difference, as the final boll weight was 34.1 times (at 600 μmol l^{-1}) and 23.3 times (at 800 μmol l^{-1}) higher compared to ambient [CO_2]. The response of final lint yield to [CO_2] was more or less similar to the response of boll weight. Lint yield showed no change when [CO_2] increased from 400 to 600 μmol l^{-1}, but it was 1.15 times higher at 800 μmol l^{-1} compared to 400 μmol l^{-1}. At the temperature of 35/25 °C, lint yield was 6.39 times higher at 600 and at 800 μmol l^{-1} was 1.79 times higher compared to ambient [CO_2]. However, increasing temperature reduced the lint yield across all [CO_2] levels (Table 3).

3.4. Interactive effects of CO_2 and temperature

The interactive effects of temperature and CO_2 on crop growth and development are very critical in determining a crop's response to changing environmental conditions. Table 4 shows the interactive effects of CO_2 and temperature on the three main growth

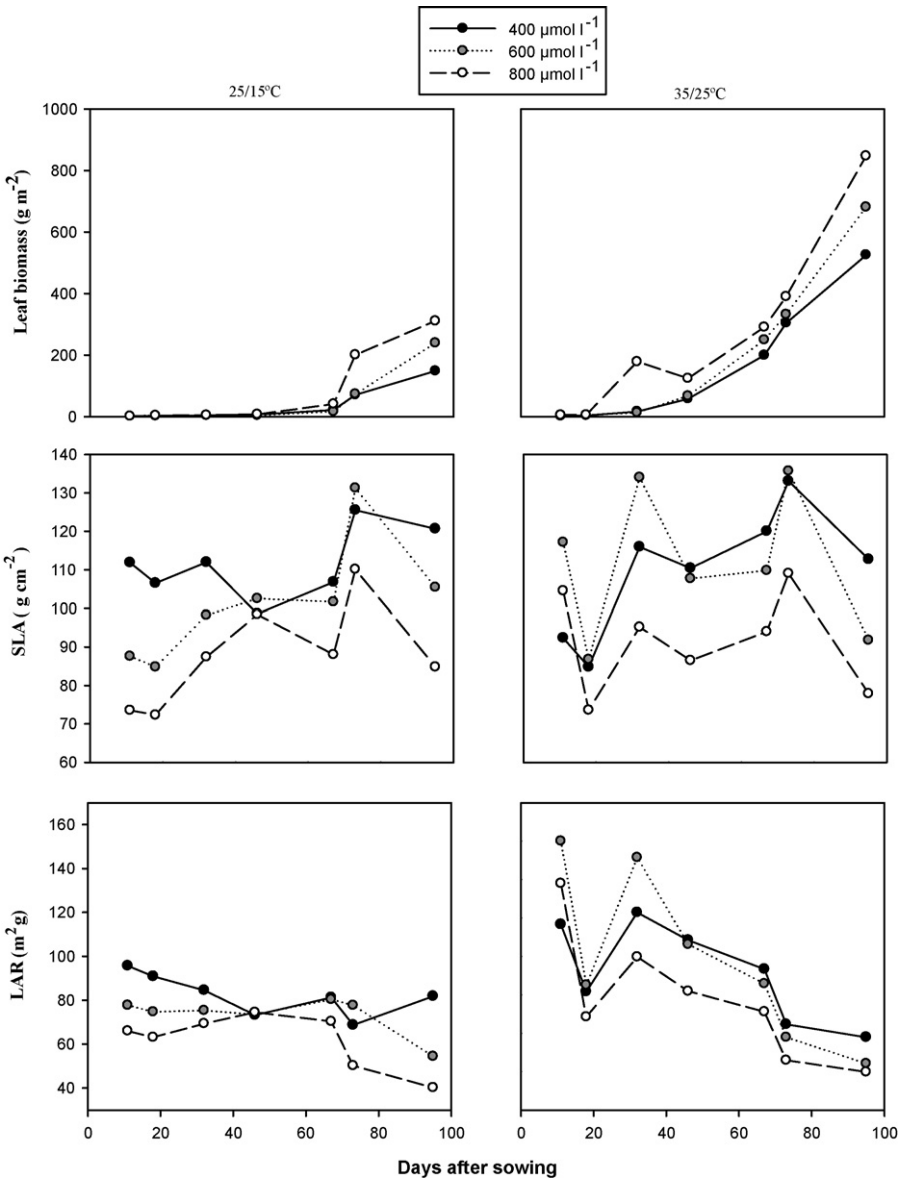

Fig. 5. Leaf biomass, SLA and LAR as a function of days after planting for two temperature regimes and three [CO_2] levels.

parameters of cotton, including biomass, LAI and boll weight. The relative response of above ground biomass and boll weight to an increase in [CO_2] from 400 to 600 µmol l^{-1} was more at higher temperature level, although it was not true for LAI_{max}. A similar response was obtained when [CO_2] increased to 800 µmol l^{-1}. The relative response of LAI_{max} to [CO_2] decreased by 1% at 600 µmol l^{-1} and 3% at 800 µmol l^{-1} compared to ambient [CO_2] with an increase in temperature. Boll weight showed a very positive response to both [CO_2] and temperature at 95 days after planting. The response to [CO_2] for boll weight at 35/25 °C indicated the dominant role of temperature compared to [CO_2] on cotton production. Among the traits shown in Table 4, boll weight showed a higher response to a change in temperature than above ground biomass and LAI_{max}. Considering that the temperature range of 20–30 °C is the optimum temperature for cotton (Reddy et al., 1998; Sawan et al., 2002; Malik et al., 2004) cool temperatures have been reported to be a major limiting factor for cotton productivity (Gipson, 1986; Ramey, 1986; Winter and Burke, 1991). [CO_2] is not able to enhance growth as much at the temperature combination of 25/15 °C compared to when the temperature increased to 35/25 °C. The results from our study showed that within the optimum range of temperature for cotton, at higher temperatures CO_2 will be more beneficial for cotton compared to lower temperatures.

Mechanisms of the plant responses to these changes need to be incorporated into process-based models of plant growth to obtain an understanding of the potential consequences of the global environmental changes (Bannayan et al., 2005). As [CO_2] increases, properly evaluated models will be important tools for predicting crop responses such as changed productivity, altered composition of plant products and changes in sink–source relationships. The information provided in this research could be useful to be incorporated into process-level simulation to enhance model applications beyond the current conditions. Further data are required for fiber quality to expand cotton model predictions. Simulating fiber quality properties as a function of local weather conditions during the fiber growth period will allow producers to predict their fiber quality, which is invaluable for the marketing process.

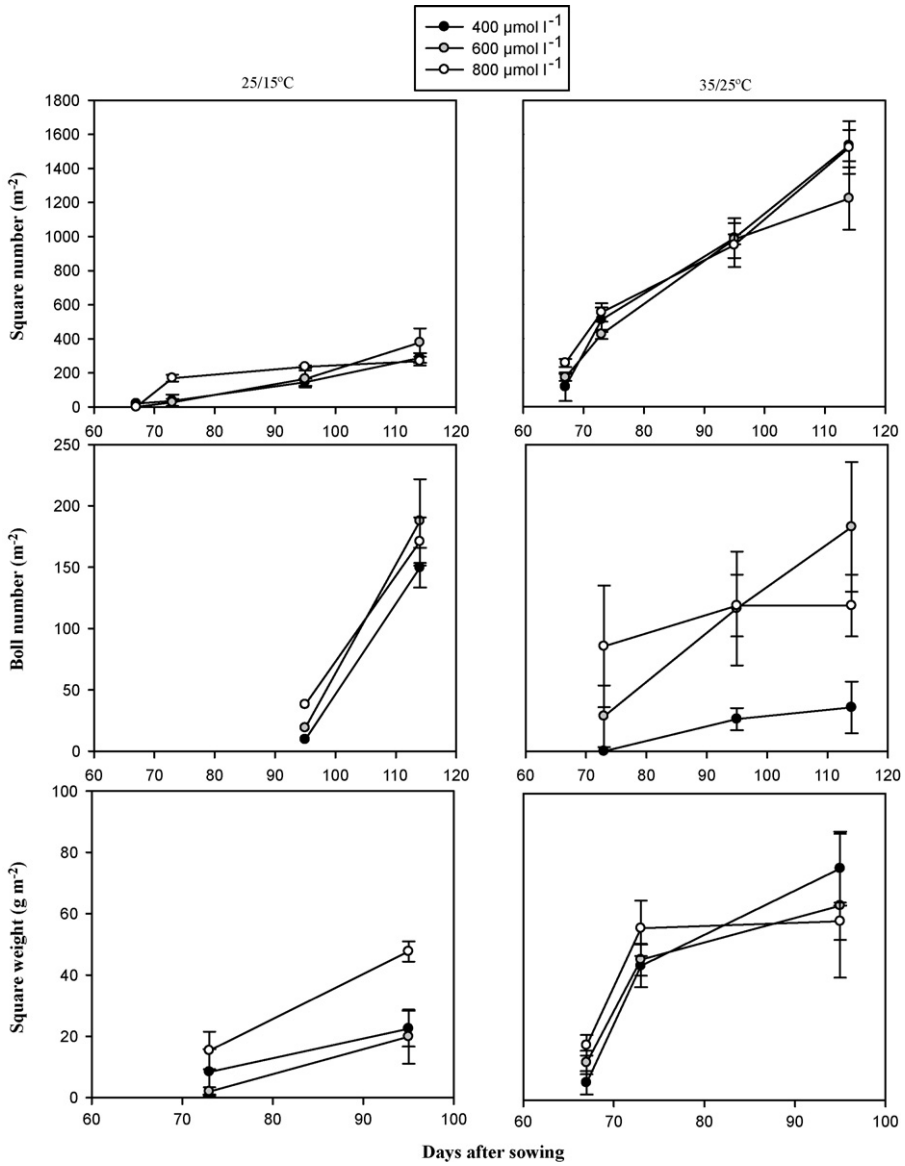

Fig. 6. The number of squares, and bolls and square mass for two temperature regimes and three [CO_2] levels.

4. Conclusion

The results of this study showed that increasing the [CO_2] compared to ambient [CO_2] could increase both above ground biomass and boll weight of cotton. However seed and lint yield could increase in response to higher [CO_2] when the plants are not exposed to temperatures that are above the optimum temperature. LAI increased in response to an increase in both [CO_2] and temperature. Our study indicated that within the optimum range of temperature for cotton, CO_2 will be beneficial for cotton production. The results from this study also supported our hypothesis that the response to elevated [CO_2] is the function of the temperature level at which the crop is grown. Further research is needed to determine the impact of climate change parameters on other economic traits, such as fiber quality.

Acknowledgement

This research was conducted while the senior author was on sabbatical leave at the University of Georgia. This work was supported by State and Federal funds allocated to Georgia Agricultural Experiment Station Hatch project GEO01654.

References

Allen Jr., L.H., Bisbal, E.C., Campbell, W.J., Boote, K.J., 1989. Carbon dioxide effects on soybean development stages and expansive growth. Soil Crop Sci. Florida, Proc. 49, 124–131.

Allen Jr., L.H., Baker, J.T., Albrecht, S.L., Boote, K.J., Pan, D., Vu, J.C.B., 1995. Carbon dioxide and temperature effects on rice. In: Peng, S., Ingram, K.T., Neue, H.T., Ziska, L.H. (Eds.), Climate Change and Rice. Springer, Berlin, pp. 258–277.

Baker, J.T., Allen Jr., L.H., Boote, K.J., Jones, P., Jones, J.W., 1989. Response of soybean to air temperature and carbon dioxide concentration. Crop Sci. 29, 98–105.

Bannayan, M., Kobayashi, K., Kim, H.Y., Liffering, M., Okada, M., Miura, S., 2005. Modeling the interactive effects of atmospheric CO_2 and N on rice growth and yield. Field Crop Res. 93, 237–251.

Bannayan, M., Tojo Seller, C.M., Garcia, A.G., Guerra, L.C., Hoogenboom, G., 2009. Interactive effects of elevated CO_2 and temperature on two long and short season peanut cultivars growth and development. Climatic Change Climatic Change 96, 389–406.

Bednarz, C.W., van Iersel, M.W., 2001. Temperature response of whole-plant CO_2 exchange rates of four upland cotton cultivars differing in leaf shape and leaf pubescence. Commun. Soil. Sci. Plan. 32 (15–16), 2485–2501.

Bhattacharya, S., Bhattacharya, N.C., Biswas, P.K., Strain, B.R., 1985. Response of cowpea (*Vigna unguiculata* L.) to CO_2 enrichment environment on growth, dry matter

production and yield components at different stages of vegetative and reproductive growth. J. Agric. Sci. (Camb.) 105, 527–534.
Bloom, A.J., 2006. Rising carbon dioxide concentrations and the future of crop production. J. Sci. Food Agric. 86 (9), 1289–1291.
Chaudhuri, U.N., Burnett, R.B., Kirkham, M.B., Kanemasu, E.T., 1986. Effect of carbon dioxide on sorghum yield, root growth and water use. Agric. For. Meteorol. 37, 109–122.
Chaudhuri, U.N., Kirkham, M.B., Kanemasu, E.T., 1990. Root growth of winter wheat under elevated carbon dioxide and drought. Crop Sci. 30, 853–857.
Cheng, W., Inubushi, K., Yagi, K., Sakai, H., Hasegawa, T., 2009. Interactions of elevated [CO_2] and night temperature on rice growth and yield. Agric. For. Meteorol. 149, 51–58.
Coleman, J.S., Bazzaz, F.A., 1992. Effects of CO_2 and temperature on growth and resource use of co-occurring C3 and C4 annuals. Ecology 73, 1244–1259.
Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A., Totterdell, I.J., 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408, 184–187.
Del Castillo, D., Acock, B., Reddy, V.R., Acock, M.C., 1989. Elongation and branching of roots on soybean plants in a carbon dioxide-enriched aerial environment. Agron. J. 81, 692–695.
Delgado, E., Mitchel, R.A.C., Parry, M.A.C., Driscoll, S.P., Mitchel, V.J., Lawlor, D.W., 1994. Interacting effect of CO_2 concentration, temperature and nitrogen supply on the photosynthesis and composition of winter wheat leaves. Plant Cell Environ. 17, 1205–1213.
Downs, R.J., Hellmers, H., 1975. Environment and the Experimental Control of Plant Growth. Academic Press, Inc., New York, NY.
Garbutt, K., Willimas, W.E., Bazzaz, F.A., 1990. Analysis of the differential response of five annual to elevated CO_2 during growth. Ecology 71, 1185–1194.
Gipson, J.R., 1986. Temperature effects on growth, development and fiber properties. In: Mauney, J.R., Stewart, J.M. (Eds.), Cotton Physiology. Cotton Foundation, Memphis, TN, pp. 47–56.
Hacour, A., Craigon, J., Vandermeiren, K., Ojanperä, K., Pleijel, H., Danielsson, H., Högy, P., Finnan, J., Bindi, M., 2002. CO_2 and ozone effects on canopy development of potato crops across Europe. Eur. J. Agron. 17, 257–272.
Heinemann, A.B., Maia, A.H.N., Neto, D.D., Ingram, K.T., Hoogenboom, G., 2005. Soybean (*Glycine max* (L.) Merr.) growth and development response to CO_2 enrichment under different temperature regimes. Eur. J. Agron. 24 (1), 52–61.
Hesketh, J.D., Hellmers, H., 1973. Floral initiation in four plant species growing in CO_2-enriched air. Environ. Control Biol. (Jpn.) 11 (5), 1–3.
Idso, S.B., Kimball, B.A., Anderson, M.G., Mauney, J.R., 1987. Effects of CO_2 enrichment on plant growth: the interactive role of air temperature. Agric. Ecosyst. Environ. 20, 1–10.
Imai, K., Coleman, D.F., Yanagisawa, I., 1985. Increase in atmospheric partial pressure of carbon dioxide and growth and yield of rice (*Oryza sativa* L.). Jpn. J. Crop Sci. 54, 413–418.
Ingram, K.T., Hoogenboom, G., Liu, L., 1998. A multidisciplinary research facility for the study of interacting environmental stresses on plants. ASAE Paper No. 984151. American Society of Agricultural Engineers, St. Joseph.
Kimball, B.A., Mauney, J.R., 1993. Responses of cotton to varying CO_2, irrigation, and nitrogen: yield and growth. Agron. J. 85, 706–712.
Kimball, B.A., Kobayashi, K., Bindi, M., 2002. Responses of agricultural crops to free-air CO_2 enrichment. Adv. Agron. 77, 293–368.
Krenzer Jr., E.G., Moss, D.N., 1975. Carbon dioxide enrichment effects upon yield components in wheat. Crop Sci. 15, 71–75.
Lawlor, D.W., Mitchel, R.A.C., 2000. Crop ecosystem responses to climatic change: wheat. In: Reddy, K.K., Hodges, H.F. (Eds.), Climate Change and Global Crop Productivity. CAB International, Wallingford, UK, pp. 57–80.
Li, A.-G., Trent, A., Wall, G.W., Kimball, B.A., Yue-Sheng, H., Pinter Jr., P.J., Garcia, R.L., Hunsaker, D.V., Lamorte, R.L., 1997. Free-air CO_2 enrichment effects on rate and duration of apical development of spring wheat. Crop Sci. 37, 789–796.
Malik, S.A., Hafeez ur Rahman, Saleem, M., 2004. Heat tolerance of upland cotton during the fruiting stage evaluated using cellular membrane thermostability. Field Crops Res. 85, 149–158.
Mauney, J.R., Kimball, B.A., Pinter, P.J., Lamorte, R.L., Lewin, K.F., Nagy, J., Hendrey, G.R., 1994. The free-air carbon dioxide enrichment (FACE) cotton project: a new field approach to assess the biological consequences of global change. Agric. For. Meteorol. 170 (1–4), 49–67.
Morgan, P.B., Bollero, G.A., Nelson, R.L., Dohleman, F.G., Long, S.P., 2005. Smaller than predicted increase in aboveground net primary production and yield of field-grown soybean under fully open-air [CO_2] elevation. Global Change Biol. 11, 1–10.
Newman, Y.C., Sollenberger, L.E., Boote, K.J., Allen Jr., L.H., Littell, R.C., 2001. Carbon dioxide and temperature effects on forage dry matter production. Crop Sci. 41, 399–406.
Nijs, I., Impens, I., Behaeghe, T., 1998. Effects of rising atmospheric carbon dioxide concentration on gas exchange and growth of perennial ryegrass. Photosynthetica 22, 44–50.
Poorter, H., 1993. Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. Vegetatio 104/105, 77–97.
Prior, S.A., Rogers, H.H., Runion, G.B., Mauney, J.R., 1994. Effects of free-air CO_2 enrichment on cotton root growth. Agric. For. Meteorol. 70, 69–86.
Ramey, H.H., 1986. Stress influence on fiber development. In: Mauney, J.R., Stewart, J.M. (Eds.), Cotton Physiology. Cotton Foundation, Memphis, TN, pp. 351–360.
Rawson, H.M., 1992. Plant responses to temperature under conditions of elevated CO_2. Aust. J. Bot. 40, 473–490.
Reddy, K.R., Prasad, P.V., Kakani, V.G., 2005. Crop responses to elevated carbon dioxide and interactions with temperature: cotton. J. Crop Improv. 13, 157–191.
Reddy, K.R., Davidonis, G.H., Johnson, A.S., Vinyard, B.T., 1999. Temperature regimes and carbon dioxide enrichment alter cotton boll development and fiber properties. Agron. J. 91, 851–858.
Reddy, K.R., Robana, R.R., Hodges, H.F., Liu, X.J., McKinion, J.M., 1998. Interaction of CO_2 enrichment and temperature on cotton growth and leaf characteristics. Environ. Exp. Bot. 39, 117–129.
Reddy, K.R., Harry, H.F., McKinion, J.M., 1995a. Carbon dioxide and temperature effects on Pima cotton development. Agron. J. 87, 820–826.
Reddy, K.K., Hodges, H.F., McKinion, J.M., 1995b. Carbon dioxide and temperature effects on Pima cotton growth. Agric. Ecosyst. Environ. 54, 17–29.
Rufty, T.W., Thomas, R.B., Cure, J.D., Cure, W.W., 1994. Growth response of cotton to CO_2 enrichment in differing light environments. Physiol. Plantarum 91, 503–509.
SAS Institute, 2001. SAS System, 8th ed. SAS Inst., Cary, NC.
Sawan, Z.M., Hanna, L.I., El Karim, G.A.G., 2002. Relationships between climatic factors and flower and boll production in Egyptian cotton (*Gossypium barbadense*). J. Arid. Environ. 52 (4), 499–516.
Schonfeld, M., Johnson, R.C., Ferris, D.M., 1989. Development of winter wheat under increased atmospheric CO_2 and water limitation at tillering. Crop Sci. 29, 1083–1086.
Tremmel, D.C., Patterson, D.T., 1993. Responses of soybean and five weeds to CO_2 enrichment under two temperature regime. Can. J. Plant Sci. 73, 1249–1260.
Winter, D.A., Burke, J.J., 1991. Dry matter production and photosynthetic capacity in *Gossypium hirsutum* L. under conditions of slightly sub-optimal leaf temperatures and high levels of irradiance. Oecologia 87, 190–197.
Yoshimoto, M., Oue, H., Kobayashi, K., 2005. Energy balance and water use efficiency of rice canopy under free-air CO_2 enrichment. Agric. For. Meteorol. 133, 226–246.
Zhao, D., Reddy, R., Kakani, V.G., Read, J.J., Sullivan, J.H., 2003. Cotton growth, development and physiological responses to elevated carbon dioxide and ultraviolet-B radiation. Plant Cell Environ. 26, 771–782.
Ziska, L.H., Weerakoon, W., Namuco, O.S., Pamplona, R., 1996. The influence of nitrogen on the elevated CO_2 response in field-grown rice. Aust. J. Plant Physiol. 23, 45–52.