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CARBON DIOXIDE AND TEMPERATURE EFFECTS ON COTTON LEAF INITIATION AND DEVELOPMENT

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REDDY V. R., REDDY K. R. and Acock B. *Carbon dioxide and temperature effects on cotton leaf initiation and development*. BIOTRONICS 23, 59-74, 1994. The current increase in atmospheric CO₂ concentration [CO₂] and the predicted increases in global surface air temperature have stimulated the need for understanding the response of agricultural crops to [CO₂] and temperature interactions. The objectives of this study were to evaluate the effects of ambient and doubled [CO₂] at a range of temperatures on leaf initiation rates, expansion rates, and final sizes of cotton leaves. Cotton plants (*Gossypium hirsutum* L., cv. DPL-50) were grown in a nearly natural environment using daylit plant growth chambers with temperature and [CO₂] as controlled variables. The average air temperatures were 17.8, 18.7, 22.7, 26.6, and 30.6°C during a 70-d experimental period with [CO₂] treatments of 350 and 700 μL L⁻¹ at each temperature. Leaf initiation, expansion, and final sizes were recorded at daily or weekly time intervals as needed. Temperature and [CO₂] had significant effects on expansion and final sizes of the mainstem leaves on the cotton plant. There was no significant effect of [CO₂] on leaf initiation rates. Temperature affected the final leaf sizes, duration of expansion, and rate of expansion. High [CO₂] increased final leaf size and rate of leaf expansion, and the effect was more pronounced at higher temperatures. The increase in whole plant leaf area with doubling of [CO₂] was due to small increases in individual leaf sizes and a large increase in the number of leaves on fruiting and vegetative branches.

Key words: *Gossypium hirsutum* L.; cotton; CO₂; temperature; leaf initiation; leaf growth.

INTRODUCTION

Interest and concern for Earth's changing atmosphere and its effect on agriculture have increased in recent years (3, 4, 9, 11, 12, 20). The carbon dioxide concentration [CO₂] of the planet's atmosphere has increased by 30% since the industrial revolution, presumably because of mankind's increasing use of fossil fuels and deforestation (12). The current level of CO₂ is about 350 μL L⁻¹, and future increases are expected to result in a CO₂ level of 600 μL L⁻¹

probably sometime between 2030 and 2070 (19).

The increases in the concentration of CO₂ will change Earth's climate and affect plant growth. Elevated CO₂ levels tend to partially close stomata in plant leaves, resulting in reduced transpiration per unit of leaf area (8) and rising tissue temperatures (6). This direct effect of [CO₂] on canopy temperature coupled with the 3 to 6°C rise in global surface air temperature predicted by atmospheric general circulation models (5) will affect crop productivity and yield.

The beneficial effects of CO₂ on growth and productivity of crops and pasture plants have been well documented (3, 9, 11). The interactive effects of long-term elevated [CO₂] and temperature on productivity of crop plants are poorly understood. Cure & Acock (3) reported that temperature x CO₂ interactions on seed yield were unavailable in their survey of eight major crops. They found only three studies of [CO₂] x temperature interaction on biomass. However, Idso *et al.* (7) showed that growth stimulation by CO₂ enrichment increases with increase in air temperature, but their studies mostly concentrated on prefruiting plants. In contrast, Baker *et al.* (2) found a downward trend with temperature in seed yield and harvest index for soybeans grown at 330 and 660 $\mu\text{L L}^{-1}$ of CO₂. We recently found well-watered cotton square and flower retention was very sensitive to daytime temperatures of 35 and 40°C (13). Cotton plants grown at 35/25°C produced only 4% as much fruit as plants grown at 30/20°C, and plants grown at 40/30°C produced no fruit (16). Thus the effects of long-term [CO₂] and temperature may be interactive and the literature is very limited. Temperatures of 35 and 40°C are frequently observed in cotton-producing areas (13), and periods with even greater temperature extremes will likely be more frequent and more detrimental to cotton production if predicted global warming occurs.

The primary objective of this study was to evaluate the interactive effects of temperature and [CO₂] on cotton leaf initiation rates, leaf expansion, and final size of the leaves. The secondary objective of this study was to collect a database for the development of a mechanistic crop model for cotton that would predict cotton responses to changing climatic conditions.

MATERIALS AND METHODS

The plant growth chambers used in this study consisted of a steel bin containing the rooting medium and measured 1.0 m high by 2.0 m long by 0.5 m wide (1, 15, 17). An acrylic base on top of the soil bin held the aerial parts of the plants and measured 2.0 m high by 2.0 m long by 1.5 m wide. A door in the bottom of each base was hinged for easy access to the plants. The soil bins were filled with a mixture of sand and vermiculite (3:1 by volume) to which was added a mixture of slow-release micronutrients at the rate of 88 mg L⁻¹ prior to filling the bins. Cotton 'Deltapine 50' (DPL-50) seeds were germinated in moistened paper towels at 28/23°C day/night temperatures for 48 h. The germinated seeds, with radicals emerging, were selected for uniformity and

planted in the naturally lighted plant growth chambers in 11 rows of five plants per row. Six rows of plants were harvested at 23 days after emergence (DAE), and two more rows were harvested at 35 DAE to avoid interplant competition for light, leaving three rows at final harvest on 70 DAE with 15 plants m⁻². Intermediate harvests were required because of the need for thick planting to get a canopy large enough to measure photosynthesis from the seedling stage and to provide short-term dry matter accumulation rates and total leaf areas. The data collected on canopy photosynthesis and dry matter accumulation are outside the scope of this paper and are therefore not presented here.

This experiment is part of a larger study in which the controlled-environment chambers were all maintained at 28/23°C (day/night) during seedling emergence and until 14 DAE. On 15 DAE, temperature and CO₂ treatments were imposed, and the air temperatures in the growth chambers were maintained at 20/12, 20/12, 25/17, 30/22, and 35/27°C. The CO₂ concentrations were maintained at 350 and 700 μL L⁻¹ for each temperature, utilizing a total of 10 controlled-environment cabinets. The daytime temperature was initiated at sunrise and returned to the nighttime temperature 1 h after sunset during the experimental period. On 24 DAE, at the time of the first destructive harvest of extra rows, the temperature treatments in two chambers were changed from 20/12°C to 15/7°C to determine if we could measure growth and development at such a low temperature. Since 20/12°C was a replicated treatment having two chambers at each [CO₂] and temperature, we were able to continue 20/12°C along with 15/7°C treatments at both CO₂ levels. However, 10 d later the plants at 15/7°C in both CO₂ levels had not grown and were found to be disease prone. On 35 DAE, we changed the 15/7°C treatment back to 20/12°C and completed the second destructive harvest. The average temperatures during the entire experiment were 17.8, 18.7, 22.7, 26.6, and 30.6°C for the day/night

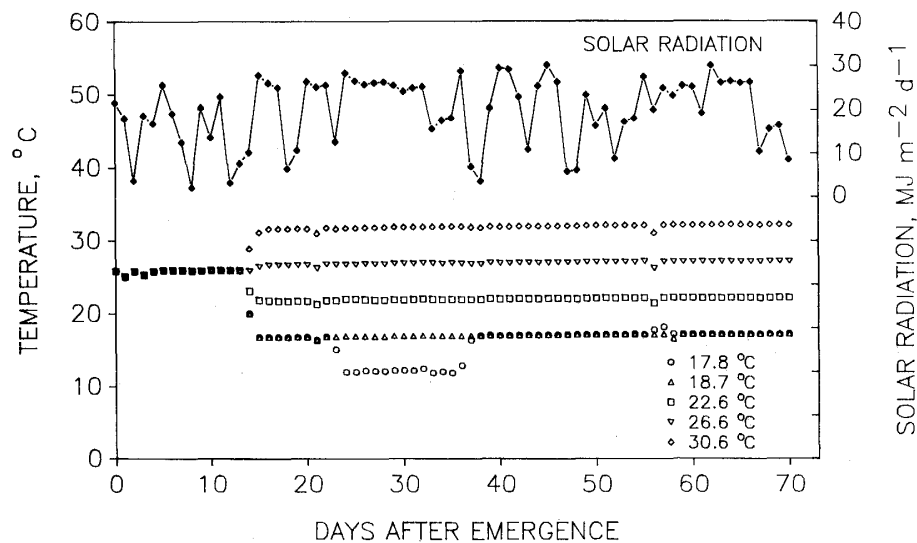


Fig. 1. Mean daily air temperature and solar radiation levels in the controlled-environment cabinets during the experiment.

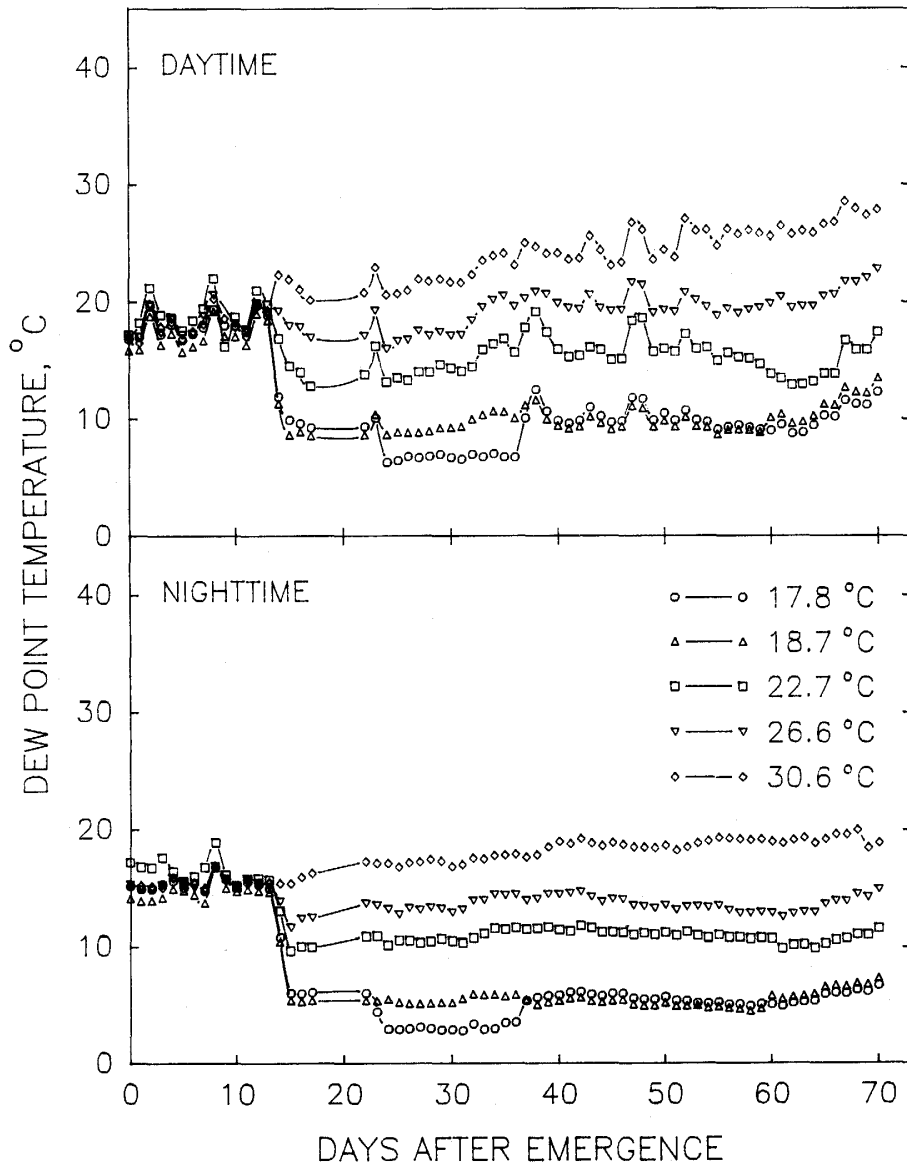


Fig. 2. Average dew point temperature during daytime and nighttime in the controlled environment cabinets during the experiment.

temperature treatments of 15/7°C with 20/12, 20/12, 25/17, 30/22, and 35/27°C (Fig. 1). The dewpoint temperatures were not controlled but were measured at 10-s intervals with gold mirror hygrometers (Fig. 2).

The chambers were monitored by a computer (Digital, Pro 380,¹ Digital Equipment Corp., Maynard, MA), which controlled carbon dioxide concentration, air temperature, and irrigation along with other environmental and plant

¹Trade name and company name are included for the benefit of the reader and do not imply any endorsement or preferential treatment of the product by USDA-ARS or Mississippi State University.

response variables. The temperatures in the growth chambers were maintained to within $\pm 0.1^\circ\text{C}$ of the set points for 95% of the time, using a secondary cooling system and resistance heaters. Continuous circulation of air maintained uniform temperatures throughout the chambers. The chambers were sealed, and the CO₂ concentration was monitored at 10-s intervals and averaged over 900-s periods. To maintain [CO₂] at 350 or 700 $\mu\text{L L}^{-1}$, pure CO₂ was injected from a gas cylinder through a pressure regulator, solenoid valve, needle valve, and flow meter into the chambers as necessary. Graded shade cloths were adjusted around the chamber sides to plant height to simulate shading effects found in a field crop. The plants were irrigated with a drip irrigation system with one emitter per plant, three times a day. The cotton plants were treated with proper insecticides as necessary to control insects, but any insecticide application necessary in one chamber was given to all the chambers.

Non-destructive data on leaf initiation and growth of the nine plants in each chamber were collected at daily, three-day, or weekly intervals. Leaf areas were estimated non-destructively during the experiment by measuring the distance from the site of petiole attachment to the leaf tip of the center lobe. These values were well correlated ($r=0.98$) with measured leaf area taken on leaves of different ages at each harvest. For this experiment the relationship between leaf length and leaf area was:

$$\text{Leaf Area (cm}^2\text{)} = 12.67 + (-0.513 \times \text{length}) + (0.012 \times \text{length}^2)$$

Where leaf area is in square centimeters and length is in millimeters. Leaf expansion rate was determined during the linear phase of leaf growth (between 5 and 80% of final leaf area).

Statistical analysis was conducted by using procedures outlined in the General Linear Model (10, 18). The standard error of each mean was calculated and is presented wherever appropriate.

RESULTS AND DISCUSSION

Initiation and Growth of Mainstem Leaves

The number of leaves on the cotton plants increased with increasing temperature, resulting in the highest number of mainstem leaves at 30.6°C and the lowest at 17.8°C (Table 1). There was no significant increase in the number of mainstem leaves due to high CO₂ level except at 30.6°C, where there was a 9.2% increase in the high [CO₂] treatment on 70 DAE. Overall, it appears there was a slight increase in the number of leaves on the mainstem in high [CO₂]. However, this effect may be associated with an increased supply of carbohydrates rather than any direct effect of [CO₂] on leaf production in cotton.

The number of days per new leaf initiation remained in a narrow range across temperatures during the first 22 DAE (Fig. 3). This is partly because temperature treatments were only started on 15 DAE and partly because the response of cotton seedlings to temperature is minimal during this period (14). The number of days per new leaf initiation during 23–36 DAE varied among the

Table 1. The effects of [CO₂] and temperature on the number of mainstem leaves.

DAE	Average Temperature, °C									
	17.8		18.7		22.7		26.6		30.6	
	[CO ₂], µL L ⁻¹									
	350	700	350	700	350	700	350	700	350	700
22	3.83± 0.16	3.67± 0.21	3.83± 0.16	3.67± 0.21	3.67± 0.23	3.78± 0.14	3.78± 0.22	4.0 ± 0.0	3.89± 0.11	4.0 ± 0.0
29	4.0 ± 0.0	3.67± 0.21	4.0 ± 0.0	3.83± 0.16	4.78± 0.22	4.44± 0.17	5.67± 0.28	6.11± 0.26	7.44± 0.33	7.44± 0.24
36	4.0 ± 0.0	3.67± 0.21	5.33± 0.21	5.0 ± 0.36	7.0 ± 0.23	6.78± 0.22	8.89± 0.20	9.44± 0.17	11.0± 0.44	11.44± 0.33
43	4.33± 0.51	4.0 ± 0.25	6.33± 0.21	5.83± 0.30	8.67± 0.16	8.56± 0.29	11.22± 0.27	12.11± 0.26	13.56± 0.37	14.11± 0.35
50	5.17± 0.98	5.33± 0.33	7.50± 0.22	7.50± 0.22	10.33± 0.28	10.44± 0.41	13.78± 0.22	14.22± 0.22	16.22± 0.43	17.0 ± 0.33
57	6.50± 0.83	6.50± 0.42	8.0 ± 0.0	8.17± 0.16	11.67± 0.16	12.33± 0.37	15.89± 0.20	16.44± 0.24	18.44± 0.33	19.44± 0.66
64	7.50± 0.83	7.67± 0.33	9.33± 0.21	9.17± 0.16	13.67± 0.28	14.00± 0.40	18.0 ± 0.16	18.67± 0.16	20.44± 0.33	21.67± 0.37
70	8.67± 0.91	9.17± 0.30	10.67± 0.21	10.17± 0.30	15.67± 0.28	16.67± 0.40	20.0 ± 0.23	20.33± 0.33	21.78± 0.40	23.78± 0.52

temperature treatments, ranging from 14.0 d at 12.7°C to 2.01 d at 31.8°C in 350 µL L⁻¹ CO₂. The rate of leaf initiation in 700 µL L⁻¹ CO₂ was very similar and ranged from 14.0 d at 12.7°C to 1.91 d at 31.8°C. The leaf initiation rate thus increased 7-fold from 12.7 to 31.8°C (Fig. 3). However, there were no significant differences in leaf initiation rates due to [CO₂]. The number of days per new leaf initiation decreased from 23–36 DAE to 37–70 DAE at two lower temperatures in both [CO₂] levels. The leaf initiation rates declined during 37–70 DAE from the 23–36 DAE period, resulting in an increase in the number of days per new leaf initiation at higher temperatures. This was probably due to the initiation of fruiting organs, which compete with vegetative growth for available carbohydrates. Overall, it appears that the number of days per new leaf initiation varied with time within each temperature treatment, and decreased with increase in temperature, while remaining insensitive to the CO₂ level at all temperatures during the early part of the growing period.

Growth and Expansion of Prefruiting Leaves

The final area, duration of growth, and rate of expansion of leaf 4 are presented in Fig. 4. The final area of leaf 4 increased with an increase in temperature starting from 20.62 cm² at 17.8°C and reaching 114.34 cm² at 22.7°C, and then declining to 71.68 cm² when the temperature increased to 30.6°C. No

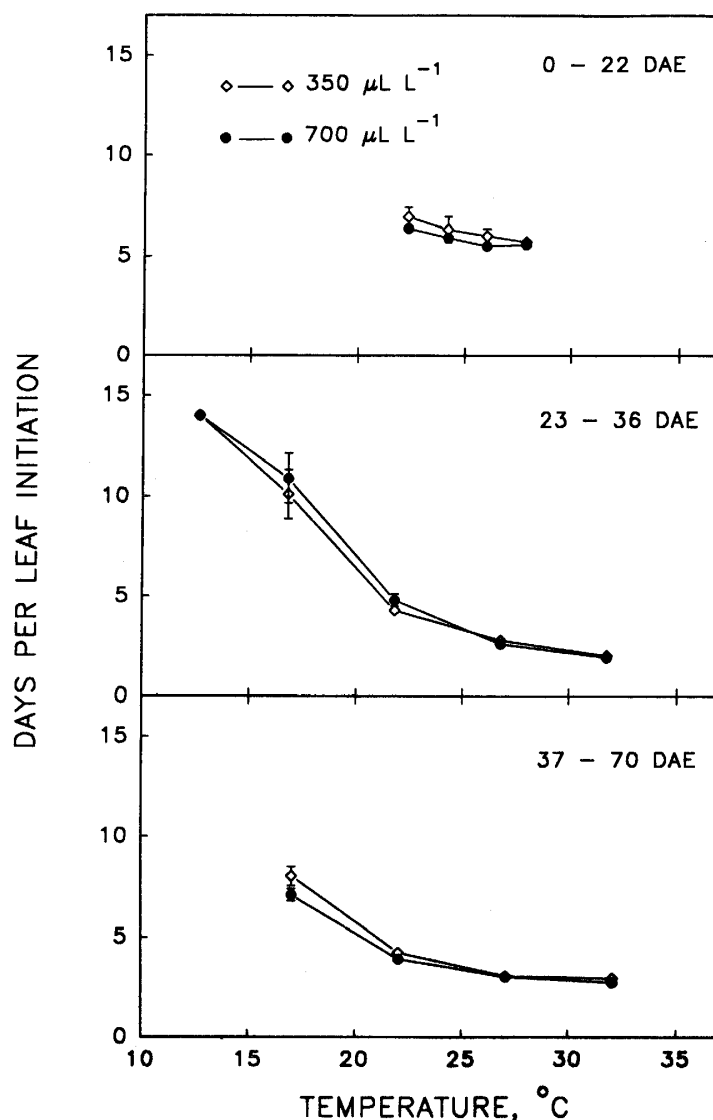


Fig. 3. Effect of temperature and [CO₂] on cotton leaf initiation during different periods after emergence. Bars indicate standard errors of the mean and are shown when greater than the symbol size.

differences in final area of leaf 4 were observed at 17.8°C between the CO₂ levels, but higher CO₂ concentration increased leaf area at higher temperatures.

The duration of leaf growth from 5 to 80% of the final area decreased with increase in temperature at both CO₂ levels. The longest duration of growth was 31.2 d at 17.8°C and 700 $\mu\text{L L}^{-1}$ CO₂, and the shortest duration of growth was 19.2 d at 30.6°C and 350 $\mu\text{L L}^{-1}$ CO₂. No significant differences were observed in duration of growth due to CO₂ doubling at any temperature.

The rate of leaf expansion increased with increases in temperature up to 22.7°C and declined thereafter as temperature increased to 30.6°C at both CO₂ levels. The rate of leaf expansion was 5.43 cm² d⁻¹ at 17.8°C and increased to 32.67 cm² d⁻¹ at 22.7°C, an increase of 502%. It then declined to 29.87 cm² d⁻¹ at

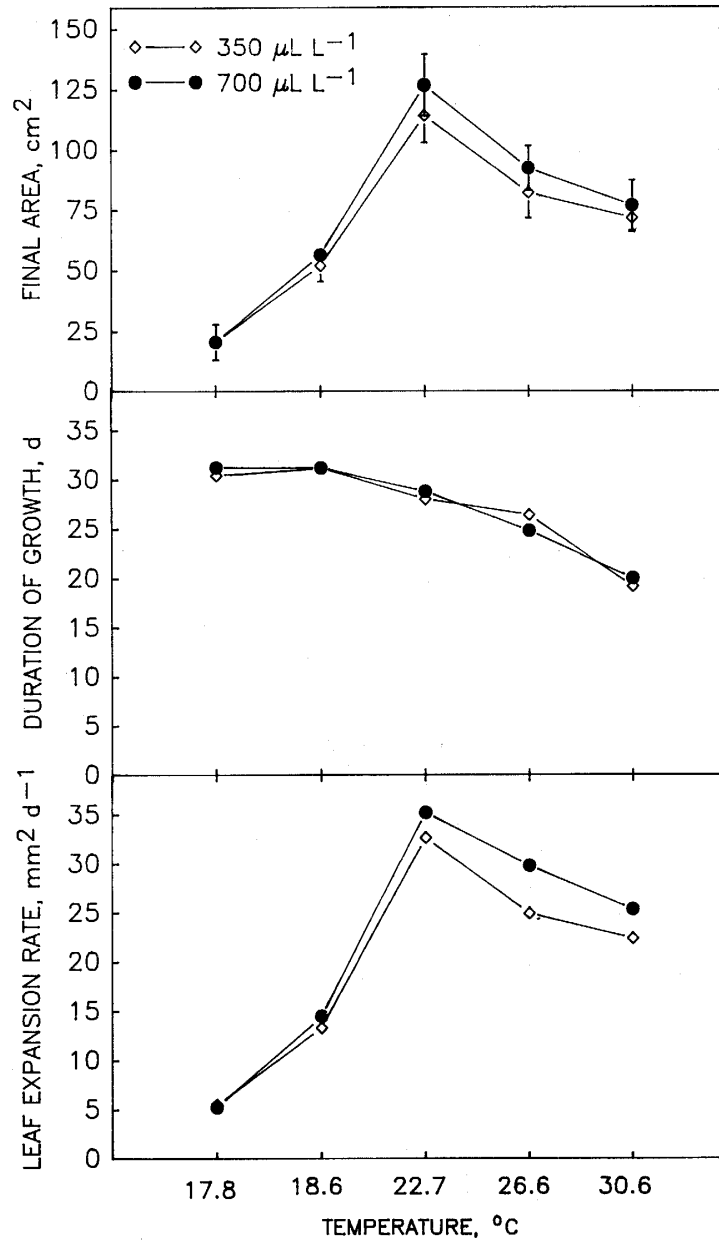


Fig. 4. Final leaf area, duration of leaf growth (5-80% of final area), and leaf expansion rate (5-80% of final area) of the 4th prefruiting leaf on the mainstem of cotton at various temperature and [CO₂] regimes. Bars indicate standard errors of the mean and are shown when greater than the symbol size.

30.6°C in 350 $\mu\text{L L}^{-1}$ CO₂. At 700 $\mu\text{L L}^{-1}$ CO₂, the rate of leaf expansion was 5.22 cm² d⁻¹ at 17.8°C and increased to 35.23 cm² d⁻¹ at 22.7°C, which is an increase of 575%. The leaf expansion rates were similar at both CO₂ levels at lower temperatures. However, at higher temperatures, CO₂ increased the rate of leaf expansion. This indicated that the limiting factor at lower temperatures, at least for cotton, was expansion rate, whereas at higher temperatures the limiting factor seemed to be carbon availability.

Growth and Expansion of Fruiting Leaves

Figure 5 shows the daily growth in area of leaf 10 on the mainstem at the three higher temperatures. This leaf did not develop at the two lower temperatures in either CO₂ level. No significant differences were observed in final size of leaf 10 between temperature treatments 22.7°C (25/17) and 26.6°C (30/22) at either CO₂ level. However, at 30.6°C (35/27) the final size of leaf 10 was significantly lower than at 22.7 or 26.6°C. The mature leaf size was significantly higher in high [CO₂] at all three temperature treatments (Fig. 5). At 22.7°C, the highest leaf area was 315.8 cm² in 700 $\mu\text{L L}^{-1}$ [CO₂] and 285.9 cm² in 350 $\mu\text{L L}^{-1}$ [CO₂], a difference of 11%. At 26.6°C, a leaf area of 278.7 cm² was recorded in 350 $\mu\text{L L}^{-1}$ [CO₂] and 317.4 cm² in 700 $\mu\text{L L}^{-1}$ [CO₂], a significant difference in leaf area (a 14% increase) due to the doubling of [CO₂]. The mature leaf area was lower at 30.6°C in both CO₂ levels. However, the area at 700 $\mu\text{L L}^{-1}$ [CO₂] was 12% higher than that at 350 $\mu\text{L L}^{-1}$ [CO₂].

The rate of leaf expansion for leaf 10 measured on a daily basis is presented in Fig. 6. At 22.7°C the rate of leaf expansion increased to 23.8 cm² d⁻¹ at 700 $\mu\text{L L}^{-1}$ CO₂ and 21.5 cm² d⁻¹ at 350 $\mu\text{L L}^{-1}$ CO₂ by 10 d after unfolding, and then declined to negligible levels by day 22 in both CO₂ levels. At higher temperatures, the maximum rate of leaf expansion occurred at 6 to 7 d after leaf unfolding and declined thereafter to near zero at 18 d after unfolding. The highest differences in leaf expansion rates due to CO₂ were observed on or around the day of highest leaf expansion rates at 22.7, 26.6, and 30.6°C, indicating that the leaf growth rates are limited by carbon supply.

Mainstem and Branch Leaf Area

Whole plant leaf area at 23, 35, and 70 DAE is presented against running average temperature in Fig. 7. Leaf area taken from the destructive sampling on 23 DAE did not show any trend due to CO₂. Again, this is probably because CO₂ treatment was imposed on 15 DAE and the duration of CO₂ treatment exposure had been short. There is a clear temperature response, showing an initial increase in leaf area followed by a slight decrease as temperature increased. By 35 DAE the plants had been exposed to both [CO₂] and temperature treatments for 22 d. At the two higher temperatures leaf area increased 31% because of [CO₂] doubling. Both [CO₂] and temperature treatments had significant impact on leaf area by 70 DAE except at the two lowest temperatures (Fig. 7). The greatest increase in leaf area occurred between the temperature treatments of 18.7 and 22.7°C, with an increase of 337 and 617% at the 350 and 700 $\mu\text{L L}^{-1}$ CO₂

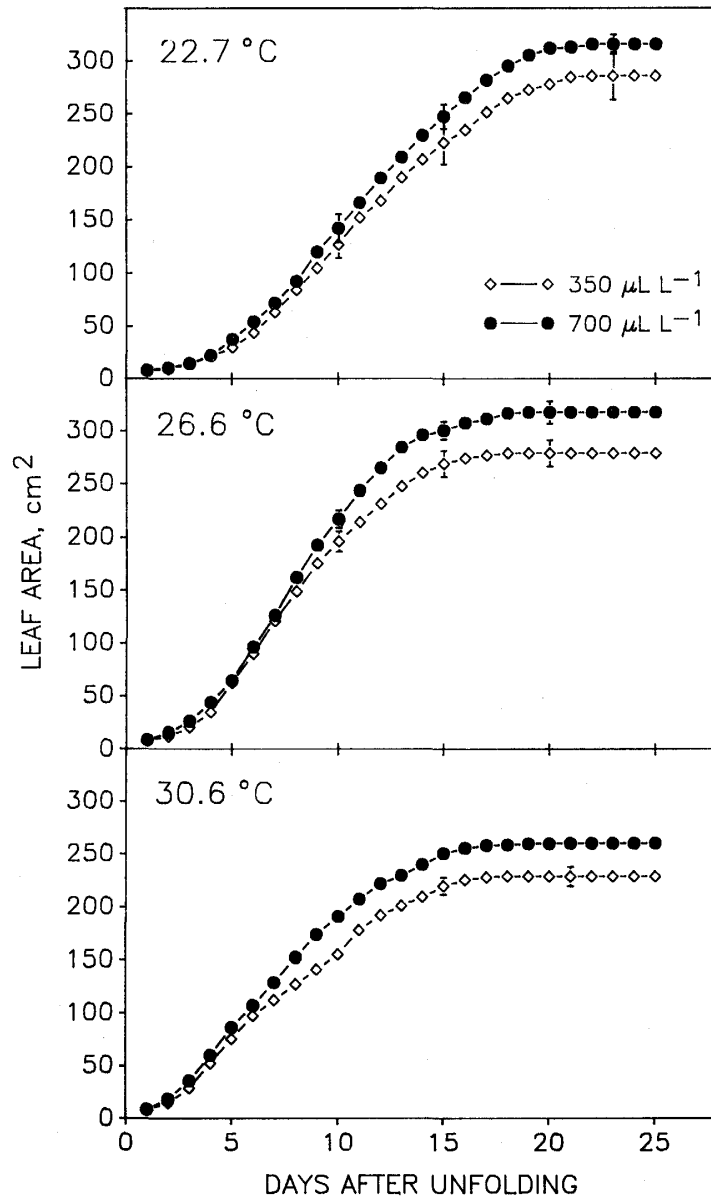


Fig. 5. The effects of [CO₂] and temperature on growth and final size of leaf 10 on the mainstem of cotton. Bars indicate standard errors of the mean and are shown when greater than the symbol size.

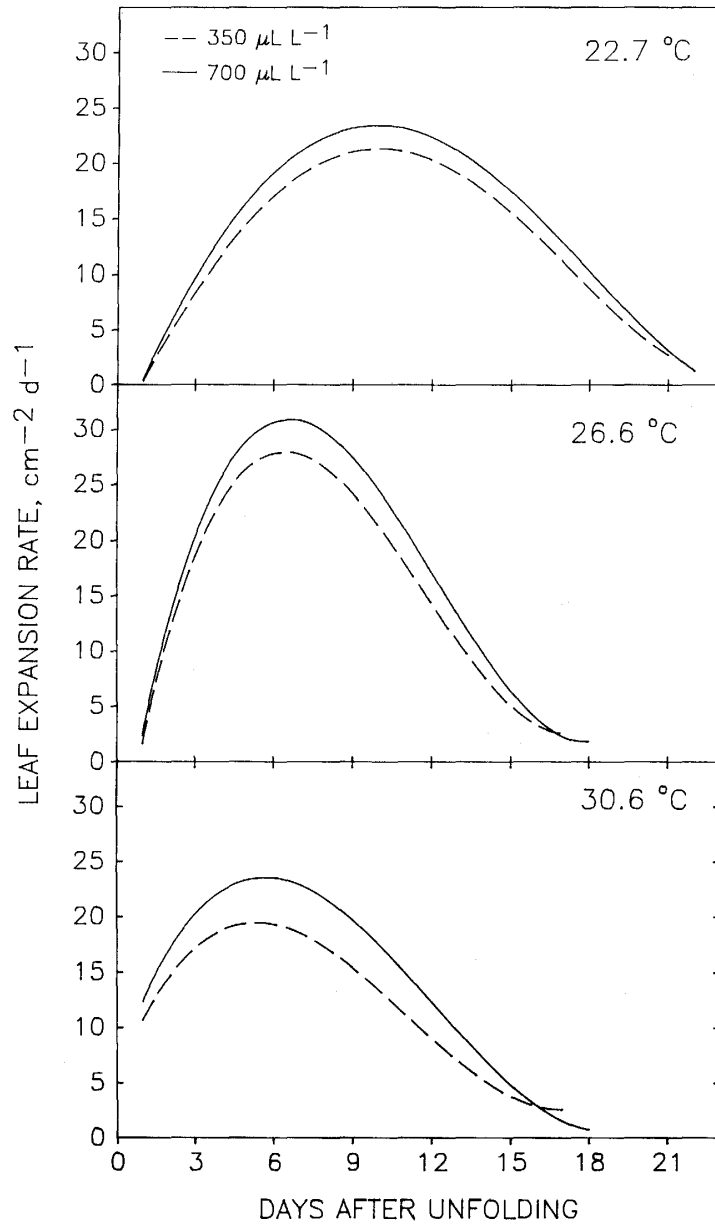


Fig. 6. The rate and duration of leaf expansion of leaf 10 on the mainstem of cotton as influenced by [CO₂] and temperature.

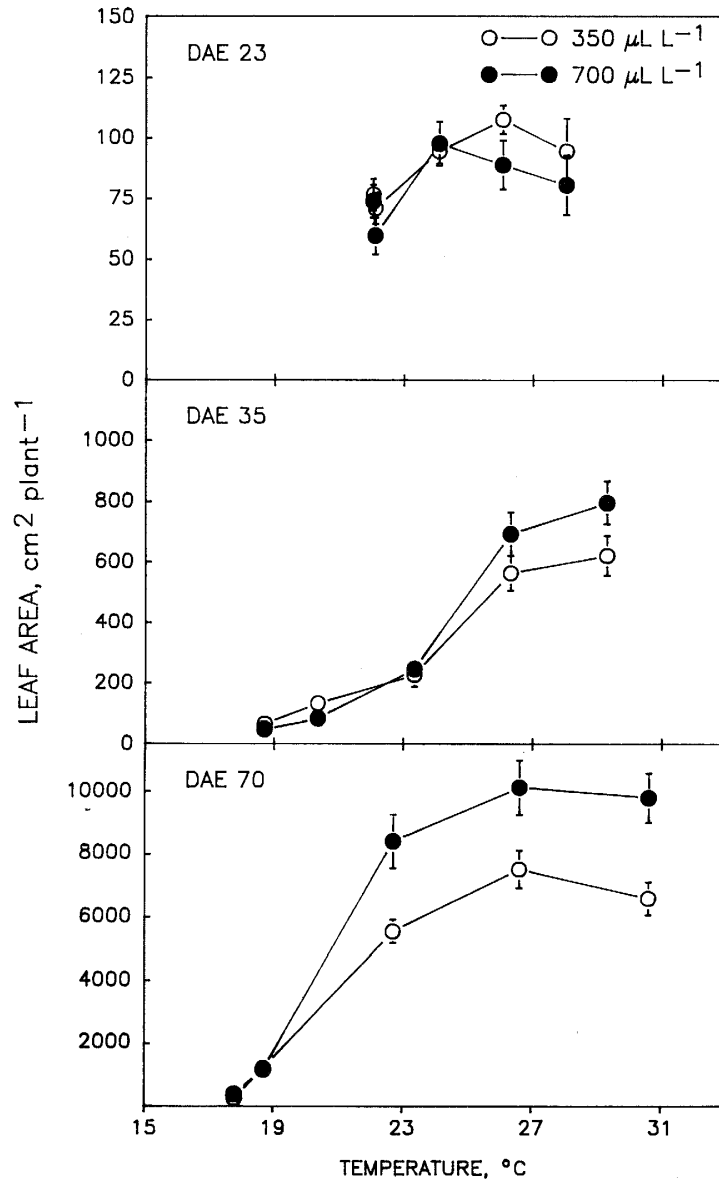


Fig. 7. Total leaf area of cotton at three different times during the growing period as affected by temperature and [CO₂]. Bars indicate standard errors of the mean and are shown when greater than the symbol size.

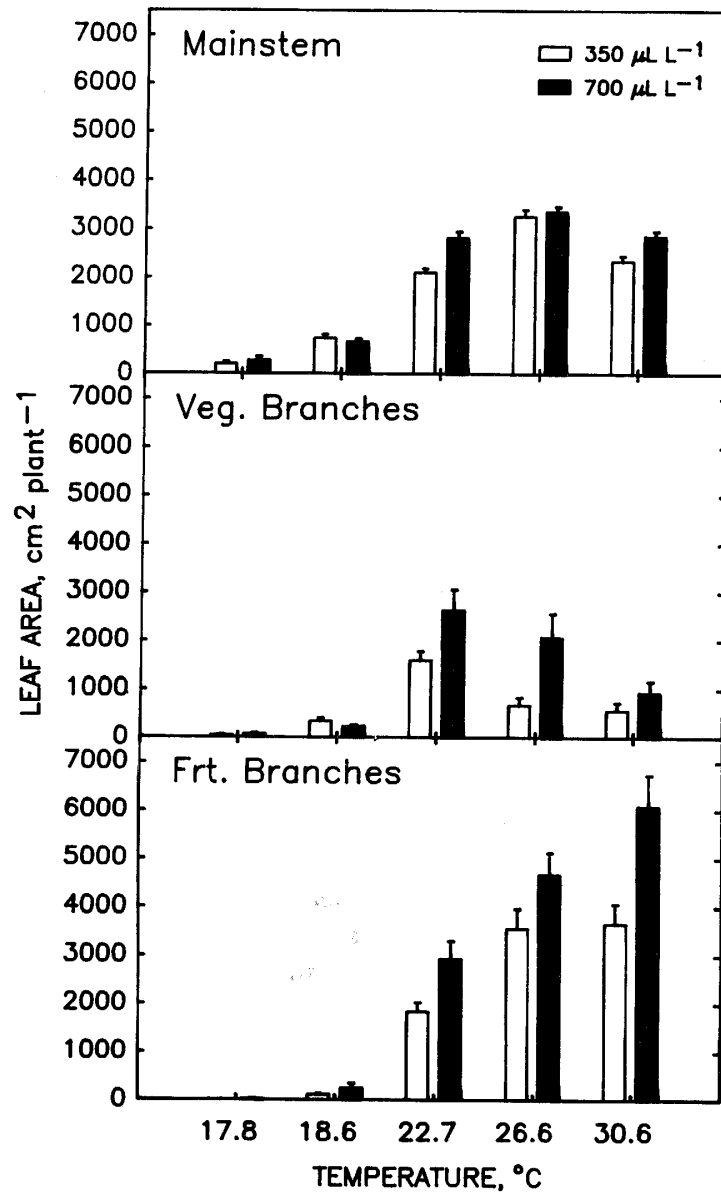


Fig. 8. Leaf area on the mainstem, vegetative branches, and fruiting branches of cotton at 70 DAE as influenced by temperature and [CO₂]. Bars indicate standard errors of the mean and are shown when greater than the symbol size.

levels, respectively. Leaf area increased with temperature up to 26.6°C and then slightly decreased at 30.6°C. The high CO₂ treatment significantly increased leaf area at 22.7, 22.6, and 30.6°C.

After separating leaf area into leaf area from mainstem, vegetative branches, and fruiting branches, it is evident that high [CO₂] enhanced leaf area more dramatically on fruiting and vegetative branches than on the mainstem (Fig. 8). High CO₂ level increased mainstem leaf area significantly at 22.7 and 30.6°C. It

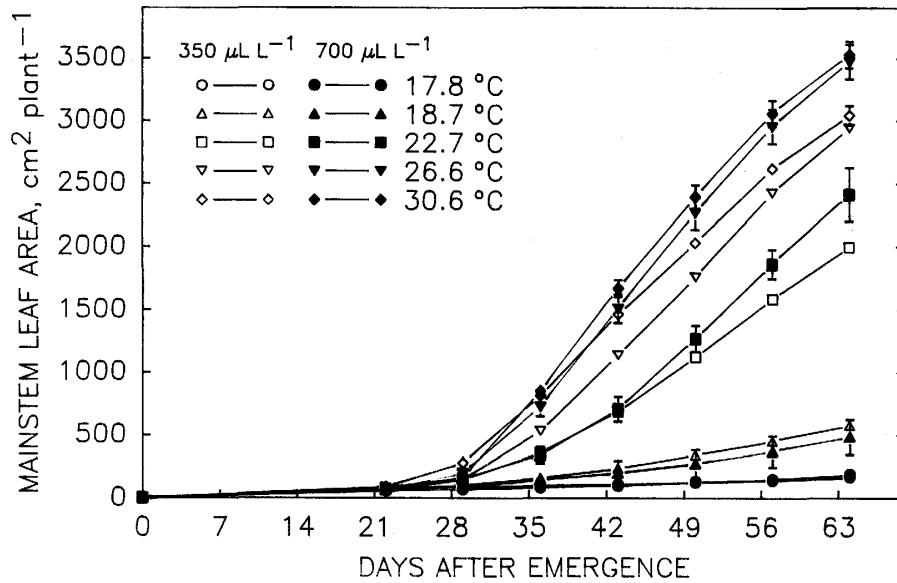


Fig. 9. Temperature and $[CO_2]$ effects on the total area of the mainstem leaves during the prefruiting period. Bars indicate standard errors of the mean and are shown when greater than the symbol size.

appears that higher CO_2 increased leaf area because of the production of a higher number of vegetative branches and a higher number of fruiting nodes on fruiting branches (14).

The non-destructive measurements of leaf area on the mainstem collected at weekly intervals also show that the effects of both $[CO_2]$ and temperature on leaf area were less pronounced during early seedling growth (Fig. 9). However, by 49 DAE both $[CO_2]$ and temperature affected leaf area growth on the mainstem. The effect of CO_2 was more pronounced at higher temperature treatments, especially at 22.7°C, which shows an increase of 34% in mainstem leaf area due to doubling CO_2 by 63 DAE. The effect of $[CO_2]$ on mainstem leaf area was not significant at the two lower temperature treatments during the entire experimental period (Fig. 9).

The data on mainstem leaf sizes recorded on 63 DAE show the interactive effects of CO_2 and temperature (Fig. 10). At 17.8°C, all the leaves were less than 50 cm², and there was no effect of leaf position on leaf area. When the temperature was 18.7°C, the leaf sizes increased to as high as 100 cm². CO_2 did not significantly affect individual leaf sizes. However, there were differences between leaves at various positions on the mainstem. As the temperature increased, more leaves were grown to their full size and a higher number of leaves were produced on the mainstem. The high $[CO_2]$ increased individual leaf sizes significantly at the three higher temperatures and produced more nodes on vegetative and fruiting branches (15), resulting in higher whole plant leaf area.

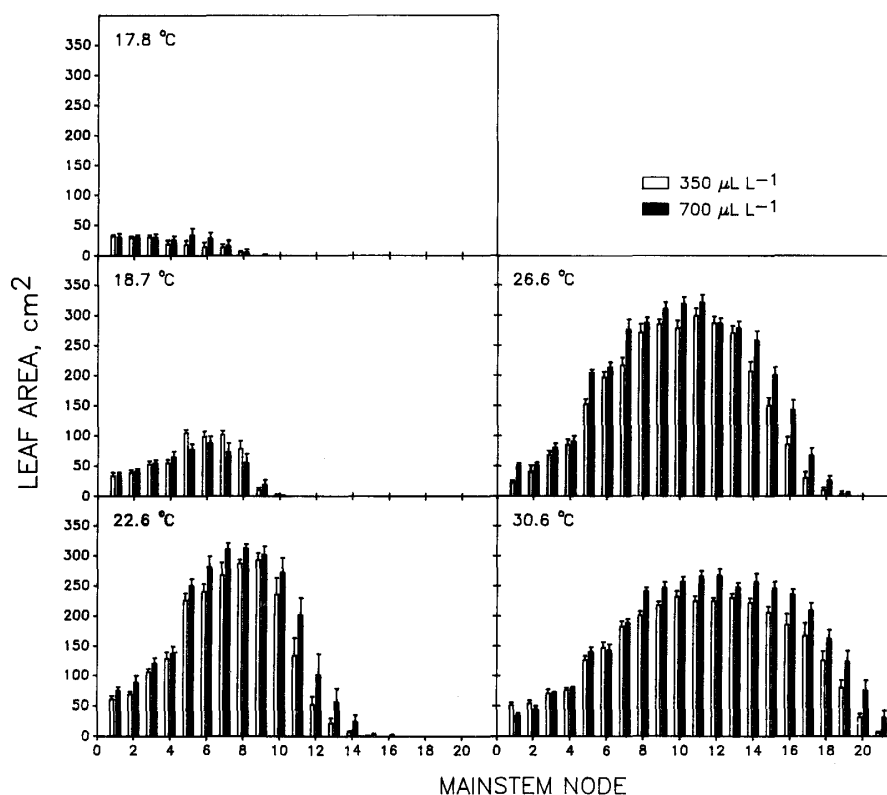


Fig. 10. Profile of mainstem leaf sizes as influenced by temperature and [CO₂]. Standard errors of each mean are presented.

CONCLUSIONS

Temperature and [CO₂] significantly affected expansion and final size of the cotton leaves. Leaf initiation rates on the mainstem were primarily temperature dependent and not limited by carbon supply in the ambient [CO₂] environment. Temperature significantly affected final sizes of the prefruiting and fruiting leaves, and the duration and rate of leaf expansion. High [CO₂] increased final leaf sizes and rate of leaf expansion, but the effect was more pronounced at higher temperatures, showing an interaction between [CO₂] and temperature. The rate of leaf expansion increased with temperature up to 26.6°C, and declined at higher temperatures in both [CO₂] levels. The duration of leaf expansion was not influenced by carbon supply but was strongly influenced by temperature. High [CO₂] increased total leaf area because of small increases in individual leaf sizes and also because more nodes were produced on fruiting and vegetative branches.

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