

Interactive effects of elevated [CO₂] and temperature on growth and development of a short- and long-season peanut cultivar

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Abstract Temperature and CO₂ are two of the main environmental factors associated with climate change. It is generally expected that elevated [CO₂] will increase crop production. However, other environmental factors such as temperature along with management practices could further modify a crop's response to CO₂. The goal of this study was to determine the interactive effects of elevated [CO₂] and above-optimum temperature on growth, development and yield of two peanut (*Arachis hypogaea* L.) cultivars, e.g., Pronto and Georgia Green. One of the objectives was to determine if there was any variation in response between these two cultivars with respect to possible adaptation to climate change. Peanut plants were grown in controlled environment chambers in the University of Georgia Envirotron under conditions of non-limiting water and nutrient supply. Plants were exposed to day/night air temperatures of 33/21°C (T_A), 35.5/23.5°C ($T_A + 2.5^\circ\text{C}$), and 38/26°C ($T_A + 5^\circ\text{C}$) along with CO₂ treatments of 400 and 700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air. The selected range of temperatures was based on the temperatures that are common for southwest Georgia during the summer months. The results showed that LAI of both cultivars responded positively, e.g., 28.3% for Pronto and 49.3% for Georgia Green to elevated [CO₂]. Overall, elevated [CO₂] alone resulted in a significant increase in total biomass at final harvest across all temperatures ($P < 0.0001$), but decreased final seed yield ($P < 0.0005$), except for Georgia Green at ($T_A + 5^\circ\text{C}$). The higher temperatures compared to T_A reduced the relative response of total biomass to CO₂ for both cultivars. It can be concluded that final seed yield response to CO₂ depends on the sensitivity of individual cultivars to temperature, especially during the reproductive development stage.

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1 Introduction

Elevated $[\text{CO}_2]$ together with other factors which cause climate change may greatly affect the worldwide agricultural production in the future (IPCC 1995). Various studies have shown an increase in growth and yield of C3 crops in response to CO_2 (e.g. Kimball et al. 2002; Kim et al. 2003). Higher temperature individually or along with the ongoing global increase of atmospheric CO_2 could affect various physiological and morphological traits, which subsequently influence growth and final yield. Studying the effects of CO_2 on crop performance would be more meaningful if considered in interaction with other environmental and management factors (Kim et al. 2003; Bannayan et al. 2005; Heinemann et al. 2005). What could jeopardize crop production under future climate change would be extreme occurrences of weather variables, among them high temperatures. However, these negative effects could be offset by any expected positive response of crops to elevated $[\text{CO}_2]$. CO_2 mitigation of the hazardous effects of extreme temperature can be considered a positive response. However, other factors, such as introducing new cultivars which are more efficient under future climate change, could change the magnitude and direction of response to both CO_2 and extreme temperatures. It is well-recognized that the CO_2 concentration, management factors and other environmental factors will interact in complex ways that determine the ultimate impact of climate change on crop production. Any crop yield stimulation due to elevated $[\text{CO}_2]$ could either be diminished or amplified by a warmer climate, depending on the sensitivity of various growth traits of the cultivar to temperature. About 90% of the world peanut production is in tropical and semi-arid tropical regions that are characterized by high temperatures (Prasad et al. 2003). Baker et al. (1989) reported positive effects of an increasing temperature on the response of soybean to CO_2 , but Boote and Allen (1999) reported negative effects for peanut. They applied double $[\text{CO}_2]$ (700 vpm) and a 4.5°C increase above Florida ambient temperature and found a positive response to CO_2 at ambient temperatures, but increasing the temperature by 4.5°C above ambient did not show any beneficial effect from elevated $[\text{CO}_2]$. Peanut exposure to air and soil temperatures above optimum temperature can cause a significant loss in yield (Prasad et al. 2000; Craufurd et al. 2002). For instance, a high air temperature, e.g., 38°/22°C, day/night, reduced total biomass and pod yield of peanut significantly (Prasad et al. 2000).

The beneficial effects of elevated $[\text{CO}_2]$ have been reported for many crops. Elevated $[\text{CO}_2]$ increased the photosynthetic rate of peanut under different soil moisture regimes (Chen and Sung 1990; Clifford et al. 1993). It is expected that above-optimum temperatures would counterbalance the useful effects of CO_2 (Prasad et al. 2005; Reddy et al. 2005), but intra-species variation in response to CO_2 (Johannessen et al. 2005) may provide an opportunity to mitigate the deleterious effects of high temperature at elevated $[\text{CO}_2]$. Thus, the response of individual genotypes to combinations of CO_2 and high temperatures is a critical research issue in order to be able to predict peanut production under possible future climate change. The hypothesis of this study was that the responses to elevated $[\text{CO}_2]$ and temperature may differ among different cultivars (Long 1991) and that yield reduction due to high temperatures is more relevant in studying the effect of elevated $[\text{CO}_2]$ on crop performance under future climate change (Baker 2004). The overall goal of this study

was to improve our knowledge of peanut performance under high levels of $[\text{CO}_2]$ and high temperature and their corresponding interactions. The specific objective was to determine if there is a variation in response to CO_2 and temperature between two different peanut maturity groups.

2 Materials and methods

The experiment was conducted in the Georgia Envirotron of the University of Georgia Griffin Campus. The experimental design consisted of a three-way randomized block with four replications. The treatments consisted of two peanut cultivars, Pronto and Georgia Green, three day/night temperature levels, 33/21°C (T_A), 35.5/23.5°C ($T_A + 2.5^\circ\text{C}$), and 38/26°C ($T_A + 5^\circ\text{C}$) and two CO_2 concentrations, 400 and 700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air. The temperature and CO_2 treatments were randomly allocated in each of the six growth chambers as follows:

- Chamber 1- $T_A + 5^\circ\text{C}$ and 400 $\mu\text{mol CO}_2 \text{ mol}^{-1}$,
- Chamber 2- $T_A + 2.5^\circ\text{C}$ and 400 $\mu\text{mol CO}_2 \text{ mol}^{-1}$,
- Chamber 3- $T_A + 5^\circ\text{C}$ and 700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$,
- Chamber 4- T_A and 700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$,
- Chamber 5- $T_A + 2.5^\circ\text{C}$ and 700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$,
- Chamber 6- T_A and 400 $\mu\text{mol CO}_2 \text{ mol}^{-1}$.

2.1 The growth chambers

Six large walk-in Conviron growth chambers with an internal chamber height of 2.20 m and a growth area of 8.64 m² were used for the experiment. All chambers have high intensity lighting with air temperature, relative humidity and carbon dioxide control. Each chamber was individually controlled with a touch screen unit that included alarm condition information, programming, diagnostics, and data-logging features. A central dedicated personal computer allowed for programming of the desired climatic conditions in the chambers and for storing the environmental data. Photosynthetic active radiation (PAR) was 1,500 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ during the course of the experiment. Carbon dioxide was injected automatically into the chambers and its concentration inside the chambers 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, Nebraska, USA) was used to monitor the $[\text{CO}_2]$ levels for each chamber independently. The accuracy of the analyzer was 2% at a level of 700 ppm (Ingram et al. 1998).

2.2 The controlled conditions

The air temperature in the chambers was set to mimic the weather conditions in the southwest region of Georgia during the warmer period of the peanut growing season using weather data from Camilla, Mitchell County (31.2°N, 84.2°W, and 56 m above mean sea level). A set of temperatures based on the day/night air

temperature of 33/21°C with treatment increments of 2.5°C (35.5/23.5°C) and 5°C (38/26°C) was established for the temperature treatments. Based on these the three maximum temperatures (33, 35.5 and 38°C) and three minimum temperatures (21, 23.5 and 26°C), the temperature in the chambers was changed in 15-min steps using a sinusoidal wave function during the day and a decay function during the night (Parton and Logan 1981). A fixed daylength of 14 h, which corresponds to the daylength during the month of July in Camilla, was used. Four hundred micromole CO₂ mol⁻¹ air was set for ambient conditions while 700 μmol CO₂ mol⁻¹ air was selected for future climate change.

2.3 The peanut cultivars

The peanut cultivars in this study were Pronto and Georgia Green, which belong to different maturity groups. Pronto (subsp. *fastigiata* var. *vulgaris*) is a large-seeded Spanish market-type cultivar that has good shelling characteristics and good production potential (Banks and Kirby 1983). The primary advantages of Spanish types are their short growing season (an average of 120 days after planting), which should give farmers greater flexibility in adjusting planting and harvesting dates, as well as their bunch-type growth habit (Banks and Kirby 1983; USDA Peanut Crop Germplasm Committee 2003). Georgia Green (subsp. *hypogaea* var. *hypogaea*) is a Runner market-type cultivar (Branch 1996) and is currently the most widely-grown peanut cultivar in the southeastern USA.

Each peanut cultivar was planted in 144 plastic containers that had a 625 cm² surface area and a 20-l volume, for a total of 288 containers. Then, 24 containers of each cultivar were placed in each chamber. Holes were drilled at the bottom of the containers to allow for drainage. The containers were filled with sand, manually irrigated to saturation and then left for 24 h to drain the excess water. The containers were placed together, which permitted a plant population of 16 plants m⁻² that is similar to the plant density used by farmers in southwest Georgia. Five peanut seeds were sown in each container and thinned to two plants at 4 days after emergence and again thinned to one plant per container at 30 days after emergence. The plants were irrigated manually on a daily basis to maintain well-watered soil conditions.

2.4 Phenology and growth analysis

Vegetative and reproductive development was recorded following the scale proposed by Boote (1982). Phenology was recorded on a daily basis and a change in stage of development was considered achieved when more than 50% of the plants exhibited the next developmental stage. Four plants were randomly tagged in each chamber and the number of flowers per plant was counted for several weeks during the reproductive stage. Plant samples for growth analysis were collected from emergence to physiological maturity, with a total of eight samplings. Plant samplings were conducted at shorter intervals during the early stages of peanut growth and the interval was increased to a maximum of 28 days near physiological maturity.

The plants that were removed from each chamber were divided equally into four replicates for the growth analysis samplings from emergence to 30 days after

sowing. For the subsequent growth analysis samples, four containers with one plant each were randomly selected from each treatment. Plant height and root length were measured during each growth analysis sampling, and then each plant was separated into its individual components: roots, stem, leaves, and pods. The roots were cleaned and washed with water. The leaf area per plant was determined using the LI 3000 leaf area meter (LI-COR, Nebraska, USA). The plant components were dried in a forced-air oven at 70°C for a minimum of 72 h and the dry matter was measured separately for each component. The 8th and final growth analysis sample was obtained at physiological maturity and the pod yield, seed yield, and harvest index were determined. Relative biomass partitioning to leaves (leaf mass fraction, LMF), stems (stem mass fraction, SMF), roots (root mass fraction, RMF) and pod harvest index (PHI), and seed harvest index (SHI), were calculated as the ratio of each of these components to total biomass.

2.5 The statistical analysis

Three-way analysis of variance was conducted using the general linear models (GLM) procedure of SAS system, Version 8.1 (SAS Ins. 2001) to analyze the effects of cultivar, temperature and CO₂ on the growth and development data. GLM procedures were also conducted to analyze the yield and yield components. When the *F*-test was significant ($P < 0.05$), the means were compared using the Least Significant Difference (LSD) test at $\alpha = 0.05$.

3 Results

3.1 Crop development

Our observations showed (Table 1) that plants emerged one day earlier at both ($T_A + 2.5^\circ\text{C}$) and ($T_A + 5^\circ\text{C}$) than at ambient temperature. From emergence to the beginning of anthesis, elevated [CO₂] hastened the development by only one day for Georgia Green and by two days for Pronto. The cultivars showed a different response to both CO₂ and temperature for the beginning of flowering (R1). Elevated [CO₂] at T_A hastened R1 of Pronto for 1 day, but delayed flowering of Georgia Green for three days (Table 1). However, these results were not significantly different ($P > 0.05$). The cultivars showed a relatively opposite response with respect to reaching R1 at above-ambient temperatures. Increased temperature ($T_A + 2.5^\circ\text{C}$) shortened the duration to R1 for the Georgia Green cultivar but lengthened it for the Pronto cultivar. However, the highest temperature ($T_A + 5^\circ\text{C}$) shortened the interval to R1 for Pronto but prolonged it for Georgia Green. Such observations across different cultivars requires more research attention.

3.2 Leaf area index

There were no differences between ambient and elevated [CO₂] effects on leaf area index (LAI) early during the growing season, but towards the beginning of anthesis

Table 1 Number of days from sowing (DAS) to emergence (VE), second leaf stage (V2), beginning of anthesis (R1), and pegging (R2) for Georgia Green and Pronto grown at different combinations of ambient and elevated $[\text{CO}_2]$ and temperature ($^{\circ}\text{C}$)

Growth stage	Georgia Green (number of days)						Pronto (number of days)					
	Ambient ($400 \mu\text{mol mol}^{-1}$)			Elevated ($700 \mu\text{mol mol}^{-1}$)			Ambient ($400 \mu\text{mol mol}^{-1}$)			Elevated ($700 \mu\text{mol mol}^{-1}$)		
	T_A	$T_A+2.5$	T_A+5	T_A	$T_A+2.5$	T_A+5	T_A	$T_A+2.5$	T_A+5	T_A	$T_A+2.5$	T_A+5
VE	6	6	5	6	5	5	6	6	6	6	5	5
V2	9	9	8	9	8	8	9	9	8	9	8	8
R1	29	31	26	32	24	25	31	28	30	30	27	25
R2	42	44	43	45	42	44	44	42	43	42	42	41

T_A Ambient temperature

until maturity, elevated [CO₂] showed a positive impact among all cultivars and temperature treatments (Fig. 1). The ANOVA results are shown in Table 2. From planting up to about 31 days, which almost coincided with the beginning of anthesis, the LAI of Pronto at elevated [CO₂] compared to ambient was not significantly different ($P > 0.05$), but after the start of anthesis and towards the end of the growing season, LAI at elevated [CO₂] was significantly ($P < 0.01$) higher (Fig. 1). This trend was observed across all temperature treatments. Between the two cultivars, Georgia Green had a more positive response in LAI to an increase in [CO₂] than Pronto.

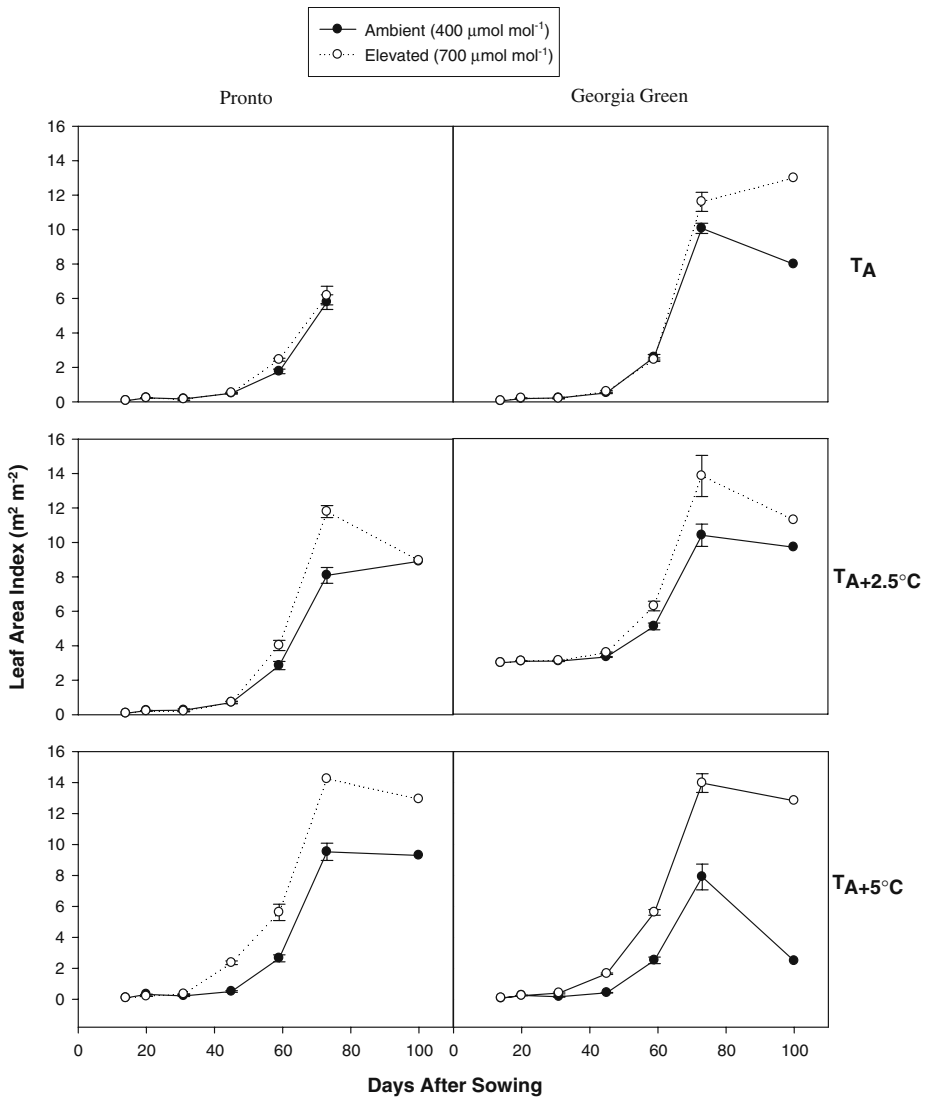


Fig. 1 LAI expansion pattern of Georgia Green and Pronto at two [CO₂] and three temperature levels

Table 2 ANOVA results for maximum LAI, total biomass (t ha^{-1}), pod yield (t ha^{-1}) and seed yield (t ha^{-1}) at harvest (** $P < 0.01$, * $P < 0.05$ and *ns* no significance)

Source	LAI _{max}	Total biomass	Pod yield	Seed yield
Cultivar	ns	*	**	**
CO ₂	**	**	ns	**
Temperature	**	ns	**	**
CO ₂ × cultivar	ns	ns	ns	ns
Temperature × cultivar	*	ns	ns	ns
CO ₂ × temperature	**	ns	*	*

The average percentage increase of LAI over the growing season and across all temperatures in response to elevated [CO₂] for Georgia Green was 49.3% and for Pronto was 28.3%. This showed the potential genotypic differences for LAI between Georgia Green and Pronto in response to CO₂.

3.3 Specific leaf area (SLA)

SLA is the amount of leaf area formed per unit of leaf biomass. The change of SLA can be considered as a morphological adaptation in response to environmental conditions. Elevated [CO₂] decreased the SLA of Pronto and Georgia Green by 6% and 1.7% respectively, averaged across the entire growing season at all temperatures. Both cultivars showed an increase in SLA with increasing temperature (Fig. 2). However, the response of SLA to both CO₂ and temperature was not significant ($P > 0.05$).

3.4 Leaf number

The number of leaves measured at the beginning of anthesis (R1), increased by 3.4% and 3.8% in response to CO₂ across all temperatures for Pronto and Georgia Green, respectively (Fig. 2). ANOVA revealed a significant ($P < 0.05$) difference between the two cultivars' leaf numbers. An increase in temperature generally increased the leaf number at both ambient and elevated [CO₂] significantly ($P < 0.05$).

3.5 Biomass and its components

Elevated [CO₂] significantly ($P < 0.05$) increased the total biomass of both cultivars (Tables 2 and 3). The average increase of biomass in response to CO₂ over the growing season for Georgia Green and Pronto across all temperatures was 26.8% and 38.6%, respectively. Our results showed that the highest response to CO₂ across various temperatures was achieved at the same point in time for both biomass and LAI. The data also showed that the belowground biomass of Pronto was significantly ($P < 0.01$) higher than Georgia Green across CO₂ and temperature levels. This indicates that the higher total biomass production of Georgia Green compared to Pronto at ambient [CO₂] was due to aboveground biomass. However at elevated [CO₂] both higher aboveground and belowground biomass of Pronto resulted in a higher total biomass than Georgia Green. Temperature did not show a significant effect on biomass production (Table 2).

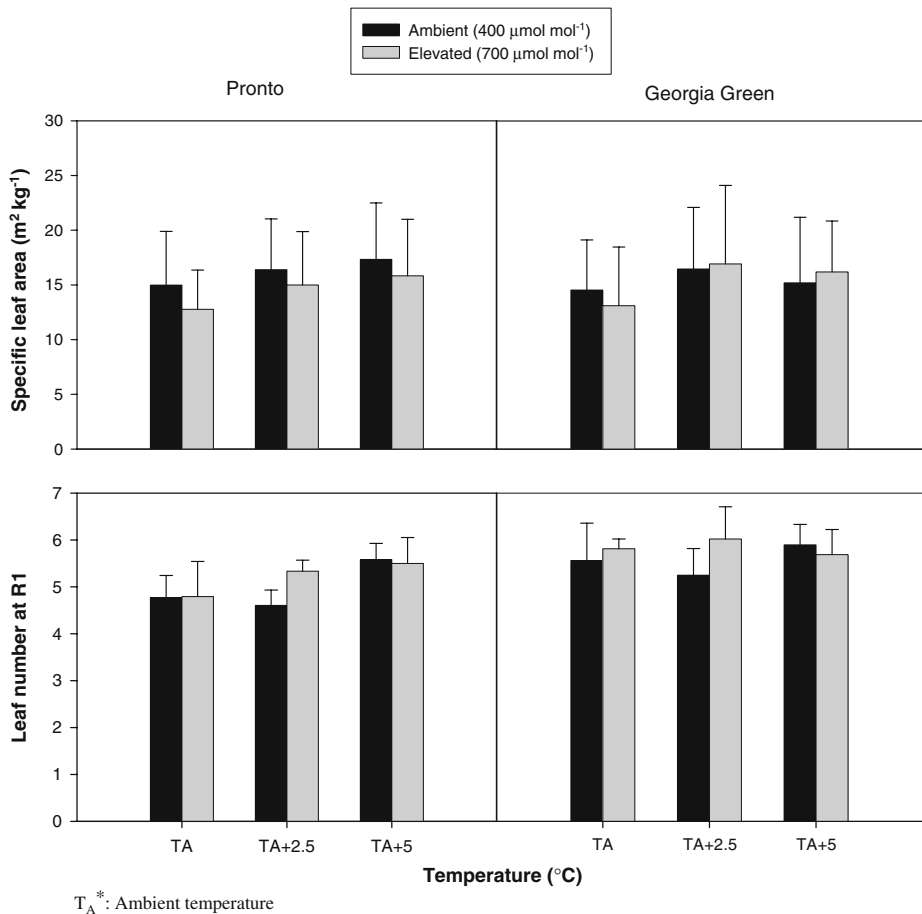


Fig. 2 Average SLA for Georgia Green and Pronto and maximum number of green leaves from emergence to beginning of anthesis at two $[CO_2]$ and three temperature levels

3.6 Biomass partitioning

Similar to total plant biomass, the individual components including leaf, stem and root mass, also showed a positive response to elevated $[CO_2]$. Among these components, stem mass, averaged over the whole growing season, was the main contributor of the response to elevated $[CO_2]$. Stem weight in response to CO_2 ($P < 0.001$) increased by 19.2% for Georgia Green and 38.3% for Pronto at ambient temperature (T_A). Increasing the temperature above ambient also significantly ($P < 0.05$) increased the stem biomass for both $[CO_2]$ levels.

Relative biomass partitioning to leaves (LMF), stems (SMF) and roots (RMF) at both ambient and elevated $[CO_2]$ are shown in Fig. 3. Increasing $[CO_2]$ increased the LMF of Georgia Green, but there was not a clear response for Pronto as LMF decreased at T_A . However, the two cultivars showed no significant difference at

Table 3 Observed maximum leaf area index (LA_{max}), total biomass, pod yield and seed yield response to CO_2 for Georgia Green and Pronto under different temperatures

	Average temperature ($^{\circ}C$)		Georgia Green		Pronto		Elevated/Ambient ratio	
			Ambient ($400 \mu mol mol^{-1}$)	Elevated ($700 \mu mol mol^{-1}$)	Ambient ($400 \mu mol mol^{-1}$)	Elevated ($700 \mu mol mol^{-1}$)	Pronto	Georgia Green
LA_{max}								
T_A^*			10.07	11.61	5.79	6.17	1.07	1.15
$T_A + 2.5$			11.40	16.67	8.09	11.79	1.46	1.46
$T_A + 5$			7.90	13.97	9.52	14.24	1.50	1.77
Total biomass ($t ha^{-1}$)								
T_A			18.58	22.36	13.78	22.48	1.63	1.20
$T_A + 2.5$			18.87	24.26	18.63	28.42	1.53	1.29
$T_A + 5$			17.70	23.80	17.33	29.40	1.70	1.34
Pod yield ($t ha^{-1}$)								
T_A			7.26	4.15	6.99	6.05	0.86	0.57
$T_A + 2.5$			2.06	2.60	4.89	4.60	0.94	1.26
$T_A + 5$			1.02	1.37	2.93	1.02	0.35	1.34
Seed yield ($t ha^{-1}$)								
T_A			5.33	2.49	5.53	4.18	0.76	0.47
$T_A + 2.5$			1.10	0.98	3.52	3.01	0.85	0.89
$T_A + 5$			0.29	0.45	1.88	0.51	0.27	1.55
T_A Ambient temperature								

both elevated $[\text{CO}_2]$ and temperature ($P > 0.05$). Increasing temperature resulted in higher partitioning to leaves, though it was not significant ($P > 0.05$) and elevated $[\text{CO}_2]$ stimulated it slightly more for Georgia Green than for Pronto. The only time that both CO_2 and temperature would significantly affect the LMF was around the beginning of flowering.

3.7 Pod and seed yield

While elevated $[\text{CO}_2]$ resulted in higher total biomass, pod yield decreased (Table 3). Elevating both $[\text{CO}_2]$ and temperature resulted in a lower pod yield for Pronto. Although the reduction due to CO_2 was only marginally insignificant ($P = 0.08$), it was highly significant ($P < 0.01$) in response to temperature (Table 2). The yield reduction due to increasing the temperature by 5°C ($T_A + 5^\circ\text{C}$) was lower at ambient than at elevated $[\text{CO}_2]$. In other words, the elevated $[\text{CO}_2]$ was not able to offset the strong negative effect of the increase in temperature.

Elevated $[\text{CO}_2]$ significantly ($P > 0.05$) reduced the seed yield of both Georgia Green and Pronto at 3.2% and 37.3%, respectively (Table 3). Increasing the temperature also significantly ($P > 0.05$) decreased the seed yield for both $[\text{CO}_2]$ levels. A comparison of the slope of seed yield reduction due to increasing temperature for both $[\text{CO}_2]$ levels showed that elevated $[\text{CO}_2]$ did not affect this rate, i.e., -1.8 for Pronto, but for Georgia Green, at elevated $[\text{CO}_2]$ this rate was reduced from -2.52 to -1.0 . Therefore, the elevated $[\text{CO}_2]$ did not mitigate the negative effect of higher temperature on the seed yield of Pronto, but it had a significant effect ($P < 0.05$) on Georgia Green (Table 2). However, the final seed yield for Pronto was significantly ($P < 0.01$) higher than the final seed yield for Georgia Green across all temperature and CO_2 levels.

The responses of the pod harvest index (PHI) to CO_2 ($P > 0.05$), temperature ($P > 0.05$) and $T_A \times \text{CO}_2$ ($P > 0.05$) were similar to pod yield (Fig. 4), except that the relative response to $T_A \times \text{CO}_2$ was only positive at $T_A + 5^\circ\text{C}$. In contrast to PHI, total pod number showed a significant response to elevated $[\text{CO}_2]$. There was also a significant difference between the two cultivars for final pod number (Fig. 4). Temperature did not impose a significant effect on pod number of either cultivar across both $[\text{CO}_2]$ levels.

By increasing the temperature, the seed harvest index (SHI) of the two cultivars at both $[\text{CO}_2]$ levels was reduced. Although the SHI decreased at elevated $[\text{CO}_2]$ compared to ambient $[\text{CO}_2]$, the relative reduction of SHI across all temperatures for Pronto and Georgia Green was 56.0% and 25.5%, respectively. This indicates that the mitigating effect of elevated $[\text{CO}_2]$ on the negative response of temperature varied between both cultivars.

The number of flowers showed a positive response to CO_2 except at T_A and $T_A + 5^\circ\text{C}$ for Georgia Green, though the differences were not significant. Across all temperatures, elevated $[\text{CO}_2]$ significantly ($P > 0.05$) increased the number of flowers by 138.3% for Pronto and 43.6% for Georgia Green. At ambient $[\text{CO}_2]$ and averaged across all temperatures, the increase in temperature resulted in a 72.4% greater number of flowers for Pronto and 149.3% for Georgia Green ($P > 0.05$). At elevated $[\text{CO}_2]$ and averaged across all temperatures, the number of flowers increased by 84.6% for Pronto and 127.3% for Georgia Green (Fig. 4).

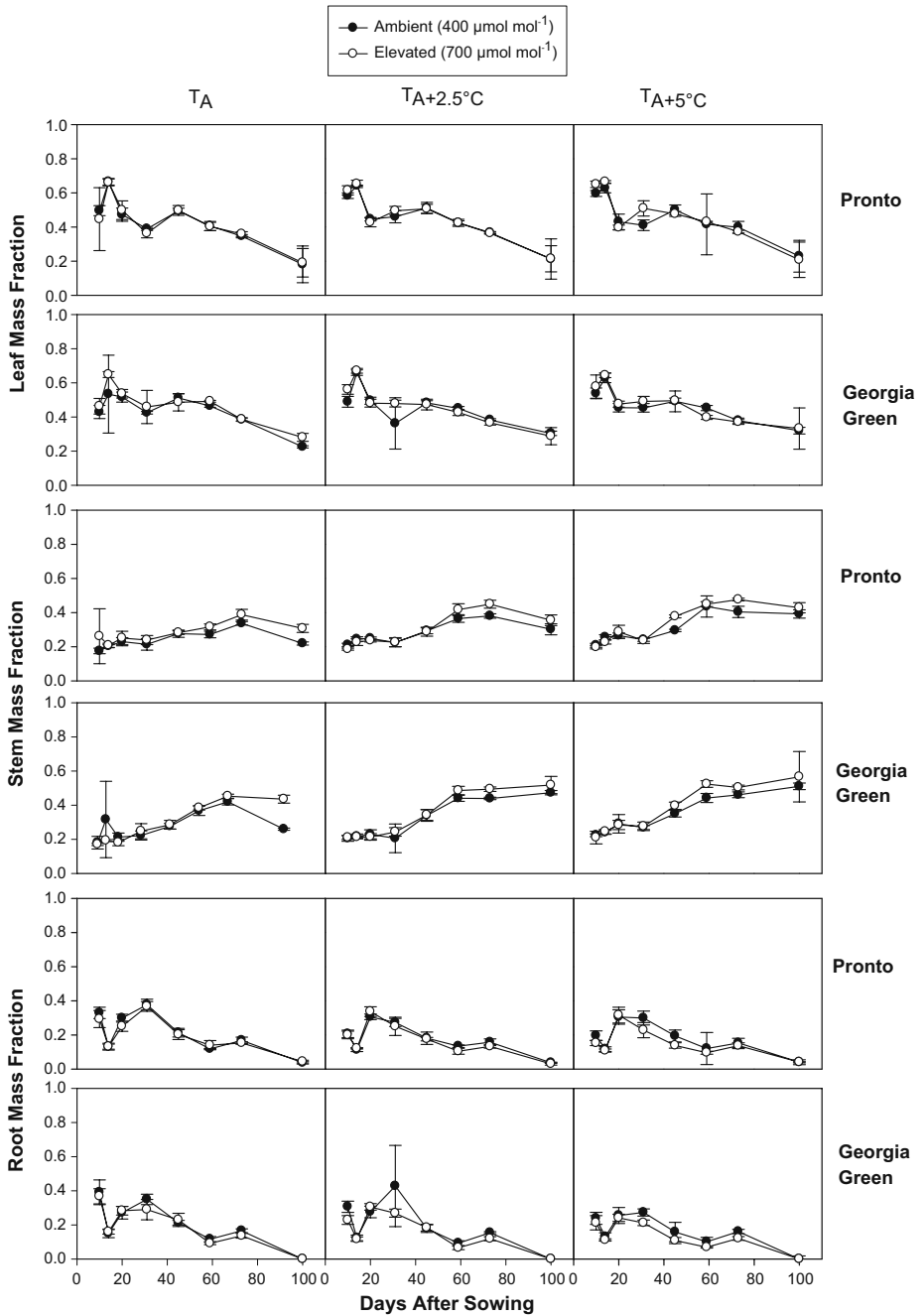


Fig. 3 Partitioning of biomass to leaves, stems, and roots at two [CO₂] and three temperature levels

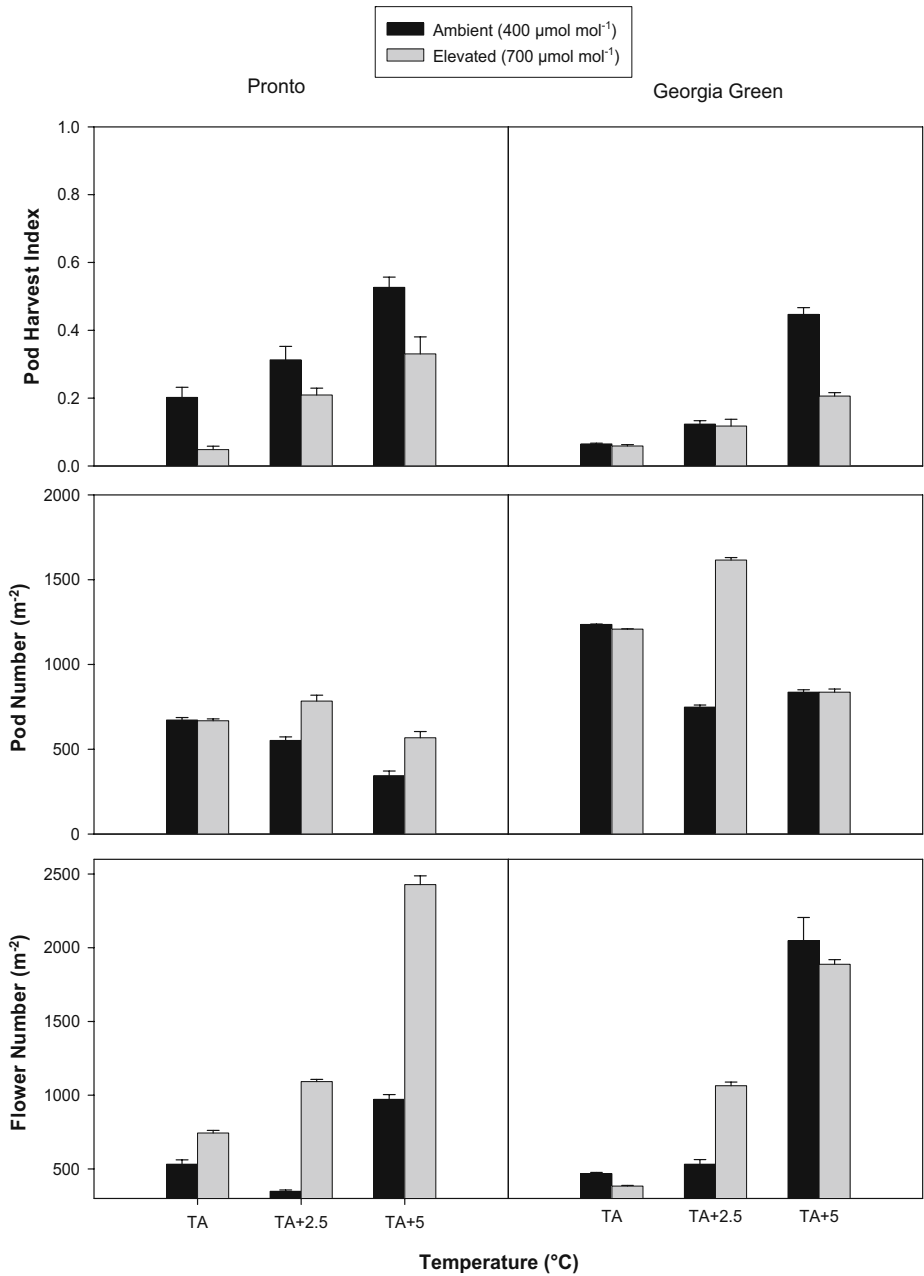


Fig. 4 Partitioned biomass to pods (PHI), pod number and maximum flower number across various temperature and [CO₂] levels for Pronto and Georgia Green at final harvest

4 Discussion

4.1 Development

Total biomass production is the product of development duration and the crop growth rate. Temperature is among the major environmental factors that determines growth and development of crops (Johnson and Thornley 1985; Atkinson 1996; Bannayan et al. 2004). The different response of the two cultivars to the interactive effects of CO₂ and temperature for development timing, though not significant, may indicate the possibility of adaptation to future climate change by selecting the appropriate cultivar(s). Ahmed et al. (1993) found no effect for cowpea on flowering under elevated [CO₂] (700 μmol l⁻¹), but Ellis et al. (1995) indicated the hastening of flowering of cowpea under enriched CO₂ conditions (720 μmol l⁻¹).

4.2 Vegetative growth

Our experiment showed that LAI for both Georgia Green and Pronto was higher in response to CO₂. Vu (2005) also showed a higher LAI for peanut at higher temperatures (1.5°C and 6°C above ambient) and elevated [CO₂] (720 μmol l⁻¹). SLA, leaf weight and leaf number are the three components that might have contributed to the larger leaf area of both cultivars in response to elevated [CO₂]. Total leaf area per plant can be considered as the product of SLA and leaf biomass. Thus both a higher SLA and leaf biomass can increase the leaf area. A larger number of leaves can also contribute to an increase in leaf area in response to environmental and management factors. In this experiment, when leaf number was higher in response to CO₂ there was no significant difference of LAI in response to CO₂. As SLA of both cultivars decreased in response to CO₂, then either the leaf number increased continuously compared to ambient (not monitored in this experiment) or leaf biomass was higher at elevated than at ambient [CO₂]. Our data showed that leaf biomass increased by 45.3% and 36.2% in response to CO₂ across all temperatures for Georgia Green and Pronto, respectively. The leaf biomass of Georgia Green was significantly ($P < 0.05$) higher than that of Pronto (Fig. 5). These modified traits at elevated [CO₂] could explain the higher LAI of Georgia Green and Pronto in response to CO₂. Mortley et al. (1997) studied the impact of [CO₂] (400 vs 700 μmol mol⁻¹) on three different peanut cultivars and found a higher LAI at elevated [CO₂]. Morison and Lawlor (1999) stated that the stimulation of total plant leaf area at elevated [CO₂] might be due to higher leaf numbers. Cure et al. (1989) found that a 31% increase in leaf area of soybean when grown at 700 μmol l⁻¹ was due to a higher leaf number, although the final size per leaf was not much affected.

In this study we found a higher final biomass induced by elevated [CO₂] which supports the common prediction of the positive response of all C3 crops to a higher CO₂ concentration. Elevated [CO₂] increases net photosynthesis and light saturated carbon assimilation rates of peanut under both irrigated and drought conditions (Clifford et al. 1993; Stronach et al. 1994). Among the total biomass components, stem biomass contributed most. Moya et al. (1998), who studied the effects of temperature and CO₂ on rice plants (*Oryza sativa* L.), also found a significant increase of stem weight at elevated [CO₂] for different cultivars at various temperatures. Allen

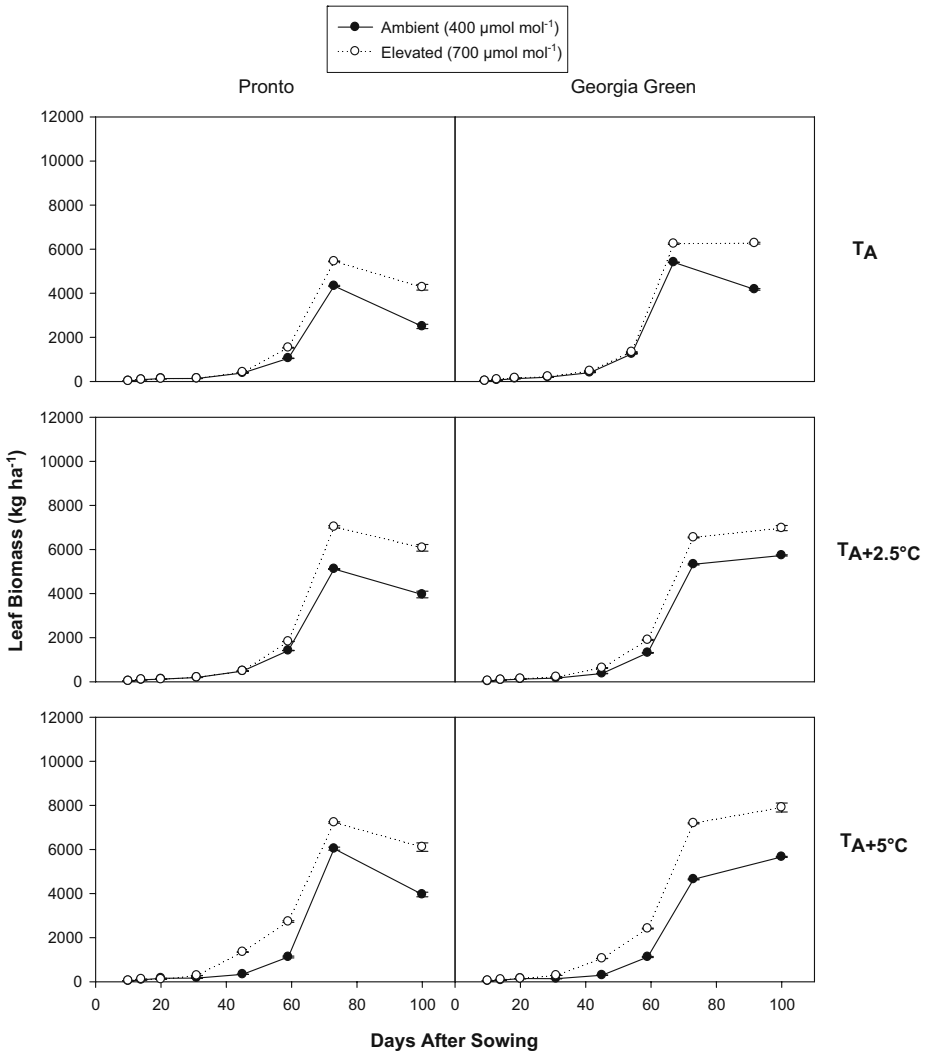


Fig. 5 Leaf biomass for Georgia Green and Pronto at two [CO₂] and three temperature levels

et al. (1991) found that CO₂ enhanced carbon partitioning to stems of soybean as a supporting structure during vegetative growth. Both Pronto and Georgia Green partitioned more biomass to stems (stem mass fraction, SMF) at elevated [CO₂] by respectively 7.7% and 3.7% and SMF was significantly (*P* < 0.05) higher for Georgia Green compared to Pronto.

4.3 Reproductive growth

A higher flower number indicates the availability of assimilates due to improved vegetative growth (Jolliffe and Ehret 1985), but the smaller number of pods and

seeds compared to the number of flowers might be due to the sensitivity of seed set to temperature (Prasad et al. 2000). Ong (1984) showed a reduction in partitioning of assimilates to pods as the temperature increased above 24°C, which demonstrates that cultivars can respond quite differently to possible changes in the future climate. Bell et al. (1993), Nigam et al. (1994), and Wheeler et al. (1997) indicated that genotypes differ in sensitivity to temperature during both vegetative and reproductive growth. However, the optimum temperature for pod growth and development is lower than for vegetative growth (Cox 1979). Similar to the results of our study, others have also reported differences in response to high temperatures among peanut cultivars (Greenberg et al. 1992; Wheeler et al. 1997; Prasad et al. 2000). Prasad et al. (2003) reported a reduction of both pod and seed harvest index by increasing the temperature at different [CO₂] levels. Prasad et al. (2002) reported a significant negative effect of temperature and non-significant interaction of temperature and CO₂ on total biomass of dry bean (*Phaseolus vulgaris* L.). The results of our study with a lower seed yield at high [CO₂], even at ambient temperature, are unexplainable here. However, higher temperatures may have influenced the poor response to elevated [CO₂] due to partial stomatal closure (Prasad et al. 2002; Matsui et al. 1997). The dominant and limiting effect of temperature on the response to CO₂ has been reported for other crops as well (Newton et al. 1994; Ziska et al. 1997). Prasad et al. (2003) found a lower seed-set of peanut at higher temperatures for both ambient and elevated [CO₂]. Lower seed-set is mostly due to a temperature effect on pollen production and viability (Hall 1992). Based on the results of our study we conclude that the magnitude and even the direction of the growth response to elevated [CO₂] at different temperatures depends on the characteristics and sensitivity to temperature of a particular cultivar. Chen and Sung (1990) found that peanut seed yield did not increase at elevated [CO₂] (1,000 µl CO₂ l⁻¹) for pot studies in semi-closed chambers. In contrast, Mortley et al. (1997) reported a higher pod and seed yield for three different peanut cultivars at elevated [CO₂]. Various other studies have also shown a reduction in seed yield due to high temperature, even under elevated [CO₂] (Baker and Allen 1993; Ziska et al. 1997; Horie et al. 2000). Both Craufurd et al. (2002) and Greenberg et al. (1992) indicated that there is a variation among peanut genotypes in their ability to maintain partitioning at high temperature. A comparison of PHI and SHI showed that the reduction percentage of PHI and SHI by increasing temperature is the same at ambient [CO₂], but at elevated [CO₂] the reduction in PHI is 15% lower than SHI.

4.4 Cultivar effect

Although the LAI and total biomass of Georgia Green was higher than Pronto, seed yield for Pronto was higher than Georgia Green across all treatments. Georgia Green showed a lower sensitivity to high temperatures during vegetative growth than Pronto, but was more sensitive during reproductive development, which ultimately resulted in a lower seed yield compared to Pronto. The effect of CO₂ on the negative effect of higher temperatures was more prominent for Georgia Green than Pronto. Based on the results from this study, we conclude that selection criteria for peanut breeding programs that consider future climate change should be more focused on cultivars that have a lower sensitivity to high temperatures, especially during seed-setting and pod filling. A shift to higher optimum temperatures will potentially

reduce the adverse effect of the increase in temperature, subsequently resulting in higher beneficial effects of elevated [CO₂].

References

- Ahmed FE, Hall AE, Madore MA (1993) Interactive effects of high temperature and elevated carbon dioxide concentration on cowpea [*Vigna unguiculata* (L.) Walp]. *Plant Cell Environ* 16:835–842
- Allen LH Jr, Bisbal KJ, Boote KJ, Jones PH (1991) Soybean dry matter allocation under subambient and superambient levels of carbon dioxide. *Agron J* 83:875–883
- Atkinson D (1996) Temperature, plant development and crop yields. *Trends Plant Sci* 1:119
- Baker JT (2004) Yield responses of Southern US rice cultivars to CO₂ and temperature. *Agric For Meteorol* 122:129–137
- Baker JT, Allen LH Jr (1993) Contrasting crop species responses to CO₂ and temperature: rice, soybean, and citrus. In: Rozema J, Lambers H, Van de Geijn SC (eds) CO₂ and biosphere. Elsevier, Amsterdam, pp 239–260
- Baker JT, Allen LH Jr, Boote KJ, Jones PH (1989) Response of soybean to air temperature and carbon dioxide concentration. *Crop Sci* 29:98–105
- Banks DJ, Kirby JS (1983) Registration of pronto peanut (Reg. No. 28). *Crop Sci* 23:184
- Bannayan M, Hoogenboom G, Crout NMJ (2004) Photothermal impact on maize performance: a simulation approach. *Ecol Model* 180:277–290
- Bannayan M, Kobayashi K, Kim HY, Liffering M, Okada M, Miura S (2005) Modeling the interactive effects of atmospheric CO₂ and N on rice growth and yield. *Field Crops Res* 93:237–251
- Bell MJ, Wright GC, Harch G (1993) Environmental and agronomic effects on the growth of four peanut cultivars in a sub-tropical environment. II Dry matter partitioning. *Exp Agric* 29:491–501
- Boote KJ (1982) Growth stages of peanut (*Arachis hypogaea* L.). *Peanut Sci* 9(1):35–40
- Boote KJ, Allen LH Jr (1999) Effects of elevated carbon dioxide and temperature on growth and yield of peanut. The American Peanut Research and Education Society, Inc. Conference Proceeding vol. 31. p 5
- Branch WD (1996) Registration of 'Georgia Green' peanut. *Crop Sci* 36:806
- Chen JJ, Sung JM (1990) Gas exchange rate and yield responses of Virginia-type peanut to carbon dioxide enrichment. *Crop Sci* 30:1085–1089
- Clifford SC, Stronach IM, Mohamed AD, Azam-Ali SN, Crout NMJ (1993) The effects of elevated atmospheric carbon dioxide and water stress on light interception, dry matter production and yield in stands of groundnut (*Arachis hypogaea* L.). *J Exp Bot* 44(269):1763–1770
- Cox FR (1979) Effects of temperature treatment on peanut vegetative and fruit growth. *Peanut Sci* 6:14–17
- Craufurd PQ, Prasad PVV, Summerfield RJ (2002) Dry matter production and rate of change of harvest index at high temperature in peanut. *Crop Sci* 42:146–151
- Cure JD, Rufty TW, Israel DW (1989) Alterations in soybean leaf development and photosynthesis in a CO₂-enriched atmosphere. *Bot Gaz* 150:337–347
- Ellis RH, Craufurd PQ, Summerfield RJ, Roberts EH (1995) Linear relations between carbon dioxide concentration and rate of development towards flowering in sorghum, cowpea, and soybean. *Ann Bot* 75:193–198
- Greenberg DC, Williams JH, Ndunguru BJ (1992) Differences in yield determining processes of groundnut (*Arachis hypogaea* L.) genotypes in varied drought environments. *Ann Appl Biol* 120:557–566
- Hall AE (1992) Breeding for heat tolerance. *Plant Breed Rev* 10:129–168
- Heinemann AB, Maia AHN, Neto DD, Ingram KT, Hoogenboom G (2005) Soybean (*Glycine max* (L.) Merr.) growth and development response to CO₂ enrichment under different temperature regimes. *Eur J Agron* 24(1):52–61
- Horie T, Baker JT, Nakagawa H, Matsui T (2000) Crop ecosystem responses to climatic change: rice. In: Reddy KR, Hodges HF (eds) Climate change, plant productivity and global implications. CABI, New York, NY, pp 81–106
- Ingram KT, Hoogenboom G, Liu L (1998) A multidisciplinary research facility for the study of interacting environmental stresses on plants, ASAE Paper No. 984151, St. Joseph, American Society of Agricultural Engineers

- IPCC (1995) In: Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K (eds) The science of climate change, 1996. Cambridge University Press, Cambridge, p 572
- Johannessen MM, Mikkelesen TN, Nersting LG, Gullord M, von Bothmer R (2005) Effects of increased atmospheric CO₂ on varieties of oat. *Plant Breed* 124:253–256
- Johnson IR, Thornley JHM (1985) Temperature dependence of plant and crop processes. *Ann Bot* 55:1–24
- Jolliffe PA, Ehret DL (1985) Growth of bean plants at elevated carbon dioxide concentrations. *Can J Bot* 63:2021–2025
- Kim HY, Lieffering M, Kobayashi K, Okada M, Miura S (2003) Seasonal changes in the effects of elevated CO₂ on rice at three levels of nitrogen supply: a free air CO₂ enrichment (FACE) experiment. *Glob Chang Biol* 9:826–837
- Kimball BA, Kobayashi K, Bindi M (2002) Responses of agricultural crops to free-air CO₂ enrichment. *Adv Agron* 77:293–368
- Long SP (1991) Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: has its importance been underestimated? *Plant Cell Environ* 14:729–739
- Matsui T, Namuco OS, Ziska LH, Horie T (1997) Effects of high temperature and CO₂ concentration on spikelet sterility in indica rice. *Field Crops Res* 51:213–219
- Morison JIL, Lawlor DW (1999) Interactions between increasing CO₂ concentration and temperature on plant growth. *Plant Cell Environ* 22:659–682
- Mortley DG, Philip A, Loretan JH, Seminara J (1997) CO₂ enrichment influences yields of ‘Florunner’, ‘Georgia Red’ and ‘New Mexico’ peanut cultivars. *Adv Space Res* 20:1905–1908
- Moya TB, Ziska LH, Namuco OS, Olszyk D (1998) Growth dynamics and genotypic variation in tropical, field-grown paddy rice (*Oryza sativa* L.) in response to increasing carbon dioxide and temperature. *Glob Chang Biol* 4:645–656
- Newton PCD, Clark H, Bell CC, Glasgow EM, Campbell BD (1994) Effects of elevated CO₂ and simulated seasonal changes in temperature on the species composition and growth rates of pasture turves. *Ann Bot* 73:53–59
- Nigam SN, Nageswara JC, Wynne JH, Williams MF, Nagabhshnam GVS (1994) Effect and interaction of temperature and photoperiod on growth and partitioning on three groundnut (*Arachis hypogaea* L.) genotypes. *Ann Appl Biol* 125:541–552
- Ong CK (1984) The influence of temperature and water deficits on the partitioning of dry matter in groundnut. *J Exp Bot* 35:746–755
- Parton WJ, Logan JA (1981) A model for diurnal variation in soil and air temperature. *Agric Meteorol* 23:205–216
- Prasad PVV, Craufurd PQ, Summerfield RJ (2000) Effect of high air and soil temperature on dry matter production, pod yield and yield components of groundnut. *Plant Soil* 222:231–239
- Prasad PVV, Boote KJ, Hartwell L, Allen JR, Thomas JMG (2002) Effects of elevated temperature and carbon dioxide on seed-set and yield of kidney bean (*Phaseolus vulgaris* L.). *Glob Chang Biol* 8:710–721
- Prasad PVV, Boote KJ, Hartwell L, Allen JR, Thomas JMG (2003) Super-optimal temperatures are detrimental to peanut (*Arachis hypogaea* L.) reproductive processes and yield at both ambient and elevated carbon dioxide. *Glob Chang Biol* 9:1775–1787
- Prasad PVV, Allen JR, Boote K (2005) Crop responses to elevated carbon dioxide and interaction with temperature: grain legumes. *J Crop Improve* 13(1/2):113–155
- Reddy KR, Prasad PVV, Kakani VG (2005) Crop responses to elevated carbon dioxide and interactions with temperature: cotton. *J Crop Improve* 13(1/2):157–191
- SAS Institute (2001) SAS system. 8th ed. SAS Inst., Cary, N.C.
- Stronach IM, Clifford SC, Mohamed AD, Singleton-Jones PR, Azam-Ali SN, Crout NMJ (1994) The effects of elevated carbon dioxide, temperature and soil moisture on the water use of stands of groundnut (*Arachis hypogaea* L.). *J Exp Bot* 45:1633–1638
- USDA Peanut Crop Germplasm Committee (2003) Report on the status of *Arachis* germplasm in the United States. http://www.ars-grin.gov/npgs/cgc_reports/status11.pdf
- Vu JCV (2005) Acclimation of peanut (*Arachis hypogaea* L.) leaf photosynthesis to elevated growth CO₂ and temperature. *Environ Exp Bot* 53:85–95
- Wheeler TR, Chatzialioglou A, Craufurd PQ, Ellis RH, Summerfield RJ (1997) Dry matter partitioning in groundnut exposed to high temperature stress. *Crop Sci* 37:1507–1513
- Ziska LH, Namuco O, Moya T, Quilang J (1997) Growth and yield response of field-grown tropical rice to increasing carbon dioxide and air temperature. *Agron J* 9:45–53