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Super-optimal temperatures are detrimental to peanut (*Arachis hypogaea* L.) reproductive processes and yield at both ambient and elevated carbon dioxide

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Abstract

Continuing increases in atmospheric carbon dioxide concentration (CO_2) will likely be accompanied by global warming. Our research objectives were (a) to determine the effects of season-long exposure to daytime maximum/nighttime minimum temperatures of 32/22, 36/26, 40/30 and 44/34 °C at ambient (350 μmol mol^{-1}) and elevated (700 μmol mol^{-1}) CO_2 on reproductive processes and yield of peanut, and (b) to evaluate whether the higher photosynthetic rates and vegetative growth at elevated CO_2 will negate the detrimental effects of high temperature on reproductive processes and yield. Doubling of CO_2 increased leaf photosynthesis and seed yield by 27% and 30%, respectively, averaged across all temperatures. There were no effects of elevated CO_2 on pollen viability, seed-set, seed number per pod, seed size, harvest index or shelling percentage. At ambient CO_2, seed yield decreased progressively by 14%, 59% and 90% as temperature increased from 32/22 to 36/26, 40/30 and 44/34 °C, respectively. Similar percentage decreases in seed yield occurred at temperatures above 32/22 °C at elevated CO_2 despite greater photosynthesis and vegetative growth. Decreased seed yields at high temperature were a result of lower seed-set due to poor pollen viability, and smaller seed size due to decreased seed growth rates and decreased shelling percentages. Seed harvest index decreased from 0.41 to 0.05 as temperature increased from 32/22 to 44/34 °C under both ambient and elevated CO_2. We conclude that there are no beneficial interactions between elevated CO_2 and temperature, and that seed yield of peanut will decrease under future warmer climates, particularly in regions where present temperatures are near or above optimum.

Keywords: carbon dioxide, climate change, global warming, groundnut, high temperature, peanut, photosynthesis, pollen viability, seed-set, yield

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Introduction

Global climate change has emerged as an important environmental challenge due to its potential impact on biological systems of planet Earth (Walther *et al*., 2002). Since the beginning of the industrial revolution (about 1750), the concentrations of CO_2, methane and nitrous oxide have increased by 31%, 150% and 16%, respectively (Houghton *et al*., 2001). The present day CO_2 concentration (370 μmol mol^{-1}) has not been exceeded during the past 420 000 years and likely not during the past 20 million years (Petit *et al*., 1999; Houghton *et al*., 2001). Human activities such as deforestation and burning of fossil fuel are mainly responsible for the recent rapid increases in atmospheric concentrations of greenhouses gases including CO_2 (Kaufmann & Stern, 1997; Houghton *et al*., 2001; Stott *et al*., 2001). At the present rate of emission, CO_2 concentration is projected to be in the range of 540–970 μmol mol^{-1} by the end of this century, which will potentially increase global near-surface temperatures by 1.4–5.8 °C (Houghton *et al*., 2001). With some degree of delay, global warming will

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occur concurrently with increases in CO_2. Therefore, it is important to quantify the interactive effects of increasing temperature and CO_2 on crop production.

Peanut or groundnut (*Arachis hypogaea* L.) is an important grain legume crop and is grown as a principal source of edible oil and vegetable protein. About 90% of the world's peanut production occurs in the tropical and semi-arid tropical regions, which are characterized by high temperature and low or erratic rainfall. In the tropics, most of the crops are near their maximum temperature tolerance; therefore, crop yields may decrease even with minimal increases in temperature. The mean optimal air temperature range for vegetative growth of peanut is between 25 and 30 °C, which is warmer than the optimum range for reproductive growth, which is between 22 and 24 °C (Wood, 1968; Cox, 1979; Ong, 1984).

Both short- and long-term exposure to air and soil temperatures above optimum can cause significant yield loss in peanut (Dreyer *et al*., 1981; Ketring, 1984; Ong, 1984; Golombek & Johansen, 1997; Prasad *et al*., 1999a, b, 2000a, b). Effects of short-term (1–6 days) exposure to daytime temperature between 28 and 48 °C during reproductive development and yield were thoroughly investigated (Prasad *et al*., 1999a,b, 2000a, 2001; Craufurd *et al*., 2002, 2003). It was observed that day temperature >34 °C decreased fruit-set and resulted in fewer numbers of pods (Prasad *et al*., 1999b, 2000a). Decreased fruit-set at high temperatures was mainly due to poor pollen viability, reduced pollen production and poor pollen tube growth, all of which lead to poor fertilization of flowers (Prasad *et al*., 1999b, 2000a, 2001). Increasing daytime temperature from 26–30 to 34–36 °C significantly reduced the number of subterranean pegs and pods, seed size and seed yield by 30–50% (Cox, 1979; Ketring, 1984; Ong, 1984). Prasad *et al*. (2000b) investigated the effects of daytime soil and air temperature of 28 and 38 °C, from start of flowering to maturity, and reported 50% reduction in pod yield at high temperatures.

Elevated CO_2 increased the photosynthetic rate and pod yield of peanut under both fully irrigated and drought conditions (Chen & Sung, 1990; Clifford *et al*., 1993, 2000; Mortley *et al*., 1997; Stanciel *et al*., 2000). The interactive effects of CO_2 and temperature on peanut have received far less attention. Although Stronach *et al*. (1994) and Clifford *et al*. (2000) studied these interactions, their focus was on the interaction of elevated CO_2 and drought, and there were only two temperature regimes (28 and 32 °C). Understanding of combined season-long effects of a range of high temperatures at ambient and elevated CO_2 on yield and its attributes is of special significance in order to predict the consequences of climate change on crop production and to develop a suitable agronomic package for production in present and future climates (Reddy & Hodges, 2000). The main objectives of this research were (a) to understand and quantify the effects of season-long exposure to a range of high temperatures (daytime maximum/nighttime minimum (°C): 32/22, 36/26, 40/30 and 44/34) at ambient (350 μmol mol^{-1}) and elevated (700 μmol mol^{-1}) atmospheric CO_2, imposed from emergence to maturity, on photosynthesis, pollen viability, seed-set, dry matter partitioning, seed yield and yield components, and (b) to examine whether higher photosynthetic rates and vegetative growth at elevated CO_2 will negate the detrimental effects of high temperature on reproductive processes and yield.

Materials and methods

This study was conducted in the sunlit, controlled-environment growth chambers located at the Plant and Soil Science Field Teaching Laboratory of the University of Florida in Gainesville (29°68′N, 82°27′W), FL, USA.

Growth conditions

Eight growth chambers located outdoors using solar radiation as the light source were used for this experiment. The upper aerial plant canopy unit of each growth chamber is 2 m wide (east–west), 1 m deep (north–south) and 1.5 m high, and is made of an aluminum frame with polyethylene telephtalate film ('sixlight', Taiyo Kogyo Co., Tokyo, Japan) walls. Each chamber also has 1.2 m^2 additional volume on the south side with a trap door at the bottom that allows a person to stand outside while working inside. The aerial unit is attached to an aluminum lysimeter (soil unit) that is 0.6 m deep. The soil unit was filled with topsoil of Kendrick fine sand (loamy, siliceous, Arenic Paleudult) from a nearby field. Each growth chamber has the ability to control air temperature, dewpoint temperature and CO_2 at independent predetermined set points. Details of chamber construction and method of operation, data acquisition and quality of environmental control are described in detail by Jones *et al*. (1984), Pickering *et al*. (1994) and Allen *et al*. (2003).

The chambers were initially maintained at a daytime maximum/nighttime minimum temperature regime of 32/22 °C from sowing of peanut seeds to full emergence (10 days after sowing, DAS). Thereafter until maturity, each chamber was exposed to one of the eight treatments obtained from the combinations of four temperatures (32/22, 36/26, 40/30 and 44/34 °C) and two CO_2 concentrations during daytime [350 μmol mol^{-1} (near ambient) and 700 μmol mol^{-1} (elevated)]. Carbon dioxide treatments were started at the first sign of seedling emergence (7 DAS). Air temperatures were

controlled as a sinusoidal wave function during the day and decay function during the night, mimicking the natural diurnal temperature cycle (Pickering *et al*., 1994). Air temperatures were measured using radiation-shielded, aspirated, copper–constantan thermocouples (Omega Engineering, Stamford, CT, USA). Air temperatures were controlled by adjustment of proportional electrical resistance heaters (AA Electric, Lakeland, FL, USA). The dewpoint temperatures in each chamber were maintained 5 °C below the target day and night temperatures. These environments provided nearly constant relative humidities (40–42%) at 15:00 hours in all treatments (Allen *et al*., 2003). General circulation models predict that under climate change scenarios, absolute humidities would increase, but the relative humidities would stay somewhat constant (Rind, 1998). Dewpoint temperatures were controlled by opening and closing bypass valves that determined the flow of chilled water through cooling coils inside the chamber ductwork. Data on environmental variables and controls were stored using a data logger (CR10, Campbell Scientific Inc., North Logan, UT, USA). Soil temperature at three locations in each chamber was measured at hourly intervals at 5 cm depth from sowing to harvest using HOBO optical stowaway tidbits (Onset Computer Corporation, Bourne, MA, USA).

Carbon dioxide concentrations of each chamber were measured every 10 s using calibrated infrared gas analyzers (Siemens Corporation, New York, NY, USA) located in a nearby building and controlled at set point by injecting pure CO_2 from a high-pressure cylinder through a mass flow controller (Brooks Instruments, Hatfield, PA, USA). During the night, the chambers were vented and flushed for 13 min with ambient air once every hour. Carbon dioxide concentrations were measured continuously during diurnal and nocturnal period.

Before the start of the experiment, all chambers were run at different temperatures and CO_2 levels to check for chamber effects. All chambers were run at a set temperature and CO_2 controlled uniformly and there were no differences among the chambers in terms of temperature control, CO_2 control and light transmission. These data are typically shown for a temperature regime of 32/22 °C for a 24 h period (Fig. 1a). After the start of temperature and CO_2 treatments, set-point temperature and actual air temperatures were overlapping and similar in both ambient and elevated CO_2 levels, as typically shown for the 24 h period when plants reached full canopy (Fig. 1b). Similarly, measured CO_2 concentrations were close to set-point CO_2 at all temperatures during the daytime (Fig. 1c). The photosynthetic photon flux density (PPFD) in each

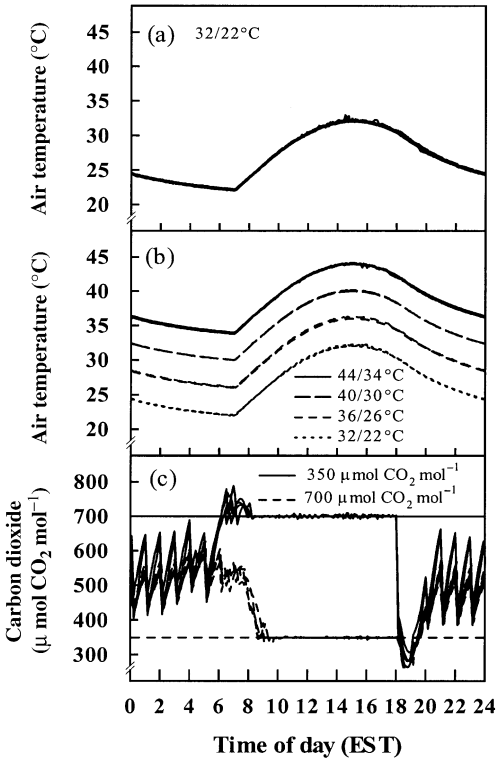

Fig. 1 Temperature and carbon dioxide controls in all eight chambers for a 24 h period: (a) actual measured and set-point air temperatures at 32/22 °C daytime maximum/nighttime minimum temperature; (b) actual measured and target temperatures under ambient and elevated CO_2 levels at temperature regimes of 32/22, 36/26, 40/30 and 44/34 °C; and (c) actual measured and set-point CO_2 concentrations at different temperature regimes.

chamber was the same and all chambers transmitted about 91% of PPFD. The soil in the chambers was from the same field and all chambers had similar irrigation control. Therefore, all chambers had similar growth environments, except for the experimental treatment differences.

Cultivar and plant husbandry

Healthy and uniform seeds of the Virginia Runner botanical-type cultivar 'Georgia Green' were selected and treated with Vitavax (a.i., Captan; Gustafson, Plano, TX, USA) as a precautionary measure against seed-borne diseases. Seeds were inoculated with peanut-type *Bradyrhizobium* (Nitragin, Liphatech, Milwaukee, WI, USA) prior to sowing. Two seeds per hill, were sown by hand on 15 July 2002 at a depth of 5 cm in a single twin-row planting system. The twin rows were spaced 24 cm apart running along a 2 m length dimension (east–west) of the chamber, and plants

within the rows were spaced 9 cm apart. Plants were irrigated by overhead sprinklers from sowing to 20 DAS, and thereafter plants were dependent on subsurface irrigation provided by a constant water level at 45–50 cm beneath the soil surface. The capillary flow within the Kendrick fine sand soil was adequate to provide the required soil water as soon as the rooting system developed. After emergence, seedlings were thinned to one plant per hill, with a uniform plant population of 20 plants per row and 40 plants per chamber (20 plants m^{-2}). To simulate field conditions and eliminate border effects, a black polypropylene shade cloth was placed around the edges of the chamber and periodically adjusted upwardly to match plant height. The crop did not receive any inorganic or organic fertilizer, except for gypsum application. The soil was rich in potassium and phosphorous, and nitrogen nutrition was dependent on symbiotic dinitrogen fixation. Due to high calcium requirements of peanut, gypsum dust was applied (75 g m^{-2}) soon after flowering. Weeding was carried out by hand as necessary from sowing to harvest. Biological agent big-eye bug nymphs (*Geocoris punctipes*; Entomos, Gainesville, FL, USA) were released three times during the season to control aphids (*Aphis craccivora* Koch) and red spider mites (*Tetranychus urticae* Koch). Sevin dust (a.i. carbaryl) was applied twice to control thrips (*Frankliniella fusca* Hinds). The crop was sprayed with Daconil (a.i. chlorothalonil) at 42, 52, 70 and 90 DAS to prevent the incidence of early (*Cercospora arachidicola* Hori.) and late [*Phaeoisariopsis personata* (Berk. & Curt.) V. Arx.] leaf spot diseases.

Gas exchange measurements

Photosynthesis, stomatal conductance and transpiration rates of upper canopy sunlit leaves were measured at 52 DAS. Measurements were taken using an LI6200 portable photosynthesis system (LI-COR, Lincoln, NE, USA), with a 0.25 L leaf chamber on a clear sunny day between 11:00 and 14:00 hours when solar PPFD was 1200–1800 μmol m^{-2} s^{-1}. A total of nine observations were taken on three fully expanded leaflets from three different plants randomly selected from the population. The trap door at the bottom of the chamber was used to stand outside and work inside. A drawstring body seal and face-cover breathing apparatus prevented chamber contamination with CO_2. Measurements were taken after the cuvette temperature and CO_2 were equilibrated with the treatment conditions in the growth chamber. Leaflets from gas exchange measurements were harvested and their leaf areas were measured with a Model LI-3100 leaf area meter (LI-COR).

Seed-set and pollen viability

To determine the effects of temperature and CO_2 on seed-set, individual flowers were tagged and followed through final harvest at maturity. A total of 40 flowers were randomly tagged in each chamber (treatment) on nine to 16 plants (about four flowers per plant) between 3 and 5 days after first flowering. Seed-set expressed as percentage was defined as the proportion of 40 tagged flowers that produced seed.

On the day of flower tagging for seed-set, pollen viability was determined through *in vitro* pollen germination in a medium consisting of 100 mg H_3BO_3, 250 mg $Ca(NO_3)_2 \cdot 4H_2O$, 200 mg $MgSO_4 \cdot 7H_2O$, 100 mg KNO_3 and 200 g of sucrose dissolved in 1 L of deionized water (Prasad *et al.*, 2001; Kakani *et al.*, 2002). To this liquid medium, 20 g agar L^{-1} was added and slowly heated on a hot plate to dissolve agar. After the agar was completely dissolved, the germinating medium was poured on the required number of microscopic glass slides and allowed to cool for 15 min so that agar solidified. Each glass slide layered with germinating medium was kept in an empty Petri dish lined with moistened filter paper at the bottom to provide a humid atmosphere and incubated at 28 °C for 30 min. Thereafter, five individual peanut flowers were collected from five different plants between 08:00 and 08:30 hours and immediately placed in plastic bags lined with moistened filter paper to avoid pollen desiccation. Pollen from each flower was collected separately on a clean glass plate by pressing the keel petal or removing pollen from the anther using a needle. Pollen grains were brushed evenly on the glass slide layered with germinating medium and were placed in darkness at 28 °C for 30 min before estimating pollen viability. For each flower, the proportion of germinating pollen was estimated by counting the total number of germinated (viable) and ungerminated pollen grains in three microscopic fields. Pollen was considered germinated if the length of the pollen tube was greater than the diameter of the pollen.

Seed growth

Once pegging started, 40 pegs at an identical stage of development were tagged on 10 plants (four per plant) and their development and growth was monitored by destructive harvests of four randomly selected pegs or pods from three to four different plants at 5, 10, 17, 27, 41, 55 and 70 days after tagging and at maturity. Plants grown at 32/22 and 36/26 °C were tagged on 45 DAS, and those at 40/30 °C on 43 DAS, under both ambient and elevated CO_2, so that the reproductive structures were of the same age (7 days) after start of pegging

(when 50% of plants started pegging). Plants grown at 44/34 °C at both ambient and elevated CO_2 did not produce pegs and therefore were not tagged. Time-series data obtained from these harvests were used to determine the individual seed growth rate and effective seed-filling duration. The individual seed growth rates were determined from the slope of the linear phase of seed growth. Effective seed-filling duration was the length of time (days) from start of seed growth ($y = 0$) to the time when the average maximum seed size was reached.

Yield and yield components

At harvest maturity (130, 133, 134 and 135 DAS, for plants grown at 44/34, 40/30, 36/26 and 32/22 °C, respectively), all plants from each chamber were carefully removed by digging. At the same time, six representative plants were randomly selected from each chamber. For each of the six plants, component parts (roots, leaves, stems, pegs and pods) were separated and respective dry weights per plant were recorded after oven-drying each component at 60 °C for 3 days. Data on plant height, vegetative stage, numbers of pegs and pods were recorded on these six plant samples. Similarly, for all the remaining plants harvested from each chamber, pods were removed and data on total vegetative dry weight (leaf, stem and root) and pod dry weights were recorded. After drying, pods were shelled and data on number of seeds per plant, shelling percentage (ratio of seed to pod weight), number of seeds per pod, seed size ($g\,seed^{-1}$) and seed yield were estimated. The total dry weight was the sum of vegetative and pod dry weights. Pod and seed harvest indices were calculated as a ratio of pod or seed to total plant dry weight, respectively.

Initially, data analyses of six plant samples and bulk samples were carried out separately. The results were similar, so data from the six plant samples were combined with the large samples ($2\,m^2$ land area), reanalyzed and presented. Data obtained from the whole chamber ($2\,m^{-2}$) were converted to m^{-2} before statistical analyses.

Data analyses

General linear model (GLM) procedures in SAS (SAS Institute Inc., Cary, NC, USA) were used to identify regression response to temperature (T). The following statistical model, $y = \beta_0 + \beta_1 T + \beta_2 T^*T + \alpha_1 CO_2 + \alpha_2 T^* CO_2$, was used to test the significance of the effects of temperature, CO_2 and their interactions on dependent variables. Carbon dioxide was used as a classification variable and temperature was the quantitative variable. Type I sum of squares was used to determine significance (P level) as temperature was a quantitative variable. The above analysis is a conservative statistical test using one mean data point for each treatment combination. Data were described either by quadratic or linear function. When the response was linear, the T^*T factor was removed from the statistical model. Based on the statistical results, either a single line with similar intercept and slope, or two lines with different intercepts and slopes were used to describe the relations between dependent and independent variables.

Results

Chamber performance

The average seasonal diurnal day/night temperatures were within ± 0.18 °C of the target temperatures under both ambient and elevated CO_2. The means and standard error of actual seasonal daytime CO_2 were 356 ± 0.8 and $698 \pm 0.6\,\mu mol\,mol^{-1}$ in ambient and elevated CO_2 treatments, respectively, when averaged across chambers. The mean daytime maximum/nighttime minimum soil temperatures from start of pod formation to maturity at air temperature regimes of 32/22, 36/26, 40/30 and 44/34 °C were 25.4/21.7, 27.9/24.5, 30.7/26.9 and 34.3/29.2 °C, respectively, under ambient CO_2 conditions. The corresponding values under elevated CO_2 were 26.4/22.3, 28.1/24.3, 30.3/26.4 and 33.9/29.9 °C, respectively.

Leaf gas exchange

There was no significant ($P > 0.28$) influence of temperature or interaction between temperature and CO_2 on the leaf photosynthetic rate (Table 1; Fig. 2a). When averaged across temperatures, leaf photosynthetic rates were 26 and 33 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$, under ambient and elevated CO_2, respectively. Elevated CO_2 significantly ($P < 0.05$) increased leaf photosynthetic rates by about 27% across all temperatures. In contrast, stomatal conductance and transpiration rates, respectively, were significantly affected by temperature ($P < 0.05$ and < 0.01, respectively) and CO_2 ($P < 0.01$) and the interaction between temperature and CO_2 ($P = 0.08$) (Table 1). Two lines with different slopes and intercepts best describe these responses. As temperature increased, stomatal conductance increased linearly by 0.12 and $0.04\,mol\,m^{-2}\,s^{-1}$ per every °C rise in temperature from 32/22 to 44/34 °C under ambient and elevated CO_2, respectively (Fig. 2b). The corresponding increases in transpiration were 1.4 and $0.8\,mmol\,m^{-2}\,s^{-1}$, respectively, per °C (Fig. 2c).

Table 1 Summary (P values) of the effects of temperature, CO_2 and interaction between temperature and CO_2, based on statistical analyses on various measured parameters of peanut

Parameter	Temperature	CO_2	Interaction
Leaf photosynthetic rate	0.2858	0.0172*	0.2997
Stomatal conductance	0.0159*	0.0092**	0.0826
Transpiration	0.0020**	0.0040**	0.0779
Pollen viability	0.0005***	0.9088	0.6508
Seed-set	0.0002***	0.5119	0.8788
Vegetative dry matter	0.0139*	0.0076**	0.1013
Total dry matter	0.0135*	0.0025**	0.1523
Pod harvest index	0.0002***	1.0000	0.4677
Seed harvest index	0.0002***	0.8361	0.4310
Seed growth rate	0.0367*	0.1114	0.2123
Seed-filling duration	0.2797	0.3243	0.9188
Pod yield	0.0006***	0.0311*	0.4663
Seed yield	0.0006***	0.0376*	0.4308
Pod number	0.0096**	0.0621	0.9616
Seed number	0.0010***	0.0316*	0.5010
Shelling percentage	0.0181*	0.9336	0.7135
Seed number per pod	0.0344*	0.5073	0.7204
Seed size	0.0010***	0.8114	0.5379

***,**,*Significant at $P<0.001$, 0.01 and 0.05, respectively.

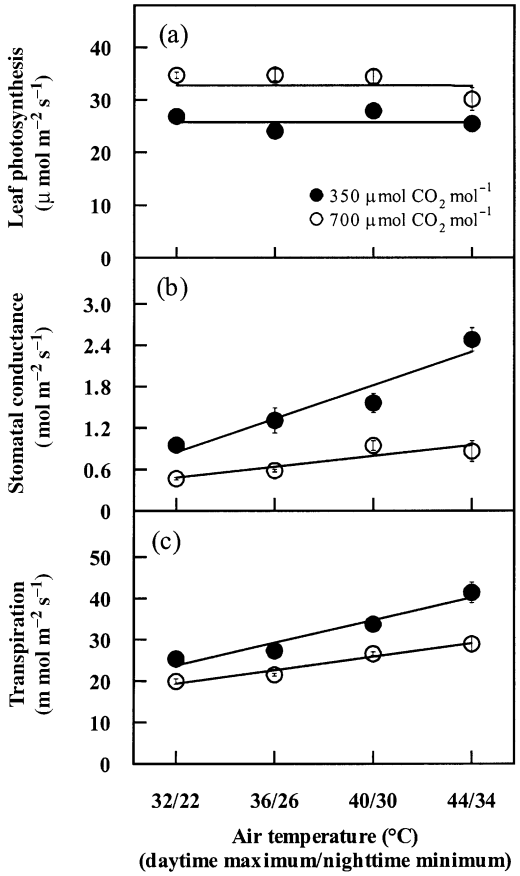

Fig. 2 Relations between daytime maximum/nighttime minimum air temperature (°C) and rates of leaf (a) photosynthesis; (b) stomatal conductance; and (c) transpiration at ambient (●, 350 μmol mol^{-1}) and elevated (○, 700 μmol mol^{-1}) CO_2. Fitted linear regressions (a) $Y = 26.01 - 0.008X$; $r^2 = 0.94$ at ambient CO_2 and $Y = 33.51 - 0.008X$; $r^2 = 0.91$ at elevated CO_2; (b) $Y = -3.0 + 0.12X$; $r^2 = 0.91$ at ambient CO_2 and $Y = -0.75 + 0.04X$; $r^2 = 0.78$ at elevated CO_2; and (c) $Y = -20.07 + 1.37X$; $r^2 = 0.94$ at ambient CO_2 and $Y = -6.32 + 0.80X$; $r^2 = 0.96$ at elevated CO_2. Vertical bars denote standard errors (±) and are shown where they exceed the size of the symbol.

Pollen viability and seed-set

There was no effect of CO_2 ($P>0.50$) or interaction between temperature and CO_2 ($P>0.65$) on pollen viability and proportion of flowers setting seed (Table 1). Therefore, these effects were best described by a single sloping line with quadratic function against temperature (Fig. 3a and b). Increasing temperature above 32/22 °C significantly ($P<0.001$) decreased pollen viability and seed-set under ambient and elevated CO_2 to a similar extent. Pollen viability was about 90–95% at 32/22 and 36/26 °C, but decreased to 68% at 40/30 °C and zero at 44/34 °C under both ambient and elevated CO_2. Similarly, seed-set was 70–80% at 32/22 and 36/26 °C, but decreased to 50% at 40/30 and zero at 44/34 °C under both ambient and elevated CO_2.

Dry matter production and partitioning

Vegetative dry matter (leaf, stem and root dry weight) was significantly influenced by temperature ($P<0.05$) and CO_2 ($P<0.01$), but the interaction was only significant at $P=0.10$ (Table 1). As temperature increased from 32/22 to 40/30 °C, vegetative dry matter increased from 382 to 577 g m^{-2} under ambient CO_2 and from 516 to 796 g m^{-2} under elevated CO_2 (Fig. 4a). A further increase in temperature to 44/34 °C decreased the vegetative dry matter to 486 and 787 g m^{-2} under ambient and elevated CO_2, respectively, but these values are still higher than those at 32/22 °C. Total dry matter production was significantly influenced by temperature ($P<0.05$) and CO_2 ($P<0.01$), but the interaction with temperature and CO_2 was not significant ($P=0.15$). Total dry matter production at temperatures between 32/22 and 40/30 °C was similar, averaging 807 g m^{-2} at ambient CO_2 and 1050 g m^{-2} at elevated CO_2. A further increase in temperature to 44/34 °C decreased total dry matter production to 530 g m^{-2} under ambient CO_2 and 850 g m^{-2} under elevated CO_2. Elevated CO_2 increased vegetative and total dry matter yield by 40% and 36% on average across all temperatures.

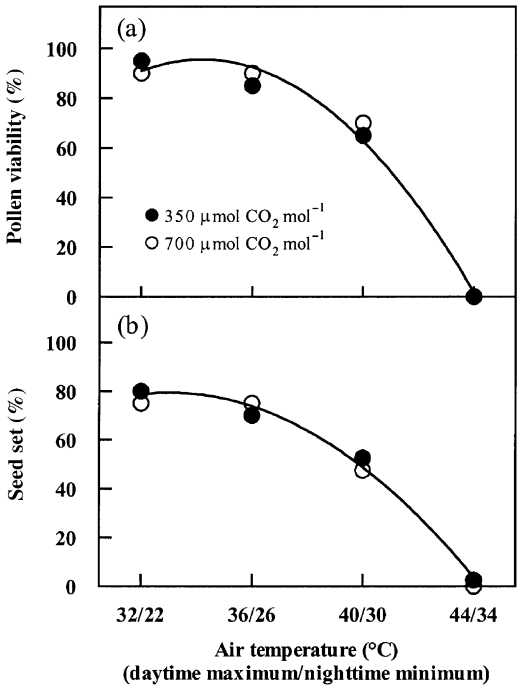

Fig. 3 Relations between daytime maximum/nighttime minimum temperature (°C) and (a) percentage of germinating pollen (pollen viability); and (b) percentage of flowers setting seed (seed-set) at ambient (●, 350 μmol mol^{-1}) and elevated (○, 700 μmol mol^{-1}) CO_2. Fitted lines for quadratic function (a) $Y = -1046 + 66.8X - 0.98X^2$; $r^2 = 0.99$ at both ambient and elevated CO_2; and (b) $Y = -601 + 41.3X - 0.63X^2$; $r^2 = 0.99$ at both ambient and elevated CO_2.

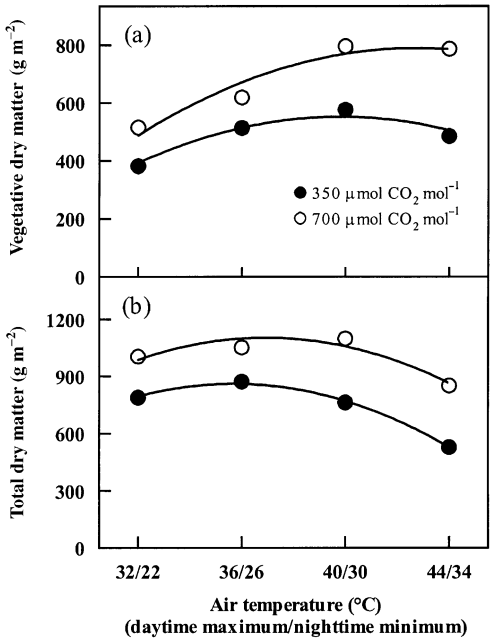

Fig. 4 Relations between daytime maximum/nighttime minimum temperature (°C) and (a) vegetative dry matter (leaf, stem and root); and (b) total dry matter (vegetative plus pod) at maturity for crops grown at ambient (●, 350 μmol mol^{-1}) and elevated (○, 700 μmol mol^{-1}) CO_2. Fitted lines for quadratic function (a) $Y = -3600 + 209X - 2.62X^2$; $r^2 = 0.96$ at ambient CO_2 and $Y = -3995 + 224X - 2.62X^2$; $r^2 = 0.96$ at elevated CO_2; and (b) $Y = -5251 + 169X - 4.80X^2$; $r^2 = 0.98$ at ambient CO_2 and $Y = -5437 + 354X - 4.80X^2$; $r^2 = 0.98$ at elevated CO_2.

Partitioning of dry matter to pods and seeds as indicated by pod and seed harvest indices, respectively, was both significantly affected by temperature ($P < 0.001$), but not by CO_2 ($P = 1.00$ and 0.83, respectively) or the interaction between temperature and CO_2 ($P = 0.47$ and 0.43, respectively) (Table 1; Fig. 5). These relations were best described by single lines with the same slopes and intercepts. As temperature increased from 32/22 to 44/34 °C, pod harvest index decreased from 0.50 to 0.07 under ambient and elevated CO_2 (Fig. 5a). Similarly, seed harvest index decreased from 0.41 to 0.05 as temperature increased from 32/22 to 44/34 °C under both ambient and elevated CO_2 (Fig. 5b).

Reproductive development and seed growth

Time (days) from sowing to flowering and from flowering to peg or pod or seed formation was influenced by temperature but not by CO_2. Time from sowing to flowering at temperatures 32/22, 36/26, 40/30 and 44/34 °C was 30, 31, 26 and 28 days, under both ambient and elevated CO_2. Time (days) from flowering to pegging at 32/22 and 36/26 °C was about 8 days, while at 40/30 °C it took about 10 days. Similarly, the period from flowering to podding was about 16 days at 32/22 and 36/26 °C, while at 40/30 °C it was 19 days. Based on the regression of seed growth, the start of effective seed filling was similar at 32/22 and 36/26 °C, but it was delayed by about 10 days at 40/30 °C. These responses were similar at both ambient and elevated CO_2. No seeds were formed from the tagged flowers at 44/34 °C; thus, no seed growth was obtained. The seed growth rates derived from the slopes of the regression lines during the effective seed-filling period (from start to near-maximum weight) show that seed growth rates were significantly ($P < 0.05$) slower at higher temperature: 0.0075 g seed^{-1} day^{-1} at 40/30 and 0.009 g seed^{-1} day^{-1} at 36/26 °C compared with 0.010 g seed^{-1} day^{-1} at 32/22 °C (Fig. 6). Similar responses were observed at elevated CO_2. In contrast, seed-filling duration was similar within ±3 days in all temperature and CO_2 treatments. Typically, effective seed-filling duration was between 50 and 60 days across different treatments.

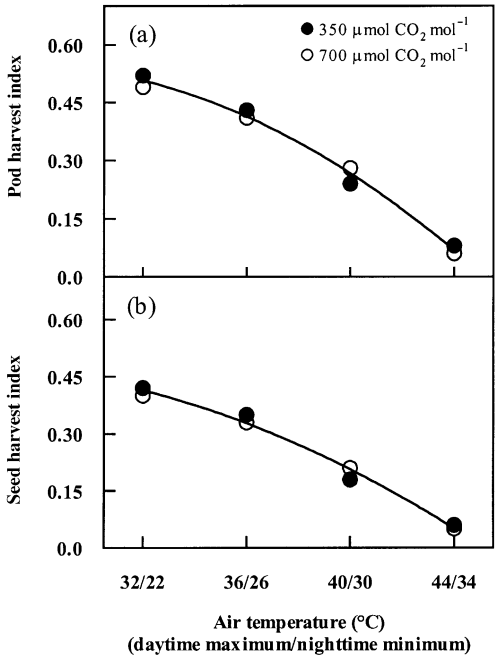

Fig. 5 Relations between daytime maximum/nighttime minimum air temperature (°C) and (a) pod harvest index; and (b) seed harvest index at ambient (●, 350 μmol mol^{-1}) and elevated (○, 700 μmol mol^{-1}) CO_2. Fitted regressions (a) $Y = -0.63 + 0.088X - 0.0016X^2$; $r^2 = 0.99$ at both ambient and elevated CO_2; and (b) $Y = -0.16 + 0.053X - 0.0011X^2$; $r^2 = 0.99$ at both ambient and elevated CO_2.

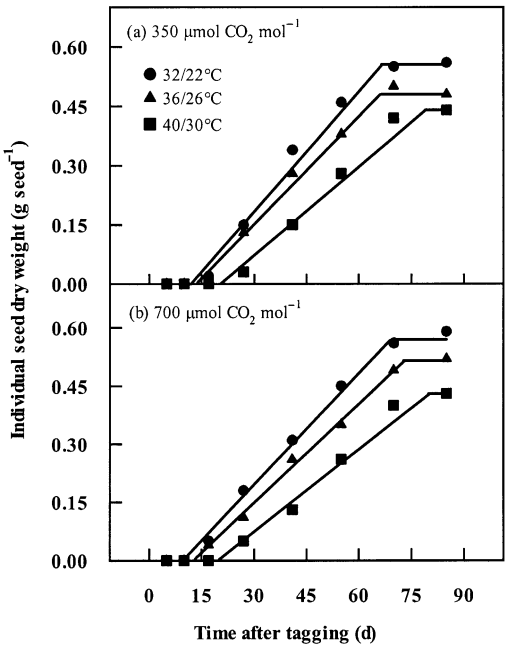

Fig. 6 Individual seed growth during the linear phase of seed-filling at different temperatures at (a) ambient and (b) elevated CO_2. Fitted linear regression (a) $Y = -0.122 + 0.011X$; $r^2 = 0.97$ at 32/22 °C (circles); $Y = -0.123 + 0.0091X$; $r^2 = 0.99$ at 36/26 °C (triangles); and $Y = -0.153 + 0.0075X$; $r^2 = 0.96$ at 40/30 °C (squares) at ambient CO_2; and (b) $Y = -0.092 + 0.0096X$; $r^2 = 0.99$ at 32/22 °C; $Y = -0.108 + 0.0085X$; $r^2 = 0.99$ at 36/26 °C; and $Y = -0.140 + 0.0071X$; $r^2 = 0.97$ at 40/30 °C at elevated CO_2.

Yield and yield attributes

There were significant negative effects of temperature on pod ($P < 0.001$) and seed yield ($P < 0.001$) and pod ($P < 0.01$) and seed numbers ($P < 0.001$) (Table 1; Fig. 7). These relations were best described by quadratic functions. As temperature increased from 32/22 to 36/26, 40/30 and 44/34 °C, the pod yield decreased from 406 to 358, 186 and 43 g m^{-2}, respectively, under ambient CO_2, and from 489 to 433, 303 and 64 g m^{-2}, respectively, under elevated CO_2. Similarly, seed yield decreased from 334 g m^{-2} at 32/22 °C to 287, 137 and 33 g m^{-2} at 36/26, 40/30 and 44/34 °C, respectively, at ambient CO_2. The corresponding decrease in seed yield at elevated CO_2 was from 404 g m^{-2} at 32/22 °C to 343, 229 and 47 g m^{-2} at 36/26, 40/30 and 44/34 °C, respectively. Elevated CO_2 increased pod and seed yield by 30% averaged across all temperatures.

As temperature increased from 32/22 to 44/34 °C, pod numbers decreased from 353 to 74 m^{-2}, under ambient CO_2, and from 407 to 116 m^{-2}, under elevated CO_2. Similarly, seed numbers decreased from 587 m^{-2} at 32/22 °C to 43 m^{-2} at 44/34 °C, at ambient CO_2, and from 709 m^{-2} at 32/22 °C to 132 m^{-2}, at elevated CO_2. Across all temperatures, elevated CO_2 compared with ambient CO_2 increased pod and seed numbers by 40% and 31%, respectively.

There were significant linear effects of temperature on shelling percentage ($P < 0.05$), seed number per pod ($P < 0.05$) and seed size ($P < 0.001$) (Table 1; Fig. 8). In contrast, there were no effects of CO_2 or interaction between CO_2 and temperature ($P > 0.50$) on any of these parameters. Shelling percentage decreased from 82% to 74% (by 0.7 U °C^{-1}) as temperature increased from 32/22 to 44/34 °C under both ambient and elevated CO_2. Similarly, an increase in temperature linearly decreased seed number per pod (Fig. 8b) and seed size (g seed^{-1}) by 0.05 seeds per pod and 0.0075 g, respectively, per every °C rise in temperature from 32/22 to 44/34 °C at both ambient and elevated CO_2.

Discussion

As expected, elevated CO_2 increased leaf photosynthesis by 27% across the range of temperatures in our study. Increased photosynthetic rates at elevated CO_2 is a common phenomenon in most C_3 plant species (Kimball, 1983), including peanut grown under irri-

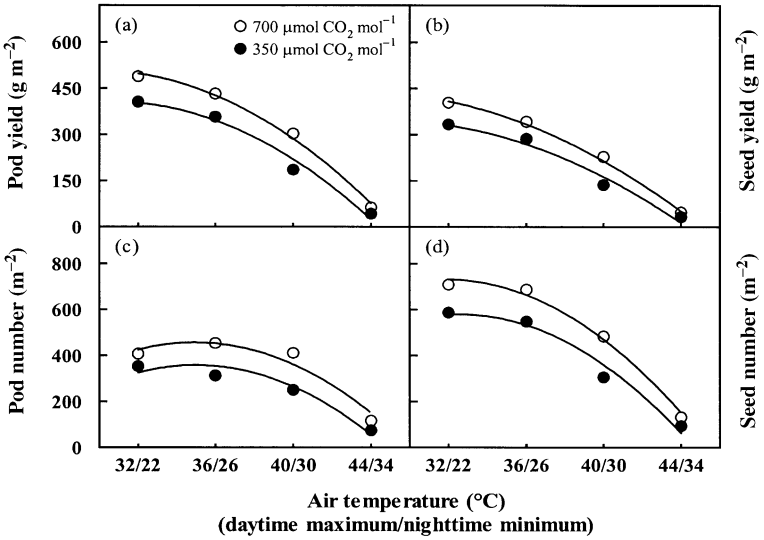

Fig. 7 Relations between daytime maximum/nighttime minimum temperature (°C) and (a) pod yield; (b) seed yield; (c) pod number; and (d) seed number at ambient (●, 350 μmol mol^{-1}) and elevated (○, 700 μmol mol^{-1}) CO_2. Fitted lines for quadratic function (a) $Y = -1651 + 134X - 2.18X^2$; $r^2 = 0.98$ at ambient CO_2 and $Y = -1442 + 130X - 2.18X^2$; $r^2 = 0.99$ at elevated CO_2; (b) $Y = -774 + 78.9X - 1.38X^2$; $r^2 = 0.98$ at ambient CO_2 and $Y = -591 + 75.6X - 1.38X^2$; $r^2 = 0.99$ at elevated CO_2; (c) $Y = -4215 + 146X - 3.73X^2$; $r^2 = 0.95$ at ambient CO_2 and $Y = -4101 + 261X - 3.73X^2$; $r^2 = 0.96$ at elevated CO_2; and (d) $Y = -3576 + 256X - 3.92X^2$; $r^2 = 0.95$ at ambient CO_2 and $Y = -3256 + 250X - 3.93X^2$; $r^2 = 0.98$ at elevated CO_2.

gated or water stress conditions (Chen & Sung 1990; Clifford *et al*., 1993, 2000; Stronach *et al*., 1994). Stomatal opening is highly sensitive to changes in CO_2; increasing CO_2 significantly decreased stomatal conductance and leaf transpiration (Fig. 2). Decreases in stomatal conductance and leaf transpiration rates at elevated CO_2 have been reported for peanut (Stronach *et al*., 1994; Clifford *et al*., 1995, 2000). However, this does not imply that total water use of plants under future climate will decrease, because higher temperature will increase transpiration due to increased vapor pressure gradient between the leaf surface and the atmosphere. In dry bean (*Phaseolus vulgaris* L.), partial closure of stomata under elevated CO_2 increased foliage temperature by 1–2 °C (Prasad *et al*., 2002) to satisfy the energy balance, resulting in higher transpiration. At the canopy level, elevated CO_2 increases total leaf area index, leading to a greater surface available for transpiration and increased water use. Allen (1999) concluded from his review that small increases in global temperature would more than offset the water-saving mechanisms of stomatal closure under elevated CO_2. In the present study, transpiration was significantly increased with temperature >32/22 °C under both ambient and elevated CO_2 (Fig. 2c).

There were clearly no beneficial interactions of temperature and CO_2 on the reproductive processes, despite the tendency for beneficial temperature by CO_2 interactions on vegetative growth ($P = 0.10$) and total dry matter ($P = 0.15$) (Table 1 and Figs 3–8). The promise of beneficial interaction on photosynthesis from temperature and CO_2 does not translate to reproductive yield. Reproductive processes and seed yield were significantly affected by increased temperature. Pollen viability, seed-set, pod and seed yield, pod and seed harvest indices and seed number per pod and seed size were all decreased by temperatures >32/22 °C under both ambient and elevated CO_2. Similar conclusions were derived from studies investigating the interactive effects of temperature and CO_2 on other legumes such as dry bean (Prasad *et al*., 2002), soybean (*Glycine max* L. Merill; Baker *et al*., 1989) and cowpea (*Vigna unguiculata* L. Walp; Ahmed *et al*., 1993). This is primarily because the reproductive processes of these crops are more sensitive to inhibition by super-optimal temperature than vegetative processes are. Our results show that the optimum temperature for seed yield was similar at both ambient and elevated CO_2 (Fig. 7b). Analyses of the curves in Fig. 7b indicated that seed yield increase from doubling of CO_2 could offset the yield loss caused by a temperature rise of 4.4 °C above ambient (32/22 °C). In other words, seed yields at 36.4/26.4 °C under elevated CO_2 were similar to those obtained at 32/22 °C under ambient CO_2 (Fig. 7d). The computed ceiling temperatures (where seed yield = 0) under ambient and elevated CO_2 were

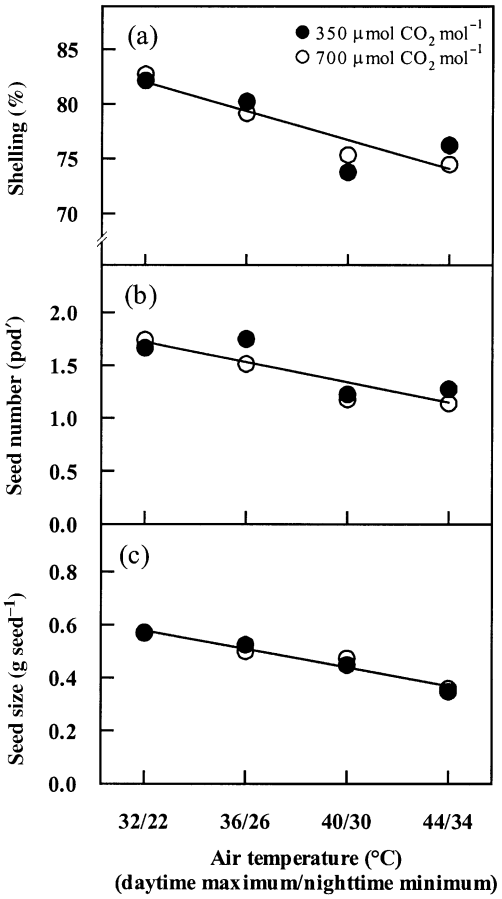

Fig. 8 Relations between daytime maximum/nighttime minimum air temperature (°C) and (a) shelling percentage; (b) number of seeds per pod; and (c) seed size (g seed $^{-1}$) at ambient (●, 350 μmol mol $^{-1}$) and elevated (○, 700 μmol mol $^{-1}$) CO_2. Fitted linear regressions at both ambient and elevated CO_2 for (a) $Y = 103 - 0.66X$; $r^2 = 0.81$; (b) $Y = 3.26 - 0.05X$; $r^2 = 0.78$ at both and ambient CO_2; and (c) $Y = 114 - 1.74X$; $r^2 = 0.96$.

44.6/34.6 and 45.3/35.6 °C, respectively. In our study, no viable pollen was formed at 44/34 °C, resulting in zero seed-set for the Runner type peanut cv Georgia Green (Fig. 3). This concurs with previous studies on Spanish bunch-type peanut cultivar ICGV 86015, which showed no fruit-set at daytime temperatures of 43 °C (Prasad *et al.*, 2000a, 2001). A few pods harvested at maturity at 44/34 °C in our study were attributed to the microclimate of some flowers being produced later in the season, which could have experienced slightly cooler temperature due to canopy closure and/or a cool spot in the soil zone for a few hours after periodic irrigation used to ensure fruit uptake of Ca from the pegging zone.

Both pollen viability and seed-set of peanut were highly sensitive to high temperatures, but were not affected by elevated CO_2 or interaction between temperature and CO_2 (Fig. 3). Elevated CO_2 caused reproductive fertility in dry bean (Prasad *et al.*, 2002) and rice (*Oryza sativa* L; Matsui *et al.*, 1997) to be more sensitive to increased temperature, presumably because of a 1–2 °C rise in canopy temperature. By contrast, Aloni *et al.* (2001) showed a positive interaction between elevated CO_2 and temperature on pollen viability of bell pepper (*Capsicum annum* L.), whereby pollen viability of plants grown under high temperature was increased by elevated CO_2. Pollen sterility at high temperature may be associated with early degeneration of tapetal layer (Suzuki *et al.*, 2001) and decrease in carbohydrates in the developing pollen (Pressman *et al.*, 2002). However, there are species and cultivar differences in the response of carbohydrate metabolism and degeneration of the tapetal layer of pollen to high temperatures (Aloni *et al.*, 2001; Porch & Jahn 2001; Pressman *et al.*, 2002). The exact physiological reasons for decreased pollen viability at high temperatures in peanut are not clearly known and need attention.

There was no effect of elevated CO_2 on phenology, i.e. days to first flower, pod, seed or maturity. However, these events were sensitive to temperature. Although the time to first flower was shorter by 3 days at 40/30 °C compared with 32/22 °C, the start of pod and seed filling at higher temperature (40/30 °C) was delayed by about 10 days in both ambient and elevated CO_2. Craufurd *et al.* (2002) reported that the start of pod and seed filling was delayed by 5–9 days when exposed to high temperature (38/22 °C) from start of flowering to maturity. Similarly, Wheeler *et al.* (1997) found that start of seed filling was progressively delayed by as much as 7 days even when exposed to a short period (6 days) of high daytime temperature between 30 and 45 °C during flowering. Soybean shows similar delays in seed formation at 40/30 °C compared with 32/22 °C (Pan, 1996; Thomas *et al.*, 2003).

Elevated CO_2 had no beneficial effects on yield attributes such as increased proportion of flowers setting seed or number of seeds per pod or seed size (Figs 3 and 8; Table 1). Elevated CO_2 increased pod and seed yield by about 30% owing to an increased total number of pods or seeds due to increased photosynthesis and growth. In contrast, elevated temperature decreased numbers of pods and seeds because of poor fertilization (seed-set), and further decreases in seed yield were attributed to smaller seed size, fewer numbers of seeds per pod and decreased shelling percentage. Although we did not count and quantify the number of flowers produced, there were no visual signs of decreased flower production under elevated temperature. Previous research on peanut indicated that high temperatures do not decrease flower production; in fact, at high air temperatures, the total number

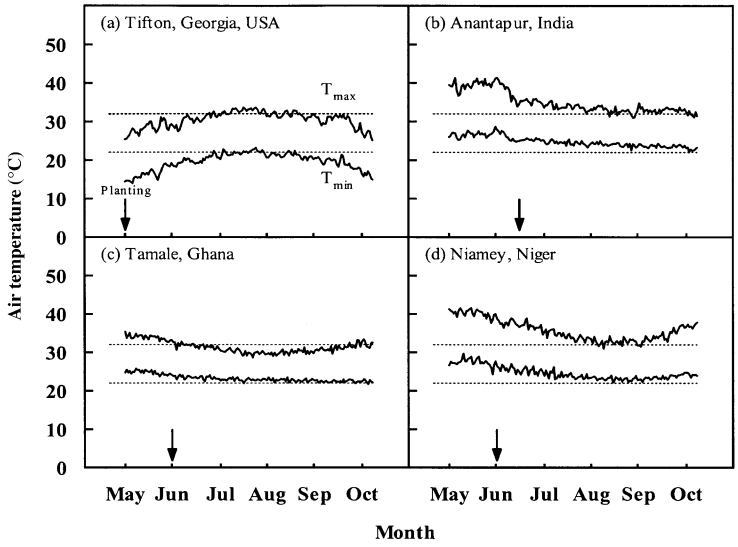

Fig. 9 Daily mean maximum and minimum temperatures (°C) for a period of 10 years (1990–1999) during the peanut-growing season for four peanut-producing regions: (a) Tifton (31.48°N latitude and 83.15°W longitude), GA, USA; (b) Anantapur (14.68°N latitude and 77.62°E longitude), Andhra Pradesh, India; (c) Tamale (9.70°N latitude and 0.92°W longitude), Ghana; and (d) Niamey (13.28°N latitude and 2.00°E longitude), Niger. Dotted straight lines on the graphs represent the base line maximum temperature (32 °C) and minimum temperature (22 °C) used in our experiment. Pointed arrows indicate the planting dates in respective locations.

of flowers produced was greater (Prasad *et al.*, 1999a, 2000b). This response is because of insufficient sinks (pod or seeds) formed at higher temperatures due to a failure of seed-set. Once seeds were set, elevated temperature decreased individual seed growth rate, but did not influence effective seed-filling duration, thus leading to decreased seed size. Neither individual seed growth rate nor effective seed-filling duration was influenced by elevated CO_2. Exposure to high temperatures has previously been reported to decrease both seed harvest index and rate of change of harvest index in peanut (Hammer *et al.*, 1995; Craufurd *et al.*, 2002). This was re-confirmed in our study, which showed the full range of decline in seed harvest index from 32/22 to 44/34 °C, projecting to zero at 45/35 °C. Clearly, the processes leading to fertilization and seed filling are highly sensitive to super-optimal temperature, but not to elevated CO_2 or the interaction between temperature and CO_2.

Our study provides an insight into the effects of season-long exposure to high temperatures starting at present-day seasonal temperatures and increasing up to and beyond those temperatures predicted by global warming. Maximum/minimum air temperatures of 32/22 °C and higher are common in many peanut-producing countries across the globe, especially those in semi-arid tropics. The daily means of maximum and minimum air temperatures for a 10-year period (1990–1999) during the peanut growing season of four important peanut-producing regions are shown in Fig. 9. The Tifton (GA, USA) location represents a highly productive peanut-growing region and is at the 32/22 °C average during the reproductive phase of growth (Fig. 9a). In warm years, Georgia, Texas, Oklahoma and other states in USA experience episodes of temperatures ≥32/22 °C during flowering and seed development. The Anantapur district in Andhra Pradesh, which is one of the largest peanut-producing regions in India, experiences season-long temperatures considerably greater than 32/22 °C from planting to maturity (Fig. 9b). Other important peanut-producing states in India such as Tamil Nadu and Gujarat also experience episodes of high temperatures during the growing season. Similar temperatures also occur in West African countries, as represented by data from Ghana and Niger (Fig. 9c and d). As the current temperatures in these peanut-growing regions are already at or higher than optimum, any further increase in temperature will decrease the productivity of peanut. The optimum temperature for peanut yield is less than 32/22 °C treatment used in this study, based on projection of data in Figs 5 and 7.

In summary, there was no interaction between temperature and CO_2 on reproductive processes, seed yield and yield components, all of which were decreased at temperatures above 32/22 °C under ambient and elevated CO_2. The beneficial effects of elevated CO_2 on photosynthesis and vegetative growth did not negate the pattern of increasingly deleterious effects of increasing temperature on reproductive

processes and seed yield. However, yield increase from CO_2-doubling offsets the seed yield loss caused by a temperature rise of 4.4 °C above 32/22 °C (near-ambient temperature treatment). Thus, if increases in atmospheric CO_2 are associated with global warming as predicted, peanut yield losses may occur in regions where current temperatures are close to or above optimum. Most peanut crops grown in tropical and subtropical regions are rainfed and experience periods of water stress during the reproductive phase, and these dry spells are likely to increase in future climates. As high temperature and water-stress events are most likely to occur in synchrony, interaction of water stress and high temperature needs attention. Research goal should be to breed for heat tolerance during the reproductive phase and to develop suitable crop management practices for future climates, which will not only have higher CO_2 but also higher mean and diurnal temperatures.

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