Effects of Temperature and Elevated CO_2 on Shoot and Root Growth of Peanut (*Arachis hypogaea* L.) Grown in Controlled Environment Chambers

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ABSTRACT: Continuing increases in atmospheric carbon dioxide concentration, $[CO_2]$, will likely be accompanied by global warming. Thus, it is important to quantify and understand the consequences of elevated $[CO_2]$ and temperature on crop growth and yield to develop suitable varieties and agronomic management practices for future climates. The objective of this study was to investigate the growth and development responses of shoots and roots of peanut (*Arachis hypogaea* L.) grown under different combinations of atmospheric $[CO_2]$ and temperature. The study comprised a long-term experiment, in which plants were grown in growth chambers for 112 days, and a short-term experiment, in which growing plants in rhizotrons for 17 days. In the long-term experiment, peanut cultivar Tainan 9 was grown in 20-L containers fitted with minirhizotron observation tubes at 5 cm soil depth and placed in controlled environment chambers under three levels of $[CO_2]$ (400, 600, and 800 µmol mol^{-1}) and two levels of air temperature (25/15ºC and 35/25ºC day/night temperature). In the short-term experiment, two peanut seedlings were grown in each of 18 acrylic rhizotrons with a 6-mm thick soil layer. Rhizotrons with plants were placed in the same growth chambers as above. At 3- to 4-day intervals, rhizotrons were placed on a flatbed scanner to collect digital images from which root length and number were measured using RMS software. At 25/15ºC, plants grown at 600 and 800 µmol mol^{-1} CO_2 had main stems that were 24 and 44% longer than those grown at 400 µmol mol^{-1}, while at 35/25ºC the main stem length was similar in all $[CO_2]$ levels. At 25/15ºC, plants showed greater area and dry weight per leaf than at 35/25ºC. At harvest, high temperature significantly reduced total leaf area to 574 cm^2 for 35/25ºC compared with 921.2 cm^2 for 25/15ºC. Specific leaf area at low temperature was 22% less than at high temperature. Above ground biomass was increased by elevated CO_2 in both temperature treatments. At high temperature, above ground biomass was 56%, 24%, and 16% higher than at low temperature at $[CO_2]$ of 400, 600 and 800 µmol mol^{-1}, respectively. Pod dry weight increased with increasing $[CO_2]$ at 25/15ºC, but was not different among $[CO_2]$ levels at 35/25ºC. At 25/15ºC, pod dry weight was 50% higher than at 35/25ºC. As the temperature increased from 25/15ºC to 35/25ºC, pod dry weight was reduced by 40% at 400, 53% at 600, and 54% at 800 µmol mol^{-1} CO_2. High temperature produced more root length in the containers, whereas low temperature did in the rhizotrons. There were significant interactions between temperature and $[CO_2]$ for their effects on main stem length and above ground biomass. High temperature enhanced growth of shoots and roots, but decreased pod dry weight. There was no interaction of elevated $[CO_2]$ with higher temperature on the reproductive growth, despite a tendency for beneficial temperature by $[CO_2]$ interaction on vegetative growth and total shoot dry weight. The beneficial effects of increased $[CO_2]$ on photosynthesis and growth were overwhelmed by the negative effect of high temperature on reproductive growth.

KEYWORDS: peanut (*Arachis hypogaea* L.); elevated CO_2; temperature; rhizotron.

INTRODUCTION

Global climate change has emerged as an important environmental challenge due to its potential impact on biological systems on Earth [1]. There is considerable concern about the increasing carbon dioxide concentration, $[CO_2]$, in the atmosphere, associated increases in temperature and their effects on crop production. At the present rate of emission, $[CO_2]$ is projected to be in the range of 540-970 µmol mol^{-1} by the year 2100. Rising concentrations of carbon dioxide and other greenhouse gases, including methane, and

nitrous oxide, will potentially increase global average near surface temperatures by 1.4-5.8ºC [2]. Therefore, it is important to quantify the interactive effects of increasing [CO_2] and temperature on crop production.

Peanut (*Arachis hypogaea* L.) is an important oil seed crop, which is grown as a principle source of edible oil and vegetable protein. About 90% of the world's peanut is produced in tropical and semi-arid tropical regions, which are characterized by high temperatures and erratic rainfall. In the tropics, most 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 30ºC, which is warmer than the optimum range for reproductive growth, which is between 22 and 24ºC [3, 4]. Both short- and long-term exposure to air and soil temperatures above the optimum level can cause significant yield loss in peanut [5, 6]. Day temperatures greater than 34ºC decreased fruit-set and resulted in fewer pods [6, 7]. 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 [6, 7].

Increases in photosynthetic rate and pod yield of peanut due to elevated [CO_2] have been reported by many researchers [8, 9]. Net photosynthesis increased linearly for some peanut genotypes as [CO_2] increased from 300 to 600 µmol mol^{-1}. The net photosynthetic rate of peanut grown under controlled environmental conditions was highest in plants grown at 800 µmol mol^{-1}. CO_2 enrichment from 400 to 800 µmol mol^{-1} had positive effects on peanut growth and yield, but above 800 µmol mol^{-1} enrichment seed yield increased only marginally [9]. High [CO_2] increased biomass and pod yields of Virginia-type peanut [8].

Although analyses of plant responses to elevated atmospheric [CO_2] have focused largely on the processes occurring above the ground, an understanding of photosynthesis alone is not sufficient to answer the important questions about terrestrial responses to a changing atmosphere. A whole-plant perspective is needed to understand the critical feedbacks and adjustments that occur within a plant and between plants and soil. Thus, an understanding of root system responses is also important. There are fewer below ground than above ground investigations in the CO_2 response literature. The most commonly reported root variable is the root dry weight [10], which has been reported to increase with elevated [CO_2] for such crops as sorghum [11], soybean [12] and winter wheat [13]. These results suggest that root systems more thoroughly exploit a given volume of soil under elevated [CO_2]. Roots of CO_2 enriched plants reach deeper soil layers [12]

or attain maximum rooting depth ahead of plants grown under ambient [CO_2] [13]. High [CO_2] increased stele and cortex diameter, root diameter in the root hair zone, length of unbranched first order lateral roots, total root length and volume of cotton [14].

Under future climate change scenarios, it is most likely that plants will be exposed to a combination of both higher temperature and [CO_2] [15]. Therefore, it is important to understand the combined effects of elevated [CO_2] and temperatures to determine the crop management or genetic improvement required to sustain peanut productivity in a future climate. Little work has been done to study the combined effects of elevated [CO_2] and temperature on peanut growth and yield. Thus, the objective of this study was to investigate the growth and development responses of peanut shoot and root under different air temperatures and atmospheric [CO_2] combinations.

MATERIALS AND METHODS

Long-term Experiment
Plant Material and Growth Conditions

Research was carried out in six controlled environment growth chambers at the Georgia Envirotron, the University of Georgia, Griffin, Georgia, USA, from 12 August to 2 December, 2002 for a total growth period of 112 days.

Uniform seeds of Tainan 9 peanut variety (*Arachis hypogaea* L.) were selected and pre-germinated on moist paper for five days. Two germinated seeds were planted in each of thirty-six 20-L containers filled with loamy sand soil. Each container was fitted with a horizontal minirhizotron tube at 5 cm below the soil surface. Six containers were placed in each of six controlled environment chambers. Chambers were set to six treatment combinations of two temperatures (25/15 and 35/25ºC, day/night temperature) and three levels of atmospheric [CO_2] (400, 600, and 800 µmol mol^{-1}). Throughout the growing period, day/night relative humidity was maintained at 70/95%, maximum light intensity was 1500 µmol PAR m^{-2}s^{-1}, and photo period was 16 h.

In the 25/15ºC temperature treatment, plants were irrigated with tap water twice weekly until drainage occurred, while those in 35/25ºC treatments were watered daily at a sufficient amount to avoid water deficit. A modified half-Hoagland nutrient solution was applied to the plants weekly to assure adequate nutrients for plant growth and development.

Measurements

Shoot growth, main stem length and number of branches, were observed weekly. The second fully

expanded leaf on the main stem was detached for leaf area, dry weight, and specific leaf area determination at 14-day intervals.

A minirhizotron camera (BTC100-X, Bartz Technology Corp., Santa Barbara, CA 93101 USA) was used to observe roots at the top of the minirhizotron tube. Digital root images were collected at 14-day intervals. Images were analyzed using RMS software, which was described by Ingram and Leers [16]. Data on root length, diameter, and number were obtained for each image taken.

Shoots, roots, and pods were harvested at 112 DAP. Fifty leaves in each container were separated and leaf area was measured using a leaf area meter. Root samples were taken by submerging the soil container upside down in the water. Roots were carefully removed from the soil. Fresh shoots and roots were dried at 70ºC for 72 hr and then dry weights were recorded. Pods were removed from each plant. Harvested pods were cleaned, air dried for 7 days, and then weighed.

Short-term Experiment
Rhizotrons and Soil

The rhizotrons were made of transparent acrylic material with a front and a back plate, and leave a soil layer of 6 mm thickness after closing the two compartments and compression of the soil layer (500 mm length x 450 mm width x 6 mm height), as described by Kuchenbuch and Ingram [17]. A loamy sand soil was used in this research. Soil was sieved twice through a 1 mm x 1 mm screen, and placed in the well of the front plate. The soil was spread evenly to give a uniform layer about 10 mm thick. The back plate was mounted and the soil layer was compressed to 6 mm thickness using a hydraulic press (Model 25 H, Dake Corp., Grand Haven, MT). Front and back plates were protected against deformation by a support system covering the entire surface and bolted firmly together while still under pressure. Soil bulk density in each rhizotron was 1.22 g cm^{-3}.

Plants

Two germinated seeds of peanut cultivar Tainan 9 were planted in each rhizotron when the radicle was 1-3 mm long, then covered with 10 mm soil. Rhizotrons with plants were placed in 6 different controlled environment chambers on racks slanted to a 45º angle with the front plate facing downward to promote root growth along the front plate and covered with opaque black plastic film to prevent light from entering the rhizotrons between observations. After planting, 360 mL of water was added to the top of each rhizotron and watered every other day thereafter until the experiment ended.

Scanning Procedure

At 3, 7, 10, 14, and 17 days after planting, the front part of each rhizotron was placed on a flatbed scanner (Model MRS-1200A3, Microtek International, Inc, Taiwan, ROC) to collected digital images of visible roots. Each rhizotron required two images from the scanner, one for the top and another for the bottom half of the rhizotron. The total image area of these initial images was 350 mm wide x 250 mm high. Optical resolution used was 300 dpi, with 256 colors. Images were cropped to 175 mm wide x 100 mm high, giving 10 images for each rhizotron. Diameter and length of roots visible on the images collected with the scanner were evaluated using RMS software. In short, an operator used a computer mouse to trace each visible root while adjusting the circular cursor to match the diameter of the root. At the end of each image, RMS computes and stores measured values of root length and diameter for each segment, and total number of roots. Root length is stored both as a total and within root diameter classes.

Measuring Total Root Length in the Soil

At 17 days after planting, the back plate of each rhizotron was removed and a soil strip of 25 mm along the sides and bottom was cut by a knife. The remaining soil was subdivided in 10 areas, each 175 mm x 100 mm, thereby matching the size and location of images taken with the scanner. Soil samples were stored at 5ºC for at most 5 days before roots were carefully washed from soil samples using a sieve with 1 mm mesh size and a low-pressure nozzle. Cleaned roots were placed in ethyl alcohol (25% v/v), to which methyl violet dye had been added. Roots were refrigerated and stored for at least 3 days to assure even coloration of roots. Total root length was analyzed using WinRhizo software (Regent Instruments, Inc., Quebec, Canada).

Data Analyses

Statistical analyses were performed using SAS (SAS Institute Inc., Cary, NC, USA.). The analysis of variance (ANOVA) was used to determine the effects of temperature, CO_2 and their interactions on measured variables.

RESULTS

Long-term Experiment

The time from planting to first flower differed between temperature treatments, but there was no effect of CO_2 levels. Duration from planting to first flower at day/night temperature of 25/15ºC was 34 days and at 35/25ºC was 22 days, for both ambient and elevated [CO_2].

Figure 1 shows the effects of temperature, CO_2 and

their interactions on the main stem length. Main stem lengths increased linearly with increasing [CO_2] from 43 to 99 DAP in both low and high temperature. Main stems of plants grown at 35/25ºC were longer than those at 25/15°C for all [CO_2] from 43 through 71 DAP, after which main stems of plants in the 25/15°C, 800 µmol mol⁻¹CO_2 treatment were longer than those at high temperature. At 25/15ºC, plants grown at 600 and 800 µmol mol⁻¹CO_2 had main stems that were 24 and 44% longer than those plants grown at 400 µmol mol⁻¹CO_2, while at 35/25ºC the main stem was similar with about 37.8 cm in all [CO_2]. There were no significant effects of [CO_2] or temperature on the number of branches per plant, and the branch number of all treatment combinations was approximately 12 branches plant⁻¹.

There was no significant effect of [CO_2] on individual leaf area at each time of observation (Figure 2a). Plants at 25/15ºC had larger individual leaf area than those at 35/25ºC. At 25/15ºC, leaf size increased rapidly from 43 to 71 DAP and increased slightly thereafter for plants exposed to 800 µmol mol⁻¹, but declined from 85 to 99 DAP at 600 µmol mol⁻¹ and from 71 to 99 DAP at 400 µmol mol⁻¹CO_2. At 35/25ºC, leaf sizes of plants growing at 400 µmol mol⁻¹ increased progressively from 43 to 99 DAP, while in those growing at 600 and 800 µmol mol⁻¹CO_2, the size of leaf increased until 71 DAP, declined at 85 DAP but increased thereafter.

Figure 2b shows the dry weight of individual leaves. Leaf dry weight of plants growing at low temperature was greater than those at high temperature. At 25/15ºC, the maximum leaf dry weight was found at 71 DAP and increased from 0.47 to 0.54 g leaf⁻¹as [CO_2] increased from 400 to 800 µmol mol⁻¹. At 35/25ºC, the

maximum leaf dry weight was attained at 99 DAP and increased from 0.19 to 0.22 g leaf⁻¹with increasing [CO_2].

At 112 DAP, there were significant effects of CO_2 and temperature on total leaf area and specific leaf area (Table 1). Increasing the temperature from 25/15ºC to 35/25ºC significantly reduced total plant leaf area at all levels of [CO_2]. Total leaf area per plant was about 921.2 cm² for 25/15ºC and 573.7 cm² for 35/25ºC. It was greatest when plants received 600 µmol mol⁻¹CO_2 with the average of 828 cm², followed by at 800 µmol mol⁻¹CO_2 with an average of 725 cm² and at 400 µmol mol⁻¹CO_2 with an average of 689 cm². Specific leaf area of plants grown at 35/25ºC was higher than those at low temperature. Specific leaf area was about 186 cm² g⁻¹ for 400 µmol mol⁻¹CO_2, 174 cm² g⁻¹ for 600 µmol mol⁻¹CO_2, and 193 cm² g⁻¹ for 800 µmol mol⁻¹CO_2.

Above ground biomass increased with increasing CO_2 from 400 to 800 µmol mol⁻¹ in plants grown at 25/15ºC, whereas at 35/25ºC, the above ground biomass was greater at 800 than 400 µmol mol⁻¹CO_2 but slightly

Fig 2. Effect of temperatures and CO_2 concentrations in the long-term experiment on individual leaf area (a) and leaf dry weight (b) at different plant ages. Letters above each plant age indicate significant differences (P≤0.05) between 25/15ºC and 35/25ºC temperature treatments, T; between CO_2 levels (400, 600, and 800 µmol mol⁻¹), T; and interaction between temperature and CO_2, T x C.
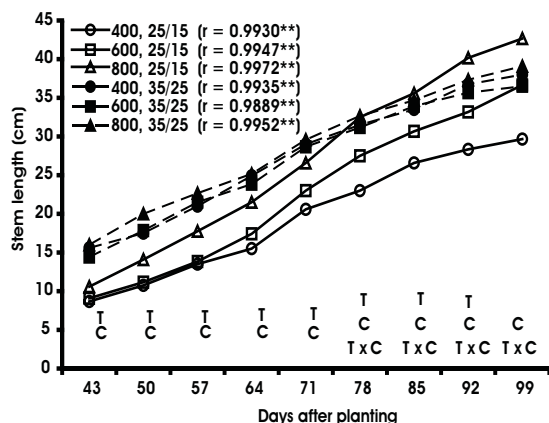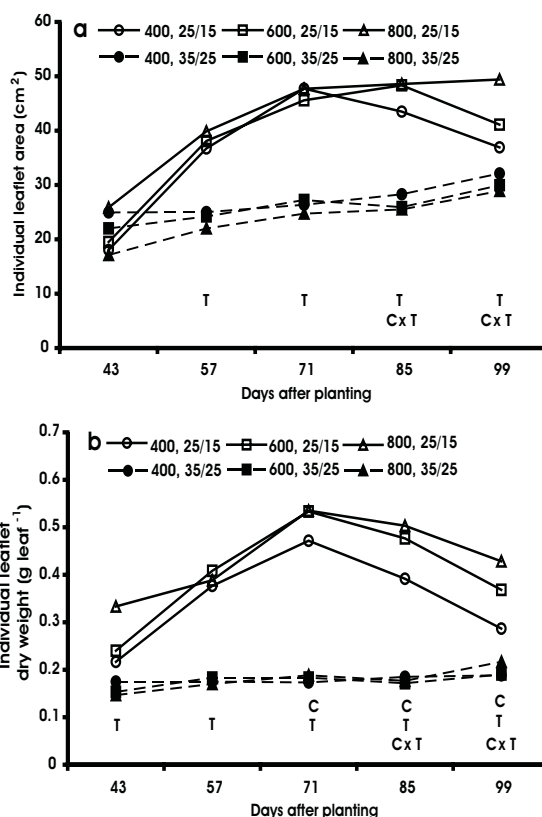
Fig 1. Effect of temperatures and CO_2 concentrations in the long-term experiment on main stem length at different plant ages. Letters above each plant age indicate significant differences (P≤0.05) between 25/15ºC and 35/25ºC treatments, T; between CO_2 levels (400, 600, and 800 µmol mol⁻¹), C; and interaction between temperature and CO_2, T x C.

less at 600 µmol mol^{-1}. At 35/25°C, plants grown at 400 µmol mol^{-1} CO_2 had an above ground biomass 56% higher, at 600 µmol mol^{-1} CO_2 had 24%, and at 800 µmol mol^{-1} CO_2 had 16% higher than those grown at lower temperature. Above ground biomass was highest when plants were grown under 35/25°C and received 800 µmol mol^{-1} CO_2 (Table 1).

Elevated CO_2 increased total pod dry weight when plants were grown at 25/15°C, but not in the 35/25°C treatment (Figure 3). In the 25/15°C treatment, pod dry weight was 50% higher than in the 35/25°C treatment. As temperature increased from 25/15°C to 35/25°C, pod dry weight was reduced by 40% at 400, 53% at 600, and 54% at 800 µmol mol^{-1}.

Fibrous root dry weight increased as $[CO_2]$ increased when plants were grown at 25/15°C, but decreased with increasing $[CO_2]$ at 35/25°C. At 35/25°C, plants had greater root dry weight by about 34% at 400, 14% at 600, and 7% at 800 µmol mol^{-1} compared with those grown at 25/15°C.

Minirhizotron observations showed significant effects of temperature at 43, 57, 85, and 99 DAP for the total visible root length and number of roots per plant, and at 57, 85, and 99 DAP for root length density, RLD (data of root number and RLD are not shown). Visible root length, number of roots, and RLD in the minirhizotron tube were significantly greater for plants grown at 35/25°C than those grown at 25/15°C for all $[CO_2]$ levels. At 99 DAP, plants grown at high temperature had 23% greater visible root length, 37% greater root number, and 23% greater RLD than those at 25/15°C. There was no effect of elevated $[CO_2]$ on those observed parameters over the course of observation. However, visible root length, root number, and RLD tended to increase with increasing $[CO_2]$ from 400 to 800 µmol mol^{-1} at 25/15°C, but decreased as $[CO_2]$ increased at 35/25°C (Figure 4).
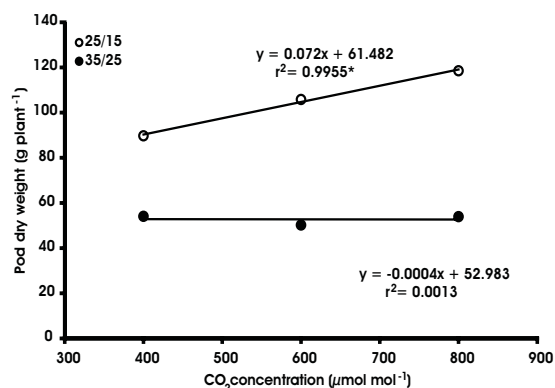

Fig 3. Relation between CO_2 concentration and pod dry weight per plant of peanut at 25/15°C and 35/25°C.

Table 1. Vegetative growth and total biomass at harvest of peanut grown in three atmospheric $[CO_2]$ levels and two air temperature treatments.

CO_2	Main stem length			Branch number			Leaf area		
(µ mol mol^{-1})	25/15°C	35/25°C	Mean	25/15°C	35/25°C	Mean	25/15°C	35/25°C	Mean
	——————cm——————						——————cm² plant^{-1}——————		
400	30	38	34	12	11	12	805	574	690
600	37	37	37	13	11	12	1052	605	829
800	43	39	41	13	13	13	908	543	723
Mean	37	38	38	13	12	13	922	574	748
LSD (T)*		n.s			n.s			79.5	
LSD (C)†		2.9			n.s			97.4	
LSD (TxC) ‡		4.1			n.s			n.s	

CO_2	Specific leaf area			Root dry weight			Shoot dry weight		
(µ mol mol^{-1})	25/15°C	35/25°C	Mean	25/15°C	35/25°C	Mean	25/15°C	35/25°C	Mean
	——————cm² g^{-1}——————			——————g plant^{-1}——————			——————g plant^{-1}——————		
400	170	203	187	57	76	67	203	317	260
600	155	193	174	63	72	68	239	296	268
800	175	212	194	65	69	67	289	336	313
Mean	167	203	185	62	72	67	244	316	280
LSD (T)*		9.4			n.s			12.9	
LSD (C)†		11.5			n.s			15.8	
LSD (TxC) ‡		n.s			n.s			22.3	

*Least significant difference (LSD) at P≤ 0.05 for comparing means among the two air temperature treatments at CO_2 concentrations of 400, 600, and 800 µmol mol^{-1}.
†Least significant difference (LSD) at P≤ 0.05 for comparing means between the three atmospheric CO_2 concentrations at day/night air temperatures of 25/15 and 35/25°C.
‡Least significant difference (LSD) at P≤ 0.05 for temperature and CO_2 interaction.

Short-term Experiment

Regardless of the rhizotron experiment, primary roots penetrated the soil nearly vertically relatives to the rhizotron and most first order laterals root grew nearly horizontal. Tap roots reached 500 mm soil depth within 13 to 14 DAP for plants growing at high temperature and 16 to 17 DAP for those at low temperature. The number of first order branch roots generated from the main root axis tended to be 11% greater for plants growing at high temperature than at low temperature.

Figure 5 shows non-destructive root length measurement using RMS to analyze images collected with a scanner at 3, 7, 10, 14, and 17 DAP. Total visible root length of plants growing under low temperature increased exponentially until 10 DAP, and increased linearly thereafter, while visible the root length of those growing at high temperature increased rapidly from 3 to 10 DAP, and 14 to 17 DAP, but from 10 to 14 DAP,
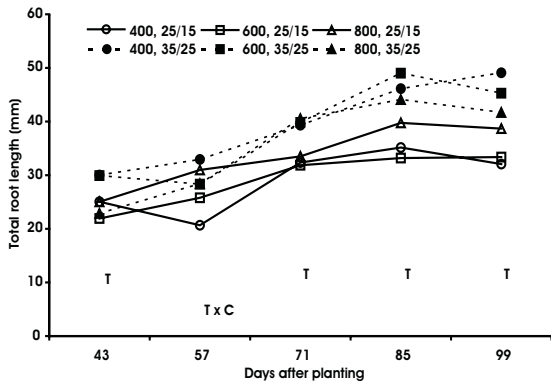
root length increased slowly . Temperature significantly affected visible root length at the beginning and toward the end of observation. Temperature significantly affected the number of roots per plant, at 3, 14, and 17 DAP, while the effect of elevated $[CO_2]$ was significant only at 10 DAP. Plants at low temperature had higher root numbers than those at high temperature. Root number was greatest at 600 μmol mol^{-1} CO_2.

Figure 6 shows the visible root length in the five 100-mm soil layers of the rhizotron as measured by RMS at the end of the study (17 DAP). Visible root lengths under 25/15ºC were higher at the three upper most depths (i.e., 0-100 mm, 100-200 mm, and 200-300 mm), whereas at 35/25ºC, the visible root length was greater only at the two upper most depths (i.e., 0-100 mm and 100-200 mm). Temperature significantly affected visible root length in the 200-300 mm and 300-400 mm soil layers. Plants grown at 25/15ºC had visible root length greater than those at 35/25ºC by 47% for the 200-300 mm and 62% for the 300-400 mm soil layers.

Fig 4. Long-term experiment; total root length development at different temperature regimes and CO_2 concentrations as observed by minirhizotron cameras with increasing days after planting. Letters indicate significant effects of temperature (T), CO_2 (C), and interaction between temperature and CO_2 (T x C), (P≤0.05).

Fig 6. Effect of CO_2 concentration and temperature on visible root length as measured by RMS at the five 100 mm soil layers.
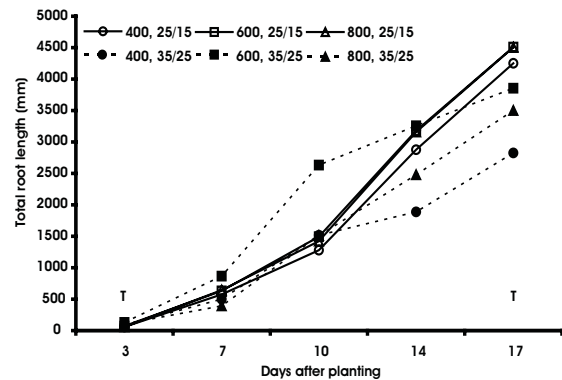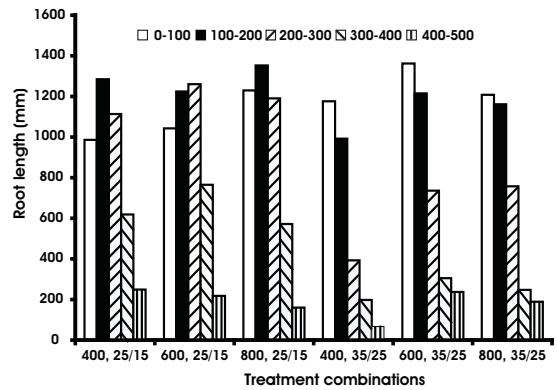

Fig 5. Short-term experiment; total root length development as measured at the transparent surface of rhizotrons with increasing days after planting (DAP).
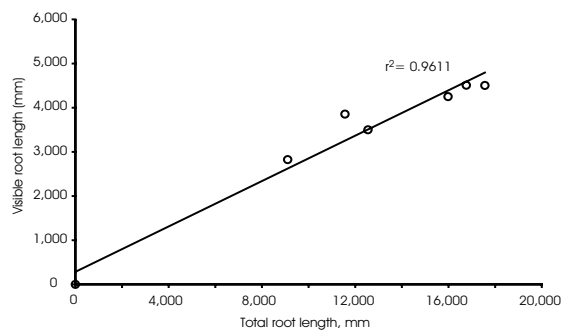

Fig 7. Relationship between visible root length at the transparent surface of rhizotrons and total root length washed from entire soil at 17 DAP response to different temperature and CO_2 regimes.

Temperature effects on root number were significant in the upper four soil layers, but not at 400-500 mm. The root numbers of 25/15ºC plants compared with 35/25ºC plants were 23% greater at 0-100 mm, 40% at 100-200 mm, 47% at 200-300, and 41% at 300-400 mm. There was no significant effect of CO_2 on the number of roots.

Figure 7 compares the root length visible at the transparent rhizotron surface as measured by RMS with roots washed from the entire soil as measured by WinRhizo. The total root length present in the soil was much greater than the visible root length at the transparent surface of the rhizotron. The visible root length was 26% to 33% of the total root length present in the soil. The coefficient of determination, $r^2 = 0.96$ indicates that it is possible to estimate total root length from root measurements conducted at the transparent surface. There were significant effects of temperature on both total root length (WinRhizo) and visible root length (RMS). Plants growing at 25/15ºC were 34% higher in total root length and 23% higher in visible root length than at 35/25ºC. Total root length present in the soil increased with increasing $[CO_2]$ from 400 to 800 µmol mol^{-1} CO_2 at both low and high temperatures. The increase was 13% greater for the plants growing at 600 µmol mol^{-1} CO_2, and 20% greater for those at 800 µmol mol^{-1} CO_2, although the difference was not significant

DISCUSSION

Stem Elongation

At the early growing period, plants growing at 35/25ºC had main stems longer than those at 25/15ºC. This result can be explained by the reports of Cox[3] and Ong[18]. They demonstrated that the mean optimal temperature range for vegetative growth of peanut is between 25 and 30ºC, while the optimum range for reproductive growth is between 22 and 24ºC. Elevated CO_2 resulted in increased stem length at 25/15ºC, but the length did not vary with $[CO_2]$ at 35/25ºC.

Leaf Growth

Individual leaf area and leaf dry weight increased with increasing $[CO_2]$, while specific leaf area decreased as CO_2 increased in both temperature treatments. Plants grown at 25/15ºC had larger leaf areas and dry weights, but smaller SLA than plants grown at 35/25ºC. These results indicated that plants grown at higher temperatures have thinner leaves due to fewer cell layers, which leads to higher SLA[19]. In contrast, a decrease SLA has been reported at elevated CO_2, which leads to extra palisade layer development[20], increased mesophyll cell size[21], and increased internal surface area for CO_2 absorption[22].

Shoots and Pods Dry Weights

There were significant effects of temperature and CO_2 and their interaction on above ground biomass. Above ground biomass increased with increasing CO_2 level and it was highest in plants grown at 800 µmol mol^{-1} CO_2 in both temperature treatments. This increase may result from increased photosynthesis. In peanut, it has been recently reported that a doubling of ambient CO_2 concentration enhances leaf photosynthesis by 27% and seed yield by 30% across a range of day-time growth temperatures from 32 to 44ºC[23]. Chen and Sung[8] reported that field-grown peanut plants produced more biomass and higher pod yield at 1000 µmol mol^{-1} CO_2 than at ambient CO_2. Stanciel *et al.*[9] also found that foliage and stem fresh and dry weights were increased as the $[CO_2]$ increased from 400 to 800 µmol mol^{-1}, but declined at 1200 µmol mol^{-1}. The increased above ground biomass obtained in this study agrees with the findings of Chen and Sung[8] and Sanciel *et al.*[9].

There was a significant effect of temperature on pod dry weight at different atmospheric $[CO_2]$. Pod dry weight was increased by elevated CO_2 when plants were grown at 25/15ºC. Pod dry weight increased 18% and 32% as CO_2 rose from 400 to 600 and 800 µmol mol^{-1}, respectively. This result can be explained by the fact that elevated atmospheric CO_2 enhances growth and productivity in C_3 plants through its beneficial effects on carbon assimilation and water use[24]. Stanciel *et al.*[9] reported that the number and the fresh and dry weights of pods increased with increasing CO_2 from 400 to 1200 µmol mol^{-1}. The total seed yield increased by an average of 37%, the mature seed yield by 25%, and the dry mass of mature seed by 38%. Prasad *et al.*[23] also found that elevated CO_2 increased pod and seed yield by about 30% owing to an increase in the total number of pods or seeds due to increased photosynthesis and growth. In contrast, elevated temperature had an adverse effect on pod dry weight. In this study, we found that as temperature increased from 25/15 to 35/25ºC, pod dry weight was reduced by 50%. The mean optimal air temperature range for vegetative growth of peanut is between 25 and 30ºC, which is warmer than the optimum range for reproductive growth, which is between 22 and 24ºC[3, 18]. Both short- and long-term exposure to air and soil temperatures above the optimum can cause significant yield loss in peanut[5, 6]. It was observed that day temperature >34ºC decreased fruit-set and resulted in fewer numbers of pods[6, 7]. 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[6, 7]. Increasing the daytime temperature from 23-30 to 34-36ºC significantly reduced the number of subterranean pegs and pods, seed size and seed yield by 30-50%[3, 18]. Prasad *et al.*[25]

investigated the effects of daytime soil and air temperatures of 28 and 38ºC, from the start of flowering to maturity, and reported a 50% reduction in pod yield at high temperature.

Root Growth

Short-term Experiment

The occurrence of a root response to different temperature and $[CO_2]$ was investigated in a rhizotron system. The primary root elongated to the bottom of the rhizotron by 13 to 14 days for plants grown at 35/25ºC and by 16 to 17 days for those at 25/15ºC. In general, a high proportion in length and number of roots were found in the three upper most soil layers (i.e. 0-100 mm, 100-200 mm, and 200-300 mm) at low temperature, but only in the two upper most soil layers at high temperature. Total root length and number of roots were significantly greater in plants grown at low than those at high temperature. The total root length present in the entire soil increased with increasing $[CO_2]$. This finding agrees with Berntson and Woodward [26]. They concluded that CO_2 enrichment resulted in a more dichotomously branched and longer root system of *Senecio vulgaris* that foraged through larger volumes of soil. Del Castillo *et at.*[4] reported that elevated CO_2 increased the number of soybean roots but not their elongation rate, from which they inferred that the soil volume explored by the root system did not increase, but a given volume of soil was explored more thoroughly.

Long-term Experiment

For the long term experiment, minirhizotron observation showed that total root length, number of roots, and RLD were significantly greater for plants grown under 35/25ºC than 25/15ºC at all CO_2 levels. Raising the concentration of atmospheric CO_2 often results in a dramatic increase in root growth. Root dry weight was found to increase at elevated atmospheric $[CO_2]$ [10]. In this study, we found that fibrous root dry weight increased as CO_2 increased when plants were grown at 25/15ºC, but decreased with increasing CO_2 at 35/25ºC. Belowground responses have been observed in cotton under free-air CO_2 enrichment [14]. Dry weights, lengths and volumes of taproots, lateral roots, and fine roots were often higher for CO_2 enriched cotton plants. Rogers *et al.*[12] demonstrated enhanced root growth in soybean with CO_2 enrichment. Root dry weight, length, diameter, and volume increased when CO_2 was increased; however, total root numbers exhibited no response. At high temperature, however, root dry weight was greater than at low temperature. This finding could have resulted from the greater total root length, RLD, and root number which were observed by minirhizotron camera.

There is a conflict in the results between short-and long-term responses of root. Thus, the greater total root length at low temperature in the short-term experiment in rhizotrons may not necessarily be indicative of the response in a long term experiment. However, the thin-layer soil rhizotron system allows researchers to simultaneously observe and quantify the time course of seedling root development without disturbance to the soil or roots.

In summary, the results from this study suggested that in peanut grown at two different air temperatures, increasing CO_2 from 400 to 800 µmol mol^{-1} had positive effects on main stem length and above ground biomass by enhancing the photosynthetic rate, while the number of branches was similar among plants grown under those treatment combinations. At low temperature (25/15ºC), leaf area increased as CO_2 increased, whereas specific leaf area declined. High temperature (35/25ºC) enhanced shoot and root growth but reduced the final reproductive biomass, which could have resulted from increased flower abortion and decreased seed size.

This study has clearly shown no beneficial interaction of elevated CO_2 with higher temperature on the reproductive processes, despite the tendency for beneficial temperature by CO_2 interaction on vegetative growth and total shoot dry weight. At all levels of CO_2 concentration, higher temperature resulted in significant yield losses. The beneficial effects of CO_2 levels on photosynthesis and growth were overwhelmed by the negative effects of high temperature on reproductive growth. Thus, if climate change is associated with increased temperature, the economic yields of crops that are sensitive to high temperature during the reproductive phase will be reduced, even after taking account of the beneficial effects of CO_2 enrichment. Therefore, a global search for plant genotypes that are more tolerant to high temperature for seed production is needed for peanut and other seed crops to improve productivity at the present and in future global climates.

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