Growth, Pod, and Seed Yield, and Gas Exchange of Hydroponically Grown Peanut in Response to CO₂ Enrichment

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Abstract. The effects of elevated CO₂ on growth, pod, and seed yield, and gas exchange of 'Georgia Red' peanut (*Arachis hypogaea* L.) were evaluated under controlled environmental conditions. Plants were exposed to concentrations of 400 (ambient), 800, and 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂ in reach-in growth chambers. Foliage fresh and dry weights increased with increased CO₂ up to 800 $\mu\text{mol}\cdot\text{mol}^{-1}$, but declined at 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$. The number and the fresh and dry weights of pods also increased with increasing CO₂ concentration. However, the yield of immature pods was not significantly influenced by increased CO₂. Total seed yield increased 33% from ambient to 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂, and 4% from 800 to 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂. Harvest index increased with increasing CO₂. Branch length increased while specific leaf area decreased linearly as CO₂ increased from ambient to 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$. Net photosynthetic rate was highest among plants grown at 800 $\mu\text{mol}\cdot\text{mol}^{-1}$. Stomatal conductance decreased with increased CO₂. Carboxylation efficiency was similar among plants grown at 400 and 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ and decreased at 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂. These results suggest that CO₂ enrichment from 400 to 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ had positive effects on peanut growth and yield, but above 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ enrichment seed yield increased only marginally.

The use of biological systems for life support in space has been studied since the early 1950s, with emphasis on the use of algae to help regenerate O₂ through photosynthesis (Golueke and Oswald, 1964; Krall and Kok, 1960). In the late 1970s, the National Aeronautics and Space Administration (NASA) created the Controlled Ecological Life Support System (CELSS) program to promote research for long-term advanced life support (ALS) (MacElroy and Bredt, 1985). Among the concepts considered for ALS is the use of higher plant photosynthesis to provide food and O₂, while removing CO₂ produced by humans and other heterotrophs. Plant transpiration may also be utilized to produce potable water. Selected for the high protein (22% to 30%) and oil content (44% to 56%) of the seed

(Ahmed and Young, 1982), peanut is among several candidate crops for ALS research.

The growth and development of peanut have been widely studied (Bagnall and King, 1991; Chen and Sung, 1990; Florh et al., 1990; Hardy and Havelka, 1977; Ketring, 1984). Bhagsari and Brown (1976) evaluated the effects of increased CO₂ on net photosynthesis and leaf characteristics of several peanut genotypes. Net photosynthesis increased linearly for some genotypes as CO₂ concentration increased from 300 to 600 $\mu\text{mol}\cdot\text{mol}^{-1}$. Hardy and Havelka (1977) grew peanut from anthesis to senescence at ambient (350 $\mu\text{mol}\cdot\text{mol}^{-1}$) or 1500 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂ in open-top field chambers. They reported that above-ground biomass was 50% greater for plants grown at 1500 $\mu\text{mol}\cdot\text{mol}^{-1}$ than for those grown under ambient conditions. The increased biomass was attributed to decreased photorespiration, delayed senescence, and retention of more reproductive structures (flowers and gynophores). Chen and Sung (1990) evaluated the effects of CO₂ at 340 (ambient) and 1000 $\mu\text{mol}\cdot\text{mol}^{-1}$ from seed filling in Virginia-type peanut. High CO₂ increased biomass and pod yields. Marketable seed yield was similar, however, because more than two-thirds of the pods on plants grown at 1000 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂ were unfilled. They hypothesized that increasing the CO₂ at the seed filling stage maximized competition among developing seeds and pegs, reducing seed growth.

Leaf photosynthetic rate was consistently higher at 1000 $\mu\text{mol}\cdot\text{mol}^{-1}$ than at 340 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂ (Chen and Sung, 1990). In

both treatments, photosynthesis was saturated at an intercellular CO₂ (C_i) of $\approx 600 \mu\text{mol}\cdot\text{mol}^{-1}$. The estimated CO₂ compensation points were 50 for the control (ambient) and 90 $\mu\text{mol}\cdot\text{mol}^{-1}$ for plants grown under high CO₂, and carboxylation efficiency was higher at 1000 $\mu\text{mol}\cdot\text{mol}^{-1}$.

In spite of concerns for increasing atmospheric CO₂, only short-term studies have been conducted on the peanut. None of these studies was carried out in controlled environments. Closed environments utilized for human life support in space may reach partial pressures of 5000 to 10,000 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂ (Wheeler et al., 1993). Although excess CO₂ will be scrubbed through physical and chemical processes, plants can also play a role in reducing CO₂ to acceptable levels by utilizing it in the photosynthetic process. The objective of this study was to evaluate the effects of increased CO₂ partial pressures on growth, pod, and seed yield and gas exchange of 'Georgia Red' peanut grown hydroponically under controlled environments.

Materials and Methods

Experiments were conducted during 1996 and 1997. Three CO₂ treatments were arranged in a randomized complete-block design with three replications over time. Three identical reach-in growth chambers (Environmental Growth Chambers, Chagrin Falls, Ohio), each with 1.39 m² of growing area, were used.

Seeding. Seeds were planted in moist commercial Jiffy Mix (Geo. J. Ball, Batavia, Ill.) media in TLC Pro-Trays transplant flats (TLC Polyform, Plymouth, Minn.) and covered with ≈ 0.6 cm of the medium. Flats were placed in a growth chamber with a 28 °C light/22 °C dark temperature, a 12-h photoperiod, and a constant relative humidity (RH) of $\approx 70\% \pm 5\%$. Seeds were watered every 3 d and seedlings were grown for ≈ 2 weeks.

Transplanting. Before transplanting, seedlings were carefully removed from each cell and excess medium was removed, ensuring that minimal damage was done to the plant root system. The roots of the plants were gently washed with running tap water to remove particles of the medium that adhered to the roots. Four 2-week-old peanut seedlings were transplanted into each of two growing channels (0.15 $\times$ 0.15 $\times$ 1.2 m) through small openings 10 cm apart in a flexible black/white vinyl covering. This covering not only supported the plants, but served to prevent the entry of light into the pod development zone. At flowering, perforations were made in the vinyl covering to facilitate the entry of the developing gynophores into the pod production zone.

CO₂ control. The CO₂ treatments were 400 (ambient), 800, and 1200 $\pm 25 \mu\text{mol}\cdot\text{mol}^{-1}$, maintained by using an infrared gas analyzer (Leybold-Heraeus, Wilhelm, Germany). The CO₂ treatments were initiated ≈ 1 week after transplanting and lasted for the duration of the experiment (110 d).

Nutrient solution. A modified half-Hoagland (Hoagland and Arnon, 1950) nutri-

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ent solution was supplied to the plants in each channel. The nutrient solution was continuously pumped (Little Giant model 2 P037; Tecumseh Product Co., Oklahoma City, Okla.) from reservoirs (30.4 L) to the high end of each growth channel at a flow rate of 1 L·min⁻¹, set by using a bypass line back to the reservoir with a control valve. Growth channels were inclined with a 1% slope to facilitate the return of the nutrient solution to the reservoir by gravity flow. The solution was replaced bi-weekly and was replenished with deionized water between changes. Nutrient solution pH was maintained between 6.4 and 6.7 by manual addition of either dilute NaOH or HCl. Electrical conductivity was maintained between 1100 and 1200 $\mu\text{S}\cdot\text{cm}^{-1}$ by adding a one-third Hoagland's stock, and solution temperature was similar to that of the air (28/22 °C).

Growth chamber conditions. Growth chamber conditions included a constant relative humidity of 70% $\pm$ 5% and a photosynthetic photon flux (PPF) of 600 $\pm$ 50 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at canopy level ($\approx$ 20 cm above the plants) supplied by a mixture of cool-white fluorescent and incandescent lamps. Photoperiod was 12 h and temperature 28 °C light/22 °C dark.

Measurements. Biweekly starting 21 d after planting (DAP), the second fully expanded leaf on the main stem (growing axis) was detached for leaf area and dry weight determination. Mainstem and cotyledonary branch lengths were also recorded bi-weekly. Single-leaf gas exchange measurements were made using a LI-6400 portable photosynthesis system (LI-COR, Lincoln, Nebr.) with a red LED light source attachment. This open-flow system is designed to measure steady-state gas exchange under controlled temperature, humidity, CO₂, and PPF conditions. Measurements were made each day between 1000 and 1500 HR, using the third or fourth fully expanded, unshaded leaf from two plants per channel on a growing axis, resulting in four replicate leaves for each CO₂ treatment. CO₂ response curves were generated by measuring CO₂ exchange rates (CER) at 11 points ranging from 55 to 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂. Measurements were made at a leaf temperature of 28 °C, a PPF of 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and a RH of 50%. Carboxylation efficiencies (Farquhar and Sharkey, 1982) were determined from the initial slope of the CO₂ response curve using linear regression on four points between 50 and 125 $\mu\text{mol}\cdot\text{mol}^{-1}$ internal CO₂.

Harvest. Plants were harvested 110 DAP and fresh weights of leaves, stems, roots, pods and seeds were determined. All fully expanded leaflets were removed from each plant and counted, and total leaflet area was determined using a LI-3100 leaf area meter (LI-COR). Fresh plant materials were dried for 72 h at 70 °C. Pods were removed from each plant, counted, weighed, and dried at 35 °C for 72 h. After drying, pods were sorted into mature and immature and weighed. Seeds were removed from pods and categorized according to the method described by Rucker et al. (1994), as mature (seeds with a smooth testa, pink to dark pink with a more rounded appearance) or immature (light-colored seeds having testae

with longitudinal wrinkles, and slightly elongated). The percentage of sound mature kernels [SMK; seeds without discoloration, mold, or sprouts (Davidson et al., 1982)] and harvest index (HI; 100 $\times$ seed dry weight/total dry weight) were also determined.

Experiments were repeated twice and treatments were rotated among chambers to minimize chamber effects. Data were combined by runs and analyzed by the General Linear Models procedure (SAS Institute, 1985).

Results

Foliage and stem fresh and dry weights were greater at 800 than at 400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂ but declined at 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$ (Table 1). Fibrous root dry weight increased linearly as CO₂ increased.

Mature pod number and total fresh weight were not significantly affected by CO₂ enrichment (Table 1), but total pod dry weight and immature pod number increased quadratically with increasing CO₂.

Total seed dry mass increased with increasing CO₂ (Table 1); the magnitude of increase was 36% from 400 (ambient) to 800 $\mu\text{mol}\cdot\text{mol}^{-1}$, but only 4% from 800 to 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$. Number of mature seeds also increased with increasing CO₂, but the yield of immature seeds and the percentage SMK were not influenced. HI increased with increasing CO₂.

Increasing CO₂ had no effect on dry matter accumulation in individual leaves (Table 2), but area per leaf and branch length (main and

cotyledonary) increased linearly with increasing CO₂. In contrast, specific leaf area decreased linearly as CO₂ concentration increased from ambient to 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$.

Leaf net photosynthetic rate (Table 2) was highest in plants grown at 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂. Stomatal conductance decreased, as expected, as the CO₂ concentration increased, and was lowest at 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$, indicating a partial closure of stomates due to the high CO₂. Carboxylation efficiency (Table 2), as determined from the initial slope of the CO₂ response curve, was similar among plants grown at 400 and 800 $\mu\text{mol}\cdot\text{mol}^{-1}$, but was lowest at 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂. Net photosynthetic rate (Fig. 1) increased with internal CO₂ concentration and was highest in those plants grown at 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂ and lowest for plants grown at 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$. Photosynthetic rates approached CO₂ saturation at an internal CO₂ concentration of $\approx$ 700 $\mu\text{mol}\cdot\text{mol}^{-1}$.

Discussion

Production of above-ground biomass (Table 1) was highest in plants grown at 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂. Pod yield (Table 1) increased linearly with CO₂ enrichment. Hardy and Havelka (1977) reported higher dry matter and vegetative growth of peanut exposed to 1000 to 1500 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂ in field studies, and attributed this response to decreased photorespiration, delayed senescence, and increased plant density. Chen and Sung (1990) reported that field-grown peanut plants produced more biomass and higher pod yield at

Table 1. Effects of CO₂ enrichment on vegetative growth, pod yield, seed yield and quality, and harvest index of 'Georgia Red' peanut.

	CO ₂ (μmol·mol ⁻¹)			
Observation	400	800	1200	Regression ²
	<i>Weight of foliage (g·m⁻²)</i>			
Fresh	3850	5570	4120	L ^{**} , Q ^{***}
Dry ^y	647	840	752	Q [*]
	<i>Weight of stem (g/plant)</i>			
Fresh	75.3	120.4	87.6	L [*]
Dry	13.5	18.9	15.2	L [*] , Q [*]
	<i>Weight of fibrous roots (g/plant)</i>			
Dry	1.96	2.04	2.83	L [*]
	<i>Number of pods/m²</i>			
Total	673	850	1057	NS
Mature	531.2	641.5	761.5	NS
Immature	123.3	197.4	309.2	Q [*]
	<i>Pod weight (g·m⁻²)</i>			
Total fresh	1043	1241	1534	NS
Total dry	326.5	479.8	510.0	Q [*]
Immature dry	7.5	12.1	10.2	NS
	<i>Number of seeds/m²</i>			
Mature	706	865	1020	Q [*]
Immature	270	334	293	NS
	<i>Dry weight of seeds (g·m⁻²)</i>			
Total	247	385	400	Q [*]
Mature	236	371	389	Q [*]
Immature	11	13	10	NS
	<i>Sound mature kernels (%)</i>			
	71	73	77	NS
	<i>Harvest index (%)</i>			
	24.5	29.1	32.0	L [*] , Q [*]

^aL = linear, Q = quadratic, significant at $P \leq 0.10$ (*) or 0.05 (**). NS = nonsignificant.

^yDry weight data are "air"-dry values.

Table 2. Effects of CO₂ enrichment on leaf and stem characteristics, net photosynthesis, stomatal conductance, and carboxylation efficiency of 'Georgia Red' peanut.

Observation	CO ₂ (μmol·mol ⁻¹)			Regression ²
	400	800	1200	
Dry weight/leaf (mg)	193.0	188.0	183.0	NS
Area/leaf (cm ²)	30.9	36.4	38.9	L***
Specific leaf area (m ² ·kg ⁻¹)	24.8	21.2	22.1	L*
Stem length (cm)				
Main	25.3	29.3	36.5	L*
Cotyledonary	23.1	26.2	33.2	L*
Net photosynthesis (μmol·mol ⁻¹)	17.1	22.1	13.0	L*
Stomatal conductance (mol·m ⁻² ·s ⁻¹)	0.468	0.261	0.234	L*
Carboxylation efficiency (μmol·m ⁻² ·s ⁻¹)	0.111	0.116	0.069	L*

²L = linear, Q = quadratic; significant at $P \leq 0.10$ (*) or 0.001 (***). NS = nonsignificant.

Fig. 1. Net photosynthesis ($\pm$ SE) as a function of internal CO₂ in 'Georgia Red' peanut plants grown at three different CO₂ concentrations. Curves are means of two to three replicate leaves from the second experiment (replicate).

1000 μmol·mol⁻¹ than at ambient CO₂. The increased biomass obtained in this study agrees with the findings of Chen and Sung (1990) and Hardy and Havelka (1977), but differs in that biomass production declined at the highest CO₂ concentration. Vegetative growth is a continuous process in the peanut and has priority for all assimilates until pod and seed set commence (Boote et al., 1986, 1992). Pods and seeds then become stronger sinks for assimilates, thereby reducing that fraction available for vegetative growth. This phenomenon could partly explain the reduced vegetative growth, as evidenced by the fact that pod production (Table 2) and seed production (Table 1) tended to be higher at the highest CO₂ level.

Pod dry weight (Table 1) was significantly higher at 1200 μmol·mol⁻¹ CO₂, reflecting both an increase in pod number as well as assimilate partitioning to the pods. According to Boote et al. (1992), physiological maturity in peanut is not as clearly defined as it is, for example, in soybean [*Glycine max* (L.) Merr.]. Pod number increases more gradually because vegetative growth continues during the seed growth phase, and pods of various stages of maturity are present at harvest.

Elevating CO₂ from 400 to 1200 μmol·mol⁻¹ increased total seed yield an average of 37%, the number of mature seeds by 25%, and dry mass of mature seeds by 38% (Table 1). These

results can be explained by a higher photosynthetic rate (35%) in the enriched CO₂ treatment (Table 2) particularly at the 800 μmol·mol⁻¹ level, and paralleled those of Chen and Sung (1990), who reported higher seed yield of peanuts under elevated CO₂ levels. Ackerson et al. (1984) attributed the high seed yields obtained for soybeans under CO₂ enrichment to more pods and seeds per plant. In this study, the number of seeds produced was also significantly higher with than without enrichment. Although total seed yield increased by 36% when ambient levels of CO₂ were raised to 800 μmol·mol⁻¹, the increase between 800 and 1200 μmol·mol⁻¹ CO₂ was only 4%. This response could be related to several factors. First, the 1200 μmol·mol⁻¹ CO₂ may be near the toxic threshold for peanuts. Wheeler et al. (1993) reported a decrease in biomass and yield of soybean when CO₂ exceeded 1000 μmol·mol⁻¹. The same may be true in peanut. Second, the decrease in foliage biomass and the marginal increase in seed yield could be an acclimation response. According to Arp (1991), long-term exposure to elevated CO₂ causes a reduction in the activity of RuBP carboxylase and feedback inhibition of photosynthesis in both C₃ and C₄ species. This acclimation does not reduce growth, but prevents the increase in photosynthesis that normally occurs with elevated CO₂. The reduction in the activity of RuBP carboxylase could

partly explain the reduced photosynthetic rate among plants grown at 1200 μmol·mol⁻¹ (Table 2). CO₂ enrichment appeared to enhance maturity, as evidenced by the higher yield of mature seeds. In contrast, neither the number nor the weight of immature seeds was significantly influenced by CO₂ enrichment (Table 1).

Harvest index (HI), which is an indication of the relative distribution of photosynthates between seeds and the remainder of the plant, was significantly increased by CO₂ enrichment (Table 1). These results are not in agreement with those of Clifford et al. (1993), who reported that HI in peanut was not significantly influenced by CO₂ enrichment. The reason for this difference may be due in part to the fact that plants were subjected to water stress in Clifford's study while in our study, plants were grown hydroponically.

Area per leaf and branch length increased with CO₂ level (Table 2), while specific leaf area decreased as CO₂ increased. Leaves of plants grown at 800 and 1200 μmol·mol⁻¹ CO₂ concentration had greater dry weights, and smaller areas, resulting in thicker leaves and thus reduced specific leaf area. Most of the difference in area per leaf occurred early in the growing period. At harvest neither total leaf area nor area per leaf was significantly affected by elevated CO₂ (data not shown).

Carboxylation efficiency (Table 2) was similar among plants grown at 400 and 800 μmol·mol⁻¹ CO₂, but decreased at 1200 μmol·mol⁻¹. Chen and Sung (1990) reported greater carboxylation efficiency in peanut grown at 1000 μmol·mol⁻¹ CO₂ than at 340 μmol·mol⁻¹ CO₂, indicating diversion of rubisco enzyme from oxygenation to carboxylation. Direct comparison of these results with ours is difficult owing to the differences in treatment levels. Perhaps the inhibitory effects of elevated CO₂ on carboxylation efficiency do not become apparent until CO₂ levels surpass 1000 μmol·mol⁻¹. Furthermore, Chen and Sung made no measurements below 200 μmol·mol⁻¹ internal CO₂, relying instead on quadratic extrapolation from the measurements made at higher CO₂ levels, leading to potentially large inaccuracies in their values.

The drop in leaf photosynthetic rates as CO₂ was raised from 800 to 1200 μmol·mol⁻¹ (Table 2) is consistent with total biomass data and occurred despite a linear increase in the harvest index. There are reports of supraoptimal effects from CO₂ on seed yield and total biomass of the soybean 'McCall' (Wheeler et al., 1993), seed set and vegetative growth in wheat (*Triticum vulgare* L.) (Bugbee et al., 1994; Grotenhuis and Bugbee, 1997; Reuveni and Bugbee, 1997), and in white potato (*Solanum tuberosum* L.) (Wheeler et al., 1996). The mechanism of varying plant responses at supraoptimal CO₂ is not entirely clear. It may be mediated by low carbohydrate supply to developing embryos or by induction of ethylene synthesis by high CO₂ (Bugbee et al., 1994; Grotenhuis and Bugbee, 1997; Reuveni and Bugbee, 1997). Developing peanut gynophores produce ethylene (Ketrings et al., 1982), with the highest rates occurring during initial

stages of growth (Lee et al., 1972), and just after penetration into the pod production zone (Hodges and Fletcher, 1979). This suggests that the high CO₂ in our study may have interacted with the natural tendency of peanut gynophores to produce ethylene by increasing CO₂-induced ethylene synthesis.

Increasing the CO₂ from 400 to 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$ decreased stomatal conductance by an average of 47% (Table 2). The partial closure of the stomates as CO₂ increased paralleled the reduction in the rate of transpiration (data not shown). This was not unexpected, since extensive reports (Cure and Acock, 1986; Field et al., 1995; Morison, 1987; Zhu et al., 1998) have documented this phenomenon under high CO₂ partial pressures.

This research clearly documents that doubling CO₂ from 400 to 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ increased total seed yield and maturity, plant dry weight, and harvest index. However, the reduction in photosynthetic rate and plant biomass at 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂ strongly indicates supraoptimal effects, the causes of which are not clearly understood, but are believed to be mediated by reduced carbohydrate supply or a CO₂-induced increase in ethylene synthesis.

Generally, these results show that peanut responded positively to CO₂ enrichment at least up to 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ and can be a useful crop in the ALS program. Although ambient CO₂ concentration is not expected to approach 800 or even 1200 $\mu\text{mol}\cdot\text{mol}^{-1}$ for several decades, in ALS, direct atmospheric exchange may be maintained between plant and human habitats in a sealed system. In such a case, CO₂ partial pressures could be elevated beyond the levels used in this study. Further studies are in progress to evaluate peanut growth and development at higher concentrations of CO₂.

Literature Cited

- Ackerson, R.C., U.D. Havelka, and M.G. Boyle. 1984. CO₂ enrichment effects on soybean physiology. II. Effects of stage-specific CO₂ exposure. *Crop Sci.* 24:1150–1154.
- Ahmed, E.M. and C.T. Young. 1982. Composition, quality, and flavor of peanuts, p. 655–688. In: H.E. Pattee and C.T. Young (eds.). *Peanut science and technology*. Amer. Peanut Res. and Educ. Soc., Yoakum, Tex.
- Arp, W.J. 1991. Effect of source-sink relations on photosynthetic acclimation to elevated CO₂. *Plant Cell Environ.* 14:869–875.
- Bagnall, D.J. and R.W. King. 1991. Response of peanut (*Arachis hypogaea*) to temperature, photoperiod, and irradiance. 1. Effect on flowering. *Field Crops Res.* 26:261–300.
- Bhagsari, A.S. and R.H. Brown. 1976. Photosynthesis in peanut (*Arachis*) genotype. *Peanut Sci.* 3:1–5.
- Boote, K.J., J.W. Jones, J.W. Mishoe, and G.G. Wilkerson. 1986. Modeling growth and yield of groundnut, p. 243–254. In: *Agrometeorology of groundnut*. Proc. Intl. Symp. 21–26 Aug. 1985, ICRISAT Sahelian Center, Niamey, Niger. Patancheru, A.P. 502324, India: ICRISAT.
- Boote, K.J., J.W. Jones, and P. Singh. 1992. Modeling growth and yield of groundnut, p. 331–343. In: *Groundnut—A global perspective*. Proc. Intl. Symp. 25–29 Nov. 1991, ICRISAT Center, India.
- Bugbee, B., B. Spanarkel, S. Johnson, P. Monje, and G. Koerner. 1994. CO₂ crop growth enhancement and toxicity in wheat. *Adv. Space Res.* 14:257–267.
- Chen, J.J. and J.M. Sung. 1990. Gas exchange rate and yield responses of Virginia-type peanut to carbon dioxide enrichment. *Crop Sci.* 30:1085–1088.
- Clifford, S.C., I.M. Stronach, A.D. Mohamed, S.N. Azam-Ali, and N.M.J. Crout. 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. Expt. Bot.* 44:1763–1770.
- Cure, J.D. and B. Acock. 1986. Crop responses to carbon dioxide doubling: A literature survey. *Agr. Forest Meteorol.* 38:127–145.
- Davidson, J.I., Jr., T.B. Whittaker, and J.W. Dickens. 1982. Grading, cleaning, storage, shelling, and marketing of peanuts in the United States, p. 501–620. In: H.E. Pattee and C.T. Young (eds.). *Peanut science and technology*. Amer. Peanut Res. and Educ. Soc., Yoakum, Tex.
- Farquhar, G.D. and T.D. Sharkey. 1982. Stomatal conductance and photosynthesis. *Annu. Rev. Plant Physiol.* 33:317–345.
- Field, C.B., R.B. Jackson, and H.A. Mooney. 1995. Stomatal responses to increased CO₂: Implications from the plant to the global scale. *Plant Cell. Environ.* 18:1214–1225.
- Flörh, M.-L., J.H. Williams, and F. Lenz. 1990. The effect of photoperiod on the reproductive developments of a photoperiod-sensitive groundnut (*Arachis hypogaea* L.) cv. NC AC 100090. *Expt. Agr.* 26:397–406.
- Golueke, C.G. and W.J. Oswald. 1964. Role of plants in closed systems. *Annu. Rev. Plant Physiol.* 15:387–408.
- Grotenhuis, T. and B. Bugbee. 1997. Super-optimal CO₂ reduces seed yield but not vegetative growth in wheat. *Crop Sci.* 37:1215–1222.
- Hardy, R.W.F. and U.D. Havelka. 1977. Possible routes to increase the conversion of solar energy to food and feed by grain legumes and cereal grains (crop production). CO₂ and N₂ fixation, foliar fertilization, and assimilate partitioning, p. 299–322. In: A. Mitsui (ed.). *Biological solar energy conversions*. Academic, New York.
- Hoagland, D.R. and D.I. Arnon. 1950. The water culture method for growing plants without soil. *California Agr. Expt. Sta. Circ.* 3407.
- Hodges, R.A. and J. Fletcher. 1979. Ethylene evolution from peanut pegs. *Plant Physiol. Suppl.* 63:66.
- Ketrting, D.L. 1984. Temperature effects on vegetative and reproductive development of peanuts. *Crop Sci.* 24:877–882.
- Ketrting, D.L., R.H. Brown, G.A. Sullivan, and B.B. Johnson. 1982. Growth physiology, p. 411–457. In: H.E. Pattee and C.T. Young (eds.). *Peanut science and technology*. APRES, Yoakum, Texas.
- Krall, A.R. and B. Kok. 1960. Studies on algal gas exchangers with reference to space flight. *Dev. Indust. Microbiol.* 1:33–44.
- Lee, T.A., D.L. Ketrting, and R.D. Powell. 1972. Flowering and growth response of peanut plants (*Arachis hypogaea* L. var. Starr) at two levels of relative humidity. *Plant Physiol.* 49:190–193.
- MacElroy, R.D. and J. Bredt. 1985. Current concepts and future directions of CELSS. *NASA Conf. Publ.* 2378.
- Morison, J.J.L. 1987. Intercellular CO₂ concentrations and stomatal responses to CO₂, p. 229–251. In: E. Zeiger, G.D. Farquhar, and I.R. Cowan (eds.). *Stomatal function*. Stanford Univ. Press, Stanford, Calif.
- Rucker, K.S., C.K. Kvien, G. Vellidid, N.S. Hill, and J.K. Sharpe. 1994. A visual method of determining maturity of shelled peanuts. *Peanut Sci.* 21:141–146.
- SAS Institute. 1985. *SAS user's guide. Statistics*, version 5 ed. SAS Inst., Cary, N.C.
- Wheeler, R.M., C.L. Mackowiak, L.M. Siegest, and J.C. Sager. 1993. Supraoptimal carbon dioxide effects on growth of soybean [*Glycine max* (L.) Merr.]. *J. Plant Physiol.* 142:173–178.
- Zhu, J., L.D. Talbot, X. Jin, and E. Zeiger. 1998. The stomatal response to CO₂ is linked to changes in guard cell zeaxanthin. *Plant Cell Environ.* 21:813–920.