Photosynthesis and growth responses of peanut (*Arachis hypogaea* L.) to salinity at elevated CO_2

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ABSTRACT

Four peanut (*Arachis hypogaea* L.) cultivars (cvs. TPT-1, TPT-4, JL-24 and TMV-2) were grown in open-top chambers at 350 and 600 µmol CO_2/mol in soil amended with 0 (control), 50, 100 and 200 mmol solutions of NaCl. The net photosynthetic rate (P_n), stomatal conductance (g_s), transpiration (E) and dry biomass of leaf, stem and root were measured on 60 days after sowing. The plant growth and photosynthesis increased in both NaCl treated and control plants with elevated CO_2. The g_s and E decreased under elevated CO_2 and the CO_2 effect was highly significant under salt stress mitigating the adverse effect on these components in all the four cultivars tested. A positive correlation was observed between P_n and dry biomass under elevated CO_2 and salt stress. Enhanced CO_2 helps to increase growth and photosynthesis in peanut cultivars and it ameliorates the adverse effects induced by salt stress.

Keywords: elevated carbon dioxide; net assimilation; stomatal conductance; NaCl; legume

Several lines of evidence suggest that agricultural ecosystem is responding to elevated atmospheric CO_2 (Kimball et al. 2002, Ratnakumar et al. 2012). Photosynthesis (Long and Drake 1992) and transpiration (Heath 1948) have long been known to be sensitive to increasing CO_2. These two processes appear to be the mechanism where increase in photosynthesis is related to the reduction in Rubisco's oxygenase activity, but the changes in transpiration related to decreased in stomatal conductance by which plants and ecosystem can sense and respond directly to rising CO_2. Many detailed and thorough reviews identifying the long list of changes at the whole plant level to rising CO_2, and the results of many open-top chamber based experiments were documented from time to time (Kimball 1983, 1986, 1993, Kimball et al. 2002, Ratnakumar et al. 2012) are of interest. Elevated CO_2 reduces stomatal conductance (g_s), transpiration (E) and improves the water use efficiency (WUE). At the same time, it stimulates higher rates of photosynthesis of leaves. The root growth often increases (Kimball et al. 2002) resulting in large leaf areas and root systems.

Elevated CO_2 also showed to ameliorate the adverse effect of salinity (Bazzaz 1989, Pérez-López et al. 2012, 2013). These observations suggest that the CO_2 enriched plants of the future will better tolerate salinity. Few investigations showed gradual decrease in net photosynthetic rate (P_n) under increased salinity and were sometimes even stimulated by low salt concentration (Heuer and Plaut 1981). Genotypic differences in the response of plants to salinity have previously been reported (Heuer and Plaut 1982).

Enhanced demand for energy and photosynthate is observed under saline conditions. Thus, treatments that increase the photosynthate supplies such as CO_2 enrichment were thought to be beneficial for salt-stressed plants. Few studies were focused on the study of interactive effect of CO_2 enrichment with salinity in barley's metabolic limitations on photosynthesis (Pérez-López et al. 2013) and peanut anti-oxidative enzymes (Ratnakumar et al. 2006). The available data indicate that CO_2 enrichment stimulates plant growth under high salt concentrations but can only partially relieve the deleterious effect of salinity (Schwartz and Gale 1984). Elevated CO_2 improved dry matter production, leaf area and tillering of wheat grown under saline condition. CO_2 fixation was increased in bean plants grown in nutrient solution containing salt were exposed to high CO_2 levels i.e., 700 μmol/mol. Variation among cultivars grown under elevated CO_2 and NaCl salt stress were understood modest with regard to photosynthesis, growth and yield. Although a large database is available on twelve of the most important crops of the world on the effects of elevated CO_2 on photosynthesis and growth (Kimball et al. 2002, Ratnakumar et al. 2012), lack of information on peanut (*Arachis hypogaea* L.) a C3 legume, as influenced by abiotic stress and climatic variables viz., change in atmospheric CO_2 and soil salinity led us to understand the response of peanut cultivars to elevated CO_2 and its interaction with salinity. In this paper we determine the relative growth and photosynthesis of four peanut cultivars grown under elevated CO_2 and three different concentrations of NaCl salinity. The peanut cultivars chosen for this study are contrast lines for drought and farmer preferred cultivars grown under rain-fed condition at Andhra Pradesh, Karnataka and Tamil Nadu states of India.

MATERIAL AND METHODS

Experimental conditions. Two open-top chambers (OTCs) were constructed at the botanical garden of Sri Venkateswara University campus, Tirupati, Andhra Pradesh, India by adapting the design of Ashenden et al. (1992). A cylindrical design of chambers 3 m tall with 5.5 m diameters was used. The chambers were constructed with iron frames covered with clear polyvinyl chloride (PVC) sheet. The maximum day sunlight/photosynthetically active radiation (PAR) varied from 1200 to 1250 μmol/m^2/s inside the chamber. The average temperature during the daytime inside the OTC was 36 ± 2°C, the wind velocity was low and constant, and the relative humidity ranged from 45% (light period) to 60% (dark period) inside the open-top chambers. The average ambient level of CO_2 was found 360 ± 20 μmol/mol during daytime under natural conditions. Pure carbon dioxide was supplied 24 h to the OTC from a CO_2 cylinder during the treatment period. The CO_2 level was regulated by computing solenoid valves to obtain a desired concentration of 600 ± 10 μmol/mol and it was monitored regularly by using IRGA (California Analytical, Model ZRH-1, USA) monitor based on non-depressive infrared optical technique as described by Vanaja et al. (2006a).

Plant material. Seeds of peanut (*Arachis hypogaea* L.) cvs. TPT-1, TPT-4, JL-24 and TMV-2 were obtained from the Regional Agriculture Research Station, Tirupati. These cultivars are contrast to drought where TPT-4, TPT-1 are tolerant to drought; JL-24 and TMV-2 were susceptible to drought. TPT-4 and TPT-1 were also successfully used by farmers in drought-prone area in southern states of India. The seeds were surface sterilized with 0.1% mercuric chloride and rinsed thoroughly with distilled water, and then they were soaked for 3 h in glass-distilled water. They were sown in fiberglass pots (98 cm diameter and 65 cm depth) with soil and farmyard manure in the ratio of 3:1. The soil (order: Alfisol) is low in available nitrogen (254 kg/ha) phosphorous (11 kg/ha) and potassium (154 kg/ha). Solutions of NaCl 50, 100 and 200 mmol concentration were added to the soil. Care was taken to prevent leaching of salt from the pots. Five seeds were sown in each pot, after germination three plants were maintained per pot. Twelve pots were maintained for each treatment. Up to 30 days after sowing (DAS) plants were grown in natural conditions at ambient atmospheric CO_2. On 30 DAS, the pots were divided into two sets and maintained in the OTCs with ambient CO_2 (360 ± 20 μmol/mol) concentration and elevated CO_2 (600 ± 10 μmol/mol) concentration for 30 days (up to 60 DAS) at grand growth period of the crop. On 60 DAS the gas exchange measurements were measured in the third leaf (fully measured) from the apex of individual plants.

Gas exchange measurements. A portable gas exchange measuring system (model LCA.3.ADC, Hearts, England) was used for determination of CO_2 and water vapor exchange in attached leaves. Gas exchange measurements were made between 10:00 and 11:30 h (IST) on sunny and generally cloud free days. For measuring P_n, g_s and E in light, photosynthetic leaf chamber model (PLC-3 (B) ADC, Hearts, England) was clipped onto the attached leaf, which had been exposed to sunlight. The chamber was held in such an angle that the enclosed leaf surface faced the sun, to avoid the shading inside the curette. The irradiance at the upper surface of the leaf chamber was measured by calibrated sensor (filtered silicon photocell, ADC, Hearts, England) mounted on the same surface of the leaf chamber. It was 1200–1250 µmol/m^2/s during the most P_n measurements. The temperatures were 36 ± 2°C; relative humidity was 60 ± 2%; CO_2 concentration 360 ± 15 µmol CO_2/mol in control chamber and 600 ± 10 µmol CO_2/mol in elevated CO_2 chamber. The P_n and g_s become stable within 2 min after clipping the selected attached leaf experiencing saturated solar irradiance and values on P_n gas exchange were then recorded. Measurements were made on six different plants on the third leaf from the stem apex.

Growth. The observations of shoot length, root length, leaf dry weight and total biomass were recorded at 60 DAS. Plants were uprooted carefully and roots were made free from soil particles by using fine brush and plant parts were separated. Root and shoot length were recorded with minimum diameter (mm) by using scale. Dry weights were recorded after keeping the plant parts at 80°C for 48 h in hot air oven.

Statistical analysis. The randomized block design was used to prepare the layout for arranging two sets of pots; each set consisting of 198 pots (with four cultivars) was kept under each OTC with two CO_2 levels (360 and 600 ppm of CO_2) and four NaCl treatments (0, 50, 100 and 200 mmol). Six replications were maintained for each treatment and each replication consisted of three plants. The data recorded on various growth and gas exchange parameters was analyzed by using statistical analysis-ANOVA package of analysis of variance (ANOVA) with two factorial randomized block design.

RESULTS

The peanut cultivars showed a positive response to elevated CO_2 and a significant increment in the stem biomass at 0 to 200 mmol of NaCl salinity (Table 1). However, the stem dry biomass decreased progressively with increasing concentration of NaCl from 0 to 200 mmol and increased with elevated CO_2 among the cultivars to altered degrees. The maximum percentage of increment in stem dry weight was recorded in cvs. TPT-1 (53%) and JL-24 (46%) grown without NaCl. Correspondingly the plant root dry biomass was also higher in treated plants under elevated CO_2 (Table 1). The percent increment in root dry weight was found high in cv. TPT-4 (79%) followed by TPT-1 (55%), TMV-2 (44%) and JL-24 (34%) under elevated CO_2 and without NaCl treatment and simultaneously also increased in those plants subjected to NaCl stress. These results indicate that the cultivars TPT-4 and TPT-1 were known to be drought resistant, had greater root biomass than shoot in response to elevated CO_2 that had a great impact to explore soil and procure more water under oxidative conditions. The leaf dry biomass decreased with increasing salinity levels and it was increased in salt treated and untreated plants under elevated CO_2. The maximum percentage of leaf dry biomass was recorded in cv. TPT-1 (44%) and minimum in cv. JL-24 (19%) with elevated CO_2 in salt untreated plants (Table 1). The elevated CO_2 ameliorate the adverse effect of different concentrations of NaCl to various degrees among the cultivars (Table 1). The total dry biomass of the untreated plants under elevated CO_2 varied from 7.5% to 53%, and in NaCl treated plants from 17% to 63%. The maximum percentage (63%) of total biomass was recorded in cv. TPT-1 at 200 mmol under elevated CO_2 when compared with the plants at 200 mmol under ambient CO_2. The salinized plants, which were exposed to increased CO_2 levels showed a greater increase of total dry biomass from 17% to 63% among the four cultivars (Table 1).

Stimulated photosynthesis under elevated CO_2 varied among the four peanut varieties (Figure 1). The extent of stimulation of photosynthesis varied from about 24.7% to 37.5% among the cultivars. The maximum percent of P_n was recorded in cv. TPT-4 (34%) at 200 mmol NaCl and elevated CO_2 than their ambient grown controls. The CO_2 effects were highly significant under different regimes of salt stress. The results on the stomatal conductance and transpiration showed a decrease in control plants (unstressed) and salt-treated plants (stressed) grown at 350 and 600 µmol CO_2/mol. The g_s and E values of ambient CO_2 stressed with 50, 100 and 200 mmol concentration of NaCl showed a gradual reduction, while in enhanced CO_2 stressed plants with three different concentration of NaCl, g_s were decreased by about 16% to 28% and E by 14% to 23%. Stomatal conductance and transpiration was decreased considerably in the salt treated plants of all the four cultivars by the influence of the elevated CO_2 (Figure 2). The reduction percentage was maximum (53%) in cv. TMV-2 at 200 mmol NaCl under elevated CO_2 compared to ambient treatment; at plants stressed with 200 mmol NaCl it eventually caused reduction in photosynthesis. A positive correlation (r^2 = 0.930) was observed between photosynthesis and dry biomass under different salinity levels as influenced by elevated CO_2 concentration in all cultivars.

Table 1. Stem, root, leaf dry weight, total biomass (g/plant) and % increase in biomass at 60 days after sowing of peanut (*Arachis hypogaea* L.) cultivars grown under elevated CO_2 and ambient CO_2 at different levels of NaCl stress

Cultivated variety (cv)	Treatment		Stem dry weight	Root dry weight	Leaf dry weight	Total biomass	% increase
	CO_2	NaCl (mmol)					
TPT-1	A	control	14.87	0.87	2.74	18.48	53.32
	E	control	31.63	1.93	4.03	37.59	
	A	50	13.07	0.58	2.15	15.80	47.24
	E	50	25.36	1.56	3.03	29.95	
	A	100	12.21	0.47	1.76	14.44	41.51
	E	100	20.29	1.80	2.60	24.69	
	A	200	05.73	0.35	1.28	07.36	63.12
	E	200	16.94	1.01	2.01	19.96	
TPT-4	A	control	18.42	0.57	2.21	21.20	21.16
	E	control	22.63	2.77	2.49	26.89	
	A	50	15.91	0.28	2.04	18.23	24.13
	E	50	19.73	1.82	2.48	24.03	
	A	100	13.53	0.27	2.05	15.85	29.20
	E	100	18.53	1.86	2.33	22.39	
	A	200	10.17	0.25	2.00	12.42	33.00
	E	200	15.57	0.84	2.13	18.54	
JL-24	A	control	18.58	0.61	2.15	21.34	44.16
	E	control	34.76	0.93	2.66	38.22	
	A	50	16.56	0.43	2.05	19.04	46.81
	E	50	32.47	0.80	2.43	35.80	
	A	100	13.97	0.40	1.90	16.27	48.3
	E	100	28.96	0.50	2.03	31.49	
	A	200	10.63	0.30	1.55	12.48	56.5
	E	200	26.51	0.43	1.75	28.69	
TMV-2	A	control	17.28	1.25	2.79	21.32	7.50
	E	control	27.79	2.25	3.01	23.05	
	A	50	11.94	0.88	2.26	15.08	32.9
	E	50	18.17	1.57	2.76	22.50	
	A	100	11.79	0.63	1.72	14.14	17.50
	E	100	13.34	0.90	1.90	17.14	
	A	200	10.50	0.36	1.46	12.32	17.31
	E	200	12.46	0.67	1.77	14.90	
C.D. ($P > 0.01$)							
Cultivars (cv)			0.111	0.081	0.091		
Treatments (T)			0.157	0.115	0.128		
cv × T			0.314	0.229	0.256		
Coefficient variation (%)			10.54	22.45	9.91		

Values are means of six replication; three plants in each replication. A – ambient CO_2; E – elevated CO_2; C.D. – critical difference

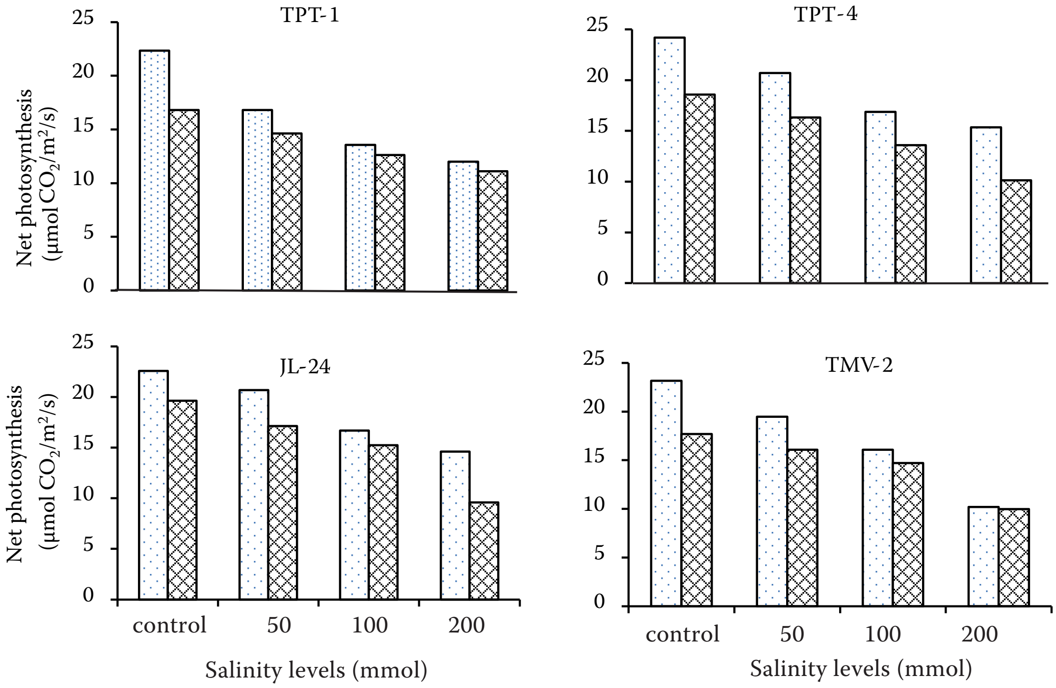

Figure 1. Net photosynthesis (P_n) in peanut cultivars grown under elevated CO_2 (dotted) and ambient CO_2 (crossed) at different concentrations of salinity. Values are means of six replication; three plants in each replication

DISCUSSION

Overall results of the present experiment showed that improved response of photosynthesis and biomass of peanut cultivars under CO_2 enrichment were attributed to tolerance/resistance to salinity stress. As it was known from the literature (Kimball et al. 2002, Ratnakumar et al. 2012) that crop plants generally showed a greater increase in biomass production than non-crop plants (58% vs. 35%) and that of N_2 fixing species responded more readily to CO_2 fertilization than N_2 non-fixing species (50% vs. 42%) (Vanaja et al. 2006b). Peanut is a C3 legume that has a great potential to fix nitrogen through root nodules and CO_2 by Rubisco enzyme activity to reduce oxygenase activity instigated by salinity stress. Similar findings in blackgram, a C3 legume, cum pulse showed better growth response to elevated CO_2 under moisture stress (Vanaja et al. 2006c). However, dry matter production is often used to characterize plant response to salt stress (Flowers et al. 1977, Greenway and Munns 1980), in the current study an average increment in dry biomass as influenced by elevated CO_2 at different concentrations of NaCl improved in terms of root growth in cvs. TPT-4 and TPT-1, those were known as drought tolerant cultivars. Similarly, elevated CO_2 had high impact leaf area at different concentration of NaCl that further increased photosynthesis. Though limited experiments were conducted using several CO_2 levels on long-term basis to estimate the stimulation of biomass production (Kimball et al. 2002) nevertheless with raising CO_2, the rate of biomass production gradually approaches to a point of saturation. That exact saturation of CO_2 is determined by the species/variety/study, as well as experimental conditions (Idso et al. 1989). The selected cultivar known for drought tolerant cv. TPT-4 performed high photosynthesis under elevated CO_2 at 0 to 200 mmol of salinity than other cultivars. Further, to strengthen the above statement this cultivar viz TPT-4 responded better in protecting its photosynthetic apparatus from ROS generated at salinity stress through modulating their antioxidative mechanism (Ratnakumar et al. 2006, 2012) in order to reach their full potential in biomass production.

Enhanced net photosynthesis varied from 25% to 37% among the peanut cultivars under elevated CO_2 at 0 to 200 mmol levels of salinity. Similarly, net photosynthesis was increased up to 40% in *Syzyzium cumini* seedlings, a C3 plant, under elevated CO_2 (Ratnakumar and Swamy 2003); in

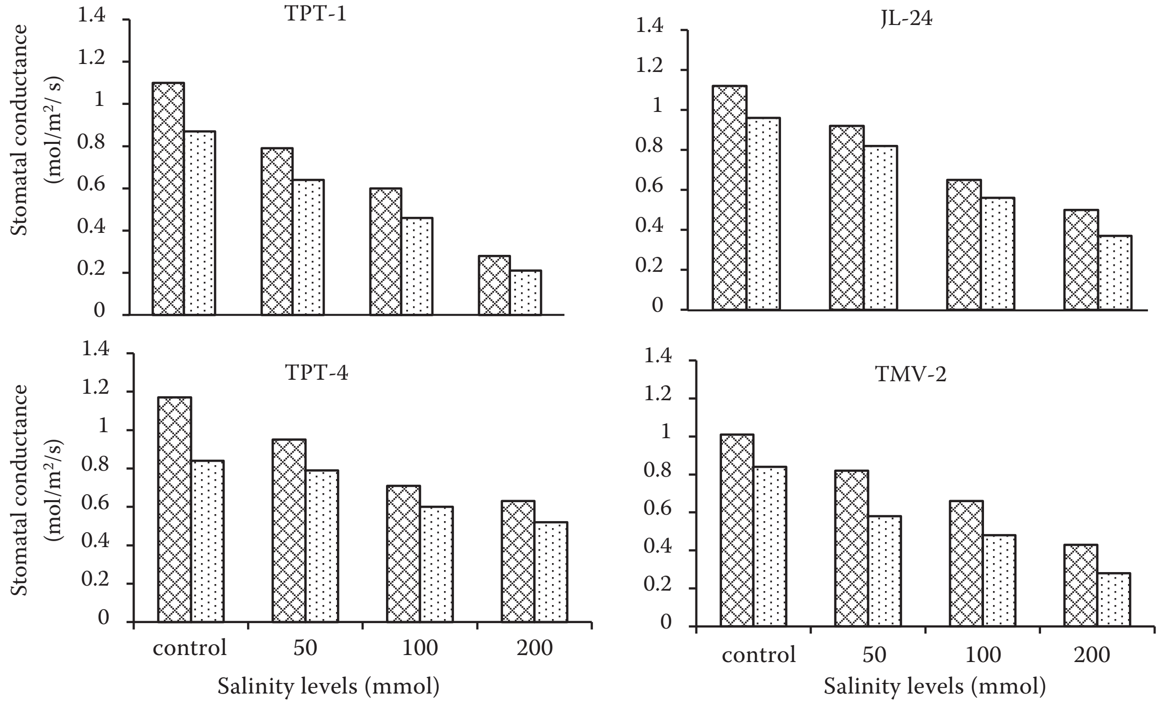

Figure 2. Stomatal conductance (g_s) in peanut cultivars grown at different concentrations of salinity under ambient CO_2 (crossed) and elevated CO_2 (dotted). Values are means of six replication; three plants in each replication

barley (Pérez-López et al. 2012) under the combination of elevated CO_2 at salt stress. The percent of P_n increment varied from cultivar to cultivar and among the treatment. The maximum percent of P_n was recorded in cv. TPT-4 34% under elevated CO_2 at 200 mmol NaCl compared to its ambient grown respective control. Likewise, peanut cv. Kadiri-3 grown under high levels of CO_2 in combination with water stress showed an increased rate of photosynthesis up to 40% (Clifford et al. 1993, Stronoch et al. 1994). These results were strongly indicated that increased conversion efficiency of carbon in salt imposed peanut plants under elevated CO_2.

Our understanding of g_s and E as influenced by interactive effect of elevated CO_2 and salt stress had great impact on reduction in g_s and E, which further enhance the effective use of water (EUW). The cv. TMV-2 showed decrease in g_s under elevated CO_2 and 200 mmol salt stress, which ultimately resulted in reduction in photosynthesis and biomass. In the same way g_s decreased under increasing CO_2 was documented for maize, soybean, barley and sweet gum (Mbikayi et al. 1993, Pérez-López et al. 2012); in few cases no response or very large responses were reported (Liang et al. 1995) and in most of the studies it was observed that elevated CO_2 decreases transpiration rate (Gondriaan and van Laar 1978, Rogers et al. 1983). These comprehensive results specify that enhanced CO_2 helps to increase growth and photosynthesis in peanut cultivars by inducing the tolerance to NaCl stress.

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