

Elevated CO₂ ameliorate the negative effects of high temperature on groundnut (*Arachis hypogaea*) - Studies under free-air temperature elevation

M. VANAJA¹, P. SATHISH¹, N. JYOTHI LAKSHMI¹, G. VIJAY KUMAR², P. VAGHEERA¹, CH. MOHAN¹, S.K. YADAV¹, B. SARKAR¹, M. MAHESWARI¹, K. SAMMI REDDY¹

¹Central Research Institute for Dryland Agriculture, Santoshnagar, Hyderabad-500 059, India

²Department of Genetics, Osmania University, Hyderabad-500 007

*Corresponding author: vanajamaddi@gmail.com

ABSTRACT

Four groundnut (*Arachis hypogaea* L.) genotypes- Narayani, Dharani, K-6 and K-9 were assessed for growth and yield responses at elevated temperature of $3.0 \pm 0.5^\circ\text{C}$ above ambient canopy temperature (eT) and its interaction with elevated CO₂ of $550 \pm 50\text{ppm}$ (eT+eCO₂) under Free Air Temperature Elevation (FATE) facility. The study revealed that eT significantly decreased photosynthetic rate (A_{net}) of all groundnut genotypes whereas eT+eCO₂ condition ameliorated the ill effects of eT. The impact of eT on A_{net} was higher than transpiration rate (Tr) and this reflected in decreased WUE with all genotypes. WUE improved significantly at eT+eCO₂ with increased A_{net} and decreased Tr. Increase in canopy temperature (eT) resulted decreased relative water content (RWC), cell membrane stability and increased osmotic potential, Malondialdehyde (MDA) content and accumulation of proline. Elevated CO₂ along with eT (eT+eCO₂) facilitated these parameters to recover to that of ambient controls, revealing the ameliorative effect of eCO₂. Similar responses were recorded for biomass and yield parameters. Among the selected groundnut genotypes, superior performance for seed yield at high temperature of $>40^\circ\text{C}$ by K-9 was due to ability to maintain better reproductive capacity and Dharani was responsive to elevated CO₂ even at high temperature, indicating the genotypic variability.

Keywords: CO₂ elevation, temperature stress, photosynthetic rate, transpiration rate, water use efficiency, biomass, seed yield

Global climate change is a serious challenge to crop production across the world. Temperature is one of the most important environmental factors controlling the agro-ecological distribution of crop species and their productivity. The increasing risk of global warming due to climate change is already having a substantial impact on agricultural production as heat waves are causing significant yield loss with great risks for future global food security. The mean annual global surface temperature is projected to increase by 1.8°C - 5.8°C by the end of this century, depending on the greenhouse emission scenario (IPCC, 2013).

Fluctuations in temperature take place naturally during plant growth as plants experience variation in diurnal temperature as well as at different phenophases. Change in temperature to below or above the optimum range of the specific crop species often result in loss of yield due to rate-limited photosynthesis or reduced vegetative and reproductive growth (Siebers *et al.*, 2015). Elevated temperatures can disrupt metabolic processes involved in plant growth and development. Decrease in soybean and corn yield by 17% in

the United States was reported with rise in every 1°C growing season temperature (Lobell and Asner, 2003).

The atmospheric carbon dioxide concentration has increased from 300 to 402 ppm (NOAA 2016) and is likely continue to double from the current level by the year 2100 (IPCC 2013). The responses to elevated CO₂ range from least to four fold increases in biomass and yield as compared with current CO₂ concentration (Kimball, 2016; Yadav *et al.*, 2016). Various studies revealed that plants have better ability to tolerate abiotic stresses like high temperature, drought, salinity, and pollutants under CO₂-enriched conditions (Vu and Alen, 2009).

Groundnut (*Arachis hypogaea* L.) is an important edible oil seed crop grown mainly in arid and semi-arid areas of the world. Globally India ranks first in area and second in production (FAOSTAT 2014) with 31% of the cultivated area (24.6 mha) and 22% of the total production (41.3mt). Temperatures during flowering and pod filling stages are critical for yield realization in groundnut and temperature effect on crop yield varies with genotypes. In groundnut crop

threshold high temperature is 34°C at the stage of pollen production (Prasad *et al.*, 2000) and the simulated studies of Mote *et al.* (2018) revealed that the pod yield of groundnut will be compensated by elevated CO₂ of 500ppm if maximum temperatures increase by 2°C. The present study was formulated to quantify the impact of elevated canopy temperature (+3°C) and its interaction with elevated CO₂ (550ppm) on performance of physiological, biochemical, biomass and yield parameters of groundnut crop as well as variability within genotypes.

MATERIALS AND METHODS

Plant material and experimental design

A field experiment was conducted with four released and popular groundnut genotypes- Narayani, Dharani, Kadiri-6 (K-6) and Kadiri-9 (K-9). The genotypes were planted in FATE facility during summer 2016 at ICAR- Central Research Institute for Dryland Agriculture (CRIDA), located between 17.20°N latitude and 78.30°E longitude, Hyderabad, Telangana, India. The spacing was 0.10 m within row and 0.30 m between rows. The recommended dose of fertilizers were applied @ 20 kg N, and 40 kg P₂O₅ and 50 kg K₂O ha⁻¹ as urea, single super phosphate and muriate of potash respectively. Gypsum @ 500 kg ha⁻¹ was applied by placement at flowering stage. The crop was irrigated at regular intervals and maintained pest and disease free by adopting plant protection measures.

Free Air Temperature Elevation (FATE) facility consisting of nine rings with 8m diameter. Among the nine rings, six rings were fitted with 24 arrays of 2000 W capacity ceramic infrared heaters (Elstein, model FSR-1000W) above the canopy to maintain elevated crop canopy temperature (eT) of ambient +3°C ± 0.5°C. The heating system delivers warming only with no photo-morphogenic effects and no significant radiation emitted at wavelengths shorter than 850 nm. Three warming rings were also provided with CO₂ release system at 0.3m height from the base of the ring to study the interactive effects of elevated temperature and CO₂ (eT+eCO₂). The polyurethane (PU) tubing with perforations releases the CO₂ within ring to maintain the elevated concentration of 550ppm. The CO₂ release was controlled by solenoid valves which in turn regulated by the SCADA based control system linked with CO₂ analyser, wind direction and wind speed. The CO₂ concentration at the centre of the ring was continuously monitored by IRGA based CO₂ analyser (Priva, model-200821), the duration of CO₂ release was based on the set CO₂ concentration for the specified area as well as

wind direction and wind speed.

The canopy temperatures are monitored with infrared sensor (Ray teck Fluke, model-RAYCMLTJ3) fitted in each ring. The duration and intensity of heating is regulated by canopy temperatures of control plots and uses a proportional-integral-derivative (PID) feedback system to maintain the heating treatment (Kimball *et al.*, 2008). Signals from each sensor are being recorded and monitored and controlled by Program Logic Control (PLC) and Supervisory Control and Data acquisition (SCADA) system.

Temperatures during crop growth

The maximum air temperatures during vegetative stage of the crop ranged from 31.6 to 37.6°C with an average of 33.8°C while minimum temperature ranged from 15.2 to 20.6°C with an average of 18.5°C. During the vegetative to pod maturity, the crop experienced maximum air temperature from 32.4 to 42.2°C with an average of 37.9°C and minimum temperature from 20.8 to 27.4°C with an average of 22.9°C.

Physiological and biochemical parameters

The physiological and biochemical observations were recorded at flowering stage of groundnut plants from ambient (aT), elevated temperature (eT) and elevated temperature and CO₂ (eT+eCO₂) conditions. The photosynthetic rate (A_{net}), stomatal conductance (gs), transpiration rate (Tr), relative water content (RWC), osmotic potential (ψ_s), total soluble sugars, proline, Malondialdehyde (MDA) and cell membrane stability (CMS) of all the genotypes were recorded at aT, eT and eT+eCO₂ conditions.

Net photosynthetic rate (A_{net}), stomatal conductance (gs) and transpiration rate (Tr) were measured with a portable photosynthesis system (LI-6400, LI-COR, Nebraska, USA) at flowering stage on fully expanded young leaves of three plants of each genotype from all treatments. Water use efficiency (WUE) was calculated as the ratio of A_{net} and Tr using the formula $WUE = A_{net}/Tr$.

Fully expanded third leaves from the top of the main stem were sampled from each treatment to measure the relative water content (RWC). RWC was calculated based on the formula suggested by Gonzalez and Gonzalez-Vilar (2001).

$$RWC (\%) = (FW - DW) / (TW - DW) \times 100$$

Where, FW is the sample fresh weight, TW is turgid weight and DW is dry weight.

The unused leaflets of the same trifoliolate leaves used for RWC measurements were excised and dipped in liquid nitrogen. The cell sap was squeezed out to analyse osmotic potential (Scholander *et al.*, 1966) using a vapour pressure osmometer (Wescor- 5500 Wescor Inc., USA) and expressed in MPa. Cell membrane stability was estimated with expressions of electrolyte leakage by method of Blum and Ebercon (1981) with slight modification. The cell membrane stability was calculated by the following formula.

$$\text{CMS (\%)} = \{[1-(T_1/T_2)] / [1-(C_1/C_2)] \times 100\}$$

Where C and T refer to electrical conductivity of control and heat treated samples and the subscripts 1 and 2 refer to electrical conductivity readings before and after boiling, respectively.

The lipid peroxidation was estimated with expression of malondialdehyde (MDA) according to De Vos *et al.* (1991). The final concentration of MDA was calculated by using an extinction coefficient ($\epsilon = 155 \text{ mM}^{-1} \text{ cm}^{-1}$) and expressed as $\mu\text{mol g}^{-1} \text{ FW}$. Proline was extracted from 0.5g of fresh leaf material in 3% (w/v) aqueous sulphosalicylic acid and estimated with ninhydrin reagent (Bates *et al.*, 1973) and expressed as $\mu\text{g g}^{-1} \text{ FW}$. For estimation of total soluble sugars, 1.0 g leaf material was homogenized in 80% ethanol and the clarified supernatant was used for estimation. Total soluble sugars were estimated by the method of Dubois *et al.* (1956) and expressed in $\text{mg g}^{-1} \text{ FW}$.

Biomass and yield parameters

At harvest, three plants of each genotype were up rooted carefully from three replicated treatments of aT, eT and eT+eCO₂. The biomass of leaves and stems was measured after drying them in hot air oven at 60°C till constant weights were attained. The data on yield parameters such as pod number, pod weight (g), seed number, seed weight (g) per plant and test weight (of 100 seed weight) were recorded. From the recorded data sets total biomass, vegetative biomass and HI was calculated.

Statistical analysis

The analysis of variance (ANOVA) was carried out to assess the significance of treatments, genotypes and their interaction for the traits.

RESULTS AND DISCUSSION

The response of all the physiological, biochemical, biomass and yield parameters of selected four groundnut genotypes were significantly altered at both eT, eT+eCO₂

conditions. The ANOVA of physiological and biochemical parameters was presented in Table 1, biomass and yield parameters are presented in Table 2 and the reduction (%) of biomass and yield parameters at eT and eT+eCO₂ over aT condition are presented in Fig.1.

Phenology of flowering

With exposing the plants to eT, phenology of 50% flowering was early in groundnut genotypes and it was 1.0 day with K-9, 1.7 days with Narayani and K-6 while 2.3 days with Dharani. No impact of eT+eCO₂ condition was observed on flowering behaviour of selected groundnut genotypes. In mungbean, shortened phenology of flowering and podding duration was reported under eT condition (Sharma *et al.*, 2016).

Physiological and biochemical parameters

The variation in photosynthetic rate, stomatal conductance, transpiration rate and WUE were highly significant ($P < 0.01$) for genotypes, treatments, and interaction of genotypes and treatments except A_{net} was significant ($P < 0.05$) for interaction of genotypes and treatments (Table 1). The eT and eT+eCO₂ conditions impacted all physiological parameters of selected four groundnut genotypes. Among the selected four groundnut genotypes, K-9 recorded significantly higher A_{net} followed by K-6 under all conditions. The increased temperature (eT) significantly reduced the A_{net} and it ranged from 31% (Narayani) to 35% (K-6). However, significant recovery of A_{net} was recorded with eT+eCO₂ in all the four genotypes as compared with eT condition and it was comparable with values of aT. This response clearly revealing that the impact of eT on photosynthetic rate was ameliorated by elevated CO₂. In groundnut, Prasad *et al.* (2003) reported that elevated CO₂ enhanced leaf photosynthesis by 27% and seed yield by 30% across a range of daytime growth temperatures from 32 to 44°C. Dwivedi *et al.* (2015) also observed that photosynthetic rate increased with elevated CO₂ and reduced with elevated temperature across the rice genotypes and the effect of eT on photosynthetic rate was ameliorated by elevated CO₂.

Similar to A_{net} response, higher stomatal conductance was recorded with genotype K-9 followed by K-6 under all conditions. Under the eT and eT+eCO₂ conditions, reduced values of g_s were recorded with all the genotypes as compared with aT. Stomatal conductance significantly reduced at eT and it ranged from 48% (Narayani) to 63% (K-9). While under eT+eCO₂ condition the response of g_s varied with genotype. The transpiration rate (Tr) of all the genotypes was reduced at

Table 1: Mean performance and ANOVA of physiological and biochemical parameters of groundnut genotypes at aT, eT and eT+eCO₂ conditions

Genotypes	Treatments	A _{net}	gs	Tr	WUE	RWC	OP	MDA	CMS	Proline	TSS
K-9	aT	42.54	0.844	13.98	3.05	88.34	-2.00	6.14	100.00	43.67	7.93
	eT	27.74	0.310	9.95	2.79	81.1	-1.64	9.70	72.86	46.25	9.70
	eT+eCO ₂	42.76	0.374	8.47	5.11	83.04	-2.12	7.64	94.48	73.83	9.00
K-6	aT	33.62	0.505	10.49	3.21	85.68	-1.63	6.35	100.00	42.17	9.75
	eT	21.86	0.240	9.59	2.29	76.4	-1.72	7.43	70.60	134.33	7.12
	eT+eCO ₂	31.20	0.227	4.44	7.11	79.34	-1.72	6.19	90.01	65.25	10.82
Narayani	aT	27.40	0.361	8.76	3.18	85.17	-1.78	5.78	100.00	51.33	6.77
	eT	18.80	0.188	8.28	2.29	73.9	-1.81	7.85	69.22	98.51	7.73
	eT+eCO ₂	26.58	0.265	5.89	4.59	78.81	-2.18	6.55	93.28	71.50	11.27
Dharani	aT	27.16	0.385	8.83	3.07	87.57	-1.81	5.11	100.00	42.75	9.24
	eT	17.78	0.191	7.01	2.59	79.2	-1.56	8.57	72.28	163.08	8.21
	eT+eCO ₂	27.02	0.180	5.30	5.15	81.83	-2.06	6.76	91.50	138.70	11.28
ANOVA	Genotypes df (3)	367.876**	0.124**	24.683**	1.140**	44.557**	0.107**	2.747	8.032	5686.204**	1.633
	Treatments df (2)	463.326**	0.309**	61.177**	29.981**	252.890**	0.344**	19.830**	2660.794**	13261.459**	21.111**
	G x T df (6)	9.670*	0.027**	3.858**	1.363**	2.501	0.059**	1.126	5.866	2765.968**	5.455*
	Error df (22)	3.094	0.002	0.61	0.128	2.324	0.007	1.106	3.14	3.785	1.586

*significant at 0.05%; **significant at 0.01%; df = degrees of freedom

aT-ambient canopy temperature; eT-elevated canopy temperature; eT+eCO₂- combination of elevated temperature and elevated CO₂

A_{net}- photosynthetic rate [$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$]; gs- stomatal conductance [$\text{mol m}^{-2} \text{ s}^{-1}$]; Tr- transpiration rate [$\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$]; WUE- water use efficiency [$\mu\text{moles CO}_2 \mu\text{mol H}_2\text{O}^{-1}$]; OP- osmotic potential [MPa]; RWC- relative water content [%]; MDA- malondialdehyde content [$\mu\text{mol/g FW}$]; CMS- cell membrane stability [%]; Proline [$\mu\text{g/g FW}$]; TSS- total soluble sugars [$\text{mg g}^{-1} \text{FW}$].

Table 2: Mean performance and ANOVA of biomass and yield parameters of groundnut genotypes at aT, eT and eT+eCO₂ conditions

Genotypes	Treatments	LDW	SDW	RDW	TBM	VBM	Pod number	Pod weight	Seed number	Seed weight	100 seed weight	HI
K-9	aT	28.37	25.70	1.35	80.62	55.41	42.67	25.20	74.33	17.43	23.93	21.57
	eT	20.50	23.17	1.00	69.87	44.67	51.33	25.20	61.67	18.41	30.70	26.47
	eT+eCO ₂	28.53	26.30	1.13	71.43	55.97	36.67	15.46	38.67	11.14	29.02	15.56
K-6	aT	32.80	26.87	1.27	89.55	60.94	51.67	28.61	68.00	17.62	25.71	19.69
	eT	22.57	19.77	1.12	54.79	43.45	28.33	11.34	26.33	6.12	26.24	11.19
	eT+eCO ₂	38.33	27.73	1.27	85.02	67.34	39.67	17.68	42.00	10.94	26.09	12.82
Narayani	aT	25.20	22.23	1.18	68.19	48.61	40.00	19.58	45.33	13.18	28.53	19.40
	eT	15.50	22.70	0.96	48.88	39.16	22.33	9.72	27.00	5.75	21.62	11.82
	eT+eCO ₂	36.23	26.23	1.15	78.79	63.61	31.33	15.17	42.67	9.62	22.67	12.28
Dharani	aT	31.53	29.67	1.07	85.97	62.27	42.33	23.70	59.67	17.26	29.77	20.08
	eT	25.10	27.97	0.98	73.67	54.04	38.33	19.63	54.00	14.00	21.29	19.03
	eT+eCO ₂	34.80	22.97	1.23	80.04	59.00	42.67	21.04	54.33	15.29	28.16	19.13
ANOVA	Genotypes df (3)	79.95**	15.4	0.033	350.0**	134.8**	259.4**	95.2**	778.4**	82.7**	19.9*	103.5**
	Treatments df (2)	564.2**	24.87	0.146**	1320.7**	819.3**	264.2**	219.6**	1383.1**	99.96**	13.4	83.4**
	G x T df (6)	28.99**	29.90**	0.019	217.05**	87.1**	186.3**	63.5**	417.1**	32.1**	42.2**	39.82**
	Error df (22)	6.169	7.930	0.024	17.15	14.5	9.02	5.58	20.962	3.023	5.47	5.37

*significant at 0.05%; **significant at 0.01%; df = degrees of freedom

aT- ambient canopy temperature; eT- elevated canopy temperature; eT+eCO₂- combination of elevated temperature and elevated CO₂

LDW- leaf dry weight [g/pl]; SDW- shoot dry weight [g/pl]; RDW- root dry weight [g/pl]; VBM- vegetative biomass [g/pl]; TBM- total biomass [g/pl]; Pod weight [g/pl]; Seed weight [g/pl]; 100 seed weight [g]; HI- harvest index [%]

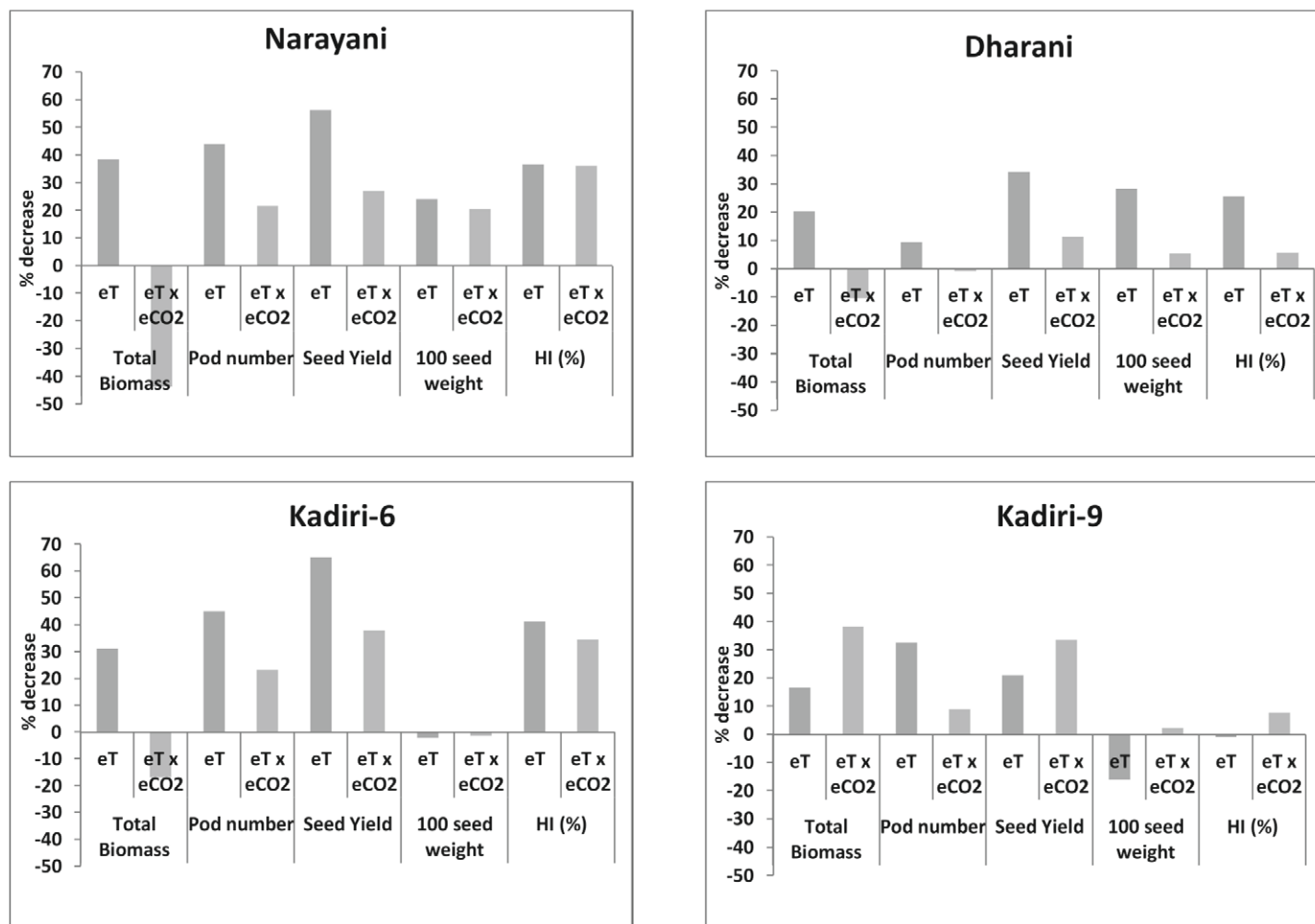


Fig. 1: Reduction (%) of biomass and yield parameters of four groundnut genotypes at eT and eT+eCO₂ over aT condition eT-elevated canopy temperature; eT+eCO₂- combination of elevated temperature and elevated CO₂; HI-harvest index

eT and it ranged from 5% (Narayani) to 28% (K-9) as compared with aT. The eT+eCO₂ further reduced the Tr in all the genotypes, revealing that elevated CO₂ impacting more of Tr than gs. The response of WUE calculated as the ratio of A_{net} and Tr clearly indicating that eT impacted more of A_{net} than Tr, hence all the genotypes recorded lowest values for WUE. It is interesting to observe that eT+eCO₂ condition recorded highest values for WUE of all the genotypes as elevated CO₂ enhanced the A_{net} and reduced the Tr. The studies of Vu (2005) with peanut revealed that the increase in photosynthetic rate under elevated CO₂ with near ambient growth temperature (+1.5°C) was higher than under high growth temperature (+6°C) and the elevated CO₂ grown plants recorded increased WUE of 56%, 41% at near a high temperature conditions respectively.

Relative water content (RWC) of groundnut genotypes was measured to assess impact of treatments on the water status of the plants. The RWC of all genotypes was recorded highest at aT condition, while it reduced in plants exposed to

eT condition. Among the genotypes, K-9 was able to maintain highest RWC in all the treatments, while Narayani was the lowest. The extent of reduction of RWC with eT condition varied significantly with genotypes as lowest was recorded with K-9 (8%) and highest with Narayani (13.3%). The eT+eCO₂ condition improved the plant water status in all the genotypes though it was lower than that of aT revealing that eCO₂ ameliorated the impact of eT to some extent. Dwivedi *et al.* (2015) reported that the impact of elevated temperature on RWC was ameliorated by elevated CO₂ in all the rice genotypes.

Accumulation of compatible solutes is known to impart high temperature stress tolerance through active reduction in osmotic potential. The eT condition induced higher accumulation of proline in all groundnut genotypes except K-9 and higher accumulation was recorded in Dharani (281%) followed by K-6 (218%) and Narayani (92%) as compared with aT, while change in proline content of K-9 was not significant with eT. Total soluble sugars (TSS) also recorded

higher accumulation under eT condition with K-9 (22%) and Narayani (15%) but decreased with Dharani (11%) and K-6 (27%). The presence of eCO₂ lowered the content of proline, osmotic potential and increased TSS in all four groundnut genotypes as compared with eT. It is evident from this study that in all the groundnut genotypes proline accumulation was triggered with eT, while content of total soluble sugars was higher with elevated CO₂. Among the genotypes, response of K-9 was significantly different at both eT and eCO₂ conditions for these parameters. Vu (2005) reported high temperature reduced the levels of total soluble sugars by 21% in peanut leaf at ambient CO₂ while the reduction was very less under elevated CO₂ as increased sucrose was recorded in elevated CO₂ grown plants.

High temperature stress leads to the disruption of cellular membranes, making them more permeable to ions by increased solubilisation and peroxidation. Lipid peroxidation is used as an index of oxidative damages caused by various abiotic stresses in plants. Membrane lipid peroxidation and electrolyte leakage can be determined by measuring malondialdehyde (MDA) content and cell membrane stability (CMS). The plants grown with eT+eCO₂ recorded lower MDA content thereby increased CMS as compared with only eT condition. The eT condition reduced the CMS to 69 to 73% of all the four groundnut genotypes while it improved to above 90% with eT+eCO₂. The magnitude of response of individual genotype clearly indicates variability in their tolerance to high temperature and their responsiveness to eCO₂. Dharani and K-9 has the ability to maintain relatively better membrane stability with lower MDA content under eCO₂ with eT. Mishra and Agrawal (2014) reported that lower MDA content at elevated CO₂ in different mungbean cultivars as compared with ambient CO₂ condition. However Koti *et al.* (2007) reported that elevated CO₂ moderately compensated the injurious effects of high temperature and enhanced UV-B radiation levels on vegetative growth and physiology in soybean.

Dry matter accumulation and partitioning

The dry matter accumulation and its partitioning in four groundnut genotypes was quantified under aT, eT and eT+eCO₂ conditions. The variability in genotypes, treatments, interaction of genotypes and treatments were highly significant ($P < 0.01$) for all the biomass parameters. At eT and eT+eCO₂, the magnitude of response differed with selected groundnut genotypes for leaf biomass, stem biomass root biomass, total biomass, vegetative biomass and its partitioning. At harvest, reduced biomass of leaf and root was

recorded with eT in Narayani, Dharani and K-6 while the impact was not observed with K-9. The presence of eCO₂ along with eT improved these components than at aT. Significant reduction in total biomass was recorded at eT while eT+eCO₂ condition improved it with all selected groundnut genotypes and similar trend of response was also observed with vegetative biomass. The increase in biomass of this C3 crop can be explained by its ability to maintain elevated photosynthetic rates at eCO₂ even at elevated temperature of >40°C. The increased temperature reduced the reproductive biomass of maize while it improved the vegetative biomass (Vanaja *et al.*, 2017).

Yield and yield attributes

Among the four groundnut genotypes, the pod number, pod weight, seed number and seed weight at aT was lowest with Narayani and highest with K-6 except for seed number. It is interesting to observe that among the genotypes, the reduction of all these yield components was highest with K-6 under eT and eT+eCO₂ conditions followed by Narayani. The amelioration of these components due to eCO₂ was also high with K-6 and Narayani showing that these genotypes are sensitive to high temperature and responsive to eCO₂. The eT condition improved the pod number and seed weight in K-9 while eT+eCO₂ reduced all these yield components revealing that this genotype has better tolerance to higher temperature of >40°C, however it is not responsive to eCO₂. The genotype K-6 maintained its test weight at all conditions irrespective of its seed yield response to eT and eT+eCO₂, while K-9 recorded increased test weight under these condition with reduced yield components. The variability in seed filling ability of genotypes is clearly evident under different conditions. Similar observations at high temperature of >40°C at reproductive stage on mungbean crop was reported as highly detrimental for production of flowers and pod set, which resulted in fewer number of pods and seeds leading to decreased seed yield (Bindumadhava *et al.*, 2016). In grain legume crops such as soybean, dry bean, peanut and cowpea, improved yield with elevated CO₂ due to increased photosynthesis and growth was observed (Prasad *et al.*, 2005).

CONCLUSION

High temperature and its interaction with elevated CO₂ significantly affected physiological, biochemical, biomass and yield parameters of groundnut genotypes. There was significant variability between the selected groundnut genotypes for their performance including seed yield under eT and eT + eCO₂ conditions. The superior performance for seed yield of groundnut genotype K-9 at high temperature of

>40°C, while Dharani responsiveness to elevated CO₂ even at high temperature were due to their ability to maintain better pod and seed number as well as improved test weight indicating their role under these conditions. The eCO₂ significantly improved the total biomass and pod number and pod weight of the selected groundnut genotypes even at high temperature. Among the four groundnut genotypes, the better performance of K-9 under high temperature was attributed to its capacity to accumulate significantly higher concentrations of osmotic solutes especially proline and total soluble sugars, which led to better RWC and increased cell membrane stability. The significant observation of this study was that the presence of eCO₂ ameliorated the negative impacts of elevated temperature of >40°C on this C3 leguminous oil seed crop. The identified traits will form a base for the future breeding programs to develop the climate ready genotypes.

ACKNOWLEDGEMENTS

The present work was carried out under ICAR Network project on 'National Innovations in Climate Resilient Agriculture (NICRA)' funded by Indian Council of Agriculture Research (ICAR), Government of India.

REFERENCES

- Bates, L.S., Waldren, R.P. and Teare, I.D. (1973). Rapid determination of free proline for water stress studies. *Plant Soil*, 39: 205–207.
- Bindumadhava, H., Nair, R.M. and Nayyar, H. (2016). Salinity and high temperature tolerance in mungbean (*Vigna radiata* L. Wilczek) from a physiological perspective. *Front. Plant Sci.*, 7: 1–20.
- Blum, A. and Ebercon, A. (1981). Cell membrane stability as a measure of drought and heat tolerance in wheat. *Crop Sci.*, 21: 43–47.
- De Vos, C.H., Schat, M., De Waal, Voijis, R. and Ernst, W. (1991). Increased resistance to copper-induced damage of the root cell plasmalemma in copper tolerant *Silene cucubalus*. *Plant Physiol.*, 82: 523–528.
- Dubois, M., Gilles, K.A., Hamilton, J.K., Rebers, P.A. and Smith, F. (1956). Colorimetric method for the determination of sugars and related substances. *Anal. Chem.*, 28: 350–356.
- Dwivedi, S.K., Kumar, S., Prakash, V., Mondal, S. and Mishra, J.S. (2015). Influence of rising atmospheric CO₂ concentrations and temperature on morpho-physiological traits and yield of rice genotypes in sub humid climate of Eastern India. *AJPS*, 6: 2339–2349.
- Gonzalez, L. and Gonzalez-Vilar, M. (2001). Determination of relative water content. In: Handbook of Plant Ecophysiology Techniques. (Ed. M.J. Reigosa Roger). pp 207–212, Springer, Netherlands. ISBN, 978–0-7923-6,
- IPCC (2013). Summary for policy makers, in Climate Change 2013. In: The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. (Eds. T.F. Stocker, D. Qin, G.K. Plattner, M.M.B. Tignor, S.K. Allen and J. Boschung). pp 1–27, Cambridge University Press.
- Kimball, B.A. (2016). Crop responses of elevated CO₂ and interactions with H₂O, N, and temperature. *Curr. Opin. Plant Biol.*, 31: 36–43.
- Kimball, B.A., Conley, M.M., Wang, S., Lin, X., Luo, C., Morgan, J. and Smith, D. (2008). Infrared heater arrays for warming ecosystem field plots. *Glob. Change Biol.*, 14:309–320.
- Koti, S., Reddy, K.R., Kakani, V.G., Zhao, D. and Gao, W. (2007). Effects of carbon dioxide, temperature and ultraviolet-B radiation and their interactions on soybean (*Glycine max* L.) growth and development. *Environ. Exp. Bot.*, 60: 1–10.
- Lobell, D.B. and Asner, G.P. (2003). Climate and management contributions to recent trends in U.S. agricultural yields. *Science*, 299: 1032.
- Mishra, A.K. and Agrawal, S.B. (2014). Tropical mung bean (*Vigna radiata* L.) cultivars: ROS generation, antioxidant status, physiology, growth, yield and seed quality. *J. Agro. Crop. Sci.*, doi:10.1111/jac.12057.
- Mote, B. M., Pandey V. and Patil, D. D. (2018). Effects of change in temperature and CO₂ concentration on summer groundnut in middle Gujarat- A simulation study. *J. Agrometeorol.*, 20 (3): 219–222.
- NOAA (2016). Trends in atmospheric carbon dioxide. Retrieved from <https://www.esrl.noaa.gov/gmd/ccgg/trends/>.
- Prasad, P.V.V., Allen, Jr. L.H. and Boote, K.J. (2005). Crop responses to elevated carbon dioxide and interaction with temperature: grain legumes. In: Ecological responses and adaptations of crops to rising atmospheric carbon dioxide. (Ed. Zoltán Tuba). pp 113–

- 155, Food Products Press, An imprint of The Haworth Press, Inc.
- Prasad, P.V.V., Boote, K.J., Allen, Jr.L.H. and Thomas, J.M.G. (2003). Super-optimal temperatures are detrimental to peanut (*Arachis hypogaea* L.) reproductive processes and yield at both ambient and elevated carbon dioxide. *Glob. Change Biol.*, 9: 1775-1787.
- Prasad, P.V.V., Craufurd, P.Q., Summerfield, R.J. and Wheeler, T.R. (2000). Effect of short episodes of heat stress on flower production and fruit set of groundnut (*Arachis hypogaea* L.). *J. Exp. Bot.*, 51: 777-784.
- Scholander, P.F., Hammel, H.T., Bradstreet, E.D. and Himminosen, E.A. (1966). Sap pressure on vascular plants. *Science*, 148: 339-346.
- Sharma, L., Priya, M., Bindumadhava, H., Nair, R.M. and Nayyar, H. (2016). Influence of high temperature stress on growth, phenology and yield performance of mung bean (*Vigna radiata* (L.) Wilczek) under managed growth conditions. *Sci. Hort.*, 213: 379-391
- Siebers, M.H., Yendrek, C.R., Drag, D., Locke, A.M., Rios Acosta, L. and Leakey, A.D.B. (2015). Heat waves imposed during early pod development in soybean (*Glycine max*) cause significant yield loss despite a rapid recovery from oxidative stress. *Glob. Change Biol.*, 21: 3114-3125.
- Vanaja M., Sathish P., Vijay Kumar G., Abdul Razzaq, Vagheera P., Jyothi Lakshmi N., Yadav S.K., Sarkar B. and Maheswari M. (2017). Elevated temperature and moisture deficit stress impact on phenology, physiology and yield responses of hybrid maize. *J. Agrometeorol.*, 19 (4): 295-300.
- Vu, J.C.V. and Allen, L.H. (2009). Growth at elevated CO₂ delays the adverse effects of drought stress on leaf photosynthesis of the C₄ sugarcane. *J. Plant Physiol.*, 166: 107-116.
- Vu, J.C.V. (2005). Acclimation of peanut (*Arachis hypogaea* L.) leaf photosynthesis to elevated growth CO₂ and temperature. *Environ. Exp. Bot.*, 53: 85-95.
- Yadav, M. K, Singh, R. S. Singh, K. K, Mall, R. K, Patel, C, Yadav, S. K. and Singh, M. K. (2016). Assessment of climate change impact on pulse, oilseed and vegetable crops at Varanasi, India. *J. Agrometeorol.*, 18 (1): 31-32.