



Impact of elevated CO₂ and Temperature on Nodulation and Crop Weed Competition in Groundnut (*Arachis hypogaea* L.)

T. Ram Prakash¹, B. Padmaja¹, M. Vanaja², T. Bala Srikanth Reddy¹,
Shobha Sondhia³, M. Prabhakar², J.S. Mishra³

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ABSTRACT

Background: Rising atmospheric CO₂ and temperature due to climate change pose significant threats to agricultural productivity, particularly in semi-arid tropics. These changes can alter weed distribution, population dynamics and crop-weed interactions. Assessing groundnut's adaptability to changing climates, weed competition and herbicide efficacy is crucial for developing resilient cultivars and effective herbicide management systems to mitigate yield and quality losses, thereby enhancing global food security.

Methods: A two-year (2022-23 and 2023-24) experiment was conducted in a Carbon Dioxide and Temperature Gradient Chamber (CTGC) at the Central Research Institute for Dryland Agriculture, Hyderabad. The study evaluated groundnut under four climate variables: ambient CO₂ + ambient temperature (aCO₂ + aT) (396-405ppm), elevated CO₂ (eCO₂, 550 ± 50 ppm), elevated temperature (eT, +2°C) and combined eCO₂ + eT (550 ± 50 ppm and +2°C), three crop-weed combinations (groundnut + C₃ weeds, groundnut + C₄ weeds, groundnut + C₃ + C₄ weeds) and four herbicide rates (0X, 1X, 1.5X, 2X) using a completely randomized design. Growth parameters, soil rhizobium population and nodulation were assessed at 60 days after sowing (DAS).

Result: Pooled data revealed that eCO₂ significantly enhanced groundnut growth and nodulation, with increases in plant height (25%), leaf area (26%), chlorophyll content (12%), *Rhizobium* population (22%), nodulation (58%) and dry matter production (22%) compared to ambient conditions. Combination of elevated CO₂ and temperature also showed positive effects, though less pronounced, while eT alone reduced all parameters. Herbicide application at various rates showed suppressive effect on *Rhizobium* population, nodulation and chlorophyll content compared to no application. However, plant height, leaf area and dry matter production were significantly higher at 1.5 X rate over no application under eCO₂ conditions in contrast to 1.0X rate under aCO₂ + aT, eCO₂ + eT and eT conditions. Groundnut exhibited better competitiveness against C₄ weeds compared to C₃ weeds or their combination. The findings revealed that groundnut growth and nodulation were significantly enhanced in treatments eCO₂ and eCO₂ + eT but reduced under eT. Herbicide efficacy declined under eCO₂, suggesting the need for higher application rate under future climate scenarios. These findings highlight the importance of adaptive strategies to sustain groundnut productivity under climate change scenario.

Key words: Climate change, Crop-weed competition, CTGC, Dry matter partitioning, Elevated CO₂ (eCO₂), Elevated temperature (eT), Herbicide efficacy, Nodulation.

INTRODUCTION

The global population is projected to reach 8.6 billion by 2030 and 9.6 billion by 2050, placing increasing pressure on agriculture to ensure food security, address climate change and improve soil health (Sharma *et al.*, 2025). Groundnut (*Arachis hypogaea* L.), is an annual legume with high quality edible oil and easily digestible protein of its seeds (Vasanthi *et al.*, 2015). The crop is cultivated mainly for its seed and it comprises 40-50% oil, 20-30% protein (Naik *et al.*, 2022). It is cultivated on 7.74 million hectares in India, producing 7.8 million tonnes annually (FAO, 2023). It is vital for nutritional security and livestock fodder, especially as global demand for protein-rich diets grows. However, rising atmospheric CO₂ levels, driven by human activities, threaten agricultural productivity through climate change, altering weather patterns, increasing temperatures and intensifying pest and disease pressures. Since 1850, CO₂ concentrations have risen from 280 ppm to 407 ppm in 2017 (Asha *et al.*, 2017), with projections reaching 421-936 ppm by 2100 (IPCC, Climate change, 2013).

¹AICRP on Weed Management, Professor Jayashankar Telangana State Agricultural University, Hyderabad-500 030, Telangana, India.

²ICAR-Central Research Institute for Dryland Agriculture, Hyderabad-500 059, Telangana, India.

³ICAR-Directorate of Weed Research, Jabalpur-482 004, Madhya Pradesh, India.

Corresponding Author: T. Ram Prakash, AICRP on Weed Management, Professor Jayashankar Telangana State Agricultural University, Hyderabad-500 030, Telangana, India.

Email: trp.soil@gmail.com

ORCID: 0000-0001-6992-7769, 0000-0002-2594-7554, 0000-0002-6634-4055, 0009-0007-3912-0332, 0000-0002-0776-5546, 0000-0002-6899-3390, 0000-0001-8030-5546

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Carbon dioxide in the C₃ pathway of photosynthesis promotes growth and productivity and is an example of a positive effect on C₃ plants (Pawar, 2025). C₃ plants like groundnut generally benefit from elevated CO₂, showing improved growth and CO₂ assimilation (Laza *et al.*, 2021), but associated temperature rises can reduce yields (Vanaja *et al.*, 2019). Weeds, with their diverse gene pools and physiological plasticity, may adapt better to changing climates, intensifying crop-weed competition (Ziska, 2001; Varanasi *et al.*, 2016). Elevated CO₂ can also delay herbicide efficacy (Naidu *et al.*, 2023), while higher temperatures may reduce herbicide effectiveness (Rudell *et al.*, 2023). Understanding these interactions is crucial for optimizing weed control and ensuring food security under future climates. Hence, this study investigates the effects of climate change on groundnut growth, weed competition and herbicide efficacy.

MATERIALS AND METHODS

Location of the experimental site

The experiment was conducted in Carbon dioxide and Temperature Gradient Chamber (CTGC) facility located at ICAR-CRIDA, Hayathnagar Farm, Hyderabad (17°34'54.65"N latitude and 78°59'42.85"E longitude).

CTGC facility

The Carbon Dioxide and Temperature Gradient Chamber (CTGC) facility consists of four chambers, aT + aCO₂: Maintains ambient temperature and CO₂ levels (396-405 ppm), eT: Elevates temperature by 2°C above ambient using infrared heaters, eCO₂: Elevates CO₂ concentration to 550±50 ppm) and eT + eCO₂: Combined elevated temperature (+2°C) and CO₂ (550±50 ppm). The facility uses solar radiation and heaters to regulate temperature, with cooling pads and exhaust fans maintaining airflow. A Programming Logical Controller (PLC) monitors and controls temperature and CO₂ levels, ensuring precise environmental conditions.

Treatment details

The experiment studied groundnut response under three factors:

Climate variables (4 levels)

- aT + aCO₂: Ambient temperature and CO₂ (396-405 ppm).
- eT: Elevated temperature (+2°C).
- eCO₂: Elevated CO₂ (550 ± 50 ppm).
- eT+eCO₂: Elevated temperature (+2°C) and CO₂ (550±50 ppm).

Herbicide rates (4 levels)

- 0X: No herbicide.
- 1X: Recommended dose (75 g/ha Imazethapyr + 50 g/ha Propaquizafop).
- 1.5X: 150% recommended dose (112.5 g + 75 g/ha).
- 2X: 200% recommended dose (150 g + 100 g/ha).

Crop-weed combinations (3 levels)

- Groundnut + C₃ weeds (*Parthenium hysterophorus* and *Alternanthera sessilis*).

- Groundnut + C₄ weeds (*Cyperus rotundus* and *Cynodon dactylon*).
- Groundnut + C₃ + C₄ weeds.

The present experiment was taken under pot culture and popular groundnut cultivar in Telangana K6 was sown on 7-12-2022 and 6-12-2023 during both the years of study. Pot size of (12" diameter, 14" height) were filled with 18-19 kg red sandy loam soil. C₃ weed seeds and C₄ weed rhizomes were sown/transplanted alongside. Fertilizers (30 kg N + 40 kg P₂O₅ + 50 kg K₂O + 40 kg S/ha) and vermicompost (2 tons/ha) were applied. 75 g/ha Imazethapyr + 50 g/ha Propaquizafop herbicide was sprayed post-emergence at 4 ml/L (1X), 6 ml/L (1.5X) and 8 ml/L (2X).

Sampling

At 60 DAS, parameters on crop growth and nodule number was recorded, Plant height was measured from the base to the top leaf tip. SPAD readings (chlorophyll content) were taken using a SPAD-502 meter. Rhizosphere soil samples were collected to assess Rhizobium population using Yeast Mannitol Agar Media (Al-Mujahidy *et al.*, 2013). Plants were carefully uprooted, washed, air-dried for 30 minutes and nodules counted. Leaves were separated and leaf area was measured using a LICOR 3100 leaf area meter. Stem, root and leaf dry weights were recorded after oven-drying at 60°C and total biomass was calculated by summing them.

Statistical analysis

Data were analyzed using three-way ANOVA at 5% significance to assess variability among climate variables, herbicide rates, crop-weed combinations and their interactions using WINDOSTAT software.

RESULTS AND DISCUSSION

Plant height

Pooled data from two years (Fig 1) showed that groundnut height increased significantly by 25% under elevated CO₂ (eCO₂, 550±50 ppm) compared to ambient conditions, followed by eT + eCO₂ (12.4%) and eT (3.8%). The tallest plants (39.4 cm) were recorded with a 1.5X herbicide dose (Imazethapyr 3.75% + Propaquizafop 2.5% ME), similar to 1.0X but superior to 0X and 2X doses. Plants grew taller with C₄ weeds than with C₃ weeds or their combination. Naidu *et al.* (2023) noted that C₄ weeds like *Sorghum halepense* were less competitive than C₃ weeds like *Euphorbia geniculata* under eCO₂. The eCO₂ + 1.5X herbicide combination produced the tallest plants, outperforming other combinations except eCO₂ + 2.0X. Under ambient and eT conditions, plant height increased at 1X but declined at 1.5X and 2X, while under eCO₂ and eT + eCO₂, height increased up to 1.5X before declining at 2X. Other interactions were non-significant. Geethalakshmi *et al.* (2017) and Chander *et al.* (2023) also reported positive effects of elevated CO₂ and temperature on plant height, leaf area and nodulation in soybean.

Leaf area per plant

Leaf area was significantly influenced by all three factors independently, as well as by climate × herbicide and climate × crop-weed interactions (Fig 1). Maximum leaf area was observed under eCO₂, being 3%, 10% and 26% higher than eT, eT + eCO₂ and aT + aCO₂, respectively. Laza *et al.* (2021) found that long-term exposure to eCO₂ (650 ppm) enhanced CO₂ assimilation, transpiration efficiency, biomass and pod yield in peanuts. Leaf area was highest at the 1.5X herbicide rate, 10% greater than no application. C₄ weeds resulted in significantly higher leaf area compared to C₃ weeds or their combination. The interaction effect showed that leaf area with C₄ weeds was highest under eT + eCO₂. Climate × herbicide interactions revealed that the recommended dose increased leaf area over no application, but higher rates were ineffective under aT + aCO₂, eT and eT + eCO₂. Under eCO₂, 1X did not enhance leaf area, but 1.5X and 2X rates achieved maximum leaf area, suggesting higher herbicide rates may be needed for effective weed control under elevated CO₂ and temperature. Varanasi *et al.* (2016) noted that herbicide efficacy is reduced under high temperature and CO₂ conditions.

Leaf chlorophyll content (SPAD readings)

Chlorophyll content in groundnut leaves was significantly influenced by individual factors and climate × herbicide interactions (Table 1). eCO₂ resulted in the highest SPAD readings (43.3), significantly surpassing other climate variables, while eT recorded the lowest (35.9). Enriched CO₂ increased leaf area, photosynthetic rate and chlorophyll content, as reported by Dey *et al.* (2017). Similar trends were observed in maize, with eCO₂ showing the highest physiological parameters, comparable to eT + eCO₂. Herbicide application reduced chlorophyll content, with the

highest SPAD (41.4) under no herbicide treatment, significantly higher than 1X, 1.5X and 2X rates. Makarian *et al.* (2016) also noted high concentrations of herbicide caused a significant decline in leaf chlorophyll content in maize and barley. Chlorophyll content was higher with C₄ weeds (41.1) in comparison to the C₃ weeds or their combination (40.2 and 39.1, respectively). Weeds under elevated temperatures revealed that the C₃ weeds compete better in cooler conditions, while C₄ weeds adapt to higher temperatures (Upasani and Barla, 2018).

Soil Rhizobial population

The *Rhizobium* population (CFU/g soil) was significantly influenced by all three factors and due to their interactions (Table 2). eCO₂ increased *Rhizobium* colonies by 22%, while eT reduced them by 30% compared to ambient conditions. The combination (eT + eCO₂) partially offset this loss, showing an 11% increase. Herbicide application negatively impacted *Rhizobium* colonization, with higher rates causing greater declines. Groundnut with C₃ weeds had higher *Rhizobium* populations (19.7 CFU/g soil) than with C₄ weeds (16.4 CFU/g soil) or their combination (18.1 CFU/g soil). Vu *et al.* (2023) noted that soil microbial populations decreased with increased weed biomass. The highest *Rhizobium* population was observed under eCO₂, with C₃ weeds and in treatments with no herbicide application. Ruan *et al.* (2023) reported that CO₂ enrichment alone accelerated microbial growth, while combined temperature increases delayed it. Raghavendra *et al.* (2017) reported that herbicide application reduced *Rhizobium* populations in the soil, primarily because many herbicides are directly toxic to these beneficial microorganisms. In addition, herbicides can alter rhizosphere conditions by affecting root exudation, soil microbial balance and nutrient

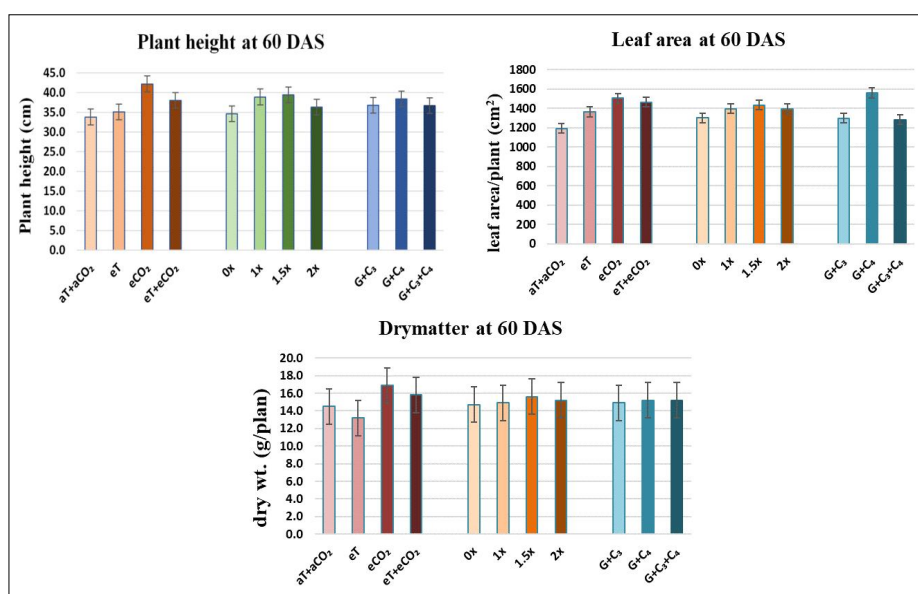


Fig 1: Growth parameters of groundnut as influenced by the climate variables, rates of herbicide application and crop weed interaction.

Table 1: Groundnut SPAD values as influenced by the climate variables, rates of herbicide application and crop weed interaction at 60 DAS.

Climate	Ambient				Elev. Temp				Elev. CO ₂				Elev. Temp + Elev.CO ₂							
	Herbicide		Mean		Mean		Mean		Mean		Mean		Mean		Mean					
Crop-weed	0X	1X	1.5X	2X	(Climate × Crop-weed)	0X	1X	1.5X	2X	(Climate × Crop-weed)	0X	1X	1.5X	2X	(Climate × Crop-weed)	Mean				
Groundnut × C ₃	40.3	40.4	39.2	37.5	39.4	37.7	37.9	37.3	36.2	37.3	43.4	41.7	42.7	42.1	42.5	41.2	40.0	40.9	40.0	40.5
Groundnut × C ₄	41.2	40.9	39.6	37.9	39.9	38.4	38.5	38.1	36.4	37.8	43.5	41.7	43.5	42.5	42.8	41.8	40.4	41.2	40.7	41.0
Groundnut × C ₃	40.0	40.2	38.7	36.5	38.8	37.6	37.6	36.9	35.8	37.0	42.6	41.1	42.1	41.1	41.7	41.1	39.4	40.9	39.7	40.3
and C ₄																				
Mean (Climate × Herbicide)	40.5	40.5	39.2	37.3		37.9	38.0	37.4	36.1		43.2	41.5	42.8	41.9	41.4		39.9	41.0	40.1	
Mean (Climate)																				
Mean (Herbicide)																				
Mean (Crop-weed)																				

Table 2: *Rhizobium* population (CFU/g soil) in soil rhizosphere as influenced by climate variables, rates of herbicide application and crop weed interaction at 60 DAS.

Climate	Ambient				Elev. Temp				Elev.CO ₂				Elev. Temp + Elev.CO ₂							
	Herbicide				Mean				Mean				Mean							
	0X	1X	1.5X	2X	(Climate × Crop-weed)	0X	1X	1.5X	2X	(Climate × Crop-weed)	0X	1X	1.5X	2X	(Climate × Crop-weed)	0X	1X	1.5X	2X	(Climate × Crop-weed)
Crop-weed	23.3	21.0	16.2	18.7	19.8	16.2	13.3	11.5	10.0	12.8	30.5	18.7	21.8	23.3	23.6	27.0	24.7	19.3	20.3	22.8
Groundnut + C ₃	18.6	16.3	17.5	12.5	16.2	14.0	11.2	12.3	11.3	12.2	24.8	22.5	13.6	16.6	19.4	21.8	14.0	20.2	14.7	17.7
Groundnut + C ₄	20.8	20.5	14.2	14.7	17.5	16.6	13.3	11.0	10.0	12.7	27.5	25.7	19.3	18.3	22.7	23.5	24.2	16.3	13.3	19.3
Groundnut + C ₃ and C ₄																				
Mean (Climate × Herbicide)	20.9	19.3	15.9	15.3		15.6	12.6	11.6	10.4		27.6	22.3	18.3	19.4		24.1	20.9	18.6	16.1	
Mean (Climate)	aT+aCO ₂ : 17.9						eT: 12.6					eCO ₂ :21.9					eT+eCO ₂ :19.9			
Mean (Herbicide)	0X: 22.1						1X: 18.8					1.5X: 16.1					2X: 15.3			
Mean (Crop-weed)	G+C ₃ :19.7						G+C ₄ :16.4					LSD (P=0.05)					G+C ₃ +C ₄ :18.1			
Factors	Climate						1.415					NS					NS			
Herbicide	Crop-weed						1.415					NS					NS			
Crop-weed	Climate × Herbicide						1.225					NS					NS			
Climate × Herbicide	Climate × Crop-weed						2.451					2.451					2.451			
Herbicide × Crop-weed	Climate × Herbicide × Crop-weed						4.902					4.902					4.902			

Table 3: Nodulation (No. of nodules/plant) in groundnut as influenced by climate variables, rates of herbicide application and crop weed interaction at 60 DAS.

Climate	Ambient				Elev. Temp				Elev. CO ₂				Elev. Temp + Elev. CO ₂			
	Herbicide				Mean				Mean				Mean			
Crop-weed	0X	1X	1.5X	2X	(Climate × Crop-weed)	0X	1X	1.5X	2X	(Climate × Crop-weed)	0X	1X	1.5X	2X	(Climate × Crop-weed)	Mean
Groundnut + C ₃	249	242	224	203	229	199	179	187	138	176	422	388	320	305	358	364
Groundnut + C ₄	258	247	227	216	237	210	192	187	153	185	440	402	339	325	377	367
Groundnut + C ₃ and C ₄	235	238	219	212	226	189	183	181	136	172	401	359	340	327	357	352
Mean (Climate × Herbicide)	247	242	223	210		199	184	185	142		421	383	333	319		361
Mean (Climate)	aT+aCO ₂ : 231					eT: 178					eCO ₂ :364					eT+eCO ₂ :320
Mean (Herbicide)	0X: 307					1X: 284					1.5X: 262					2X: 239
Mean (Crop-weed)	G+C ₃ :271					G+C ₄ :282					LSD (P=0.05)					G+C ₃ +C ₄ :266
	Factors															
	Climate										4.653					
	Herbicide										4.653					
	Crop-weed										4.030					
	Climate × Herbicide										9.307					
	Climate × Crop-weed										NS					
	Herbicide × Crop-weed										8.060					
	Climate × Herbicide × Crop-weed										16.12					

availability, creating a toxic or unfavorable environment for *Rhizobium* survival and activity.

Nodule number

Nodulation, a key indicator of groundnut's nitrogen-fixing ability, was significantly influenced by climate variables, herbicide doses, crop-weed competition and their interactions (Table 3). Nodulation increased by 58% under eCO₂ and 39% under eT + eCO₂ compared to ambient conditions but decreased by 23% under eT. Libault (2014) noted similar trends, with eCO₂ enhancing nodulation and eT reducing it due to soil moisture changes. Growth, nodule dry weight and nitrogenase activity are inversely related to temperature (Day *et al.*, 1978). Herbicide application reduced nodulation by 7%, 15% and 22% at 1.0X, 1.5X and 2.0X rates, respectively, consistent with Zaidi *et al.* (2005). The highest nodulation (440 nodules/plant) was observed under eCO₂ with C₄ weeds and no herbicide application while the lowest was under ambient conditions with 2X herbicide and C₃ weeds. Elevated CO₂ may boost plant growth, but weed competition for resources can affect nodulation outcomes. Climate change modifies plant-herbicide interactions by altering crop physiology, herbicide uptake and effectiveness and weed competitiveness. These changes can either suppress or stimulate nodulation, depending on crop species, environmental conditions and the intensity and type of weed competition (Burul *et al.*, 2022).

Dry matter production

Dry matter accumulation in groundnut was significantly influenced by climate variables, herbicide doses and their interactions (Fig 1). The highest dry matter (16.9 g/plant) was recorded under eCO₂ (550±50 ppm), followed by eT + eCO₂ (15.8 g/plant), while eT resulted in the lowest (13.2 g/plant). Similar increases in biomass under eCO₂ were reported by Saha *et al.* (2012) in pigeon pea and by Vanaja *et al.* (2019) and Guna *et al.* (2024) in groundnut and black gram, respectively. Dey *et al.* (2017) noted a 20.7% and 17.3% increase in photosynthetic rate at 25 and 45 DAS in mung bean under eCO₂, enhancing biomass production. Among herbicide doses, the highest dry matter (15.6 g/plant) was observed at 0X, significantly higher than 1.0X and 2.0X but similar to 1.5X. Interaction effects were non-significant. While herbicides improve growth by reducing weed competition, excessive doses can cause phytotoxicity, reducing productivity (Galon *et al.*, 2015).

CONCLUSION

Elevated CO₂ (eCO₂) significantly enhanced groundnut growth, increasing plant height, leaf area, chlorophyll content, nodulation and dry matter production, while elevated temperature (eT) reduced these parameters. The combination of eCO₂ + eT partially offset the negative effects of eT. Herbicide application improved growth at moderate rates but suppressed *Rhizobium* populations and nodulation at higher doses. Groundnut competed better with

C₄ weeds than with C₃ weeds. Under future climate scenarios, higher herbicide rates may be needed for effective weed control, as herbicide efficacy is reduced under elevated CO₂ and temperature. These findings highlight the need for adaptive management strategies to sustain groundnut productivity under changing climatic conditions.

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Disclaimers

The views and conclusions expressed in this article are solely those of the authors and do not necessarily represent the views of their affiliated institutions. The authors are responsible for the accuracy and completeness of the information provided, but do not accept any liability for any direct or indirect losses resulting from the use of this content.

Informed consent

All animal procedures for experiments were approved by the Committee of Experimental Animal care and handling techniques were approved by the University of Animal Care Committee.

Conflict of interest

The authors declare that there are no conflicts of interest regarding the publication of this article. No funding or sponsorship influenced the design of the study, data collection, analysis, decision to publish, or preparation of the manuscript.

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