R-2827
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REVIEW ARTICLE Agricultural Reviews

Resilience under Pressure: A Review on Cowpea's Tolerance to Heat and Elevated CO_2 in the Context of Climate

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10.18805/ag.R-2827

ABSTRACT

Climate change presents a significant threat to global survival affecting ecosystems and human health through increased frequency and intensity of extreme weather events. In agriculture, abiotic stresses including drought, heat, floods and salinity severely undermine plant survival and crop productivity, threatening food security worldwide. Livestock production, a cornerstone of rural economies is also compromised by declining crop yields, which reduce the availability and quality of animal fodder, thereby diminishing livestock health and productivity. To combat these challenges, there is a pressing need for sustainable agricultural practices, including the development of climate-resilient crop varieties. Cowpea (*Vigna unguiculata*), a nutrient-rich and drought-tolerant legume holds immense potential to address future food and fodder demands, especially in arid and semi-arid regions. Its rich genetic diversity makes it a valuable resource for breeding programs aimed at enhancing resilience to environmental stresses. However, climate change adds complexity, rising carbon dioxide concentrations and temperatures intensify heat stress, impairing physiological functions and limiting yield. While elevated CO_2 may improve photosynthesis and water-use efficiency, heat stress can negate these benefits by disrupting reproductive development and metabolic processes. A deeper understanding of these interactions is critical for advancing cowpea breeding strategies to ensure stable productivity under future climatic scenarios.

Key words: Cowpea, Heat, Carbon dioxide, Legume, Temperature stress, Climate change, Livestock.

Global climate change and the increasing threat of elevated carbon dioxide (eCO_2) and temperature

The ongoing climate change presents a significant threat to humanity's survival, as it impacts diverse areas globally leading to extreme weather events, ecological imbalances and disruptions to agriculture, health and economic sectors. Global crop productivity is highly sensitive to variations in temperature and precipitation patterns. Since 1880, the global mean temperature has risen by approximately 1°C and is projected to increase by an additional 1.5°C primarily by greenhouse gas emissions from industrialization, urbanization and transportation has resulted in a persistent rise in global temperatures and altered rainfall patterns, posing a critical threat to agricultural productivity and food security worldwide (Zafar *et al*., 2018). The agricultural sector, especially in developing countries is particularly vulnerable to the adverse effects of climate change including increased frequency of floods, droughts and heat stress (Daryanto *et al*., 2016). Abiotic stresses including drought, heat stress, floods and salt-stressed conditions are categorized as extreme weather events that can have a significant impact on plant survival (Bita and Gerats, 2013). As a consequence of climate change, eCO_2 contribute to rising temperatures which in turn subject crops to heat stress. Heat stress poses a significant decline in plant metabolic, physiological and biochemical processes limiting crop yield (Bita and Gerats, 2013). However, it has been reported from various studies that increased CO_2 levels have a profound positive effect on the photosynthetic rates and consequently the growth and yield in plants (Long *et al*., 2004).

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How to cite this article: Rajasekharan, A. and Gayathri, G. (2026). Resilience under Pressure: A Review on Cowpea's Tolerance to Heat and Elevated CO_2 in the Context of Climate. *Agricultural Reviews.* 1-10. doi: 10.18805/ag.R-2827.

Submitted: 27-09-2025 **Accepted:** 14-01-2026 **Online:** 12-02-2026

Role of cowpea in livestock production under climate-stressed conditions

Cowpea (*Vigna unguiculata*) is a versatile crop that serves as a source of both human food and livestock feed. It is recognized as an important drought-tolerant legume with significant production potential to meet the increasing demands for food and fodder for both humans and livestock. Additionally, it improves soil fertility by contributing significant amounts of nitrogen through biological nitrogen fixation (Abebe and Alemayehu, 2022). Recent findings highlight the substantial carbon sequestration potential of cowpea-based intercropping systems, with NPKEC fertilization contributing up to 0.30 Mg C ha^{-1} yr^{-1} and intercropping systems enhancing SOC storage by an additional 0.17 Mg C ha^{-1} yr^{-1}, thereby improving the overall numerical clarity of carbon dynamics in such systems (Roohi *et al*., 2022). Cowpea is a resilient legume that thrives in environments characterized by high temperatures and limited water availability. (Carvalho *et al*., 2017). The wide genetic variability of the crop can be harnessed to develop crop varieties tolerant to extreme climatic conditions.

Livestock production is a key sector of the economy that is notably affected by reduced crop production caused by climate changing patterns. Alterations in the availability of good quality fodder and water sources has significantly impaired livestock productivity and in turn the availability of livestock produce for human consumption (Nardone *et al*., 2010). A projected temperature increase of 2-3°C across the country coupled with higher humidity driven by climate change, is expected to intensify heat stress in dairy animals, thereby diminishing both their growth and milk production (Das, 2018). To address the growing demands and ensure global food security, it is imperative to adopt sustainable practices and secure long-term viability of crop and livestock production. As climate change becomes more prevalent worldwide, examining how plants react to stress is crucial for evaluating their significant morphological and physiological features. This review aims to understand how cowpea responds to heat stress and elevated CO_2 by examining its growth, physiology, yield and to identify ways to improve its tolerance for future climate conditions.

Impact of eCO_2 and high temperature on plant physiology

Increased CO_2 levels often stimulates photosynthesis in C_2 plants through the CO_2 fertilization effect, enhancing carbon assimilation and biomass accumulation (Baig *et al*., 2015). This is accompanied by partial stomatal closure, reducing stomatal conductance and transpiration rates (typically by 20–30/ %), thereby improving water-use efficiency (Wei *et al*., 2022). Leaf structural and biochemical adaptations occur including increased chloroplast size, starch storage and altered chlorophyll and hormone status (Müller and Munné-Bosch, 2021). However, eCO_2 can also dilute mineral and protein concentrations in plant tissues due to carbohydrate accumulation and reduced transpiration driven nutrient uptake (Ahammed *et al*., 2021). These nutrient declines pose concerns for crop quality and food nutrition. eCO_2 may moderate heat and drought stress by boosting thermotolerance and antioxidant responses, although interactions with rising temperatures can complicate outcomes (Adireddy *et al*., 2024). The heat tolerance mechanisms of cowpea is listed in Table 1.

Table 1: Heat tolerance mechanisms in cowpea and associated traits.

Mechanism type	Specific traits/responses	Effect on plant	Reference
Heat avoidance	Transpirational cooling, leaf orientation, canopy shading	Reduces internal leaf temperature, delays stress impact	Nadeem *et al.* (2018), Hall (2019)
Thermomorphogenesis	Hypocotyl elongation, early flowering, altered leaf architecture	Enhances transpiration efficiency and avoids peak heat periods	Kan *et al.* (2023), Fatima *et al.* (2020)
Reproductive resilience	Maintained floral bud development, pollen viability, reduced pod abortion	Prevents yield loss under high day/night temperatures	Mohammed *et al.*(2024), Ahmed and Hall (1993)
Antioxidant defense	Elevated activities of SOD, CAT, APX, GPX	Detoxifies ROS, protects cell structures, reduces lipid peroxidation	Amorim *et al.* (2018), Hasanuzzaman *et al.* (2013)
Heat shock proteins (HSPs)	Upregulation of sHSP17.6I/II, HSP22, chaperones (BAG6, MBF1C)	Stabilizes proteins, enhances thermotolerance	Selinga *et al.* 2022), Asthir (2015)
Osmolyte accumulation	Proline, glycine betaine	Maintains turgor, supports pollen viability, protects enzymes	Priyanka *et al.* (2024), Amorim *et al.* (2018)
Stomatal regulation	Modulated stomatal conductance under heat/eCO_2	Enhances water-use efficiency and thermoregulation	Cavalcante *et al.* (2016), Al-Salman *et al.* (2023)
Photosynthetic stability	Preserved PSII function, high A_{net}, reduced photorespiration under eCO_2	Maintains carbon assimilation under stress	Mohammed *et al.* (2024), Adireddy *et al.* (2024)
Hormonal signaling	ABA, CK, auxin, ethylene modulation; ABA-triggered HSP expression	Coordinates stress responses, supports reproductive development	Ahammed *et al.* (2021), Angon *et al.* (2024), Li *et al.* (2021)

Developmental and physiological responses of cowpea to heat stress

Temperature is a key environmental variable that influences multiple physiological and developmental processes ultimately determining crop growth and yield. One of the most temperature-sensitive processes is the rate of crop development, which generally accelerates under higher temperatures (Hatfield and Prueger, 2015). This acceleration can shorten the crop growth duration, thereby limiting cumulative radiation interception by the canopy and ultimately reducing potential biomass accumulation and yield (Fatima *et al*., 2020). Under elevated temperatures, plants exhibit a suite of developmental changes referred to as thermo-morphogenesis, which includes elongation of hypocotyls, early flowering and modifications in leaf architecture. The process is governed by a network of temperature sensors, core regulatory genes and downstream effectors which together improve plant growth and form under mild to moderate heat conditions (Kan *et al*., 2023).

High temperatures negatively affect cowpea seed germination and seedling survival, especially when seeds are sown deeply or in saline soils (De Lima Nunes *et al*., 2019). Various studies have indicated that temperatures exceeding 35°C lead to flower abortion, accelerated leaf senescence and reduced photosynthetic capacity (Zandalinas *et al*., 2018). Elevated night temperatures affect floral bud development, pollen viability, anther dehiscence, embryo formation, pod and seed development (Mohammed *et al*., 2024). The most heat-sensitive stage of floral development occurs 7-9 days before anthesis. High night temperatures also reduce sugar supply to peduncles and restrict proline translocation in heat-sensitive genotypes (Ahmed and Hall, 1993).

In response to heat stress, plants reduce their chlorophyll content, photosynthesis rate and transpiration to minimize water loss (Taiz *et al*., 2017). To cope with abiotic stresses, they have developed defense mechanisms that include the activity of ROS scavenging enzymes including Superoxide Dismutase (SOD), Catalase (CAT), Glutathione Peroxidase (GPX) and Ascorbate Peroxidase (APX) (Merwad *et al*., 2018). Therefore, characterizing these defense mechanisms at the cellular level is crucial for breeding, genetic engineering and developing cultivars that are tolerant to environmental stresses.

Photosynthesis and carbon assimilation

eCO_2 significantly enhances photosynthetic carbon assimilation in C_2 plants by increasing the substrate concentration available to Rubisco, thereby improving carboxylation efficiency and reducing photorespiration (Ekele *et al*., 2025). Meta analyses and FACE (Free Air CO_2 Enrichment) studies consistently report average increases in net photosynthesis of 20-40% under elevated CO, leading to enhanced biomass production especially in leaves and stems ((Hu *et al*., 2021). Initially, stomatal conductance (g›) declines by roughly 20-30%, reducing transpiration and improving intrinsic water use efficiency (iWUE), allowing plants to fix more carbon per unit of water lost (Wang *et al*., 2022). However, over prolonged exposure, many species exhibit photosynthetic acclimation, where biochemical capacity declines as leaf internal carbohydrate pools increase and leaf nitrogen is diluted (Bellasio *et al*., 2018; Singer *et al*., 2020). Under heat stress, eCO_2 also helps preserve photosynthetic efficiency by stabilizing PSII and PSI function enhancing electron transport, preserving redox balance and improving recovery through increased ratios of ascorbate-glutatione (ASA-GSH) and better NADPz NADPH regulation, as in tomato (Pan *et al*., 2018).

In a controlled growth chamber study, Angelotti *et al*. (2020) reported up to a 45% increase in cowpea pod yield under eCO_2 (700 µmol mol^{-1}) compared to ambient levels (350–360 µmol mol^{-1}), along with higher photosynthetic rate (A_{net}), leaf area and biomass. Similarly, Mohammed *et al*. (2024) showed that eCO, enhances A_{net}, leaf area and biomass by up to 45 % under optimal temperatures (25-30°C). Under high temperature stress (>35°C), tolerant genotypes maintain elevated A_{net}, sugar content and pod set under eCO_2 while sensitive lines suffer flower abortion and male sterility due to disrupted starch and proline partitioning (Selinga *et al*., 2022). Controlled studies further confirm that eCO_2 partly offsets heat-induced declines in photosynthesis by sustaining Calvin-cycle activity and reducing Rubisco inhibition from photorespiration (Adireddy *et al*., 2024). eCO_2 also strengthens antioxidant defenses, increasing heat shock proteins and ROS-scavenging enzymes (SOD, CAT, APX) which stabilize proteins and membranes under heat (Selinga *et al*., 2022). Heat stress alone accelerates phenology, reduces time to flowering and increases flower abortion but eCO_2 alleviates these effects by supporting assimilate supply and enhancing pod sink strength (Roy *et al*., 2023).

Stomatal conductance and water relations

Stomatal conductance (g_s) governs the trade-off between CO_2 uptake for photosynthesis and water loss via transpiration. Under eCO_2 plants often reduce g› partly as the internal CO_2 concentration (C_i) rises, enabling sufficient carbon fixation with fewer open stomata, thereby enhancing water use efficiency (Cavalcante *et al*., 2016). However, under heat stress (>35°C), increased vapor pressure deficit typically triggers stomatal closure to curb excessive water loss which impairs transpirational cooling and risks overheating despite high CO_2 levels (Ferreira *et al*., 2021). eCO_2 may partially offset this by lowering transpiration demand, helping conserve water and maintain moderate leaf temperature. However, reduced evaporative cooling capacity under combined high CO_2 and heat can lead to elevated leaf temperatures, especially if g_s is too low (Al-Salman *et al*.,2023).

In cowpea, g_s exhibits strong plasticity in response to water and heat stress. Under drought, cowpea rapidly downregulates g_s to conserve water and maintain leaf turgor, which concurrently reduces photosynthesis and biomass accumulation (Al-Salman *et al*., 2023). Despite this, cowpea demonstrates a conservative water use strategy and limited variation in leaf water potential reflecting its isohydric behaviour (Goufo *et al*., 2017). Under eCO_2 stomatal frequency and g_3 are significantly reduced (28-35%), leading to decreased transpiration but improved relative water content and membrane stability even during combined water deficit and heat stress. Cowpea genotypes also show variation in g_3 under heat where some genotypes maintain higher g_3 during moderate soil drying and correlate positively with yield and biomass under stress (Tankari *et al*., 2019). Therefore, breeding for genotypes with moderated stomatal responsiveness under eCO_2 and heat may support improved thermoregulation, photosynthetic maintenance and drought resilience in cowpea production systems.

Plant growth and biomass allocation

eCO_2 typically enhances net photosynthesis and stimulates plant growth in C_3 species, often leading to biomass increases of 20-30% or more under non-stressful conditions (Delahunty *et al*., 2018, Sabagh *et al*., 2020). This CO_2 fertilization effect results in greater carbon assimilation and improved water-use efficiency *via* reductions in stomatal conductance, lowering transpiration. However, when heat stress (>35°C) is superimposed, the benefits of eCO_2 can be partially offset, wherein high temperature shortens phenological stages, accelerates development and impairs reproductive success (Yamaguchi *et al*., 2023). Under combined heat and eCO_2 plant dry mass may still increase modestly, but many crops show reduced yield components due to thermal injury during flowering and grain filling wherein heat reduces fertility and grain weight even when vegetative biomass increases (Sehgal *et al*., 2018). Biomass partitioning often shifts under stress in which drought and heat favour root allocation at the expense of shoot growth but eCO_2 may moderate this by supporting both above and belowground growth (Xi *et al*., 2025).

Controlled environment studies in cowpea indicate that eCO_2 (550–700 ppm) enhances both shoot and root biomass under optimal temperatures/ (29°C day23°C night) compared to ambient CO_2 (Angelotti *et al*., 2020). Higher temperature regimes (32°C/29°C) accelerated crop phenology and reduced reproductive biomass in sensitive genotypes even with CO_2 enrichment (Angelotti *et al*., 2020, Roy *et al*., 2023). Heat tolerant cowpea lines maintained biomass allocation to pods and seeds under combined CO_2 and temperature stress suggesting genotype-specific resilience in partitioning assimilates to reproductive sinks (Mohammed *et al*., 2024). Studies shows that tolerant cultivars under eCO_2 preserved root allocation to support water uptake, whereas sensitive lines redirected resources to rapid but short-lived vegetative growth reducing seed yield (Poudel *et al*., 2025).

Nutrient dynamics

Rising atmospheric CO_2 combined with elevated heat fundamentally alters the nutrient dynamics of crops. eCO_2 often stimulates photosynthesis in C_3 plants and increases biomass (CO_2 fertilization effect), but concurrently leads to a "dilution" of vital nutrients, especially nitrogen based protein and micronutrients such as iron, zinc, magnesium, potassium, calcium and phosphorus, with declines frequently in the 5-15% range or more (Food, Fibre and Other Ecosystem Products, 2023). Heat stress particularly during reproductive phases impairs photosynthetic apparatus, accelerates leaf senescence, disrupts carbohydrate translocation and damages reproductive tissues, thereby reducing grain filling and yield quality (Farooq *et al*., 2017). When heat and eCO_2 occur together, the negative effects on nutrient concentration may be moderated in some cases: higher temperatures can restore mineral concentrations to near ambient levels by reducing biomass dilution effects, but only for specific crops under certain conditions (Köhler *et al*., 2018). Additionally, eCO_2 tends to increase the carbon to nitrogen ratio, which shifts resource allocation toward carbon based defense compounds (*e.g.* phenolics) at the expense of nitrogen rich proteins and alkaloids, potentially influencing both nutritional value and pest resistance (Hill and Shlisel, 2024).

Cowpea, a C_3 legume widely grown in hot, semiarid regions, exhibits both promise and vulnerability under eCO_2 and heat. Under CO_2 enrichment (700 ppm), pod yield may increase by around 45% compared to ambient (350 ppm) and eCO_2 can partially offset heat stress impacts on leaf area, net photosynthesis and dry matter production, especially in heat tolerant genotypes (Mohammed *et al*., 2024). However, exposure to short term elevated heat in growth chamber trials reveals strong sensitivity during the flowering stage: crude protein (%N) in shoots increased under moderate heat (≈30°C) but declined sharply under higher heat (≈35°C) specifically at flowering, indicating severe disruption of nitrogen allocation at this critical phase (Nevhulaudzi *et al*., 2020). Heat tolerant cowpea lines accumulate more sugars in peduncles and maintain pod set under high nighttime temperatures (~33/30°C), whereas heat sensitive lines fail to flower or set pods even under eCO_2 (Ahmed *et al*., 1993). At the same time, eCO_2 may promote symbiotic nitrogen fixation in legumes, potentially mitigating crude protein losses compared to other C_3 cereals (Singer *et al*., 2020).

Hormonal changes and signalling

The combination of eCO_2 and high temperatures significantly alters plant hormonal signalling networks, impacting growth, stress tolerance and adaptation. eCO_2 often enhances photosynthesis and biomass, but it also modulates phytohormone levels including abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA), ethylene (ET), auxin, cytokinins (CKs), brassinosteroids (BRs) and gibberellins (GAs) which together govern stress responses (heat, drought) *via* complex crosstalk (Li *et al*., 2021). Under heat stress, eCO_2 enhances thermotolerance partly by modulating ROS signalling through RBOH pathways and increasing HSP expression, which are often hormone mediated (*e.g.* ABA triggered HSP70 up regulation) (Ahammed *et al*., 2021). Auxin promotes heat induced morphological changes (thermomorphogenesis), while cytokinin/ABA ratios shift in response to heat with high CK relative to ABA improving flower retention and antioxidant responses under elevated temperatures (Angon *et al*., 2024). Salicylic acid and ethylene enhance antioxidant defence and HSP levels, mitigating cellular damage during heat episodes (Li *et al*., 2021). eCO_2 also modifies stomatal regulation via ABA and SA shifts under drought or heat with plants grown at eCO_2 show altered ABA GE and SA accumulation patterns, affecting stomatal control and water use efficiency (WUE) (Jensen *et al*., 2024).

General legume studies suggest that CO_2 enrichment can improve nitrogen fixation and growth. Elevated CO_2 may alleviate heat induced ABA accumulation resulting in stomatal closure and improving WUE, while CK may support floral organ retention under heat stress (Li *et al*., 2021). Ethylene signalling may also be upregulated under the dual stress to trigger HSP expression and boost thermotolerance. Moreover, auxin and BR mediated pathways could support thermomorphogenic adjustments under elevated temperature (Wu and Yang, 2019). These interactions suggest that breeding cowpea cultivars with eCO_2 responsiveness and hormonal regulation tuned to heat may preserve reproductive success and yield.

Stress tolerance and antioxidant defense

eCO_2 generally enhances plant tolerance to abiotic stresses like drought, heat and ozone exposure. This is often attributed to improved WUE, enhanced antioxidant enzyme activities (SOD, CAT, APX) and stabilization of cellular membranes. Plants may show higher levels of osmo-protectants (proline, soluble sugars), which help maintain cell turgor and enzyme function under stress (Zinta *et al*., 2018). Elevated temperatures sharply increase the production of reactive oxygen species (ROS) such as superoxide (O_2•–), hydrogen peroxide (H_2O_2) and hydroxyl radicals in crop tissues, causing oxidative damage to lipids, proteins, membranes and photosystems particularly in chloroplasts and mitochondria (Kumar *et al*., 2022). In response, crops activate enzymatic antioxidants including SOD, APX, CAT, glutathione reductase (GR), GPX and non enzymatic compounds like ascorbate, glutathione and phenolics to detoxify ROS and restore redox balance (Hasanuzzaman *et al*., 2013). eCO_2 often mitigates heat induced oxidative stress by reducing photorespiration and ROS generation, maintaining a more reduced redox state (higher ASA/DHA and GSH/GSSG ratios) even under heat stress, as shown for tomato and other crops (Pan *et al*., 2018). In a study conducted by Jincy *et al*. (2020) green gram genotypes, VGG 17003, VGG 17019 and VGG 16069 accumulated markedly higher proline under drought and high-temperature stress compared to sensitive genotypes such as VGG 16027 and CO 8. Enhanced antioxidant activity evident from higher catalase levels in VGG 17019 and VGG 16069 further reflects the superior oxidative stress tolerance of these genotypes. In legumes and C_3 crops, eCO_2 also improves antioxidant defense and lowers oxidative damage more effectively compared to grasses and C_4 species (AbdElgawad *et al*., 2014). Thus, combined eCO_2 and heat can partially protect crops by boosting antioxidant capacity along with improved photosynthetic energy fluxes and redox stability.

In cowpea, responses to heat and oxidative stress reflect classic antioxidant defense mechanisms and enhanced stress protein expression. Under acute heat stress (above 35^{o}C), cowpea genotypes variably induce heat shock proteins (HSPs) and ROS scavenging enzymes to stabilize proteins, membranes and metabolic processes (Pan *et al*., 2018). Proteomic analyses have identified small HSPs and other stress protective proteins in heat resilient lines, indicating genotype specific antioxidant responses (Mohammed *et al*., 2024). Meanwhile, transgenic cowpea lines overexpressing a constitutively active DREB2A transcription factor demonstrated enhanced osmotic adjustment, antioxidant systems and yield stability under combined drought and heat regimes (28-52^{o}C) (Kumar *et al*., 2022).

Physiological and molecular basis of heat tolerance in cowpea

Heat stress tolerance in plants is primarily governed by two adaptive strategies: avoidance and tolerance (Hall, 2019). Heat avoidance encompasses mechanisms that enable plant tissues to maintain temperatures lower than those of control plants under elevated thermal conditions. Avoidance mechanisms include transpirational cooling, leaf orientation and leaf shading (Nadeem *et al*., 2018). These strategies collectively help mitigate the detrimental effects of heat stress on plant tissues. In contrast, heat tolerance refers to a plant's ability to maintain vital physiological functions even when exposed to high temperatures. The various adaptive strategies of cowpea in response to heat stress is depicted in Fig 1.

Cowpea, cultivated in hot and arid regions is expected to express HSPs and heat-responsive proteins as part of its thermotolerance mechanisms (Asthir, 2015). While earlier studies reported no significant differences in HSP expression between heat-tolerant and susceptible cowpea varieties, recent proteomic analyses have provided deeper insights into the molecular responses of cowpea to heat stress. In a recent proteomic study conducted by Selinga *et al*. (2022), cowpea genotype IT-96D-610 demonstrated enhanced heat stress tolerance compared to IT-16. Under controlled conditions, IT-96D-610 upregulated small HSPs such as HSP17.6I, HSP17.6II and HSP22, along with chaperones like BAG6, MBF1C and CSDP1.

At the physiological and biochemical level, tolerant genotypes maintain photosynthetic efficiency, stomatal conductance and transpiration at high temperatures, helping sustain carbon fixation and leaf cooling. Conversely, susceptible cultivars show reduced stomatal conductance, elevated leaf temperature, chlorophyll loss and reduced biomass and yield (Priyanka *et al*., 2024). Heat stress often accelerates leaf senescence and reproductive organ abortion, particularly under high night time temperatures, causing poor pollen viability, anther indehiscence, suppressed floral bud development and reduced pod set and seed fill (Liu *et al*., 2019). Heat stress triggers oxidative damage via accumulation of ROS which damage membranes, DNA and proteins. Cowpea genotypes tolerant to heat maintain higher activities of antioxidants to scavenge ROS and mitigate cellular injury (Amorim *et al*., 2018).

Impact of eCO_2 and heat stress on cowpea productivity

Climate change, characterized by rising atmospheric CO_2 levels and increasing temperatures poses complex challenges to plant growth and productivity. While eCO_2 generally enhances photosynthesis and plant growth, its interaction with high temperatures can yield variable outcomes (Roy *et al*., 2023). In C_3 plants, eCO_2 can mitigate some detrimental effects of heat stress by maintaining photosynthetic efficiency and improving WUE (Roy *et al*., 2023). However, under supra-optimal temperatures, the benefits of eCO_2 may diminish leading to reduced photosynthetic performance (Hamilton *et al*., 2008). Conversely, C_4 plants which already operate with a CO_2-concentrating mechanism may experience diminished thermotolerance under eCO_2 conditions (Al-Salman *et al*., 2023). Additionally, eCO_2 can alter plant biochemical compositions by increasing carbon-based secondary metabolites and decreasing nitrogen content which may affect nutritional quality and plant-herbivore interactions (Kaur *et al*., 2023). The interactive effects of heat and eCO_2 in cowpea plants with respect to crop growth, yield and biochemical compounds are depicted in Fig 2.

Genetic diversity provides a crucial foundation for developing cowpea varieties with improved tolerance to climate-induced stresses. By broadening the genetic base and using wild or landrace relatives in breeding, cowpea can adapt more effectively to shifting environmental conditions (Vaishna *et al*., 2025). eCO_2 and increased temperatures have been shown to positively influence cowpea (*Vigna unguiculata*) growth, enhancing parameters such as plant height, number of branches, leaf area and overall yield components (Lamichaney *et al*., 2021). These improvements are attributed to increased photosynthetic rates and reduced photorespiration, leading to greater carbon assimilation (Adireddy *et al*., 2024). eCO_2 typically reduces stomatal conductance, thereby enhancing transpiration efficiency and limiting water loss through stomata in both C_3 and C_4 plants. However, this response is primarily observed at the leaf level. At the canopy scale, water use in C_3 crops may actually increase under eCO_2 largely due to expanded leaf area associated with increased biomass accumulation and improved water status (Wang *et al*., 2015). A study by Angelotti *et al*. (2020) concluded that both temperature and CO_2 concentration significantly influence the development and yield of cowpea cultivars. Specifically, the BRS Tapaihum cultivar exhibited superior performance under eCO_2 conditions, showing the highest number of pods, seeds and seed weight. The study also noted that high temperatures (32°C day29°C night) led to increased flower abortion in BRS Tapaihum, highlighting the cultivar's sensitivity to extreme heat despite its enhanced performance under eCO_2. Cavalcante *et al*. (2016) assessed the effects of temperature and CO_2 concentration on cowpea development and evapotranspiration in the semi-arid region. Their findings indicated that an increase in temperature accelerates crop development, leading to a reduction of 14 to 23 days in the cowpea crop cycle. However, these benefits are accompanied by significant alterations in the plant's phytochemical composition. Under eCO_2 conditions, there is an observed increase in carbon-based compounds, including phenols, tannins and sugars, which are secondary metabolites often associated with plant defense mechanisms (Palit *et al*., 2020). Conversely, nitrogen-based compounds notably proteins exhibit a decline which is likely due to a dilution effect caused by the accumulation of carbohydrates as well as a decrease in the nitrogen pool available for protein synthesis. Such changes in the phytochemical profile may influence the nutritional quality of cowpea and its interactions with herbivores and pathogens (Sola *et al*.,

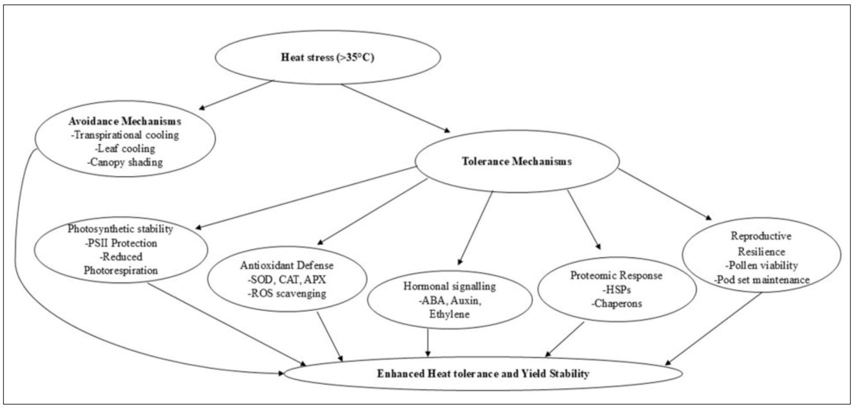

Fig 1: Adaptive strategies of cowpea under elevated temperature conditions.

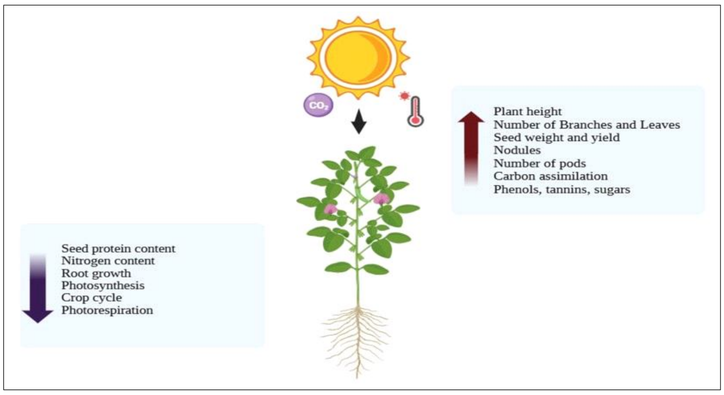

Fig 2: Interactive effects of eCO_2 and heat Stress on cowpea growth, yield and biochemical components.

2025). Therefore, while eCO_2 and elevated temperatures can enhance cowpea growth and yield, they also necessitate careful consideration of the associated biochemical shifts that could impact crop quality and pest dynamics (Megha *et al*., 2022).

Future directions and research needs

Despite significant progress in understanding the effects of elevated CO_2 (eCO_2), drought and heat stress on crop performance, several important knowledge gaps remain particularly concerning the resilience mechanisms of cowpea. The crop is recognized for its inherent tolerance to heat and water limitation. However, the physiological and ecological pathways that enable this resilience are still insufficiently characterized. Recent studies highlight that cowpea's ability to maintain photosynthetic efficiency under stress is linked to traits such as efficient stomatal regulation, osmotic adjustment, deeper rooting patterns and enhanced antioxidant defense systems. However, the extent to which these traits interact under simultaneous climate stressors requires further investigation.

Future research should focus on evaluating cowpea responses under multi-stress field environments, as many existing studies rely on controlled chambers that do not fully replicate fluctuating climatic conditions. Understanding crop behaviour under real-time heat stress, intermittent drought and rising CO_2 concentrations will provide more ecologically relevant insights. Comparative assessments with other legumes and drought-tolerant cereals would also strengthen the identification of key resilience attributes unique to cowpea.

Additionally, genotype × environment (G×E) interactions must be explored in greater depth to pinpoint physiological traits including canopy temperature depression, stay-green characteristics, carbon assimilation efficiency and root hydraulic conductivity which are key contributors to superior performance under combined stress. Integrating high-throughput phenotyping tools, remote sensing and trait-based modelling will accelerate the identification of promising genotypes suitable for climate-smart breeding programs.

Although major cereals like wheat, rice and maize have dominated climate-stress research, regionally important crops such as cowpea remain underrepresented in global adaptation studies. Expanding investigations across diverse agroecological zones will be essential to capture the full spectrum of cowpea's adaptive strategies, particularly in regions most vulnerable to climate variability. A more holistic understanding of cowpea's ecological role, including its contribution to soil fertility, carbon sequestration and intercropping benefits, will further strengthen its position as a climate-resilient crop.

CONCLUSION

Climate change, characterized by rising temperatures, altered precipitation patterns and increasing atmospheric CO_2 concentrations poses significant challenges to global crop productivity. While eCO_2 may enhance photosynthetic efficiency and biomass accumulation, especially in C_3 crops, its benefits can be offset by temperature-induced reductions in growing period, radiation interception and yield potential. The complexity of crop responses at both the leaf and canopy levels underscore the importance of integrating physiological understanding with whole plant and ecosystem scale assessments. These projections underscore the urgent need to develop and deploy heat-tolerant crop varieties capable of maintaining or enhancing yield under elevated temperature conditions. Ongoing interdisciplinary research, supported by advances in genetics, crop modelling and remote sensing, will be critical for informing and developing sustainable agricultural practices in response to climate change.

ACKNOWLEDGEMENT

The present study was supported by Kerala Agricultural University, Thrissur.

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Informed consent

No animal procedures were involved.

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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