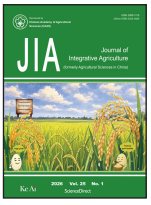
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RESEARCH ARTICLE

Impacts of abiotic stresses on cotton physiology and vigor under current and future CO_2 levels

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Highlights

- Cotton cultivars are sensitive to abiotic stress during the vegetative stage.
- Stresses and CO_2 levels significantly influence the expression of physiology and phenotypic traits.
- Elevated CO_2 partially mitigates stress-induced damage to biomass under heat, salt, and drought.

Abstract

Elevated CO_2 (eCO_2) may mitigate stress-induced damage to cotton (*Gossypium* spp.) growth and development. However, understanding the early-stage responses of cotton to multiple abiotic stressors at eCO_2 levels has been limited. This study quantified the impacts of chilling (CS, 22/14°C, day/night temperature), heat (HS, 38/30°C), drought (DS, 50% irrigation of the control), and salt (SS, 8 dS m^{-1}) stresses on pigments, physiology, growth, and development of 14 upland cotton cultivars under ambient CO_2 (aCO_2, 420 ppm; current) and eCO_2 (700 ppm; future) levels during the vegetative stage. The eCO_2 partially negated the effects of all stresses by improving one or more of the pigments, physiological, growth, and development traits, except CS. For instance, HS at aCO_2 significantly increased stomatal conductance by 36% compared with non-stressed plants at aCO_2. However, HS at eCO_2 significantly decreased stomatal conductance by 18% compared with HS at aCO_2. The first squaring was delayed by one day under SS at aCO_2 but two days earlier under SS at eCO_2 than non-stressed plants at aCO_2. Root and shoot dry mass and the total leaf area were significantly higher under all stresses, except for CS, at the eCO_2 compared with similar stresses at the aCO_2. Most growth and development traits, including plant height, leaf area, and shoot dry mass, displayed a mirroring response pattern between aCO_2 and eCO_2 under all environments except CS. Cultivars exhibited significant interaction with stressed environments. Further, results revealed differential sensitivity and adaptation potential of cultivars to stress environments at varying CO_2 levels. This study highlights the need to consider eCO_2 in designing breeding programs to develop stress-tolerant varieties for future cotton-growing environments.

Keywords: abiotic stress, eCO_2, cotton, vegetative vigor, multi-stress tolerance

1. Introduction

Historically, atmospheric CO_2 levels have risen from 260 ppm pre-industrially to ~420 ppm, with projections exceeding 700 ppm by 2100 (IPCC 2023; Keeling 2024). Under eCO_2, crops can potentially enhance several physiological and growth processes (Leakey *et al.* 2009; Shreevani *et al.* 2022), the foundation for successful reproductive performance and higher yields (Virk *et al.* 2020). However, this increase in CO_2 is likely accompanied by multiple abiotic stresses and alters crop-growing environments (Cassia *et al.* 2018). The beneficial effects of eCO_2 on growth can be compromised by the increasing prevalence and intensity of abiotic stressors (Munawar *et al.* 2021; Gupta *et al.* 2023). Thus, to develop effective strategies for sustained cotton production under future conditions, it's crucial to understand how cotton cultivars respond to abiotic stresses under varying CO_2, especially during the early vegetative stage.

Abiotic stressors significantly impact physiological

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processes in plants, leading to decreased leaf water potential and photosynthesis efficiency (Noreen *et al.* 2020; Chaudhry and Sidhu 2022; Dos Santos *et al.* 2022). Stressors such as chilling, drought, and salt lead to reduced stomatal conductance to minimize water loss, resulting in decreased photosynthate production. Conversely, heat stress increases stomatal conductance to cool the canopy. However, non-stomatal limitations lead to Rubisco inactivation and increased photorespiration, also hindering photosynthesis (Zhang and Sonnewald 2017). Additionally, these stresses lead to changes in growth traits, such as stunted growth, altered root-to-shoot ratios, and variations in leaf structure and root growth (Zhang and Sonnewald 2017; Yousaf *et al.* 2023). Despite having moderate glycophytic properties (Maryum *et al.* 2022), cotton plants experience physiological drought and ion toxicity under salt stress due to increased Na^+ and Cl^- uptake and reduced levels of essential nutrients (Zafar *et al.* 2022). These responses are reported to be cultivar-dependent. Cultivars with a wide genetic base are likely to be tolerant/stable across environments, whereas those with narrow genetic bases are likely to be responsive to specific environments (Liu *et al.* 2023).

Studies indicate that cotton can utilize higher CO_2 levels for photosynthesis, as increased CO_2 enhances intercellular concentration in chloroplasts while facing higher stomatal resistance (Bange *et al.* 2016). This alleviates limitations in C_3 crops and boosts photosynthesis and intrinsic water use efficiency (Ainsworth and Rogers 2007; Thompson *et al.* 2017; Chavan *et al.* 2019). As Rubisco carboxylation is reported to be not saturated at the current level of CO_2 (~420 ppm), it is suggested that eCO_2 enhances the ratio of Rubisco carboxylation to oxygenation (Thompson *et al.* 2017; Shreevani *et al.* 2022). The morphological and physiological responses of cotton to specific stresses at aCO_2 conditions have been studied (Saini *et al.* 2023; Bista *et al.* 2024). However, limited studies focus on how eCO_2 and abiotic stress affect the physiology and vigor of cotton plants.

Previous studies suggest that eCO_2 has a positive impact, with improved physiology and vigor in cotton exposed to heat and drought stresses. Notably, eCO_2 appears to be more effective in reducing damage caused by heat stress compared to drought stress (Yoon *et al.* 2009; Broughton *et al.* 2016; Zhang *et al.* 2017). Considering future cotton-growing environments, quantifying variability in cotton trait responses to eCO_2 in combination with abiotic stresses is the first step towards developing mitigation strategies and designing new breeding targets. Identifying multi-stress adaptive traits and tolerant donors is crucial for addressing the simultaneous prevalence of various stresses in current and near-future crop-growing conditions. To date, limited studies have quantified the physiology, growth, and development of cotton under eCO_2 levels combined with multiple abiotic stresses (chilling, heat, drought, and salt) using a set of diverse cotton cultivars. In this study, we hypothesized that eCO_2 alleviates the physiological and vigor-related damage induced by multiple individual stresses. Our specific objectives were to (i) quantify genetic variability in the response of cotton to chilling, heat, drought, and salt stresses under varying CO_2 levels, (ii) assess the responsiveness of physiological, growth, and developmental traits to eCO_2 level, (iii) elucidate the relationships between traits under abiotic stressors at aCO_2 and eCO_2 levels and (iv) identify cultivars that exhibit tolerance to multi-stress at both aCO_2 and eCO_2 levels.

2. Materials and methods

2.1. Plant materials

In this study, we examined a diverse panel of 14 upland cotton cultivars (*Gossypium hirsutum* L.), comprising 13 cultivars and one genetic standard line (Appendix A). Among 13 cultivars, AU, C315, DP90, FM966, M240, HS26, PSC355, TP, ST474, ST825, and SG747 have been used as parental lines in U.S. cotton breeding programs in developing a multiparent advanced generation inter-cross (MAGIC) population (Fang *et al.* 2014; Islam *et al.* 2016; Wang *et al.* 2022). Notably, cultivars UA 222 and FM958 stand out for their exceptional combination of high yield and fiber quality, serving as popular commercial checks in varietal trials within U.S. breeding programs (Bourland and Jones 2018; Bechere *et al.* 2020). The genetic standard line, TM-1, has been widely utilized in genomic studies as a reliable tester stock (Li *et al.* 2015; Perez *et al.* 2022).

2.2. Crop husbandry

The study was conducted at Soil–Plant–Atmospheric Research (SPAR) units at Rodney Foil Plant Science Research Center, Mississippi State University, Mississippi, USA (33°28′N, 88°47′W). The SPAR units consisted of a Plexiglas chamber (2 m long×1.5 m wide×2.5 m tall) and a steel soil bin (2 m long×0.5 m wide×1 m deep) to accommodate above and below-ground plant parts, respectively. Each SPAR unit was equipped with facilities to control environmental factors, including air temperature, soil moisture, atmospheric CO_2, and nutrient supplies (Reddy *et al.* 2001). A total of 560 polyvinyl chloride (PVC) pots (15.2 cm diameter and 30.5 cm height) were filled with 500 g gravel at the bottom and then filled with a mixture of farm soil:sand (1:3; v/v). Pots were arranged in a steel soil bin of 10 SPAR units in (10×14) factorial completely randomized design with four replicates. Each SPAR unit consisted of 56 PVC pots (14 cultivars×4 replications). Four seeds of each cultivar were sown in PVC pots at a depth of 2 cm. At the first true leaf emergence stage, seedlings were thinned to one plant per pot. Hogland's nutrient solution (Reddy *et al.* 1996) was supplied daily using an automated, computer-controlled drip irrigation system. Optimum day/night temperature (30/22°C), volumetric soil moisture content (~0.15 m^3 m^{-3}), and soil electrical conductivity (EC) of 0 dS m^{-1} at current CO_2 level (420 ppm) were maintained in all the SPAR units before the imposition of treatments.

2.3. Treatment imposition

After 14 days of sowing, 10 different growing environments (treatments) were created in 10 SPAR units, each representing a unique growing condition. The 10 growing environments were (i) aCO_2, (ii) eCO_2, (iii) CS+aCO_2, (iv) CS+eCO_2, (v) HS+aCO_2, (vi) HS+eCO_2, (vii) DS+aCO_2, (viii) DS+eCO_2, (ix) SS+aCO_2, and (x) SS+eCO_2 (Fig. 1). The

aCO_2 units were set at the current CO_2 level (420 ppm), whereas eCO_2 units were supplied with the future predicted CO_2 level (720 ppm). CO_2 concentrations were precisely regulated through automatic injection from a gas cylinder into the chambers, monitored every 10 s by a CO_2 analyzer. Chilling stress was applied at a diurnal/nocturnal temperature regime of 22/14°C (day/night), while the heat stress units were set at 38/30°C (day/night). Cooling/heating was achieved through the circulation of chilled ethylene glycols, controlled *via* parallel solenoid valves, with short-term heat spikes administered by electrical resistance heaters to ensure accurate temperature regulation. Thermocouples were employed to monitor temperatures at 10 s intervals. Irrigation frequency was reduced to 50% of the non-stress treatment to create drought stress (Narayana *et al.* 2024). Soil moisture sensors (Model EM5b Soil Moisture, Decagon Devices, Inc., Pullman, Washington, USA) were installed at 15 cm depth to monitor soil moisture levels every 15 min. A mixture of NaCl (2,160 g) and $CaCl_2$ (432 g) at the ratio of 5:1, equivalent to 80 mmol L^{-1}, was added to irrigation tanks to achieve (EC) levels of 8 dS m^{-1} (Vennam *et al.* 2024) to create salt stress. The soil EC levels were monitored using a soil EC meter (FieldScout Direct Soil EC Meter, Spectrum Technologies, Aurora, IL, USA). These treatments were used to understand and quantify trait responses in current and future cotton-growing environments.

2.4. Data collection

Plant pigments and physiological traits Plant pigments (chlorophyll index, flavonoid index, anthocyanin index, and nitrogen balance index) were measured using a handheld Dualex® Scientific instrument (Force A DX16641, Paris, France). Stomatal conductance, transpiration, the quantum efficiency of photosystem II, and leaf temperature were measured using a portable handheld LI-600 porometer system integrated with a fluorometer (LI-COR Biosciences, Lincoln, USA) on sunny hours between 10:00 a.m. and 12:00 p.m. Both plant pigments and physiological traits were measured on the fully expanded leaf from the third node down from the apex of each plant, 25 days after stress treatment (37 days after sowing (DAS)).

Growth and development traits When 50% of plants developed the first pinhead square, days to the first square and the first square node number were recorded. The plants were harvested 26 days after stress treatment (38 DAS) during the squaring stage. After harvesting, leaves were separated from the stem and scanned for single and total leaf area using LI-3100C area meter (LI-COR Biosciences, Lincoln, USA). The fully expanded leaf, used for physiological and pigment measurements, was used for the single leaf area. Subsequently, plant components such as stems and leaves were separately packed. After washing roots, all plant components were oven-dried at 70°C for three days to determine the leaf, stem, and root dry weights. Leaf and stem dry weights were summed up to get the shoot dry weight, whereas the dry weights of all parts were summed up to get the total plant dry weight. Finally, the root-to-shoot ratio was calculated as a ratio of root dry weight to shoot dry weight.

2.5. Statistical analysis

Statistical analyses were carried out using various packages in R version 4.2.2 (https://www.R-project.org/, R Core) and Sigma Plot 15.0 (Systat Software, San Jose, CA, USA). A two-way analysis of variance was performed for all the parameters to assess the significance of treatments, cultivars, and their interaction using the library "doebioresearch". *Post-*

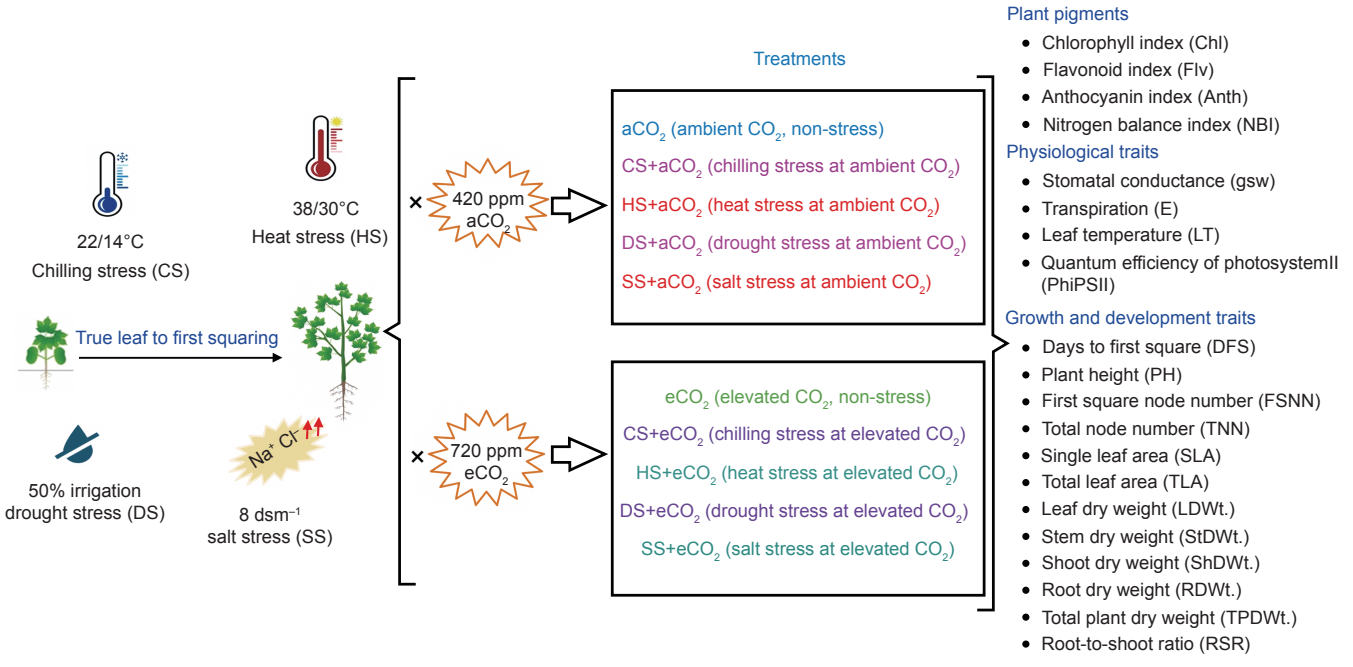


Fig. 1 Illustration of experimental methodology. Ten treatment combinations were imposed from the true leaf to the first squaring stage, and 20 traits related to plant pigments, physiology, and growth and development were collected.

hoc analysis was performed using the LSD (Least Significant Difference) test at a significance level of 5%. To check the stability of traits between CO_2 levels under multiple stresses, Pearson's correlation coefficients between treatments at aCO_2 and eCO_2 were calculated using the library "metan" and visualized using the Sigma plot.

The stress tolerance index (STI) for the individual traits of all the studied 14 cultivars was calculated using a formula defined by (Fernandez 1992).

$$STI=\frac{Y_s \cdot Y_c}{(X_c)^2}$$

Y_s=Average value of a trait of a given cultivar under stress environment

Y_c=Average value of a trait of a given cultivar under non-stress at aCO_2

X_c=Grand mean value of a trait of all cultivars under non-stress at aCO_2

The heat maps were generated using the library "pheatmap," using average STI values for pigments, physiological traits, and growth and development traits.

The genotype plus genotype-*vs*.-environment interaction (GGE) biplot analysis, as proposed by (Olivoto and Lúcio 2020), was done to visualize the genotype (G)×environment (E) interaction using the library "metan". The GGE model is expressed as,

$$\hat{y}_{ij}=\mu+\alpha_i+\beta_j+\Phi_{ij}$$

where $\hat{y}$ is the mean of total plant dry weight of ith (i=1…14) genotype in jth (j=1…10) environment; μ represents the grand mean of total plant dry weight; further, α_i, β_j, and Φ_{ij} are the main effect of genotype i, the main effect of environment j, and the interaction effect between genotype i and environment j, respectively.

The multi-trait stability index (MTSI), as proposed by (Olivoto *et al.* 2019), was also calculated to evaluate the simultaneous selection for mean and stability across all the measured traits using the library "metan". The MTSI was calculated based on the WASSBY index as,

$$WASSBY_i=\frac{(rG_i\times\theta_y)+(rW_i\times\theta_s)}{\theta_y+\theta_s}$$

where $WASSBY_i$ represents the simultaneous selection index for the ith genotype. rG_i and rW_i are the scaled values (0–100) for the dependent variable and *WASSB*, respectively. Further, θ_y and θ_s are the weights for the dependent variable and *WASSB*, respectively. The lower the MTSI value, the higher the mean and stability based on all the traits across the environments and *vice versa*. Box and whisker plots were constructed using Sigma Plot 15.0 (Systat Software, San Jose, California, USA).

3. Results

3.1. Plant pigments

The effects of varied growing environments significantly affected the plant pigments (P<0.001) (Table 1). The chlorophyll index significantly increased by 50% under drought, followed by chilling (21%), heat (8%), and salt (8%) stresses at aCO_2 compared with aCO_2 alone. The eCO_2 significantly decreased the chlorophyll index under drought (7%), and salt (6%) stresses in comparison with those stresses at aCO_2 (Fig. 2-A). The flavonoid index was significantly increased under drought (33%) and chilling (31%) stresses at aCO_2 relative to aCO_2 alone. Notably, plants under eCO_2 without stress exhibited a 12% higher flavonoid index than those grown at aCO_2 alone. Further, eCO_2 enhanced flavonoid levels under drought (8%), chilling (10%), and salt (19%) stresses when compared with identical stresses at aCO_2 (Fig. 2-B). The anthocyanin index demonstrated a significant increase only under chilling at aCO_2 compared with aCO_2 without stress. Drought and heat stresses at aCO_2 reduced the anthocyanin index by 15 and 8%, respectively, compared with aCO_2. eCO_2 did not induce any changes in the anthocyanin index except under drought stress (10% increase compared with drought stress at aCO_2) (Fig. 2-C). The nitrogen balance index was significantly affected by drought (9% increase) and chilling (11% decrease) stresses under aCO_2 compared to aCO_2. In contrast, cultivars under eCO_2 alone exhibited a 12% decline in the nitrogen balance index compared with aCO_2. Except for heat stress, all other stressed plants at eCO_2 exhibited significant reductions in nitrogen balance index: salt (19%), chilling (18%), and drought (14%) compared to their aCO_2 counterparts (Fig. 2-D).

Table 1 Analysis of variance for pigments, physiological, growth, and development traits of cotton cultivars[1)]

Trait	T	C	T×C
Chlorophyll index (Chl)	***	***	***
Flavonoid index (Flv)	***	***	**
Anthocyanin index (Anth)	***	***	*
Nitrogen balance index (NBI)	***	***	**
Stomatal conductance (gsw, mol m^{-2} s^{-1})	***	***	*
Transpiration (E, mmol m^{-2} s^{-1})	***	***	ns
Leaf temperature (LT, °C)	***	ns	ns
Quantum efficiency of photosystem II (PhiPSII)	***	ns	ns
Days to first square (DFS)	***	***	**
Plant height (PH, cm)	***	***	ns
First square node number (FSNN)	***	***	*
Total node number (TNN)	***	***	***
Single leaf area (SLA, cm^2)	***	***	*
Total leaf area (TLA, cm^2)	***	***	***
Leaf dry weight (LDWt., g)	***	***	*
Stem dry weight (StDWt., g)	***	***	***
Shoot dry weight (ShDWt., g)	***	***	**
Root dry wright (RDWt., g)	***	***	ns
Total plant dry weight (TPDWt., g)	***	***	**
Root-to-shoot ratio (RSR)	***	***	ns

[1)] T, C, and T×C represent treatment, cultivar, and interaction between treatment and cultivar, respectively.
*, **, and *** represent significant differences at P<0.05, P<0.01, and P<0.001, respectively; ns represents a non-significant difference.

3.2. Physiological traits

All physiological traits significantly (P<0.001) varied across different growing environments or treatments (Table 1). On average, cultivars grown at eCO_2 showed significantly lower (17%) stomatal conductance compared to those at aCO_2. Plants under HS+aCO_2 demonstrated a 36% increase in stomatal conductance compared with aCO_2 alone. In contrast, HS+eCO_2 exhibited a 19% decrease in stomatal

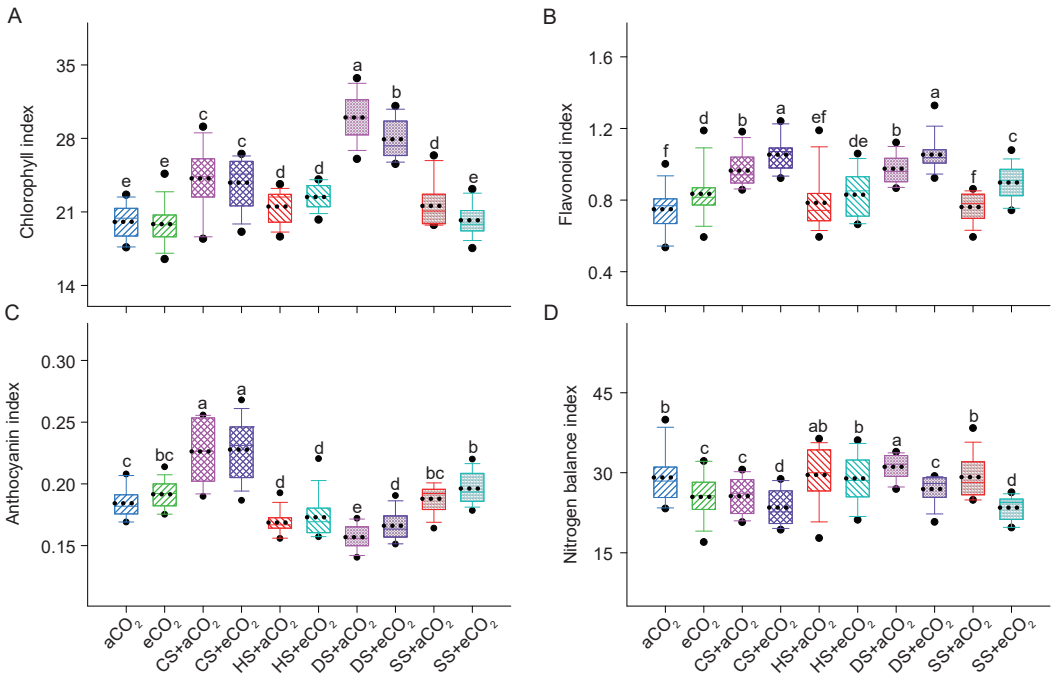


Fig. 2 Effect of chilling, heat, and drought stressors at ambient and elevated CO_2 levels on chlorophyll index (A), flavonoid index (B), anthocyanin index (C), and nitrogen balance index (D) of cotton cultivars. The dotted lines on the box plots represent the treatment means. aCO_2, ambient CO_2; eCO_2, elevated CO_2; CS, chilling stress; HS, heat stress; DS, drought stress; SS, salt stress. Common lowercase letters on the top of the box and whiskers indicate a non-significant difference between treatment means at $P>0.05$.

conductance compared to those under HS+aCO_2. Unlike under heat stress, cultivars showed a significant decline in stomatal conductance under drought (77%), chilling (66%), and salt (45%) stresses when compared to aCO_2 without stress. eCO_2 reduced stomatal conductance under chilling (21%) and salt (13%) stresses compared to their counterparts at aCO_2 (Fig. 3-A). Compared with aCO_2 alone, transpiration rate was higher in heat-stressed plants at aCO_2 (26%), but decreased under chilling (59%), drought (58%), and salt (37%) stresses in the same conditions. In contrast, eCO_2 did not significantly change transpiration across any stressors but decreased it by 13% compared to aCO_2 without stress (Fig. 3-B). Leaf temperature increased under heat (+5°C) and drought (+2.4°C) but decreased under chilling (–4.1°C) stresses at aCO_2 (Fig. 3-C). No significant difference in leaf temperature was found between plants at eCO_2 and aCO_2 under drought, but increases were noted under chilling (1.8°C), heat (1.03°C), and salt (1.2°C) stresses at eCO_2. The quantum efficiency of photosystem II (PhiPSII) was significantly affected by chilling (29% decrease) and salt (9% increase) stresses at aCO_2, while heat stress did not change PhiPSII. At eCO_2, heat and salt stresses significantly decreased PhiPSII by 16 and 4 % compared to their counterparts at aCO_2 (Fig. 3-D).

3.3. Growth and development traits

Growing environments at aCO_2 and eCO_2 levels significantly impacted cotton growth traits ($P<0.001$) (Table 1). Heat-stressed plants at aCO_2 reached first squaring three days earlier than those without stress. In contrast, chilling and salt stresses delayed squaring by three days and one day, respectively. The time to squaring was similar between aCO_2 and eCO_2 under no stress, but eCO_2 accelerated squaring under heat, drought, and salt stresses by one to two days compared to similar stress conditions at aCO_2 (Fig. 4-A). Heat stress led to a 15 cm height increase, while chilling, drought, and salt stresses reduced height (by 64.9, 51.8, and 45.8 cm, respectively) at aCO_2 compared with aCO_2 alone. Plants grown under eCO_2 were taller than their aCO_2 counterparts, except under chilling stress (Fig. 4-B). The initial squaring node was consistent across environments at aCO_2. Heat-stressed plants at eCO_2 initiated squaring at lower nodes (Fig. 4-C). eCO_2 conditions resulted in a 28% increase in node number for heat-stressed plants compared to aCO_2 without stress, while chilling, drought, and salt stresses at aCO_2 significantly reduced node counts. Under eCO_2, total node number increased across stress conditions, with notable gains under drought (15%), salt (12%), and heat (5%) compared to aCO_2 (Fig. 4-D).

Under drought stress, single leaf area decreased significantly by 47%, with chilling, salt, and heat stresses causing decreases of 36, 32, and 7%, respectively, at aCO_2 compared to non-stressed aCO_2 plants (Fig. 5-A). Notably, eCO_2 without stress resulted in an 18% lower single-leaf area compared to aCO_2 without stress. Under eCO_2, heat stress caused a 19% decrease in single leaf area, while drought and salt stresses increased by 13 and 24%, respectively. Total leaf area was significantly reduced by drought (74%), chilling (73%), and salt (54%) stresses at aCO_2, while under heat stress, it increased by 27%, compared with aCO_2 alone. Similar to non-stress conditions, eCO_2 showed an increased total leaf area by 31%, and under stress conditions, it

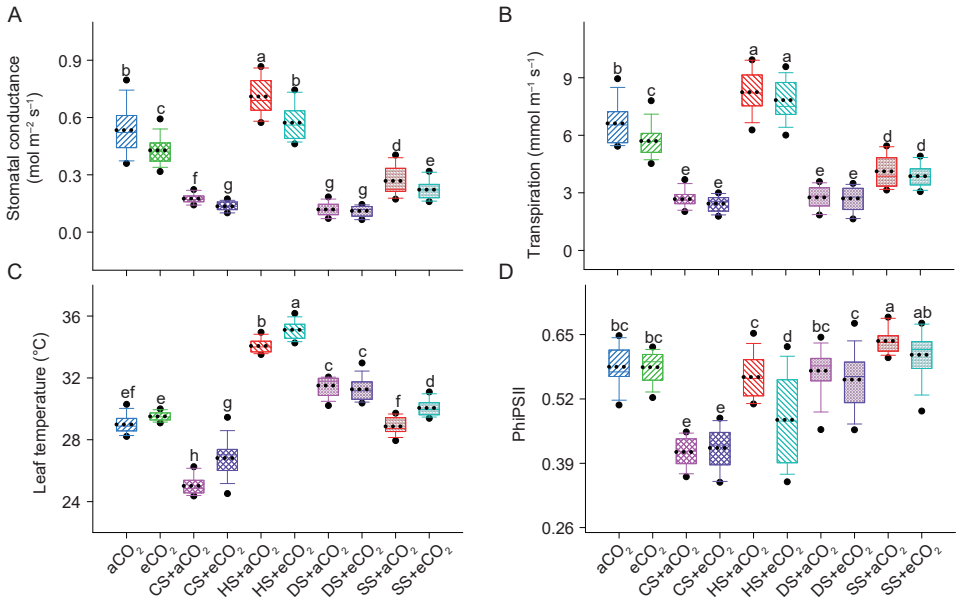


Fig. 3 Effect of chilling, heat, and drought stressors at ambient and elevated CO_2 levels on stomatal conductance (A), transpiration (B), leaf temperature (C), and quantum efficiency of photosystem II (PhiPSII) (D) of cotton cultivars. The dotted lines on the box plots represent the treatment means. aCO_2, ambient CO_2; eCO_2, elevated CO_2; CS, chilling stress; HS, heat stress; DS, drought stress; SS, salt stress. Common lowercase letters on the top of the box and whiskers indicate a non-significant difference between treatment means at $P>0.05$.

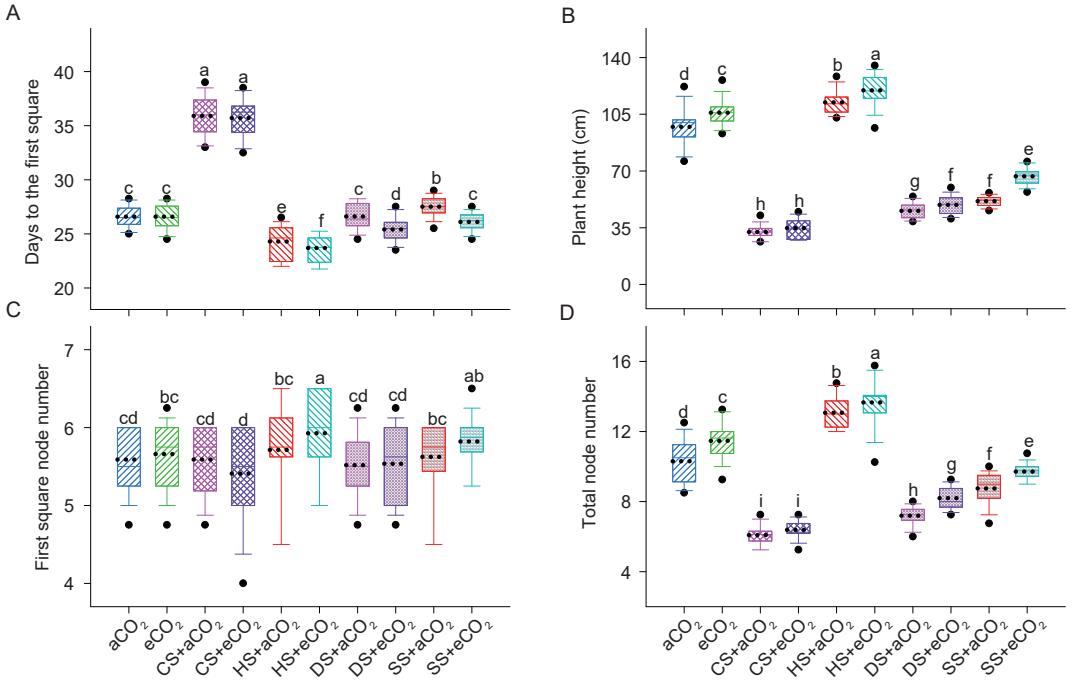


Fig. 4 Effect of chilling, heat, and drought stressors at ambient and elevated CO_2 levels on days to the first square (A), plant height (B), first square node number (C), and total node number (D) of cotton cultivars. The dotted lines on the box plots represent the treatment means. aCO_2, ambient CO_2; eCO_2, elevated CO_2; CS, chilling stress; HS, heat stress; DS, drought stress; SS, salt stress. Common lowercase letters on the top of the box and whiskers indicate a non-significant difference between treatment means at $P>0.05$.

increased total leaf area significantly under heat (17%), and salt (44%) stresses compared to their counterparts at aCO_2 (Fig. 5-B). Leaf dry weight was notably impaired under chilling (60%), drought (52%), and salt (40%) stresses at aCO_2 compared with aCO_2 alone (Fig. 6-A). In contrast, eCO_2 increased leaf dry weight by 49% compared with aCO_2 under non-stress conditions. eCO_2 significantly boosted leaf dry weight under heat (28%), drought (51%), and salt (61%)

stresses compared to their counterparts at aCO_2 (Fig. 6-A). Stem dry weight increased under eCO_2 without stress by 47%, and in stress conditions, it rose significantly, particularly under salt (87%) relative to respective counterparts at aCO_2 (Fig. 6-B).

Shoot dry weight decreased under chilling (70%), drought (48%), and salt (43%) stresses at aCO_2 but increased by 47% under eCO_2 compared with aCO_2 alone. Under HS+eCO_2, shoot dry weight increased by 31%, with significant increases of 77, 36, and 31% observed under salt, drought, and heat stresses relative to similar stresses at aCO_2, respectively (Fig. 6-C). Root dry weight remained unchanged under heat stress at aCO_2 but decreased under chilling (37%), drought (28%), and salt (9%) stresses compared to aCO_2 without stress. At eCO_2, root dry weight increased by 30% compared to aCO_2. Under eCO_2, root dry weight also improved under heat, drought, and salt stresses (30, 30, and 61%, respectively) compared to aCO_2. However, no significant changes were observed under chilling stress at eCO_2 compared to aCO_2 (Fig. 6-D). Total plant dry weight increased by 21% under heat stress compared to aCO_2, while chilling stress caused a 66% decrease. Further, under drought and salt stresses, respectively, reductions were 46 and 39% compared with aCO_2 alone. Plants at eCO_2 had 45% higher dry weight than those at aCO_2. eCO_2 improved dry weight under all stresses except chilling: 73% under salt, 36% under drought, and 31% under heat compared to those stresses at aCO_2 (Fig. 6-E). The root-to-shoot weight ratio increased by 117% under chilling, followed by salt (64%) and drought (42%), but decreased by 20% under heat compared with aCO_2. At eCO_2, root-to-shoot weight ratio remained unchanged under stress, except for a 9% decline under salt stress compared with similar growing environments at aCO_2. (Fig. 6-F).

3.4. Correlation of traits between stresses at aCO_2 and eCO_2 levels

The study observed variations in the linear relationships of various traits between aCO_2 and eCO_2 under different stress conditions (Fig. 7). The chlorophyll index demonstrated strong positive correlations under drought (r=0.88, P<0.001) and chilling (r=0.70, P<0.01) stresses similar to without stress condition (r=0.55, P<0.05). Flavonoid index showed a strong positive correlation between aCO_2 and eCO_2 (r=0.87, P<0.001), followed by heat (r=0.80, P<0.001), drought (r=0.74, P<0.01), and chilling (r=0.72, P<0.01) stresses. Although the anthocyanin index lacked significant correlation under non-stress conditions, it was significantly positively correlated between aCO_2 and eCO_2 under chilling (r=0.75, P<0.01), salt (r=0.75, P<0.05) and drought (r=0.59, P<0.05) stresses. The nitrogen balance index consistently correlated positively across all conditions. Stomatal conductance showed no significant relationships between aCO_2 and eCO_2 under all stress conditions, while transpiration showed a perfect positive relationship between aCO_2 and eCO_2 under drought stress. Leaf temperature showed significant correlations under chilling (r=0.81, P<0.01) and drought (r=0.59, P<0.05) stresses. PhiPSII correlated positively (r=0.55, P<0.05) only between HS+aCO_2 and HS+eCO_2 levels. In terms of growth and development traits, days to the first square (r=0.59, P<0.05), first square node number (r=0.65, P<0.05), and total node number (r=0.64, P<0.05) had significant correlations between CS+aCO_2 and CS+eCO_2. Notably, all the growth and development traits showed positive correlations between aCO_2 and eCO_2 under non-stress conditions, except for root dry weight and root-to-shoot ratio. Unlike other growing environments, all the studied growth and development traits showed a significant positive correlation between DS+aCO_2 and DS+eCO_2 or HS+aCO_2 and HS+eCO_2 (Fig. 7).

3.5. GGE biplot analysis

Three different GGE biplots were used to examine the G and G×E interaction effect on the vigor (total plant dry weight) of cotton cultivars (Fig. 8). The which-won-where biplot demonstrated broad and narrow adaptation of cultivars across environments. Cultivars near the biplot origin have broad adaptation (stable across the tested environments). In contrast, the vertex cultivars have narrow adaptation (highly responsive to the environments included in the same sector). Therefore, vertex cultivars (M240 and ST825) were the

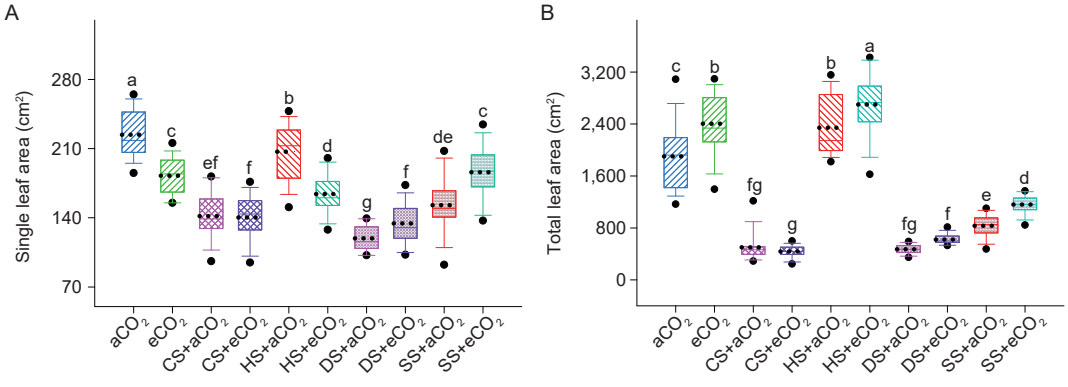


Fig. 5 Effect of chilling, heat, and drought stressors at ambient and elevated CO_2 levels on single leaf area (A) and total leaf area (B) of cotton cultivars. The dotted lines on the box plots represent the treatment means. aCO_2, ambient CO_2; eCO_2, elevated CO_2; CS, chilling stress; HS, heat stress; DS, drought stress; SS, salt stress. Similar lowercase letters on the top of the box and whiskers indicate a non-significant difference between treatment means at P>0.05.

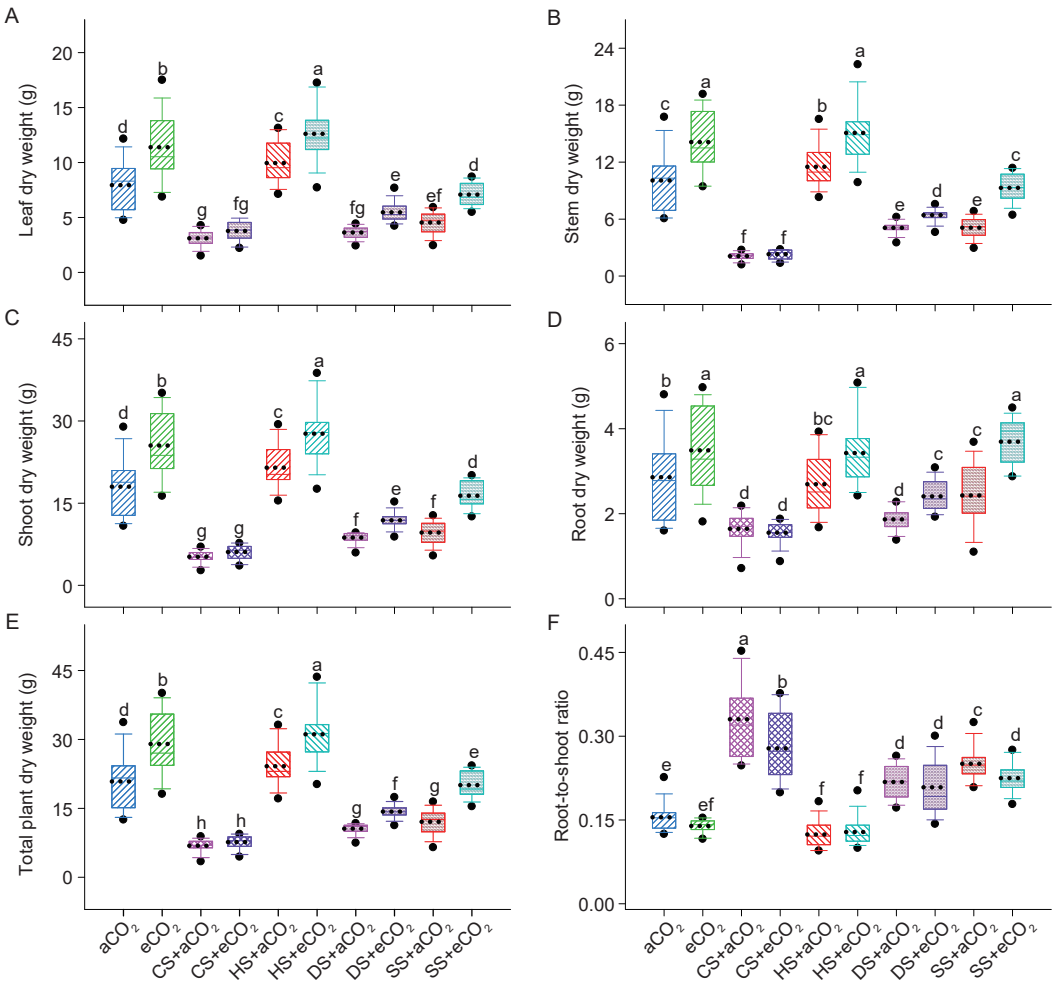


Fig. 6 Effect of chilling, heat, and drought stressors at ambient and elevated CO_2 levels on leaf dry weight (A), stem dry weight (B), shoot dry weight (C), root dry weight (D), total plant dry weight (E), and root to shoot ratio (F) of cotton cultivars. The dotted lines on the box plots represent the treatment means. aCO_2, ambient CO_2; eCO_2, elevated CO_2; CS, chilling stress; HS, heat stress; DS, drought stress; SS, salt stress. Similar lowercase letters on the top of the box and whiskers indicate a non-significant difference between treatment means at $P>0.05$.

winners (better performers) in all the environments in terms of plant vigor that shared a sector. Cultivar M240 showed the highest vigor under aCO_2 conditions without stress and chilling or heat stress at both aCO_2 and eCO_2 levels, while ST825 excelled under the remaining environments (Fig. 8-A). The mean *vs*. stability biplot indicated that M240 ranked as the most vigorous cultivar, while SG747 was the least across all 10 tested environments. Cultivars, TP and ST825, were the most and least stable across the tested environments, respectively (Fig. 8-B). The ranking biplot highlighted M240, FM958, UA222, PSC355, and DP90 as the top five cultivars capable of maintaining high vigor across environments (Fig. 8-C).

3.6. Selection of cultivars based on MTSI

The MTSI model allowed simultaneous selection for higher mean performance and stability across many traits. Among 20 studied traits, 10 traits (chlorophyll index, flavonoid index, nitrogen balance index, days to the first square, total node number, single leaf area, total leaf area, stem dry weight, shoot dry weight, and total plant dry weight) which showed significant G×E interaction ($P<0.05$) were included in the model. MTSI value ranged from 1.05 to 4.54, with an average of 2.49. Among the studied cultivars, PSC355 and C315 had the lowest MTSI values (1.05 and 1.15, respectively) and were selected as multi-stress tolerant cultivars. Further, cultivars AU and TP were closest to the cutoff point with MTSI values of 1.17 and 1.31, respectively (Fig. 9). Though cultivar M240 had the highest plant vigor or total dry mass among the studied cultivars, it was identified as an inferior cultivar based on the selection of multiple traits across environments (Figs. 8-B and 9).

4. Discussion

Traits related to pigments, physiology, growth, and development are highly responsive to environmental changes (Yousaf *et al.* 2023; Bista *et al.* 2024). Optimizing these traits during the early growth stage improves the vegetative vigor (Kramer 1980), which serves as the foundation for reproductive performance (Virk *et al.* 2020). Notably, accumulation and

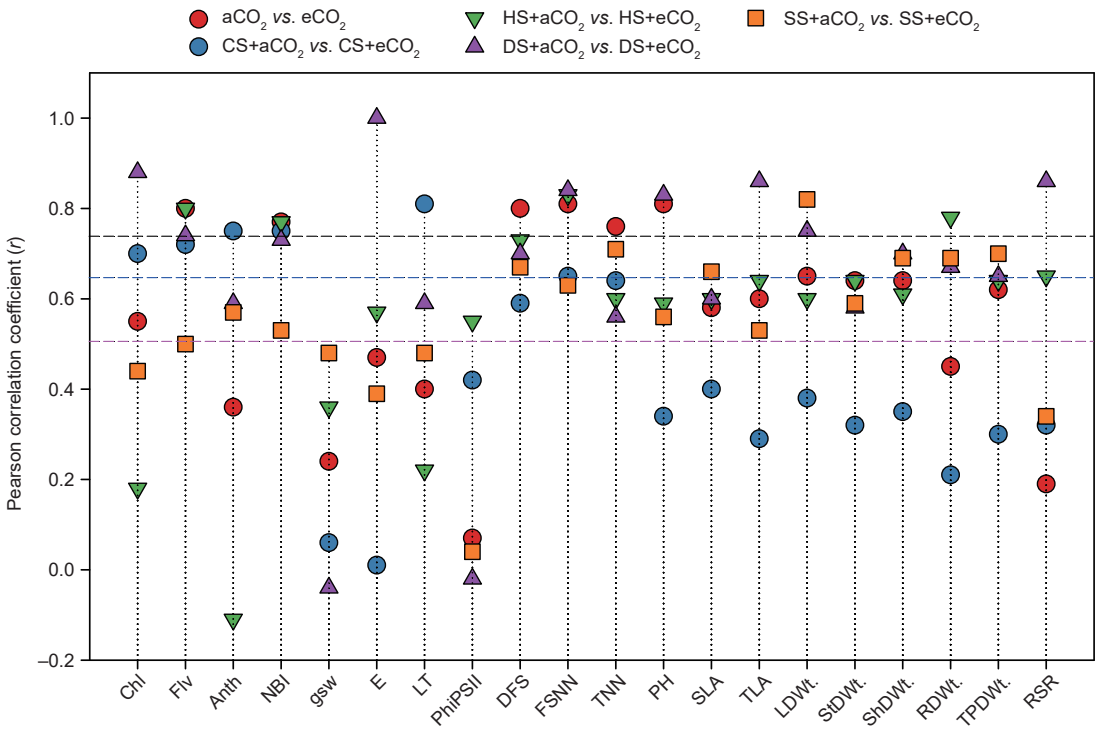


Fig. 7 Correlation of traits between stress treatments at ambient CO_2 (aCO_2) and elevated CO_2 (eCO_2) levels. Correlation coefficients above the black, blue, and pink reference lines are significant at $P<0.001$, $P<0.01$, and $P<0.05$, respectively. CS, chilling stress; HS, heat stress; DS, drought stress; SS, salt stress. Chl, chlorophyll index; Flv, flavonoid index; Anth, anthocyanin index; NBI, nitrogen balance index; gsw, stomatal conductance; E, transpiration; LT, leaf temperature; PhiPSII, quantum efficiency of photosystem; DFS, days to first square; FSNN, first square node number; TNN, total node number; PH, plant height; SLA, single leaf area; TLA, total leaf area; LDWt., leaf dry weight; StDWt., stem dry weight; ShDWt., shoot dry weight; RDWt., root dry weight; TPDWt., total plant dry weight; RSR, root-to-shoot ratio.

mobilizing assimilate reserves from vegetative to reproductive tissues are essential for seed cotton yield (Kloth and Turley 2010). This study found that eCO_2 partially alleviates damage from heat, drought, and salt stresses during the vegetative stage. The results showed variability in trait resilience under stresses and illustrated the interaction of cultivars with stressors at aCO_2 and eCO_2 levels, highlighting the need for tailored ideotypes.

4.1. eCO_2-induced thermal tolerance in cotton cultivars

Both heat and chilling stress adversely affected the growth and developmental traits of cotton at aCO_2 level, suggesting poor thermal acclimation capabilities. eCO_2 levels markedly mitigated heat stress-induced damage to physiological, growth, and development traits, findings consistent with previous studies (Zhang *et al.* 2017; Chavan *et al.* 2019). However, eCO_2 did not mitigate the damage induced by chilling stress. Under both CO_2 levels, pigments in heat-stressed plants remain unchanged. The stomatal conductance was increased under HS+aCO_2, whereas the same trait significantly decreased under HS+eCO_2. This response was reported to be linked to guard cell membrane depolarization (Ainsworth and Rogers 2007) and RBOH1-dependent H_2O_2 production in guard cells (Ahammed *et al.* 2021). Initial increases in stomatal conductance help in cooling the canopy under heat stress (Yousaf *et al.* 2023). However, this strategy poses risks by amplifying the high transpiration demand under low rainfall. In contrast, eCO_2 promotes water use efficiency by minimizing excessive transpiration while still supplying sufficient CO_2 (Ainsworth and Rogers 2007; Leakey *et al.* 2009). This stomatal limitation serving physiological adaptation was observed in plants under HS+eCO_2.

Moreover, eCO_2 improved key growth traits such as height, node number, leaf area, and root biomass of heat-stressed plants compared to HS+aCO_2. The diminished growth under HS+aCO_2 may be attributed to a lower carboxylation-to-oxygenation ratio owing to the reduced affinity of rubisco to CO_2 compared with O_2 (Ainsworth and Rogers 2007). In contrast, eCO_2 enhances this ratio, contributing to the improved growth and biomass accumulation in the HS+eCO_2 (Ainsworth and Rogers 2007; Leakey *et al.* 2009; Huang and Xu 2015). In addition, eCO_2 is known to promote non-structural carbohydrate accumulation, such as glucose and starch, with implications for auxin biosynthesis (Thompson *et al.* 2017). This process may potentially improve root architecture and biomass of heat-stressed cotton plants at the eCO_2. In addition, an increased ethylene production at eCO_2 may stimulate downstream transcription factors like ERF1, enhancing heat shock proteins' expression and consequently offering protection from oxidative damage (Ahammed *et al.* 2021). Furthermore, alterations in meristem function, such as increased cell number and expansion alongside reduced cell cycle duration (Thompson *et al.* 2017),

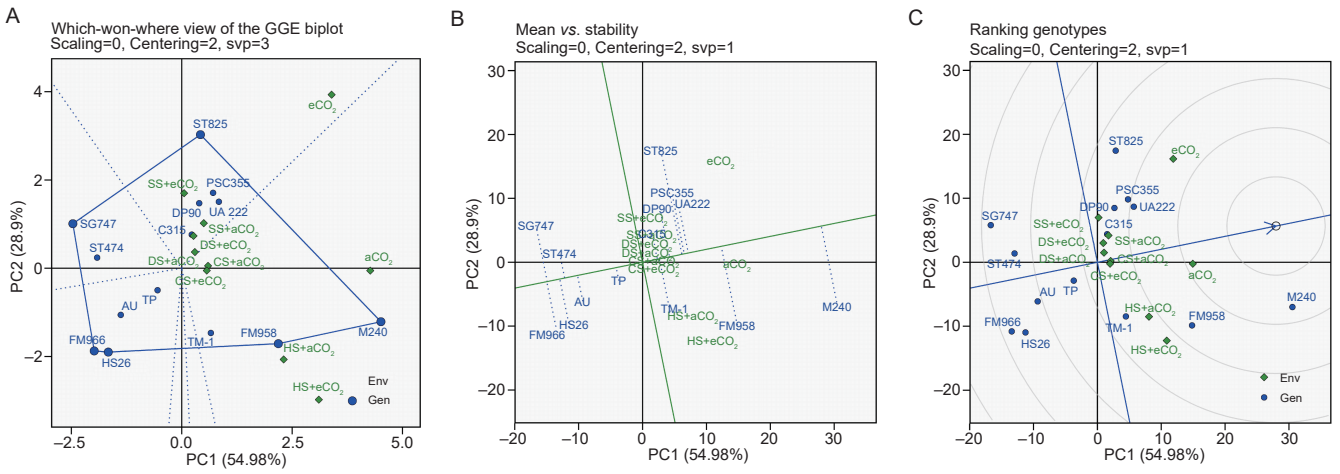


Fig. 8 Which-won-where (A), mean *vs.* stability (B), and ranking genotype plus genotype *vs.* environment interaction (C) biplots based on the total plant dry weight of 14 cotton cultivars. Centering=2 and scaling=0 indicate that environment-centered data without scaling was used in the analysis. The singular value partitioning (svp) of 1 indicates its partitioning only into genotype eigenvectors, whereas the svp of 3 indicates symmetrical partitioning into genotype and environment eigenvectors. Markers for cultivars and environments are represented in blue and green, respectively. In the mean *vs.* stability biplot, the average environment coordinates (AEC) abscissa represents the mean performance of cultivars, whereas dotted lines drawn from the AEC ordinate, regardless of direction, represent stability. In ranking genotypes biplot, a small circle at the center of the concentric circle (indicating the highest mean performance) with an arrowhead (indicating the highest stability) represents the ideal cultivar. aCO_2, ambient CO_2; eCO_2, elevated CO_2; CS, chilling stress; HS, heat stress; DS, drought stress; SS, salt stress.

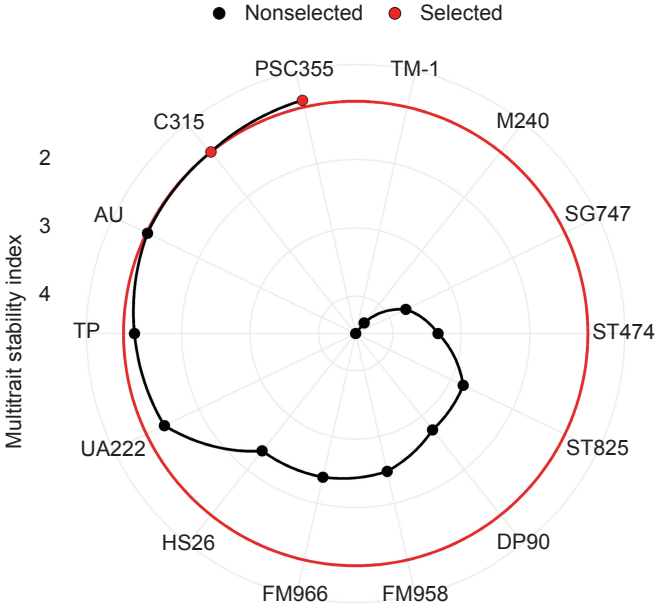


Fig. 9 Ranking of cultivars based on the multi-trait stability index. Red and black markers represent selected and non-selected cultivars, respectively. The higher the distance of the cultivar from the concentric circle, the higher the multi-trait stability index value and *vice versa*.

might have contributed to increased height and overall growth of plants under HS+eCO_2.

Our data suggest that even under optimum temperature, eCO_2 causes a decline in stomatal conductance due to the closing of their stomata and leads to a slight increase in leaf temperature. Further, eCO_2 under chilling negatively aggregated this response due to reduced enzyme activity involved in stomatal opening and closing, decreased ability of guard cells to respond to low air temperature, and overall decrease in energy production. In addition, damage to chloroplast integrity, reduced leaf area, compromised rubisco stability, or inactivation of enzyme activities under chilling could potentially cause weaker performance of cotton under chilling with varied CO_2 (Zhou *et al.* 2006; Thompson *et al.* 2017). These results indicated that eCO_2 can exacerbate the chilling effect in certain situations, rather than mitigating. Thus, further investigations are needed to explore the relationship between chilling stress and eCO_2 (Boese *et al.* 1997; Arena and Vitale 2018).

4.2. Partial mitigation of drought stress damage on cotton cultivars at the eCO_2 level

In this study, cotton plants showed increased levels of anthocyanin and flavonoid under DS+eCO_2 compared to DS+aCO_2. This indicates that eCO_2 may mitigate oxidative damage in drought-stressed plants (Li *et al.* 2024). However, chlorophyll level was significantly lower in DS+eCO_2 relative to DS+aCO_2, potentially attributed to changes in nitrogen metabolism (Leakey *et al.* 2009; Thompson *et al.* 2017). While eCO_2 did not affect drought-induced damage to physiological traits, it mitigated damage to growth and development traits, as seen in other C_3 plants (Barickman *et al.* 2021a, b; AbdElgawad *et al.* 2023; Li *et al.* 2024). The mechanisms for this response remain unclear (AbdElgawad *et al.* 2023). Potentially, the eCO_2-induced overcoming of stomatal limitations might have improved photosynthetic rate (Ainsworth and Rogers 2007; Leakey *et al.* 2009). In addition to the direct effect *via* increased photosynthesis, activated sugar-sensing pathways (Thompson *et al.* 2017) and glucosinolate biosynthesis (AbdElgawad *et al.* 2023) likely contributed to improved growth and development under

DS+eCO_2. Further, potential mitigation of oxidative damage accompanied by upregulation of genes related to peroxidase and proline synthesis might have improved vegetative vigor in cultivars like ST825 and PSC355 under DS+eCO_2 (Li *et al.* 2024).

4.3. Improvements in pigments, physiology, and vigor of salt-stressed cotton at eCO_2 level

Cotton is generally considered a glycophytic field crop compared to other crops (Ashraf 2002; Maryum *et al.* 2022). However, our findings revealed a significant negative impact of salt stress on both the physiological processes and developmental traits of cotton (Figs. 2–5). Previous research corroborates these findings in cotton *via* osmotic stress, ion toxicity, and nutritional imbalances (Ma *et al.* 2021; Nawaz *et al.* 2023). In this study, salt-stressed plants had higher anthocyanin and flavonoid at aCO_2 compared with eCO_2, suggesting eCO_2-induced mitigation of oxidative damage. Mirroring patterns were seen under drought stress (Li *et al.* 2024). eCO_2-induced mitigation further indicated that eCO_2 could trigger adaptive mechanisms for salt stress tolerance, such as osmotic adjustments and ion homeostasis (Huang and Xu 2015; Lv *et al.* 2024). Increased growth and photosynthetic functions in salt-stressed cotton under eCO_2 are consistent with findings from other C_3 crops like soybean (Lv *et al.* 2024). The reductions in stomatal conductance and transpiration rates in salt-stressed plants at aCO_2 compared with aCO_2 alone were further reduced under eCO_2, suggesting improved osmotic tolerance and water use efficiency. Key growth traits such as leaf area, plant height, and root and shoot biomass were increased, likely owing to decreased stomatal limitation/enhanced CO_2 availability for photosynthesis (Huang and Xu 2015). Hormonal changes related to sugar sensing may also have contributed to this growth enhancement, comparable to mechanisms in heat and drought-stressed plants at eCO_2 (Thompson *et al.* 2017). Additionally, an increased accumulation of soluble sugars at eCO_2 might have contributed to reducing Na^+ ion toxicity and promoting osmotic adjustments in salt-stressed cotton. Further, increased ATPase activity under eCO_2 may have improved Na^+ exclusion boosting salt stress tolerance (Geissler *et al.* 2010).

4.4. Stability of traits and cultivars under stresses at aCO_2 and eCO_2 levels

Most growth and development traits exhibited a strong positive correlation between aCO_2 and eCO_2 levels across all environments except for chilling (Fig. 7), underscoring similar manifestations of eCO_2-driven improved vegetative vigor under stresses like optimal conditions. However, the associations of physiological traits were generally weaker between CO_2 levels, indicating differential physiological adaptations and tolerance mechanisms under different stresses (Huang and Xu 2015). These variabilities in trait relationships suggested that the mechanisms for alleviating one type of stress damage may not be the same for others. Cultivars such as TP and AU exhibited broad adaptability, while others, such as M240, demonstrated narrower adaptability across the environments, highlighting the significance of determining G×E interaction. The observed crossover effects emphasized the necessity for diverse genotype panels in stress physiology studies. Differential ranking of cultivars like PSC355 and M240 based on vigor and MTSI (Figs. 8 and 9) suggested that selection based on a single trait might not be reliable for developing multi-stress tolerant cultivars under eCO_2. Ultimately, results emphasized that the significance of vigor in cotton or any other crop under stress is meaningful only if that cultivar can maintain high performance and stability across various stress conditions.

The study highlights cultivars' varied sensitivity and adaptation to different stresses at varying CO_2 levels. Thus, present stress mitigation strategies may not be effective at future CO_2 levels, indicating the need to focus on unique selection traits suited for these conditions. Results also emphasize the importance of incorporating novel traits into breeding programs for developing stress-tolerant cotton varieties for future environments. While the research primarily examined vegetative growth, considering the primary effects of CO_2 on vegetative organs, further research is needed to explore the interactions between these treatments and their impacts on cotton yield and quality.

5. Conclusion

The impact of abiotic stressors on the vegetative vigor of cotton cultivars at aCO_2 was highest under chilling stress, followed by drought, salt, and heat. Cotton cultivars displayed the complex interaction between eCO_2 and abiotic stresses. eCO_2 partially mitigated the damage induced by all stresses (heat, drought, and salt) except chilling through improvement in pigments, physiology, or growth and development traits. Mitigation of stress-induced damage by eCO_2 on total plant dry weight followed the order: HS>SS>DS. The phenotypic expression of traits was significantly affected by the interaction between cultivars and the stress environments at aCO_2 and eCO_2 levels. Cultivar PSC 355 was identified as a multi-stress tolerant cultivar at both aCO_2 and eCO_2 levels compared to other cultivars. These findings highlight the need to consider eCO_2 while designing breeding targets for future cotton-growing environments. Further, cotton breeders and physiologists may have to prioritize formulating ideotypes for developing unique stress-tolerant varieties for future CO_2 levels.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

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