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Exploring Adaptative and Susceptible Mechanism in Selected Tomato Genotypes Employing Physiological Modulations and Antioxidative Pathways under Drought Stress

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ABSTRACT

Background: Drought is a critical abiotic stress that affects the productivity, growth and yield of crops. The current study was evaluated to screen six widely grown tomato (*Solanum lycopersicum*) genotypes *viz*, Shivam, Siri, Bhagyashree, Arka Samrat, Arka Rakshak, Arka Apeksha, in the south part of India to drought stress.

Methods: The studies were performed mostly on leaves in pot experiments using a complete randomized arrangement (CRD), polybags were divided into two sets for each genotype-one set of polybags consist of four bags were given drought treatment by withholding irrigation for 10 days which includes sampling days and another set of polybags consisting of four bags were routinely watered considered as a control for preceding sampling days. The set standard protocols were used for each experiment conducted.

Result: This studies on morpho-physiology showed a significant reduction along with oxidative damage in all genotypes including increase in malonaldehyde content (MDA content) and hydrogen Peroxide and superoxide radical localization that led to increase in antioxidative activity such as superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX), as well as their isozymes. Photosynthetic parameters such as the net photosynthesis rate, stomatal conductance and *Fv*/*Fm* and other related measurements drastically decreased in drought-stressed plants. Moreover, stomatal structure showed flaccid guard cells and the closure of the stomata in all genotypes of tomatoes, but with fewer variations in 'Arka Samrat' and 'Shivam'.

Key words: Drought, Photosynthetic mechanisms, Physiological modulations, *Solanum lycopersicon.*

INTRODUCTION

Drought is a state of water scarcity caused by low rainfall over an extended period of time, as well as an increase in air temperature and atmospheric CO_2 (Seleiman *et al*., 2020). Drought stress is a prominent abiotic stress factor that significantly diminishes grain yields on a global scale, so exerting an adverse impact on the food requirements of an expanding global population (Tester *et al*., 2010; Razi and Muneer, 2023). Morphologically, drought stress results in reduced leaf area, plant height, root architecture, biomass and early leaf senescence (Ranjan *et al*., 2022). Drought stress also impairs photosynthesis as well as other important physiological activities, like synthesis of chlorophyll, nutrients, uptake of ions, translocation, respiration and carbohydrate metabolism (Ximénez-Embun *et al*., 2016; Muneer *et al*., 2016; Hou *et al*., 2019; Kumar *et al*., 2021; Razi *et al*., 2021). As a result, drought stress also upshots imbalance between the production and utilization of electrons that lead to the production of reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2) and the hydroxyl radical (OH). Drought stress furthermore triggers metabolic processes, including the production of sugar, carbohydrates, lipids and growth hormones (Mahantesh *et al*., 2018; Gupta *et al*., 2020; Yang *et al*., 2020; Kapoor *et al*., 2020). The traditional approaches to crop enhancement *via* plant breeding are tedious and time-consuming (Olivieri, 2020). The effects of climate change on farmers are growing more evident and it suggests a greater implementation of diversified

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agricultural systems may be a successful way of including resilience into agricultural systems.

Tomato (*Solanum lycopersicum* L.) is sensitive to drought stress and is directly affected by it as reduces its growth, yield and fruit quality and is also at the risk of several diseases (Zhao *et al*., 2021). Tomato is one of the perishable vegetable crops that is widely cultivated worldwide but its production is limited due to drought stress. Drought stress inhibits the tomato yield and fruit quality (Liang *et al*., 2020). It has been also observed that drought stress reduced the relative water content and abscisic acid (Liu *et al*., 2023). In other studies, it has been observed drought negatively affected physiological characteristics and hormones such as indole acetic acid, gibberellic acids and salicylic acid (Turan *et al*., 2023). Tomatoes grown in regions with high temperatures and difficult growing conditions are at the verge of significant economic. The future of tomato production and food security relies on conservation efforts to preserve tomato genetic resources, but it is unclear what those efforts involve or how successful they will be. Thus, it is hypothesized that characterizing the vast tomato genetic diversity is crucial for the development of more resistant cultivars. It has been hypothesized that traits like resilience to drought could exist on a variety of scales, from genes and proteins to physiological mechanisms (Conti *et al*., 2023). A number of studies has been focused on drought stress mechanisms by conventional or nonconventional ways to mitigate it (Manonmani *et al*., 2025; Mahala *et al*., 2025). The current study focused on finding a drought-resilient rootstock in one of the major horticultural crops: tomato by analyzing its morpho-physiochemical properties, photosynthetic mechanisms and antioxidative properties. Tomato is a common vegetable crop and has high economic significance as well as several favorable genetic and agronomic features. In addition, tomato is a model plant among horticultural crops due its genetic traits, thus to progress its quality and resistance to abiotic stresses including drought must be addressed.

MATERIALS AND METHODS

Plant material and treatments

Three genotypes of *Solanum lycopersicum* (tomato): Shivam, Siri-9005 and Bhagyashree were collected from a locally situated government-certified seed vendor (named Rajamanickam seed shop) while the rest of the three tomato genotypes: Arka Samrat, Arka Rakshak and Arka Apeksha, were purchased from the Indian Institute of Horticulture Research, India, Bengaluru. Three genotypes that are Shivam, Siri-9005, Bhagyashree from the local shops were collected based on their growth in local farming areas, whereas IIHR genotypes were collected based on their susceptibility and resistance towards stress.

The collected seeds from all genotypes were surface-sterilized with 1% sodium hypochlorite followed by distilled water, 3-4 times. The sterilized seeds were sown in portrays filled with red soil, sand and vermicompost, with a ratio of 1:1:1. The trays were kept in the greenhouse with a photoperiodism of 12 hours light and 12 hours dark in School of Agriculture Innovation and Advance Learning, Vellore Institute of Technology, Vellore, India from 2020-2023. The maximum temperature was 25-30°C and the relative humidity of 60-80%. After 25 days of germination, the seedlings were transferred to polybags (24 × 24 × 40 cm) filled with the mixture mentioned above. In each bag, 2 seedlings were transplanted and kept for acclimatization for 15 days until the 40th day. Then, using a complete randomized design (CRD), polybags were divided into two sets for each genotype-one set of polybags consist of four bags were given drought treatment by withholding irrigation for 10 days which includes sampling days and another set of polybags consisting of four bags were routinely watered considered as a control for preceding sampling days. The drought severity well thought-out to be low (5th day) and moderate (10th) for treatment. The drought conditions were measured by moisture sensors along with pH and electrical conductivity. The pH and EC were maintained to 5.6 and less than 2 dS/m. After drought treatments, the mature leaf samples were pooled down at all the nodes on the 5th and 10th day of the drought treatment and kept at -80°C for further experimentation.

Morphological characteristics

The morphological measurements, including height of the plant, shoot length and root length, were measured in centimeters by uprooting the plants carefully from the grow bags. The uprooted plants were then washed with distilled water, measured with a measuring scale and recorded.

Relative water content

The relative water content (RWC) percentage was measured concurring to Turner and Kramer (1978).

MDA and proline content

For determining lipid peroxidation, also known as malondialdehyde (MDA), approximately 0.5 g of fresh samples were homogenized with 5 mL of 1% (*w*/*v*) TCA (Tricarboxylic acid) and centrifuged at 7000 × g for 10 min according to Heath and Packer (1968).

For estimation of proline, 0.3 g of fresh leaf samples were homogenized in 5 mL of 3% (*w*/*v*) sulfosalicylic acid in a chilled mortar and pestle and centrifuged for 20 min at 3300× *g* at 4°C. Following that, 2 mL of aliquot was mixed with 2 mL of glacial acetic acid and 2 mL of acid ninhydrin. The samples were incubated at 100°C in a water bath for 1 h and absorbance was taken at 520 nm using spectrophotometer. The standard curve for proline was performed according to Bates *et al.* (1973).

Localization of stress markers H_2O_2 and O_2^{-1}

For H_2O_2 and O_2^{-1} localization, fresh leaves were taken and then immersed in a 0.1% solution of 3,3′-diaminobenzidine (DAB) and nitro blue tetrazolium (NBT) for 12 h in dark condition to avoid oxidation after vacuum infiltration. Then,

the leaves were submerged in 90% boiling ethanol for bleaching for 2 h in a water bath. The leaves were visualized with brown and blue spots respectively and documented using a digital camera.

Determination of photosynthetic parameters

SPAD meter-502DL (Konica Minolta, Tokyo, Japan) was used to determine the net photosynthesis rate, transpiration rate and stomatal conductance. SPAD values (chlorophyll values) were recorded and the equations based on the modulations given by Hutingford *et al*. (2015) were used to derive the net photosynthesis rate, transpiration rate and stomatal conductance.

A mini-PAM 2000 chlorophyll fluorescence meter (Heinz Walz, GmbH, Zarges 40,860, Weilheim, Germany) was used to measure F_v/F_m, that is, chlorophyll fluorescence. The leaves were kept in dark conditions using black clips for 30 min before taking measurements. PSII quantum yield (*Fv*/*Fm*) was calculated from:

$$\frac{F_v}{F_m} = \frac{(F_m - F_0)}{F_m}$$

Scanning electron microscope

Fresh leaves were collected and cut into squares of 1 cm × 1 cm and immersed in 2 mL of glutaraldehyde for 5 h at 4°C. Following fixation, the leaves were washed in ethanol series and were observed under a scanning electron microscope (Model: EVO-18 Research, Carl Zeiss, Dublin, CA, USA).

Antioxidant enzyme activities and their relative staining

Superoxide dismutase (SOD) was performed according to Dhindsa (1981); approximately 0.2 g fresh leaves were taken and homogenized in an extraction buffer containing 0.5 M of K-Phosphate buffer (pH 7.5), 1% of PVP, 1% Triton X-100 and 3 mM of EDTA, following which centrifugation was conducted at 15,000× *g* for 20 min at 4°C followed by a reaction mixture and absorbance was taken at 450 nm.

Catalase was performed according to the method of Aebi (1984); 0.2 g of fresh leaves were taken and homogenized in extraction buffer same for SOD. The absorbance was taken at 240 nm immediately after adding H_2O_2.

Ascorbate peroxidase (APX) was performed according to Law *et al*., (1983); the extraction buffer was the same as in the catalase activity. The absorbance was taken at 290 nm using spectrophotometer.

The antioxidant enzymes (30 µg) were electrophoresed in 10% resolving gel and 4% stacking gel for the APX and CAT isozymes, respectively, for native staining. The SOD isozymes were separated using 15% resolving gel and 5% stacking gel at 4°C for 4 hours at 80 V in a Tris-Glycine (pH8.3) running buffer. In accordance with Al Murad and Muneer (2023), the isozymes of SOD, CAT and APX were actively stained.

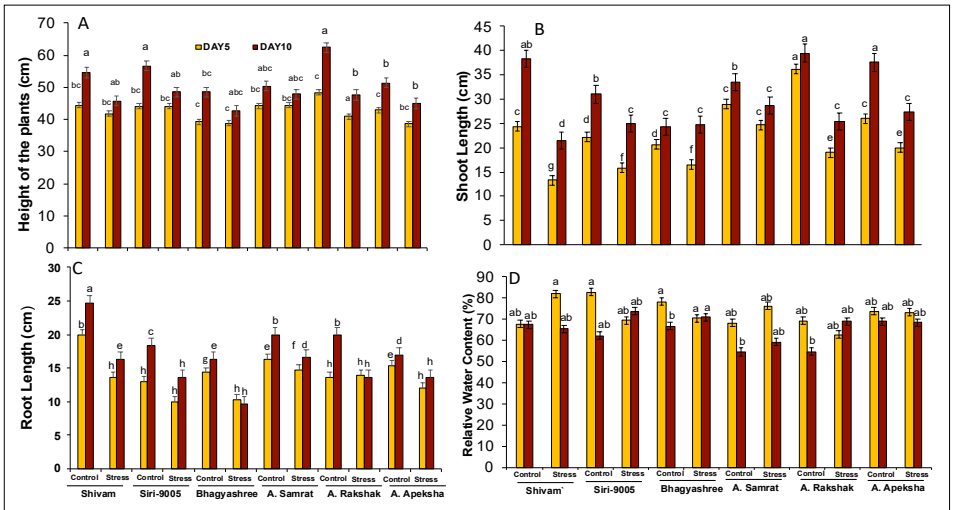
Statistical analysis

Statistical analysis software (SAS)-JMP PRO-17 tools (Cary, NC, USA) were used to conduct the statistical analysis. Three biological replicates and a totally randomized design were employed, with a significance threshold of $p<0.05$. The mean ± SE was used to express all of the results.

RESULTS AND DISCUSSION

Morphology and relative water content

The length and height of all the tomato genotypes reduced significantly on day 5 of the drought treatment and this was more pronounced on day 10 of the drought treatment (Fig 1). Relative water content is an important factor to determine



Vertical bars indicate mean±S.E. for *n* = 3. Means denoted by different letters are significant at $p \leq 0.05$ according to Tukey's studentized range test.

Fig 1: Changes in (A) height of the plant, (B) shoot length, (C) root length and (D) relative water content in tomato (*Solanum lycopersicum*) genotypes Shivam, Siri-9005, Bhagyashree, Arka Samrat, Arka Apeksha and Arka Rakshak, along with their controls.

water content in plants. In our studies relative water content significantly increased in all genotypes except for Shivam. A maximum increase of 25.91% in RWC was observed in Arka Rakshak and a minimum decrease of -2.97% was observed in Shivam under drought stress. This indicated that genotype Arka Samrat a significant resistant towards drought stress.

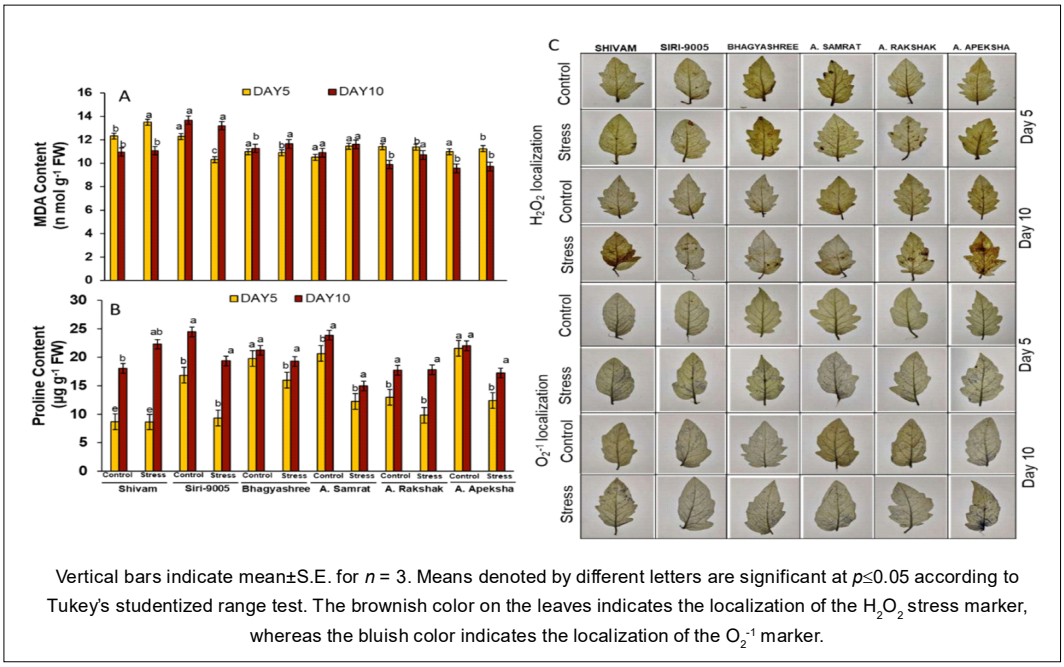
Tomatoes, like other crops, are vulnerable to drought stress due to their high irrigating requirements. Under drought conditions, the roots, shoots and height of the plants were significantly reduced in all genotypes; however, fewer variations were observed in the Shivam and Arka Samrat genotypes. This is due to the reason that under drought stress; root formation is severely affected by water deficit that will ultimately lead to lower absorption of water and cell rigidity (Hura *et al*., 2022; Ahmad *et al*., 2022). Due to less absorption and deformed roots the relative water content in all tomato genotypes was also hampered, with limited variations in Shivam and Arka Samrat (a potentially resilient genotype). A similar observation was made in tolerant varieties of peas (Upreti *et al*., 2000), okra (Razi and Muneer, 2023), wheat (Guizani *et al*., 2023). However, osmotic adjustment or changes in cell wall elasticity can improve the water status of tissues and can maintain the water influx and turgor pressure that is crucial for sustaining physiological activity during prolonged periods of drought (Al-Yasi *et al*., 2020).

Stress marekrs and photosynethsis

Drought-stressed genotypes have higher MDA (malondialdehyde) levels due to lipid peroxidation. On day 10 of drought treatment, Shivam, Arka Samrat and Arka Apeksha genotypes had significantly lower MDA content than day 5 (Fig 2A), from 9.81% to 1.13%, 9% to 6.52% and 2.27% to 1.54%, respectively. Other MDA levels increased from 16.16% to 3.42 in Siri-9005, 0.65% to 3.29% in Bhagyashree and 0.47% to 8.04% in Arka Rakshak on day 10. As an osmolyte, proline increases under plant stress and functions as a stress-responsive marker. On day 5 of drought stress, all tomato genotypes had a significant reduction in proline content (Fig 2B), but on day 10, Shivam, Siri-9005, Bhagyashree, Arka Samrat, Arka Rakshak and Arka Apeksha had significant increases of 23.50%, 20.73%, 9.12%, 37.23%, 0.50% and 21.71%, respectively.

Drought stress reduced all photosynthetic parameters. On day 10 of the drought-stress treatment, a significant reduction in the stomatal conductance and net photosynthesis was observed, while an increase in the transpiration rate was found in all tomato genotypes compared to their respective controls (Fig 3). However, a slight induction of all photosynthetic parameters was observed in the Arka Samrat and Shivam tomato genotypes. A subsequent change in the PSII quantum yield was observed in all genotypes although no or limited change was observed on day 5 of drought stress (Fig 3D). Meanwhile, a significant change was observed on day 10 of drought stress, particularly in genotypes such as Arka Samrat and Shivam.

Reactive oxygen species are produced in cytosol along with chloroplast and any kind of stress including drought, disturbs the photosynthetic pathway (Vijayaraghavareddy *et al*., 2022) particularly during non-cyclic phosphorylation.



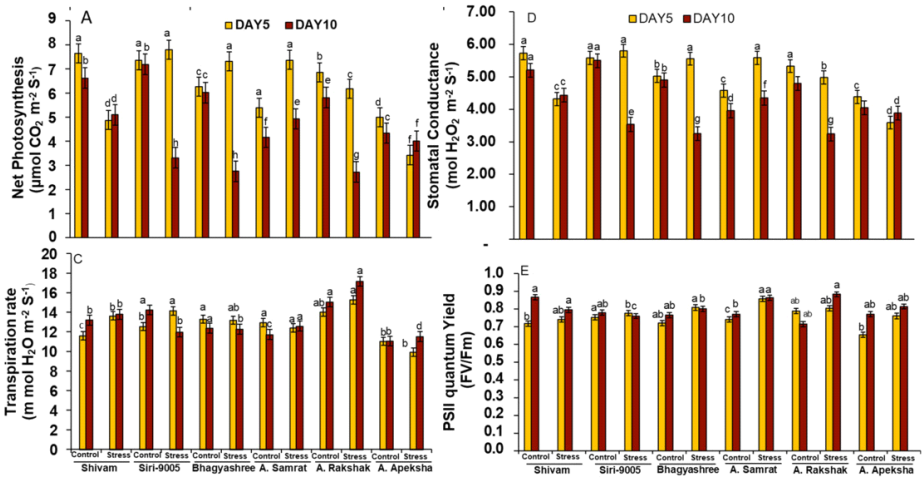
Vertical bars indicate mean±S.E. for $n = 3$. Means denoted by different letters are significant at $p \leq 0.05$ according to Tukey's studentized range test. The brownish color on the leaves indicates the localization of the H_2O_2 stress marker, whereas the bluish color indicates the localization of the O_2^{-1} marker.

Fig 2: Changes in (A) malonaldehyde content, (B) proline content, (C) histochemical localizations of H_2O_2 and O_2^{-1}, in tomato (*Solanum lycopersicum*) genotypes Shivam, Siri-9005, Bhagyashree, Arka Samrat, Arka Apeksha and Arka Rakshak, along with their controls.

The foremost disturbance is observed for pigments and membrane proteins of chloroplasts (Nankishore and Farrell, 2016; Zhuang *et al*., 2020). The short-term drought has no effect on the efficiency of the PSII's primary photochemical processes or the associated *Fv*/*Fm* percentage (Baker *et al*., 2004). When g_s decreased, photorespiration stepped in for the ATP and the NADPH protected the PSII from damage (Slabbert *et al*., 2014), which explains why the *Fv*/*Fm* of the genotypes was not affected by the drought treatment. Therefore, whereas the *Fv/Fm* in vitro was useful in a prior work, the *Fv/Fm in vivo* is not a useful metric for differentiating genotypic variance in tomatoes under drought stress (Lin *et al*., 2006). In our study, the PSII quantum yield was not significantly different between day 5 and day 10 of the drought-stress conditions, whereas some differences were observed in the genotypes of Arka Samrat and Shivam.

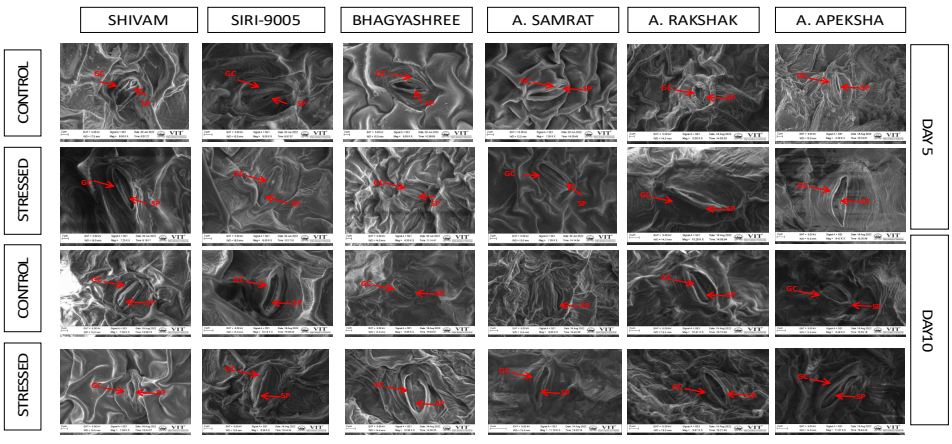
Stomatal structure

The scanning electron microscope gave us a clear structure of the stomata in drought-stressed tomatoes (Fig 4). The stomata were partially closed in genotype 'Shivam' and



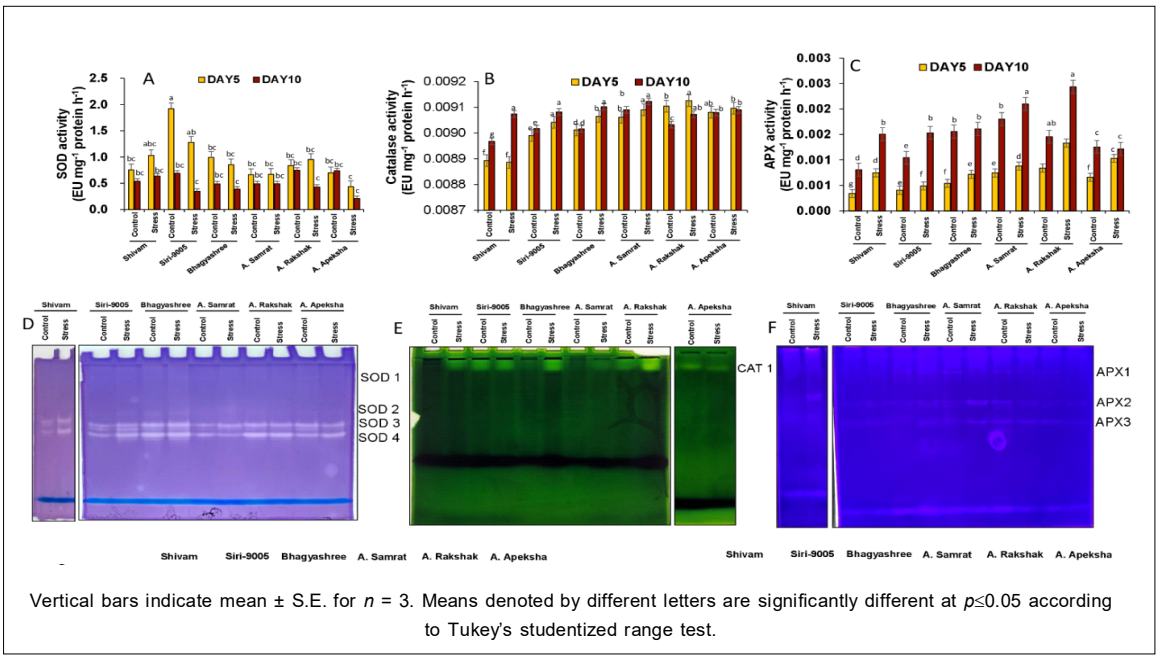
Vertical bars indicate mean±S.E. for n = 3. Means denoted by different letters are significant at $p \leq 0.05$ according to Tukey's studentized range test.

Fig 3: Changes in (A) net photosynthesis rate, (B) stomatal conductance, (C) transpiration rate and (D) PSII quantum yield in tomato (*Solanum lycopersicum*) genotypes Shivam, Siri-9005, Bhagyashree, Arka Samrat, Arka Apeksha and Arka Rakshak, along with their controls.



Observed under a scanning electron microscope (SEM). GC indicates guard cells and SP indicates stomatal pores.

Fig 4: Representative images of stomata as affected by drought stress in tomato (*Solanum lycopersicum*) genotypes Shivam, Siri-9005, Bhagyashree, Arka Samrat, Arka Apeksha and Arka Rakshak, along with their controls.



Vertical bars indicate mean ± S.E. for n = 3. Means denoted by different letters are significantly different at $p \leq 0.05$ according to Tukey's studentized range test.

Fig 5: Changes in activities of (A) superoxide dismutase, (B) catalase, (C) ascorbate peroxidase and their (D-F) isozymes in tomato (*Solanum lycopersicum*) genotypes Shivam, Siri-9005, Bhagyashree, Arka Samrat, Arka Apeksha and Arka Rakshak, along with their controls.

'Arka Smart' on day 5 and closed on day 10 of drought stress with redundant guard cells and subsidiary cells. In genotype 'Siri-9005', 'Bhagyashree', 'Arka Apeksha' and 'Arka Rakshak' stomal pore was completely closed followed by shrunken guard and subsidiary cells in day 10 and partially closed in day 5 of drought stress.

In a related study, it was discovered that the stomatal index directly correlates with photosynthesis and its structure, as observed previously in other crops such as oilseed (Muneer *et al*., 2013). The vascular bundles, in particular those that are associated with the plant stems, play a significant role in the process of water absorption (Razi *et al*., 2021). The transport of water was severely hindered during drought stress due to redundant vascular bundles, which ultimately resulted in wilted leaves, stomatal conductance, stomatal structure such as guard cells and epidermal cells. Okra (Razi *et al*., 2021) and tomato (Muneer *et al*., 2016) both exhibited a similar pattern of behavior when subjected to the effects of drought.

Enzyme activities and their isoforms

Plants/crops generate antioxidant enzymes to sustain ROS during abiotic stress, especially drought. In our results drought stress revealed three primary antioxidant enzymes and their isoforms in all tomato genotypes (Fig 5). On day 10 of the drought treatment, stressed tomato genotypes had considerably lower superoxide dismutase (SOD), a prominent stress enzyme (Fig 5A), except Shivam and Arka Samrat. All isoforms of SOD, including SOD2, SOD3 and SOD4, showed their maximum expression in all genotypes except Arka Samrat and Shivam. Our investigation indicated that drought stress enhanced catalase activity by 50-60% on days 5 and 10 compared to the control (Fig 5B). Arka Samrat and Apeksha genotypes showed a greater induction, which was validated by catalase isomer expression. In tomato genotypes under drought stress, another antioxidant, ascorbate peroxidase (APX), was also significantly induced (Fig 5C), with Shivam and Arka Samrat being most induced. APX2 and APX3, like other antioxidant enzyme isomers, showed considerably greater expression in all genotypes on day 10 of drought stress (Fig 5F). The total antioxidant enzymes and their isoforms showed that Shivam and Arka Samrat are drought-resistant, whereas the other genotypes are vulnerable. In contrast, antioxidant enzymes are crucial for reducing the effects of abiotic stress in all its forms. In our study, the activities of antioxidant enzymes such as CAT, APX and SOD were measured in all six tomato genotypes under drought stress. The results showed that under stress conditions, the activity of CAT, SOD and APX increased in all genotypes compared to their respective controls (Fig 5A-C). Under drought stress, genotypes such as Arka Samrat, Arka Apeksha and Shivam had the highest enzyme activities for CAT and APX; meanwhile, Shivam and Arka Samrat had a higher SOD activity compared to the other genotypes in drought conditions. Increased antioxidant activity is one of the stress-resistance strategies used by the tolerant tomato genotype, which supports them in scavenging hydrogen peroxide from the water in their chloroplasts, thus detoxifying them.

The drought-stressed plants showing a higher expression than the control variety indicated the presence of O_2^{-1} radicles in various parts of the cells including the

chloroplast, cytosol, peroxisome and mitochondria. As mentioned earlier, the Fe-SOD and Zn/Cu-SOD were abundantly found in the chloroplast and cytosol. A band also appeared in the PAGE gel for the CAT activity, showing the difference in expressions of all the genotypes between the drought and control conditions. Compared to CAT or guaiacol peroxidase, APX has a stronger affinity with H_2O_2 and scavenges it using ascorbate as a reductant (Soltys-Kalina *et al*., 2016). The overall isozyme activity, along with their respective activities, demonstrated that the Arka Samrat and Shivam genotypes are resistant to drought stress compared to the other genotypes; we can conclude that they can act as resilient rootstocks.

CONCLUSION

Tomatoes are a well-known vegetable crop in India, with significant commercial value as well as numerous potential genetic and agronomic characteristics. Drought stress is one of the most damaging abiotic stress on development and productivity of crops, jeopardizing long-term agricultural output. Drought stress causes a regular reduction in CO_2 integration rates, leaf size, stem extension and root proliferation, which disrupts water relations, lessens the water-use efficiency, interrupts photosynthetic pigments and decrease other necessary physiological parameters, all of which have a negative impact on plants. To select robust genotypes, this study assessed different tomato genotypes using physiological and photosynthetic approaches. Following screening, we established that the Shivam and Arka Samrat tomato genotypes are drought resistant. The robust tomato genotypes seen in our study will also be selected as scions for the plant, while the drought-resistant tomato genotypes will be used as rootstocks in the next phase of the work. The best grafted tomato will be sold for seed production following the second phase of yield analysis.

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Author contributions

Conceptualization and supervision of work (Sowbiya Muneer); Experiments and original draft of manuscript; performed the experiments and wrote the manuscript (Pritam Paramguru Mahapatra); helped in performing protein analysis (Dong Won Bae); helped in statistical analysis of data (Muthu Arjuna Samy Prakash); Edited and finalizing manuscript (Sowbiya Muneer).

Disclaimers

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Informed consent

Not applicable.

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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