Journal
Of the
Oriental Institute
M.S. University of Baroda

ISSN: 0030-5324
UGC CARE Group 1

ANALYSIS OF DROUGHT RESILIENCE, GROWTH AND RECOVERY IN TOMATO SEEDLINGS WITH PGPR-BIO-PRIMING

Deepmala Singh[1]
Plant Physiology Laboratory, Department of Botany,
Government Raza PG College, Rampur- UP, India.
Corresponding author: dr.dsingh7@gmail.com

Arpita (Banerjee) Mukherjee[2]
Department of Botany, Dum Dum Motijheel College, Kolkata- W. Bengal, India.

Abstract

The present study was conducted on a highly commercialized crop plant- tomato, a rich source of vitamin A, C and E, as well as minerals. Several antioxidants and phenolic compounds are also present. Tomato is cultivated worldwide for its high nutritional value. Undenied fact is that healthy seedlings ensure the healthy yields so it is necessary to understand the possible threats of scarcity of water to seedling growth. As we know mature plant have several stress management strategies so it is interesting to find the effect of stress at seedling stage. Healthy seeds of tomato were surface-sterilized then subjected to inoculation with plant growth-promoting rhizobacteria (PGPR). A mixture of *Azotobacter* and *Bacillus polymyxa* (1:1) was used as PGPR. Inoculated and non-inoculated seeds were grown and the seedlings were subsequently exposed to water stress for 2, 3 and 5 days respectively. Various biochemical tests were conducted in order to determine the impact of mild and severe water stress on inoculated and non-inoculated plants. We found that plants which are inoculated with PGPR exhibited a lower impact of water stress and showed a higher recovery rate in comparison to non-inoculated plants. However, mild stress had no significant impact on plant health, and plants recovered better when rewatered. Severe stress had negative effect on photosynthetic pigments and protein content while proline and carotenoids were increased. Inoculated seedlings exhibited lower MDA content, indicating reduced lipid peroxidation. This study highlights the beneficial effects of PGPR in improving drought tolerance and recovery in tomato seedlings. The findings support the use of PGPR as an eco-friendly strategy to enhance crop productivity under water-deficit conditions, offering a sustainable approach to agricultural management in stress-prone environments.

Keywords: PGPR, water stress, lipid peroxidation, compatible solute, inoculation

Abbreviations

MDA- malondialdehyde
PGPR- plant growth-promoting rhizobacteria
ROS- reactive oxygen species
RWC- relative water content

ISSN: 0030-5324
UGC CARE Group 1

Introduction

Environmental stresses impair plant growth and productivity (Abd Al-Shammari et al., 2020). Almost every plant once in its lifetime faces such stresses. These environmental stresses includes high and low temperatures, salinity, heavy metals, flood and drought. Most plants have already devised protective mechanisms against different types of stresses (Vendrusculo et al., 2007). For example, plants growing in saline region develop adaptations such as limiting uptake of dissolved salt by roots, special storage for salt in vacuoles to protect cells, production of compatible solutes, etc. To avoid temperature shock in form of heat, plants possess specialized receptors in the plasma membrane, increase membrane fluidity in response, and adjust rate of transpiration for cooling effects by managing opening and closing of stomata. In response to cold stress, antifreeze proteins are produced to prevent ice crystal damage. Additionally, well-grown root system and low transpiration rate are some adaptations of plants that survive in water-scarce conditions for long periods (Fazeli et al., 2007).

Among all abiotic stresses, drought is the most unavoidable. Commercial crops of arid and semi-arid regions are more likely to be more negatively impacted by drought due to irrigation deficit. According to Yang et.al (2010), one-third of world's land area experiences drought which is quite harmful for plant growth and food production. Scarcity of water during initial stages of plant negatively affects germination, root and shoot length, elongation and leaf development (Yordanov et al., 2003; Singh 2021). Severe water stress leads to membrane leakage, cell wall damage, inhibited photosynthesis and disrupted ion uptake (Taiz and Zeiger, 2006).

Tomatoes are considered the second most important crop of economic significant worldwide (Chandrasekaran et al., 2019). They are rich source of vitamin A, C and E, as well as minerals. Several antioxidants such as carotenoids and phenolic compounds are also present. Tomatoes are cultivated for their high nutritional values (Adalid et al., 2004). Water deficits severely affect growth and reduce yield quality (Abd Al-Shammari et al., 2020).

Plants device several short-term mechanisms to protect themselves from harmful effects of abiotic stress, and presence of plant growth-promoting rhizobacteria (PGPR) helps in this process (Sivarathri et al., 2025). PGPR enhance plant growth and development by stimulating the synthesis of phytohormones (e.g., cytokinin, abscisic acid and indole acetic acid), nitrogen fixation, increasing nutrient and water absorption, and thus improving yield quality (Backer et al., 2018; Fracasso et al., 2020). PGPR play a key role in mitigating inhibitory effects of water stress by promoting water use efficiency and root growth (Singh et al., 2015).

Material and Method

Growth, inoculation and stress condition

The seeds of tomato (*Solanum lycopersicum* cv. 'Ankur Research-308') were surface sterilized with 30% ethanol and divided into four sets for different treatments. Nitrogen fixing *Azotobacter chrooccoccum* and phosphate solubilizing *Bacillus polymyxa* were taken as PGPR in 1:1 ratio (source: IFFCO, Phulpur-India). The seeds were inoculated in heavy bacterial suspension

ISSN: 0030-5324
UGC CARE Group 1

(containing>10^8 cells/ mL) by soaking them for 20 min. The inoculated seeds were air dried in shade for 30 min. The inoculated and the non-inoculated seeds were sown in pots filled with well-manured sandy loam soil (1:4) (Temperature: 32 ± 5 °C, Relative humidity: 60 ± 5 %), 10 seeds per pot. Irrigation was done as and when required. 30 days old, seedlings of uniform size were selected for further experimentation. Each set of treatments was subdivided into 2 groups (inoculated and non-inoculated). Three sets were subjected to water stress by withholding irrigation for 2 (T-2d, Ti-2d), 3 (T-3d, Ti-3d) and 5 (T-5d, Ti-5d) days respectively while other one set was regularly irrigated and was treated as control (C, Ci). The stressed plants were rewatered and recovery was recorded after 24 h. fully expanded leaves from different treatments were sampled for biochemical analyses (Fig.1).

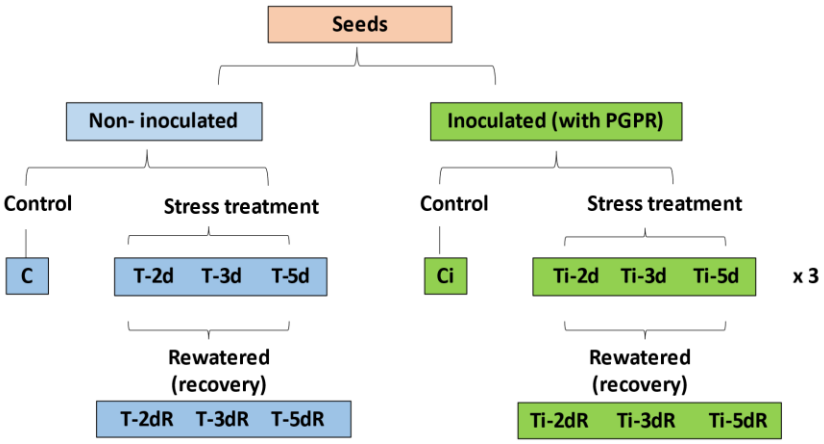

Fig. 1: Experimental Design

Relative water content

For the measurement of relative water content (RWC) leaves samples were cut into discs of uniform size, weighed for a fresh weight (FW) and then they were immediately floated on distilled water at 25 °C in darkness. The turgid weight (TW) of discs of leaf discs were taken after 12 h. The discs were dried in oven at 80 °C for 48 h for the dry weight (DW). The RWC was calculated following Bars and Weatherley (1962): RWC (%)=(FW-DW)/ (TW-DW) × 100.

Measurement of pigments and protein contents

The pigments of leaves and cotyledons viz. chlorophyll a, chlorophyll b and carotenoids were extracted with 80% acetone and quantified following Lichtenthaler (1987). Protein content was determined following Lowry et al. (1951). The amount of protein was calculated with reference to standard curve obtained from bovine serum albumin.

ISSN: 0030-5324
UGC CARE Group 1

Estimation of free proline

Extraction and determination of proline were performed according to Bates *et al*. (1973). Fully expanded leaves were harvested from water stressed and control plants (inoculated and non-inoculated). Dirt and dust were removed and leaves were weighed for sampling. 500 mg Leaf samples were extracted with 3 mL of 3% sulphosalicylic acid with the help of pestle-mortar. Homogenate was then transferred to centrifugation tubes and were centrifuged at 4000 rpm for 20 min at room temperature. Clear supernatant was separated and was used for proline test, residue was discarded. 2 mL of aliquot was treated with 2 mL of acid- ninhydrin and 2 mL of acetic acid, boiled for 1 hour at 100°C. The reaction mixture was extracted with 4 mL of toluene. Absorbance of chromophore- containing toluene was determined at 520 nm. Proline content was expressed as µmol g^{-1} FW.

Acid-ninhydrin reagent: 1.25 g ninhydrin was mixed with 30 mL glacial acetic acid and 20 mL of 6 M orthophosphoric acid.

Lipid peroxidation

Lipid peroxidation was measured in terms of malondialdehyde (MDA) content as per the method of Heath and Packer (1968). Fresh leaves were harvested from stressed and control inoculated and non-inoculated plants. Leaves (100 mg) were extracted with trichloroacetic acid (TCA 0.1% w/v) and centrifuged at 10 000 g for 10 min. MDA level was used as index of lipid peroxidation and was expressed as nmol g^{-1} fresh weight. 1 mL supernatant was added to 4 mL 0.5 thiobarbituric acid (made in 20% TCA). The mixture was incubated at 95°C for 30 min followed by rapid cooling, centrifuged at 10 000 g for 10 min. The absorbance of supernatant was determined at 532nm and corrected for non-specific absorbance at 600 nm. MDA content determined using the extinction coefficient of 155 $mM^{-1}cm^{-1}$.

Statistical Analysis

Data were statistically analysed using analysis of variance (ANOVA) by using SPSS (IBM SPSS: Ver.20). Appropriate standard error of means (±SE) was calculated for presentation with tables and graphs. The treatment means were separated by Duncan's multiple range test (DMRT) at $P< 0.05$. Graphical representation was made using PRISM software.

ISSN: 0030-5324
UGC CARE Group 1

Table 1: Effect of water stress on growth parameters of inoculated and non-inoculated tomato plants.

Treatment	RWC			Plant Height (in cms)		
C	94.36	±	0.16b	15.35	±	0.05ab
Ci	95.44	±	0.17a	15.75	±	0.06a
T-2d	88.98	±	0.04d	13.56	±	0.08d
Ti-2d	90.60	±	0.32c	15.05	±	0.40bc
T-2d-R	95.71	±	0.43a	13.66	±	0.24de
Ti-2d-R	94.88	±	0.35ab	14.53	±	0.26c
T-3d	69.05	±	0.31g	7.48	±	0.10g
Ti-3d	78.58	±	0.34f	10.61	±	0.33e
T-3d-R	85.20	±	0.07e	11.68	±	0.23e
Ti-3d-R	91.19	±	0.21c	13.66	±	0.16de
T-5d	40.48	±	0.22j	5.44	±	0.09h
Ti-5d	47.74	±	0.36i	7.63	±	0.09fg
T-5d-R	52.59	±	0.20h	5.33	±	0.15h
Ti-5d-R	69.31	±	0.47g	8.21	±	0.34f

Mean ± (SE) values followed by the same letters are not significantly different at 0.05 (ANOVA and Duncan's multiple range test) n = 3.

ISSN: 0030-5324
UGC CARE Group 1

Table 2: Effect of water stress on pigments and protein content of inoculated and non-inoculated tomato plants.

Treatment	**Pigments** (µg/mgFW)												**Protein** (mg/gFW)		
	Chl a			**Chl b**			**Chl a+b**			**Carotenoids**					
C	6.06	±	0.01bc	0.70	±	0.01f	6.76	±	0.01b	0.10	±	0.01g	10.92	±	0.03e
Ci	6.26	±	0.02ab	1.23	±	0.02c	7.49	±	0.04a	0.39	±	0.29fg	15.85	±	0.11ab
T-2d	4.80	±	0.07e	0.63	±	0.01f	5.44	±	0.06d	2.10	±	0.01b	12.65	±	0.47d
Ti-2d	3.69	±	0.14g	1.63	±	0.04a	5.33	±	0.09d	0.28	±	0.01fg	15.46	±	0.30b
T-2d-R	5.90	±	0.04cd	0.64	±	0.01f	6.53	±	0.03b	1.05	±	0.01e	13.47	±	0.12c
Ti-2d-R	6.46	±	0.08a	0.83	±	0.01e	7.28	±	0.07a	0.37	±	0.01fg	16.61	±	0.36a
T-3d	2.30	±	0.02h	1.40	±	0.06b	3.70	±	0.05e	0.17	±	0.01fg	6.69	±	0.55h
Ti-3d	2.44	±	0.06h	1.34	±	0.04b	3.78	±	0.10e	1.73	±	0.05c	7.65	±	0.17g
T-3d-R	4.94	±	0.03e	1.03	±	0.01d	5.97	±	0.04c	0.17	±	0.00fg	11.46	±	0.08e
Ti-3d-R	5.69	±	0.11d	0.95	±	0.01d	6.64	±	0.11b	1.67	±	0.01cd	10.97	±	0.35e
T-5d	1.46	±	0.13i	0.47	±	0.07g	1.93	±	0.10h	0.43	±	0.01f	5.51	±	0.10i

ISSN: 0030-5324
UGC CARE Group 1

Ti-5d	1.56	±	0.17i	1.24	±	0.03 c	2.80	±	0.15 g	2.51	±	0.10a	7.31	±	0.12g h
T-5d-R	2.27	±	0.14h	1.02	±	0.01 d	3.29	±	0.14f	1.40	±	0.13d	6.49	±	0.21h
Ti-5d-R	4.50	±	0.07f	0.96	±	0.02 d	5.46	±	0.07 d	1.68	±	0.08cd	9.12	±	0.19f

Mean ± (SE) values followed by the same letters are not significantly different at 0.05 (ANOVA and Duncan's multiple range test) n = 3.

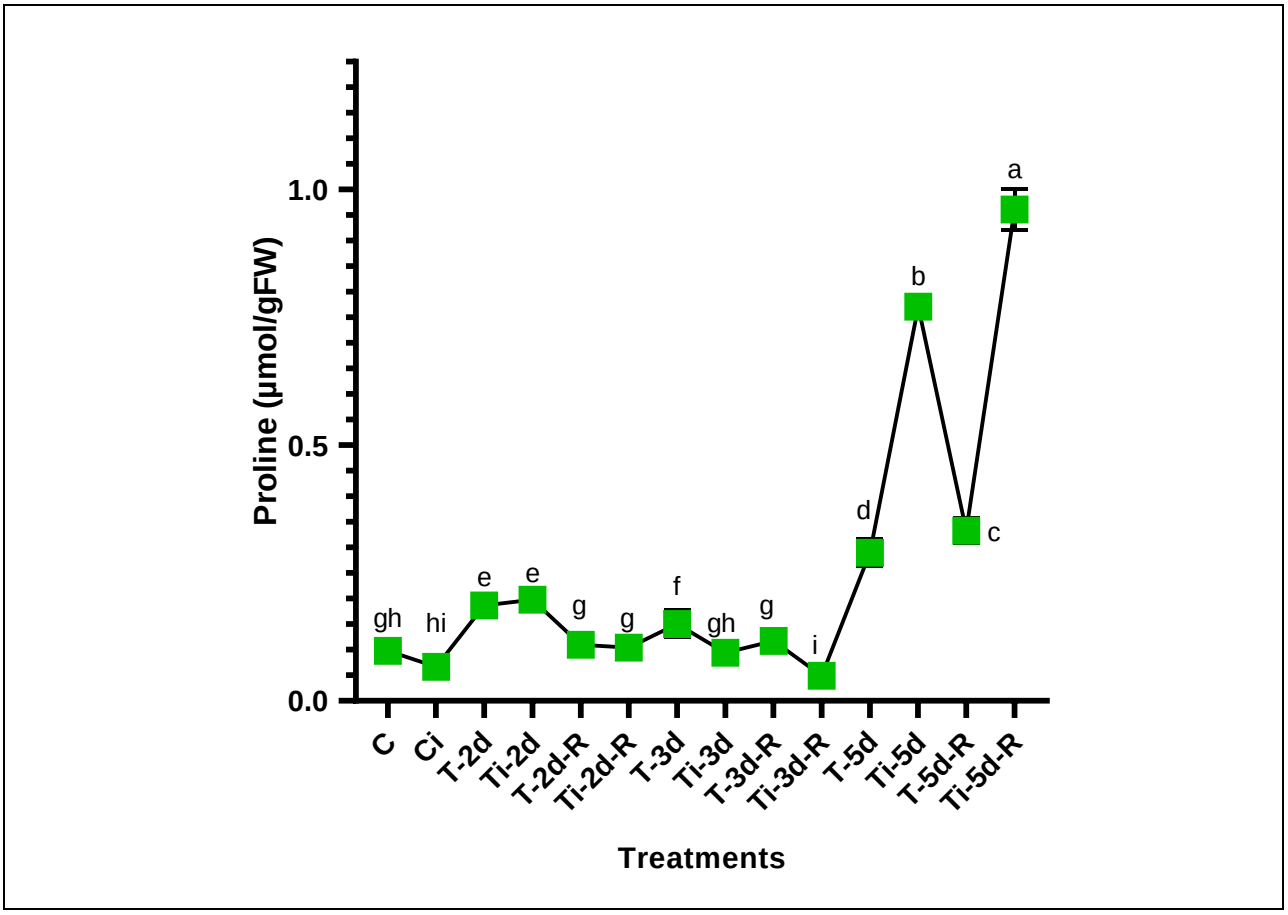

Fig.2: Effect of water stress on Proline of inoculated and non-inoculated tomato plants.

Mean ± (SE) values followed by the same letters are not significantly different at 0.05 (ANOVA and Duncan's multiple range test) n = 3.

ISSN: 0030-5324
UGC CARE Group 1

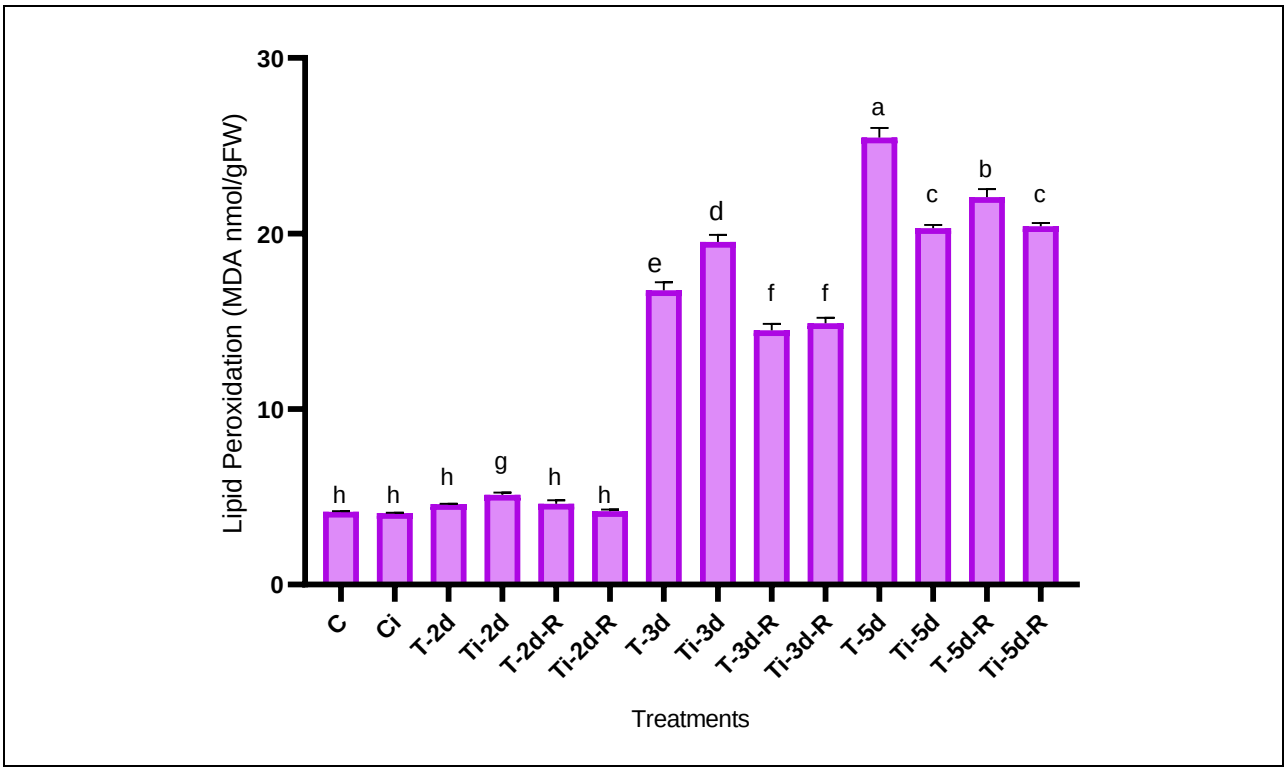

Fig.3 : Effect of water stress on Lipid peroxidation of inoculated and non-inoculated tomato plants.

Mean ± (SE) values followed by the same letters are not significantly different at 0.05 (ANOVA and Duncan's multiple range test) n = 3.

Results

Plant Height

The highest plant height was recorded in inoculated control (Ci) plants, however it was not significantly different with non-inoculated control (C) plants. Plant height was negatively impacted by water stress, with the lowest height recorded in plants subjected to 5-day water stress. PGPR inoculation helped plants in mitigating adverse effects of stress, as evident when compared height of inoculated and non-inoculated stressed plant. Rewatering helped plants regain their turgidity (Table 1).

Relative Water Content (RWC)

The lowest RWC was recorded in T-5d plants, followed by Ti-5d plants. 3 day water stress also significantly lowered RWC. However, no significant difference observed between inoculated Control (Ci) and inoculated two day recovery (Ti-2dR) plants (Table 1). Plants recovered more efficiently when rewatered after two days of water stress in comparison to three-day and five-day stress.

ISSN: 0030-5324
UGC CARE Group 1

Photosynthetic Pigments

The effect of water stress on chlorophyll a was more pronounced than chlorophyll b. the highest chlorophyll a content was recorded in Ti-2dR plants, followed by Ci and C plants, while the lowest chlorophyll a content was recorded in T-2d plants. However, chlorophyll b was lowest in T-5d plants and highest in Ti-2d plants. Total chlorophyll content were significantly different ($P<0.05$) in inoculated (Ci) and non-inoculated control (C) plants. PGPR inoculation helped plants to retain photosynthetic pigments even under stressed condition and inoculated plants recovered more rapidly upon rewatering. Carotenoids were recorded highest in Ti-5d stressed plants, with no significant differences observed among C, Ci and Ti-2d plants (Table 2).

Protein

The highest protein content was recorded in Ti-2dR plants, followed by Ci plants. Inoculated plants exhibited higher protein values than non-inoculated plants. Furthermore, inoculated stressed plants when rewatered exhibited efficient recovery compared to non-inoculated stressed plants (Table 2).

Proline Accumulation

An increase in proline content was observed with the increasing intensity of the water stress, which further increased with the duration of water-deficit. Inoculated plants subjected to five-day water stress (Ti-5d) exhibited high proline levels, which increased even further after rewatering. No significant difference ($P<0.05$) was recorded between inoculated and non-inoculated plants subjected to 2d stress and their subsequent recovery. The lowest proline content was found in Ci plants (Fig. 2).

Lipid Peroxidation (LP)

The highest lipid peroxidation, in terms of MDA content, was recorded in T-5d plants, i.e., plant subjected to five-day water stress without inoculation. Even after rewatering, LP of T-5d plants remained significantly higher than Ti-5d and Ti-5dR plants. No significant difference in LP was recorded among C, Ci, T-2d, T-2dR and Ti-2dR plants (Fig. 3).

Discussion

Plant growth and development depends upon its photosynthetic machinery, which includes photosynthetic pigments (chlorophyll a & b) and accessory pigments such as carotenoids (Mishra et al., 2012). Environmental stresses, specially drought stress, negatively impacted on photosynthetic pigments, as evidenced by our results under severe (five-day) stress conditions (Singh et al., 2015; Singh, 2021). Tomato plants can cope with mild stress; hence, no significant difference was observed between pigments of control and two-day stressed plants. However, as stress prolonged, a negative impact on chlorophyll a and chlorophyll b became evident. Photochemical events are directly affected by water stress (Mohanty and Boyer, 1976), leading to a limitation of photosynthesis under severe water deficit, which also affected total protein content.

ISSN: 0030-5324
UGC CARE Group 1

Our results suggest that inoculated plant recover more effectively from stress than non-inoculated plants.

Fluctuations in protein content are directly related to stress duration, with longer stress periods leading to lower protein content. This may be due to the degradation/modification of structural protein into functional proteins, such as antioxidative enzymes, triggered by oxidative stress caused by water deficit (Pacifice and Davies, 1990). However, photochemical reactions were restored upon rewatering (Boyer, 1971). This indicates strong defense mechanism in inoculated plants.

Inoculation with PGPR improves plant growth even under prolonged stress conditions, as evidenced by the higher chlorophyll content in inoculated stressed plants compared to non-inoculated plants under five-day stress conditions. Similar results have been reported in several other studies (Tahir et.al 2019). PGPR directly influences nutrient uptake and enhances plant health by solubilizing phosphorus and nitrogen. *Azotobacter* is capable of fixing free atmospheric nitrogen into a usable form for plants, as plants cannot fix nitrogen by their own (Zare et al.., 2011). The role of nitrogen in growth and productivity of plants is well- documented. *Bacillus polymyxa* is responsible for phosphorus acquisition of plant by mobilizing inorganic and organic phosphorus (Singh et.al, 2010; Singh, 2021). Yang et al. (2009) and Goswami and Deka (2020) reported that drought itself triggers rhizopheric symbiotic bacteria to secrete growth hormones, which ultimately benefit plant growth. Additionally, PGPR helps in minimising water loss through transpiration in plants by inducing stomatal closure due to production of ABA (Forni et al., 2017; Andryei et al. 2021).

Under water stress, elevated accumulation of proline and carotenoids were observed. The highest proline content was recorded in five-day stressed plants in this study. Both proline and carotenoids act as osmolyte and plays a crucial role in protecting plant from oxidative damage caused by water stress. Proline reduces lipid peroxidation by scavenging reactive oxygen species (ROS) and stabilizing cell membranes (Hare et al., 1999; Krishna et al.., 2024). A correlation was found between higher proline content and lower RWC in leaves of water stressed plants.

Prolonged stress led to increased MDA content, indicating membrane damage due to ROS production caused by water stress. Similar findings have been reported in several other plants under water stress (Sun et al., 2020; Esfandiari et al., 2007). Inoculation helped plant to protect themselves from membrane damage by minimising lipid peroxidation.

Conclusion

Abd Al-Shammari et al. (2020) stated that use of bio-stimulants can improve production and fruit quality of tomato. Our results also support the positive role of PGPR in the growth and development of tomato plants at the vegetative stage. Healthy plants ensure higher productivity. Gashash et al. (2022) and Andryei et al. (2021) also reported similar results. PGPR not only serve as a bio-stimulant of growth but helped plants in mitigating the adverse effect of environmental

ISSN: 0030-5324
UGC CARE Group 1

stresses. Therefore, the use of PGPR is highly recommended, as it improve soil quality, enhances water and mineral absorption, promotes plant growth and productivity by solubilizing phosphates and fixing nitrogen, and also helps plant respond positively towards adverse environmental conditions.

Declarations

Ethics approval and consent to participate
This manuscript does not contain any studies with human participants or animals performed by any of the authors.

Consent for publication
All the authors have given their consent for publication of this manuscript if accepted.

Availability of data and material
Data and materials will be made available on request

Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Funding
This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Authors' contributions
D.S. wrote manuscript with experimental design. A.M. done statistical work. All authors read and approved of the content.

Acknowledgements
Not applicable

Reference:

Abd Al-Shammari AM, Abood MA, Hamdi GJ (2020) Improvement in production, fruit quality and water use efficiency of three tomato cultivars by foliar application of tecamin flower® under water deficit conditions. *J Cent Eur Agric* 21(2):379–385.

Adalid AM, Rosello S, Nuez F (2004) Breeding tomatoes for their high nutritional value. *Recent Res Dev Plant Sci* 2:33–52.

ISSN: 0030-5324
UGC CARE Group 1

Andryei B, Horváth KZ, Agyemang Duah S, Takács S, Égei M, Szuvandzsiev P, Neményi A (2021) Use of plant growth promoting rhizobacteria (PGPRs) in the mitigation of water deficiency of tomato plants (Solanum lycopersicum L.). *J Cent Eur Agric* 22(1):167–177. https://doi.org/10.5513/JCEA01/22.1.3036

Backer R, Rokem JS, Ilangumaran G, Lamont J, Praslickova D, Ricci E, Subramanian S, Smith DL (2018) Plant growth promoting rhizobacteria: context, mechanisms of action, and roadmap to commercialization of bio-stimulants for sustainable agriculture. *Front Plant Sci* 9:1473.

Bars HD, Weatherly PE (1962) A re-examination of the relative turgidity technique for estimating water deficits in leaves. *Aust J Biol Sci* 15:413–428.

Bates LS, Waldren RP, Teare ID (1973) Rapid determination of free proline for water-stress studies. *Plant Soil* 39:205–207.

Boyer JS (1971) Recovery of photosynthesis in sunflower after a period of low leaf water potential. *Plant Physiol* 47:816–820.

Chandrasekaran M, Chun SC, Oh JW, Paramasivan M, Saini RK, Sahayarayan JJ (2019) *Bacillus subtilis* CBR05 for tomato (Solanum lycopersicum) fruits in South Korea as a novel plant probiotic bacterium (PPB): implications from total phenolics, flavonoids, and carotenoids content for fruit quality. *Agronomy* 9:838.

Esfandiari EO, Shakiba MR, Mahboob SA, Alyari H, Toorchi M (2007) Water stress, antioxidant enzyme activity and lipid peroxidation in wheat seedling. *J Food Agric Environ* 5(1):149–153.

Fazeli F, Ghorbanli M, Niknam V (2007) Effect of drought on biomass, protein content, lipid peroxidation and antioxidant enzymes in two sesame cultivars. *Biol Plant* 51(1):98–103.

Forni C, Duca D, Glick BR (2017) Mechanisms of plant response to salt and drought stress and their alteration by rhizobacteria. *Plant Soil* 410:335–356.

Fracasso A, Telò L, Lanfranco L, Bonfante P, Amaducci S (2020) Physiological beneficial effect of *Rhizophagus intraradices* inoculation on tomato plant yield under water deficit conditions. *Agronomy* 10:71.

Gashash EA, Osman NA, Alsahli AA, Hewait HM, Ashmawi AE, Alshallash KS, El-Taher AM, Azab ES, Abd El-Raouf HS, Ibrahim MFM (2022) Effects of plant-growth-promoting rhizobacteria (PGPR) and cyanobacteria on botanical characteristics of tomato (*Solanum lycopersicon* L.) plants. *Plants* 11:2732. https://doi.org/10.3390/plants11202732

ISSN: 0030-5324
UGC CARE Group 1

Goswami M, Deka S (2020) Plant growth-promoting rhizobacteria alleviators of abiotic stresses in soil: a review. *Pedosphere* 30(1):40–61. https://doi.org/10.1016/S1002-0160(19)60839-8

Hare PD, Cress WA, Van Staden J (1999) Proline synthesis and degradation, a model system for elucidating stress-related signal transduction. *J Exp Bot* 50:413–434.

Heath RL, Packer L (1968) Photoperoxidation in isolated chloroplasts. I. Kinetics and stoichiometry of fatty acid peroxidation. *Arch Biochem Biophys* 125:189–198.

Kasim WA, Osman ME, Omar MN, Abd El-Daim IA, Bejai S, Meijer J (2013) Control of drought stress in wheat using plant growth promoting bacteria. *J Plant Growth Regul* 32:122–130.

Krishna R, Ansari WA, Altaf M, Jaiswal DK, Pandey S, Singh AK, Kumar S, Verma JP (2024) Impact of plant growth-promoting microorganism (PGPM) consortium on biochemical properties and yields of tomato under drought stress. *Life* 14:1333. https://doi.org/10.3390/life14101333

Lichtenthaler HK (1987) Chlorophyll and carotenoids: pigments of photosynthetic bio-membranes. In: Packer L, Douce R (eds) *Methods Enzymol*, Academic Press, San Diego, pp 350–382.

Lowry OH, Rosenbrough RJ, Farr AL, Randall RJ (1951) Protein measurement with Folin phenol reagent. *J Biol Chem* 193:265–275.

Mishra KB, Iannacone R, Petrozza A, Mishra A, Armentano N, La Vecchia G, Trtílek M, Cellini F, Nedbal L (2012) Engineered drought tolerance in tomato plants is reflected in chlorophyll fluorescence emission. *Plant Sci* 182(1):79–86.

Mohanty P, Boyer JS (1976) Chloroplast response to low leaf water potentials. IV. Quantum yield is reduced. *Plant Physiol* 57:704–709.

Pacifici RE, Davies KJA (1990) Protein degradation as an index of oxidative stress. *Methods Enzymol* 186:485–502.

Singh D (2021) Influence of biological seed priming on pigments and superoxide dismutase activity of maize seedlings under drought stress. *Agriways* 9(2):65–68.

Singh NB, Singh A, Singh D (2010) Autotoxicity of maize and its mitigation by plant growth promoting rhizobacterium *Paenibacillus polymyxa*. *Allelopathy J* 25(1):195–204.

Singh NB, Singh D, Singh A (2015) Biological seed priming mitigates the effects of water stress in sunflower seedlings. *Physiol Mol Biol Plants* 21(2):207–214.

Sivarathri BS, Narayana NK, Bryant CJ, Dhillon J, Reddy KR, Bheemanahalli R (2025) Influence of seed-applied biostimulants on soybean germination and early seedling growth under low and high temperature stress. *Plant Physiol Rep* 30:32–44. https://doi.org/10.1007/s40502-024-00834-z

Sun Y, Wang C, Chen HYH, Ruan H (2020) Response of plants to water stress: a meta-analysis. *Front Plant Sci* 11:978. https://doi.org/10.3389/fpls.2020.00978

Tahir M, Khalid U, Khan MB, Shahid M, Ahmad I, Akram M, Ijaz M, Hussain M, Farooq AB, Naeem MA, Ahmad N (2019) Auxin and 1-aminocyclopropane-1-carboxylate deaminase activity exhibiting rhizobacteria enhanced maize quality and productivity under water deficit conditions. *Int J Agric Biol* 21:943–954.

Taiz L, Zeiger E (2006) *Plant Physiology*. 4th edn. Sinauer Associates Inc. Publishers, Massachusetts, USA.

Vendruscolo ACG, Schuster I, Pileggi M, Scapim CA, Molinari HBC, Marur CJ, Vieira LGC (2007) Stress-induced synthesis of proline confers tolerance to water deficit in transgenic wheat. *J Plant Physiol* 164:1367–1376.

Wahb-Allah MA, Alsadon AA, Ibrahim AA (2011) Drought tolerance of several tomato genotypes under greenhouse conditions. *World Appl Sci J* 15:933–940.

Yang J, Kloepper JW, Ryu CM (2009) Rhizosphere bacteria help plants tolerate abiotic stress. *Trends Plant Sci* 14(1):1–4.

Yang S, Vanderbeld B, Wan J, Huang Y (2010) Narrowing down the targets towards successful genetic engineering of drought tolerant crops. *Mol Plant* 3:469–490.

Yordanov I, Velikova V, Tsonev T (2003) Plant responses to drought and stress tolerance. *Bulg J Plant Physiol* (Special Issue):187–206.

Zare M, Ordookhani K, Alizadeh O (2011) Effects of PGPR and AMF on growth of two bred cultivars of tomato. *Adv Environ Biol* 5:2177–2181