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Pseudomonas putida KT2440 INDUCES DROUGHT TOLERANCE DURING FRUIT RIPENING IN TOMATO

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ABSTRACT

The current study investigated the effects of *Pseudomonas putida* strain KT2440 on the drought tolerance of tomato plants during fruit maturation. Plants at the ripening stage of the mature-green were not watered for 20 days to promote drought stress. Concentrations of photosynthetic pigments were determined. Bacteria-soaked tomato plants (BSS) had higher levels of chlorophyll and carotenoids than non-soaked plants (DWS) under stress conditions. Compared to the DWS, stomatal conductance, lipid peroxidation, and hydrogen peroxide content in the BSS plants decreased under drought stress. The ascorbate peroxidase (APX), catalase (CAT), and peroxidase (POD) activities increased in BSS plants compared to DWS under drought stress. Furthermore, the number and weight of fruits in both DWS and BSS plants was reduced by the stress, but the reduction in BSS plants was lower than in DWS plants. These results showed that bacteria treatment conferred tolerance to drought stress in tomato plants by reducing the peroxidation extent of polar lipids (PLs), increasing photosynthetic pigment content, and activities of the antioxidant enzymes in the leaves. Therefore, *P. putida* KT2440 has supported high fruit yield under drought stress as a biotic tolerance elicitor for this plant stress.

Additional keywords: Antioxidant enzymes, drought stress, plant growth-promoting bacteria, *Solanum lycopersicum*

RESUMEN

***Pseudomonas putida* KT2440 induce tolerancia a la sequía durante la maduración del tomate**

El estudio investigó los efectos de la cepa KT2440 de *Pseudomonas putida* sobre la tolerancia a la sequía de plantas de tomate durante la maduración de la fruta. Las plantas en etapa de fruta verde madura no se regaron durante 20 días para promover el estrés por sequía. Se determinaron los contenidos de pigmentos fotosintéticos. Las plantas que recibieron la bacteria (PCB) tuvieron mayor cantidad de clorofila y carotenoides que las plantas sin la bacteria (PSB) en condiciones de estrés. En comparación con las PSB, la sequía indujo menor conductancia estomática, peroxidación de lípidos y peróxido de hidrógeno, y mayor actividad de ascorbato peroxidasa (APX), catalasa (CAT) y peroxidasa (POD) en las PCB. El número y peso de los frutos en las PCB y PSB se redujo por el estrés por sequía, pero la reducción fue menor en las PCB. Estos resultados indican que el tratamiento con bacterias confirió tolerancia al estrés por sequía en plantas de tomate al reducir el grado de peroxidación de los lípidos polares (PLs), aumentar el contenido de pigmentos fotosintéticos y las actividades de las enzimas antioxidantes en las hojas. Se concluye que *P. putida* KT2440 facilitó un alto rendimiento de frutos bajo estrés por sequía como un inductor biótico de tolerancia a este tipo de estrés.

Palabras clave adicionales: Bacterias promotoras del crecimiento, enzimas antioxidantes, estrés por sequía, *Solanum lycopersicum*

INTRODUCTION

The stress of drought restricts plant growth and productivity and results in economic losses in agriculture, therefore, plant tolerance to drought stress should be increased. There are several ways to improve the sustainability of plants during drought. One of them is the inoculation of plants with beneficial microorganisms (Timmusk et al., 2017; Naamala and Smith, 2020), known

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as plant growth-promoting rhizobacteria (PGPR). Inoculation with PGPR provides increased tolerance of plants to abiotic stresses through physical and chemical changes (Yang et al., 2009). *Pseudomonas* spp. is an ubiquitous bacterium in agricultural soils and has many traits that make it suitable for PGPR. One of the most effective species of the *Pseudomonas* genus is *Pseudomonas putida* that has been used as inoculants on crop plants to promote growth, increase yields, and drought tolerance (Marulanda et al., 2009; Adesemoye and Egamberdieva, 2013; Ghorbanpour et al., 2013).

Inhibition of shoot and root growth is a primary symptom of drought. Stomatal closure, reduction in transpiration, CO_2 uptake, and photosynthesis are closely related to this growth reduction (Campos et al., 2014). The decrease in photosynthesis is followed by the rising generation of reactive oxygen species (ROS) such as O_2^- (superoxide), $^1O_2$ (singlet oxygen), H_2O_2 (hydrogen peroxide), and $OH^{\bullet}$ (hydroxyl) radicals. These ROSs can lead to the initiation of destructive oxidative events that damage lipids, photosynthetic pigments, proteins, and nucleic acids (Rahman et al., 2017). Plants can alleviate oxidative damage by the antioxidant system composed of both enzymatic (superoxide dismutase (SOD), peroxidases (POD), and catalase (CAT)), and non-enzymatic antioxidants (ascorbic acid, glutathione, and tocopherol) (Wang et al., 2014; Amari and Abdelly, 2021).

Tomato (*Solanum lycopersicum* L.) is one of the most widely grown vegetables globally and most commercial cultivars are susceptible to drought at all stages of plant development, been seed germination and seedling growth are the most susceptible stages (Foolad, 2004).

Tomato plants have been inoculated with various PGPRs, and after inoculating *Bacillus cereus* AR156, the plant developed resistance to drought (Wang et al., 2012). The authors found that bacteria application protected plant cells, maintained photosynthetic efficiency, and increased some peroxidase activities.

Fresh and dry weight of tomato seedlings exposed to drought stress were increased after application of the plant growth-promoting bacterium *Achromobacter piechaudii* ARV8, showing that the bacteria provided drought stress resistance to the seedlings (Mayak et al., 2004). Additionally, a great variety of biotechnological applications has been made on *Pseudomonas putida* strain KT2440 (Fonseca et al., 2011). Vilchez et al. (2016) showed that transgenic *P. putida* KT2440 overexpressed the *otsAB* gene, which participates in the synthesis of trehaloses, induced the drought tolerance of pepper plants. However, the effects of *P. putida* KT2440 on the tomato drought resistance and plant yield during fruit ripening are not known. Considering previous studies, the objective of this research was to determine the effect of *P. putida* KT2440 as a PGPR on plant yield and drought tolerance of tomato plants during fruit ripening.

MATERIALS AND METHODS

Bacterization of the seeds. Seeds of *Solanum lycopersicum* (cultivar H-2274) were obtained from Agromar (Turkey). The seeds were disinfected according to Ryu et al. (2003). The seeds were kept in 70 % (v/v) ethanol solution for 2 min, then subjected to 0.2 % (w/v) sodium hypochlorite for 2 min and rinsed with sterile distilled water five times. The seeds were inoculated with moderately drought-tolerant bacteria *P. putida* KT2440 (Molina et al., 2017). DSMZ-German Collection of Microorganisms and Cell Cultures GmbH, Braunschweig, Germany, provided the bacteria. *P. putida* (DSM 6125) cells were incubated at 30 °C in nutrient broth (NB) medium for 16 hours. Solid agar plates containing peptone (5 $g \cdot L^{-1}$), yeast extract (3 $g \cdot L^{-1}$), and agar-agar (15 $g \cdot L^{-1}$) were chosen to transfer the cells. The agar plates were kept at 30 ◦C for the proliferation of the cells (Poblete et al., 2014). A 100-mL flask containing 25 mL of NB was used to prepare the inocula. A single colony of the strain was transferred to the flask, and the colony was grown at 30 °C. A dilution was done using sterile distilled water to achieve a final concentration of 2.5×10^8 $cfu \cdot mL^{-1}$ (Kuklinsky et al., 2005). The seeds were then inoculated with the bacterial suspension containing 2.5×10^8 $cfu \cdot mL^{-1}$ of bacteria by soaking. The tomato seeds were kept in the bacterial suspension for 5 minutes; this treatment was named bacteria-soaked (BS). The control seeds were held in sterile distilled water for 5 min and were referred to as distilled water (DW).

Plant growth and drought stress treatment. The

seeds were sown into plastic pots (eight seeds each) containing 1 kg of field soil, sterilized at 105 °C for two days. Tomato plants were grown for 20 days in a growing chamber at 25 °C/20 °C day/night. The photoperiod was 16 h (07:00-23:00 h) with a light intensity of 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$. All pots were irrigated every other day with sterile distilled water. After 20 days, the pots were transferred to a rain-out-shelter located on The greenhouse field of the Karadeniz Technical University (40°59'N, 39°46'E, 179 masl). The shelter was opened at both ends to avoid rises in temperature due to greenhouse effect. The 20-day-old seedlings were transplanted in pots (30 cm diameter, 50 cm deep) filled with 14 kg of sandy soil to 30 cm height. Soil organic matter content, pH and EC values were 2.49 %, 5.63, and 0.33 $dS \cdot m^{-1}$, respectively. There was a total of 48 pots, with three seedlings per pot. After ten days, the seedlings were reduced to one in each pot. BS plants were irrigated once with 1 L of bacterial suspension containing 2.5×10^8 $cfu \cdot mL^{-1}$ per pot, then watered regularly with 3.5 L of tap water. DW plants were only irrigated with tap water. All plants were grown till the fruit ripening stage mature green (MG), which was known to be the most sensitive tomato stage to drought stress (Nuruddin et al., 2003). On the MG stage (50 days-old plants), half of all plants were kept well-watered (control), while the others were subjected to drought stress by withholding water through 20 days till maturity. The plants were split into 4 treatment groups. 1) BSC (bacteria soaked and well-watered control), 2) BSS (bacteria soaked and drought-stressed), 3) DWC (non-inoculated and well-watered control), and 4) DWS (non-inoculated and drought-stressed). At the end of the treatments, the following variables were measured: pigment content, stomatal conductance, hydrogen peroxide, lipid peroxidation, antioxidant enzyme activity, number of fruits, and fruit weight.

Chlorophyll and carotenoid contents. These variables were determined, according to Arnon (1949). Leaf samples (45 leaves from 12 plants) were ground in a mortar containing 80 % acetone. The leaf extract was subsequently centrifuged at 5000 g for 5 minutes. The supernatant was used to determine pigment content by measuring absorbance at 663, 645, and 450 nm using a spectrophotometer (Nicolet evolution 100, Thermo Scientific).

Stomatal conductance (g_s). It was measured using a porometer (AP4, Delta-T Devices) on six randomly selected leaves.

Lipid peroxidation. Measured according to Heath and Packer (1968). Leaf samples (0.5 g) were ground in a mortar, including 0.1 % (w/v) trichloroacetic acid (TCA). The extract was centrifuged at 15 000 g for 10 min at 4 °C. One mL of supernatant was taken and added to 4 mL of 20 % TCA containing 0.5 % thiobarbituric acid. Malondialdehyde (MDA) content was calculated from measurements carried out at wavelengths of 532 and 600 nm to minimize interferences.

Hydrogen peroxide assay. The hydrogen peroxide content of the leaves was determined based on Velikova et al. (2000). Leaf samples (0.25 g) were homogenized with 5 % TCA, including 0.1 g activated charcoal in a mortar at 4 °C. The extract was centrifuged at 12 000 g for 10 min at 4 °C. Then, 0.75 mL of 1 M potassium iodide and 0.5 mL of 10 mM potassium phosphate buffer (pH 7.0) were added to the supernatant (0.5 mL), then the mixture was kept in the dark for 5 min for color development. The reaction mixture was measured at 390 nm with a spectrophotometer.

Determination of antioxidant enzyme activities. Leaves (0.5 g) were homogenized with 1 % polyvinylpolypyrrolidone (PVPP) in 5 mL extraction buffer (50 mM potassium-phosphate buffer, 1 mM EDTA, pH 7.0). In the case of APX activity, 2 mL of 5 mM ascorbic acid was added. The homogenate was centrifuged at 18 000 g for 20 min at 4 °C, and conserved at -20 °C until they were used for analysis.

Ascorbate peroxidase (APX) activity. The APX (EC 1.11.1.11) activity was measured according to Nakano and Asada (1987). The decrease in ascorbic acid absorbance was followed for 3 min at 290 nm in 1 mL volume reaction medium containing 20 µL enzyme extract, 20 µL of 0.25 mM ascorbic acid, and 100 µL of 5 mM H_2O_2 in 860 µL of 50 mM phosphate buffer (pH 7).

Peroxidase (POD) activity. The POD activity (EC 1.11.1.7) was determined using a method elaborated by Mika and Luthje (2003). The increase in tetraguaiacol absorbance was monitored at 470 nm for 3 minutes in a 1 mL volume with 800 µL of a reaction mixture containing H_2O_2 in sodium acetate buffer (pH

5.6), 195 µL of 5 mM guaiacol, and 5 µL of the enzyme extract.

Catalase (CAT) activity. CAT activity (EC 1.11.1.6) was determined based on Aebi (1983). The decrease in the absorbance of H_2O_2 was monitored at 240 nm for 3 min in a 1 mL volume with 990 µL of a reaction mixture containing H_2O_2 in potassium phosphate buffer (pH 7.0) and 10 µL of enzyme extract. The method of Bradford (1976) was used to determine protein content at 25 °C using bovine serum albumin as standard

Fruit yield. The fruits of all plants were harvested at the end of treatments. Fruit weight and number were recorded to evaluate plant yield.

Statistical analysis. Fifteen leaves were used for each experiment (15 leaves x 12 plants), repeated three times. ANOVA and Tukey's test to determine differences in physiological variables between well-watered and drought-stressed plants were performed using SPSS (version 13.0, Chicago, IL, USA).

RESULTS AND DISCUSSION

Total chlorophyll content (Chl) of DW plants was significantly reduced by drought (from 9.8 in DWC to 7.2 in DWS), meaning 1.4-fold lower than that of the DWC plants. However, Chl increased in BS plants (from 9.6 in BSC to 13.7 BSS) under drought stress (Figure 1A). The content in BSS was 1.4-fold higher than that of the BSC. Inoculation with PGPR has been found to increase plant productivity under drought stress (Delshadi et al., 2017). Therefore, there is a need to understand the relationship between plants and microorganisms, which influences plant tolerance and growth. Drought stress was reported to reduce Chl in various plant species, such as tomato, periwinkle, and black henbane (Ghorbanpour et al., 2013; Yuan et al., 2016), hence this content is a parameter used to estimate the effects of drought stress on plant growth and yield (Ramírez et al., 2014). In the present study, inoculation of *P. putida* KT2440 in tomato plants mitigated the adverse effects of drought on Chl. The PGPR application on pea (*Pisum sativum* L.) was also beneficial for decreasing the impact of the drought stress on the Chl (Arshad et al., 2008). A similar result was reported by Vivas et al. (2003), who showed increased stomatal conductance and Chl of lettuce compared to a non-drought control after inoculation of the bacterial strain.

Similar to the changes in chlorophyll content, total carotenoid (car) in DW plants was also reduced by the drought stress (from 3.1 in DWC to 2.4 in DWS), meaning 1.3-fold lower than that of the DWC plants. On the contrary, drought increased the carotenoid concentration in BS plants (from 2.7 in BSC to 4.8 in BSS), 1.8-fold higher than that of the BSC plants (Figure 1B).

Carotenoid accumulation is one of the mechanisms in plants to alleviate drought stress, and in our study, carotenoid levels were significantly improved in BS drought stressed plants. Similarly, Chakraborty et al. (2013) reported an increase in carotenoid content following inoculation of drought-stressed wheat plants by bacteria. Plants maintaining high levels of photosynthetic pigments under water deficit can show an increased drought resistance (Tamburino et al., 2017). Moreover, Vurukonda et al. (2016) reported that PGPR inoculation increased plant biomass and photosynthetic pigments (Chl a-b, and carotenoids) in various species under drought stress compared to non-inoculated control. Therefore, the large quantity of pigments detected in the current study suggests that this tomato cultivar had a high tolerance to drought through bacterial inoculation.

The drought stress resulted in a decrease in stomatal conductance (g_s). The g_s of DWS plants was higher than that of BS plants under drought stress. The g_s of the BSS plants (66) was 2.2-fold lower than that of DWS plants (138). Moreover, the bacterial inoculation itself resulted in a decrease in g_s of BSC plants under well-watered conditions. DWC plants had higher g_s compared to BSC plants (Figure 1C).

Stomatal closure is a typical drought prevention response that allows plants to retain water in their tissues (Ludlow, 1980). It is also known that drought stress alters the balance of several plant hormones, changes their interactions, and can eventually change stomatal conductance (Acharya and Assmann 2009). Among the plant hormones, abscisic acid (ABA) plays the most crucial role in limiting the openings of stomata cells under drought stress conditions (Pospisilova, 2003; Kim et al., 2010). In the current study, low g_s values in BSS plants could occur due to induction of ABA synthesis by KT2440 under drought stress. In addition, *P. putida* KT2440 was

reported to produce high levels of ABA by Vilchez et al. (2016). This high ABA production by the bacteria may also explain the low g_s values of BSC plants under well-watered conditions. Planchamp et al. (2014) reported up-regulation of some ABA-related genes such as 9-cis-epoxycarotenoid dioxygenase and plasma membrane intrinsic protein 1;5 and increased ABA concentration in maize roots inoculated with *P. putida* KT2440. Likewise, *Bacillus* sp. inoculated lettuce has been shown to have elevated ABA in root tissue (Arkhipova et al. 2007), and Cohen et al. (2008) found an increase in ABA content in *Arabidopsis* inoculated with *Azospirillum brasilense* Sp245.

The high ABA content of plants can be directly linked to the high carotenoid content. Carotenoids are known to be the precursors to the plant hormone ABA, and carotenoids and ABA biosynthesis are closely related (Zhang et al., 2012). *Arabidopsis* and corn plants under drought stress were shown to have high carotenoids and, in parallel, have high ABA levels (Li et al., 2008; Ruiz et al., 2014). The reduction of stomatal conductance and high carotenoid contents under drought stress conditions in tomato plants inoculated with bacteria in our study supported the above data.

In our study, drought stress induced lipid peroxidation. As is known, drought stress causes damage to plant tissues through ROS formation that leads to oxidative stress and lipid peroxidation (Chakraborty and Pradhan, 2012). The MDA contents of the DWS and BSS plant groups under drought stress were 1.4-fold higher than their respective controls (DWC and BSC). On the other hand, bacteria treatment decreased the concentration of MDA under drought stress. MDA content of the BSS plants was 1.2-fold lower than that of DWS plants (Figure 1D). This suggested that the inoculation of KT2440 attenuated oxidative damage by decreasing lipid peroxidation during drought. The accumulation of H_2O_2 was induced by drought, but was effectively reduced by KT2440 inoculation under drought stress (BSS) as compared to DWS (Figure 2A).

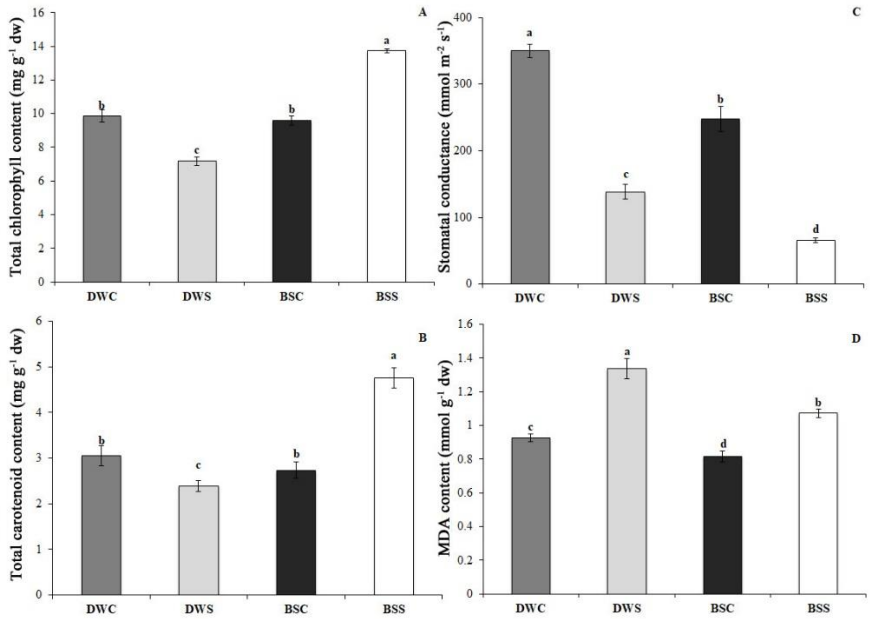

Figure 1. Total chlorophyll (A), total carotenoid (B), stomatal conductance (C), and MDA content (D) in tomato plants. DWC (non-inoculated, well-watered), DWS (non-inoculated, drought stressed), BSC (inoculated, well-watered), BSS (inoculated, drought stressed). Different letters show differences among treatments (Tukey's test, $P \leq 0.05$). Vertical bars are SD

The H_2O_2 content of DW plants (0.17) was 1.3-fold higher than that of BS plants (0.13) under drought stress. Similarly, Mohammadi et al. (2017) reported a decrease in MDA and H_2O_2 levels in *Satureja hortensis* shoots inoculated with *Pseudomonas fluorsecens* PF-135 under drought

stress. The reduction in MDA during drought stress in BS plants was likely attributed to the antioxidant system induced in the current study. As is known, the antioxidant system in plants is required in order to reduce the harmful effects of ROS. Moreover, plant stress resistance is linked to more efficient antioxidant systems. In addition, PGPR applications are accepted as one of the inducers of the antioxidant system (Bhattacharyya et. al., 2020). The major ROS scavenging mechanisms of plants include SOD, APX, and CAT (Mittler, 2002).

In the current study, POD activity was reduced in DWS and BSS plants exposed to drought stress compared to those of well-watered plants. Under drought stress, the POD activity in DW plants (190) was 2.3-fold lower than that in BSS (446) (Figure 2B). The decrease in the activity may be attributed to the inhibitory effect of high concentrations of H_2O_2 on peroxidases of DWS and BSS, as suggested in the study by Martínez et al. (2001) on strawberry plants. Even though that, in general, the POD activity was reduced by drought stress, this activity in BSS plants was higher than in DWS plants. The increase through *P. putida* KT2440 treatment under drought stress suggested that the bacteria could be an effective inducer of the antioxidant system.

In addition, inoculation of KT2440 resulted in an increase in APX and CAT activities under drought stress conditions relative to non-bacteria inoculated plants (DWS) (Figure 2C, 2D). APX activity in BSS plants (34.3) was 1.3-fold-higher than in DWS plants (26.4). Besides, CAT activity of BSS plants (13.7) was 1.5-fold higher than that of DWS plants (9.3). Heidari and Golpayegani (2012) reported that APX and CAT activities in basil plants were induced by the application of *Pseudomonas sp*. during drought. Moreover, *P. mendocina* and arbuscular mycorrhizal fungi (*Glomus intraradices* or *G. mosseae*) inoculation induced CAT activity in lettuce subjected to severe drought stress (Kohler et al., 2008).

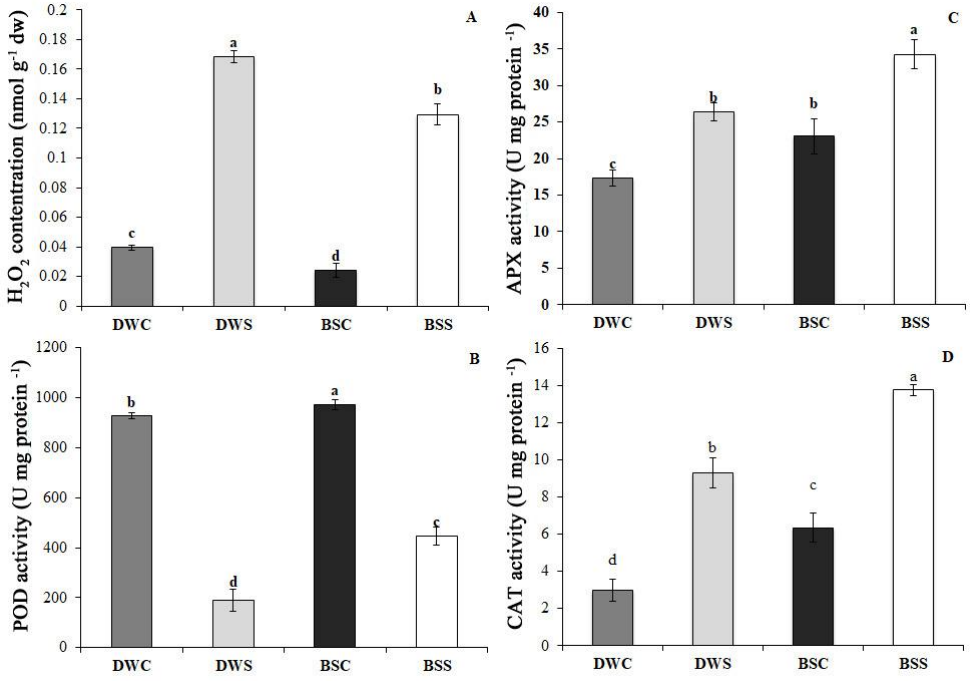

Figure 2. Leaf H_2O_2 content (A), POD (B), CAT (C) and APX (D) activities in tomato plants. DWC (non-inoculated, well-watered), DWS (non-inoculated, drought stressed), BSC (inoculated, well-watered), BSS (inoculated, drought stressed). Different letters show differences among treatments (Tukey's test, $P \leq 0.05$). Vertical bars are SD

In addition to the changes stated above, POD metabolizes phenolic compounds in lignifying tissues and scavenges hydrogen peroxide (Taheri et al., 2014). Water uptake through the cell walls

during drought stress could be achieved by reduced POD activity, which decreased lignification processes caused by drought (Yazici et al., 2007). These results suggest that the mechanisms by which KT2440 promoted drought tolerance in tomatoes involved CAT, APX and POD. The decrease in POD activity may help facilitate the plant's access to water under drought stress conditions as it may lead to a reduction in lignification. Besides, increases in CAT and APX enzyme activities induced by KT2440 were higher than the increase in H_2O_2 caused by drought stress; this means that the H_2O_2 formation caused by drought stress was lower than the H_2O_2 decomposition rate for bacteria treated (BSS) plants. The increase in CAT and APX activities in leaves of BSS plants was probably a response to the rapid rise in H_2O_2 contents generated during stomatal closure due to ABA secreted by the bacteria. PGPR play vital roles in mitigating drought stress effects due to abscisic acid (ABA) accumulation. ABA is known to induce stress resistance by activating anti-oxidant genes such as catalase, superoxide dismutase, and peroxidase by ROS induction, due to increased levels/activities of NADPH oxidase (Abdelaal et al., 2021). ABA application into stomata guard cells was reported to induce significant H_2O_2 production before stomata closure (Zhang et al., 2001). Additionally, Lu et al. (2009) suggested that endogenous H_2O_2 could be involved in ABA-induced drought tolerance of bermudagrass by increasing antioxidant enzyme activities. Also, as scavenging ROS, the carotenoids can improve tolerance to abiotic stresses such as high light conditions, UV irradiation, and salt stress (Yilmaz et al., 2020). Here, we also suggest that the synthesis of carotenoids promoted through bacterial treatment helps antioxidants to detoxify ROS. Therefore, membranes would be protected from oxidative stress due to drought.

The treatment with *P. putida* KT2440 increased the number of fruits and fruit weight per plant, respectively, to their controls. The number of fruits in the BSS plants (5.3) were 1.5-fold higher than that in the DWS plants (3.6) (Figure 3A). Fruit weights in DWS and BSS plants were reduced by drought stress compared to DW and BS plants under well-watered conditions. But, the bacteria treatment resulted in increased fruit weight even under drought stress conditions. The fruit weight of BSS plants (323.2) was 2-fold higher than those of DW plants (165.3) under drought (Figure 3B).

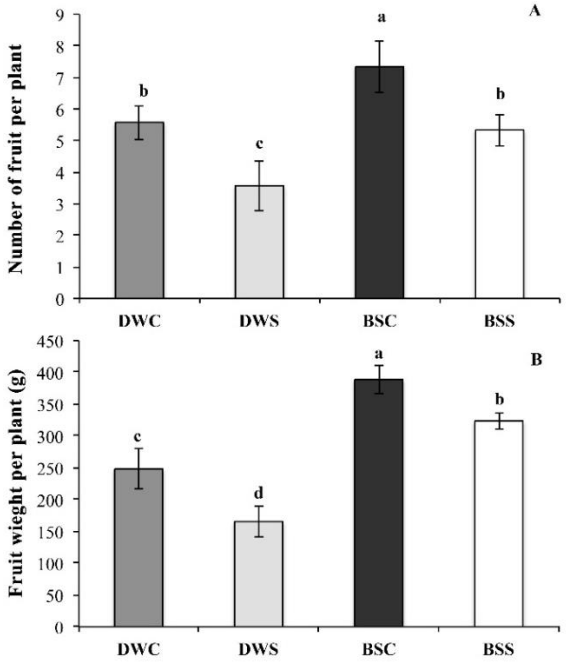

Figure 3. Fruit numbers (A) and fruit weights (B) in tomato plants. DWC (non-inoculated, well-watered), DWS (non-inoculated, drought stressed), BSC (inoculated, well-watered), BSS (inoculated, drought stressed). Different letters show differences among treatments (Tukey's test, $P \leq 0.05$). Vertical bars are SD

Mandyal et al. (2012) reported an increase in fruit yield of a variety of plants following inoculation of PGPR. Gravel et al. (2007) reported that inoculation with *P. putida* or *Trichoderma atroviride* stimulated growth and fruit yield improvement in greenhouse tomato plants. Arshad et al. (2008) reported that the grain yield of pea plants under drought stress at the flowering and pod formation stage was higher (up to 62 and 40 %, respectively) when inoculated with *P. putida* compared to the uninoculated control. The inoculation of different strains of *Azospirillum lipoferum* in wheat eased drought stress, and increased plant growth and yield (Arzanesh et al., 2011). The initiation of tomato fruit growth and fruit set are known to be related to indole acetic acid (IAA) and gibberellic acid (de Jong et al., 2009). The increased number and weights of tomato fruit can be depending on the

IAA production of strain KT2440 (Wu et al., 2011). Tomatoes with a high amount of IAA in their flower buds showed increased fruit production by improving fruit set and raising fruit weight (Mezzetti et al., 2004).

CONCLUSIONS

Pseudomonas putida KT2440 confers tolerance to drought stress in tomato plants by reducing peroxidation extent, increasing photosynthetic pigment content, and activities of the antioxidant enzymes POD, CAT, and APX in the leaves. The bacterium facilitated high fruit yield for tomatoes under drought stress as a biotic drought tolerance elicitor.

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