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Rhizobacteria alleviate the adverse effects of salt stress on seedling growth of *Capsicum annuum* L. by modulating the antioxidant enzyme activity and mineral uptake

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ABSTRACT: Salinity is one of the most important factors restricting vegetative production, especially in arid and semi-arid regions. In this study,the effects of the exogenous plant growth-promoting rhizobacteria (PGPR: *Bacillus pumilus* UG-41, *Bacillus cereus* UG-50) application on seedling growth, concentration of plant nutrient elements, antioxidant activity and chlorophyll, proline, sugar, hydrogen peroxide (H_2O_2), malondialdehyde (MDA), hormone contents of pepper seedlings under salinity stress conditions (100 mM NaCl) were investigated. Our results showed that gibberellic acid (GA), salicylic acid (SA), indole acetic acid (IAA), leaf relative water content (LRWC) and the concentration of all plant tissue nutrients investigated except for Na were decreased by salt stress. On the other hand, PGPR treatment increased the plant growth parameters by increasing the proline, sucrose, hormone and chlorophyll contents; altering the mineral uptake and increasing the antioxidant enzyme activity in pepper seedlings under salt stress. In conclusion, PGPR treatment may be used as an effective technique to protect the plants against salinity stress since the bacteria positively impact the ability of the plant to cope with the stress by particularly increasing the antioxidant enzyme activity, hormone level and mineral uptake.

KEY WORDS: Antioxidant enzyme activity, bacteria, gibberellic acid, mineral uptake, salicylic acid, salinity stress.

INTRODUCTION

Soil salinity affects twenty percent of total arable and nearly one-third of the irrigated agricultural area worldwide (Shrivastava and Kumar, 2015; Schwabe *et al*., 2006). Salinity in soil and irrigation water is one of the largest abiotic stresses in arid and semi-arid regions (Mukhopadhyay *et al*., 2020). This global challenge is predicted to be worsen in these regions due to the increased temperatures, lower rainfall and reduced snowmelt as a result of climate change (Ragab and Prudhomme, 2002; Connor *et al*., 2012) Given that the salt stress is one of the most important factors restricting vegetative production and lowering the crop yields (Parwaiz and Satyawati, 2008), there is a dire need to develop methods that would decrease salinity stress on plants to ensure food security and sustainability.

When the electrical conductivity (EC) of a soil solution reaches approximately 4 dS m^{-1} (equivalent to 40 mM NaCl), the soil is considered saline. Increased salt content increases soil osmotic pressure to around 0.2 MPa, significantly reducing the yield of most products (Munns and Tester, 2008; Acosta-Motos *et al*, 2017). Salt stress causes negative impacts on germination, vegetative growth and reproductive development of plants (Shrivastava and Kumar, 2015). The adverse effects of salinity on plants vary depending on climatic and soil conditions, light intensity and plant type. Salt stress is first perceived by the root system and weakens the plant growth in a short time by triggering osmotic stress caused by water deficiency and by causing nutrient imbalance in the cytosol due to ion toxicity associated with excessive Cl and Na uptake. These two stress factors indirectly lead to Ca and K deficiency and other nutritional imbalances as well as a decrease in photosynthetic capacity (Machado and Serralheiro, 2017). Moreover, soil salinity imposes oxidative stress on plants due to the formation of reactive oxygen derivatives (ROS).

Under saline conditions, plants activate different physiological and biochemical mechanisms to cope with the stress. Such mechanisms include changes related to morphological and anatomical structures, water response, photosynthetic activity, hormonal and biochemical response (Munns and Tester, 2008; Cassaniti *et al*., 2013; Acosta-Motos *et al*., 2017). Factors such as the concentration and type of salt, the characteristics of the plant, and the duration of exposure to stress, can change the impact of the negative effects of salinity on the growth and development of plants (Shams *et al*., 2019).

Pepper is widely cultivated in Turkey and in semi-arid

Table 1. Bacterial strains, nitrogen fixation (N) and phosphate-solubilizing activity (P) properties.

Bacterial strains	Gram stain	Growth in N free basal medium	P solubilizing
Bacillus pumilus UG - 41	+	+	+
Bacillus cereus UG - 50	+	S+	+

+: positive, S+: strong positive

regions of Mediterranean countries due to its high economic value. Studies showed that pepper plants are sensitive and moderately tolerant to salty conditions (De Pascale *et al*., 2003; Gunes *et al*., 1996). Seed germination, vegetative and generative development of pepper decrease under salt stress which reduces its productivity (Maas, 1986; Bolarin *et al*, 1993; Yildirim and Guvenc, 2006). The threshold value for salt tolerance of pepper was reported to be 1.5 dS m^{-1} (Chartzoulakis and Klapaki, 2000; Navarro *et al*., 2002; Suarez, 2010).

Plant Growth Promoting Rhizobacteria (PGPR) are beneficial microorganisms colonize in the rhizosphere/endorhizosphere and promote the growth of the plants through various mechanisms of action such as nitrogen binding, solubilizing phosphorus and other nutrients, hormone production, increasing water and mineral uptake, supporting root growth and increasing enzyme activity in the plant. PGPR mostly belong to the genera of *Acinetobacter*, *Achromobacter*, *Aereobacter*, *Agrobacterium*, *Alcaligenes*, *Artrobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Micrococcus*, *Pseudomonas*, *Rhizobium*, *Serratia* and *Xanthomonas*. PGPR were reported as promising tools to alleviate the adverse effects of abiotic stresses on plants (Shantharam and Mattoo, 1997; Esringü *et al*., 2016).

PGPR were also shown to ameliorate the adverse effects of salinity stress on the growth of pepper (*Capsicum annuum* L.) plant (Chartzoulakis and Klapaki, 2000; Navarro *et al*., 2002; Suarez, 2010; Hahm *et al*., 2017). However, the effects of PGPR on the growth parameters as well as the physiological and biochemical characteristics of pepper seedlings under salinity stress conditions have not been elucidated yet. The aim of this study was to investigate the effects of the exogenous PGPR application on the pepper seedling growth; plant nutrient element, chlorophyll, proline, sugar, H_2O_2, MDA and hormone contents of the plant as well as the antioxidant activity of pepper seedlings under salinity stress conditions.

MATERIALS AND METHODS

Plant materials, growing conditions and experimental design

In the study, pepper (*Capsicum annuum* L. cv Yalova Carliston) was used as plant material. The experiments were carried out in the greenhouses (the average temperature and humidity were about 30±2°C and 60±5%, respectively) of Atatürk University, Faculty of Agriculture, Department of Horticulture. Before planting, pepper seeds were kept in 5% sodium hypochlorite for 15 minutes, washed with sterile deionized water and dried under sterile conditions for surface sterilization Then the sterile seeds were sown at 1–1.5 cm depth in 216 celled trays filled with peat.

The seedlings that reached the 4–5 true leaf stage were transferred to 2 liter pots containing 50% soil, 25% farm manure and 25% sand. One seedling was planted in each pot and irrigated with Hoagland solution.

Experimental design was hierarchical with respect to two factors arranged in a completely randomized design with three replications. The first factor (NaCl levels) had two levels (0 and 100 mM), and the second one (PGPR treatments) had three levels (two bacterial strains and control group) (2 × 3 factorial experimental design). The total number of pots was 90, comprising three replications of each treatment, 5 plants for each replication. The temperature inside the greenhouse was measured daily and the average minimum and average maximum temperatures were calculated.

Bacterial application

The bacterial strains [*Bacillus pumilus* UG-41 (B1), *Bacillus cereus* UG-50 (B2)] were obtained from the Department of Plant Protection, Faculty of Agriculture at Atatürk University. Identification of the tested bacterial strains was confirmed by using sequence analysis (Table 1). These non-pathogenic bacterial strains were isolated from the rhizosphere of wild and traditionally cultivated plants growing in Ağrı City located in the Eastern Anatolia Region of Turkey. The bacterial strains were able to grow in N free basal medium indicating their N fixing potential. In the present study, P solubilizing activities of the two PGPR strains were measured according to the qualitative methods (Mehta and Nautiyal, 2001)

The bacterial strains were grown on nutrient agar. A single colony was transferred to 250 mL flasks containing nutrient broth and grown aerobically in flasks on a rotating shaker (95 rpm) at 27°C for 24 h. Dipping method was used for the inoculation of plant roots with the bacterial suspensions at a concentration of 10^8 cfu/mL for 30 min prior to planting into the pots. Control plants were dipped into sterile water.

Salt application

Salinity stress was created with 100 mM NaCl solution which is the level at which the stress can be clearly noticed (Chartzoulakis and Klapaki, 2000; Ozdemir *et al*., 2016; Shams *et al*., 2019). The pH of salt solution was 6.5. The SAR (Sodium Available Ratio) of

salt solution, which is one of the water quality indexes, was adjusted as < 5 (Shams and Yildirim, 2020).

Irrigation water was prepared by mixing 100mM salt solution with Hoagland solution. To determine the salinity in the soil, pH / Cond 340i / SET, WTW device was used. Irrigation continued until NaCl concentration in soil reached 100mM. Control plants (0 mM NaCl) were irrigated only with water and Hoagland solution mixed in 1:1 (v/v) ratio. Irrigation was carried out until the field capacity of the pots reached 60% in the control group. Salt application started 7 days after planting and continued until the plants were harvested.

Measurements and analysis

The pot study was terminated on the 50th day from seedling planting. At harvest, five plants from each repetition were taken to measure stem diameter, plant height, leaf number, aerial fresh-dry weights, and root fresh-dry weights. For dry weight measurements, the plant material was kept at 70°C for 48 h. To determine the content of proline, sucrose, MDA, H_2O_2, and antioxidant enzyme activity, roughly 20 g of fresh leaves were frozen in liquid nitrogen and then stored at -80°C. Analyses were performed in quadruplicate.

The chlorophyll reading values of the plant leaves and the leaf areas were determined by using a chlorophyll meter (SPAD - 502, Konica Minolta Sensing, Inc., Japan) and a leaf area meter (CID-202 Portable Laser Leaf Area Meter, CID Bio-Science, Inc., WA, USA), respectively.

To determine leaf chlorophyll concentration of plants samples were cut at 10 mm diameter from the middle leaves and put into 2 ml Eppendorf tubes. After the samples were shaken with 0.2 mL 80% cold acetone for three minutes at 50 hz, followed were centrifuged at 10,000 rpm at 5°C by brought to final volume (2 ml) with 80% cold acetone. And finally, the absorbance values was measured at 663 and 645 nm by a microplate spectrophotometer (Thermo Scientific™ Multiskan™ FC Microplate Photometer) and Chlorophyll a, chlorophyll b and total chlorophyll content were calculated as mg g fresh weight-1 (Lichtenthaler and Wellburm, 1983).

Membrane permeability (MP) and leaf relative water content (LRWC) were determined according to Yildirim *et al*. (2015). H_2O_2 content was determined according to Velikova *et al*. (2000). Thiobarbituric acid-reactive substances were measured as MDA, a degraded product of the lipid, which determines the lipid peroxidation. The concentration of MDA was determined from the absorbance curve, by using an extinction coefficient of 155 mmol l^{-1} cm^{-1} (Shams *et al*., 2019).

Sucrose concentration was measured by a method given by Chopra *et al*., (2000). Proline concentration was assayed spectrophotometrically at 520 nm (Bates *et al*., 1973). Catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD) activities were determined based on the method given by Sahin *et al*. (2018).

Extraction and purification processes of hormones were executed as described by Kuraishi *et al*. (1991) and Battal and Tilekliooglu (2001). Hormones were analyzed by high performance liquid chromatography (HPLC) using a Zorbax Eclipse- AAA C-18 column (Agilent 1200 HPLC) and by absorbance at 265 nm in a UV detector. Flow speed was set to 1.2 mL min^{-1} at a column temperature of 25°C. Gibberellic acid (GA), salicylic acid (SA), indole acetic acid (IAA) and abscisic acid (ABA) levels were determined using 13% acetonitrile (pH 4.98) as the mobile phase.

For nutrient element analyses, pepper leaves were ground after being dried at 68°C for 48 h in an oven. Determination of the total N content was achieved by the Kjeldahl method using a Vapodest 10 Rapid Kjeldahl Distillation Unit (Gerhardt, Konigswinter, Germany). An inductively coupled plasma spectrophotometer (Optima 2100 DV, ICP/OES; Perkin-Elmer, Shelton, CT) was used to determine tissue K, P, Ca, Mg, Na, Fe, Zn and B content (Mertens, 2005a,b).

Statistical analysis

In the experiment, a randomized plot design was used and the obtained data were analyzed using SPSS20 statistical package program. Data were subjected to variance analysis (ANOVA) and differences of means were determined by Duncan multiple comparison test.

RESULTS

Growth parameters of pepper seedlings dramatically decreased with the NaCl stress (Table 2 and Table 3). On the other hand, PGPR treatments generally affected these parameters positively for both control samples and stressed samples. Plant height and stem diameter were negatively affected by salt stress, which is evidenced by a decrease of 45.7% and 21.0%, respectively. However, under salt stress, PGPR inoculated plants had significantly higher plant height and stem diameter than the control treatments. Chlorophyll content of plant leaves significantly decreased with the salt stress. However, treatment with B1 positively affected the chlorophyll reading value under salinity stress compared to the non-inoculated control. Chlorophyll b and total chlorophyll values significantly decreased at 100 mM NaCl, where the decrease ratios were 48.1% and 43.1%, respectively compared to the control. However, PGPR treatments positively affected chlorophyll values for both stressed and non-stressed conditions (Table 2).

Under salt stress, treatment with B2 strain resulted in significantly higher shoot fresh weight, shoot dry weight, and root dry weight compared to the control. Treatment with B2 increased shoot fresh weight by 28.6%, shoot dry weight by 27.9%, root fresh weight by 31% and root dry weight by 22.6%, compared to the control. Salinity stress increased the MP value (by a ratio of 282.3% compared

to the control) and decreased LRWC value (by a ratio of 41.2% compared to the control). On the contrary, under stress, PGPR treatments decreased the MP value (by 9.1% and 16.2% compared to the control) and increased the LRWC values (by a ratio of 45.7% and 67.6% compared to the control) (Table 3).

Hormone content of pepper seedlings in response to PGPR treatments under salt stress is shown in Table 4. GA, SA and IAA contents of pepper were decreased by a ratio of 36.9%, 34.2% an 60.2%, respectively compared to the control under salinity stress; while ABA content increased by 108.8% compared to the control. However, PGPR treatments positively affected GA content (increased by 72.3% and 88.9%), SA content (increased by 52.9% and 67.2%) and IAA content (increased by 119.6% and 337.3%), and reduced the ABA content (by 38% and 62.7%) under salt stress condition (Table 4).

Under salinity stress, H_2O_2, MDA, proline and sucrose contents of pepper seedlings increased by 84.2%, 120%, 170.1% and 37.5%, respectively compared to the non-stressed conditions. PGPR treatments resulted in decreased H_2O_2 (18.9–31.3%), MDA (29.5–40.2%) and proline (54.1–75.9%) contents in pepper seedlings under salinity conditions. On the other hand, PGPR treated plants grown under salinity stress had more sucrose content than the control plants (Table 5).

Antioxidant activity of pepper seedlings in response to different PGPR treatments under salt stress is shown in Table 6. Salinity stress resulted in increased antioxidant activity in pepper seedlings. The increase ratios were 154% for CAT, 81.3% for POD, and 83.9% for SOD. However, PGPR treatments caused a reduced activity of CAT, POD, and SOD in pepper seedlings in both salinity and non-salinity conditions.

The concentrations of some macro and micro plant nutrient content in pepper seedlings in response to PGPR treatments are shown in Figure 1. Salinity decreased the mineral content of leaves except for Na content for all treatments: 46.1% in N, 44.7% in K, 54.3% in P, 50.5% in Ca, 46.2% in Mg, 42.1% in Fe, 68.8% in Zn, and 49.7% in B compared to the control. Plants treated with PGPR had higher mineral content under both stressed and non-stressed conditions. Under 100 mM NaCl salt stress, B2 treatment significantly decreased the Na content (by 25.9%) compared to the control (Figure 1).

DISCUSSION AND CONCLUSION

Many plant species are very sensitive to environmental stress during germination and seedling periods (Foolad *et al*., 1999). In accordance with previous studies (Shannon and Grieve, 1999; Houimli *et al*., 2010; Hussein *et al*., 2012; Ekinci *et al*., 2019), our results showed that salinity stress negatively affected the growth parameters of pepper seedlings (Table 2, Table 3). Under salt stress, the growth and development of plants are reduced due to osmotic and ionic stress (Parida and Das, 2005). In the rhizosphere, a high concentration of salt causes an increase in the soil osmotic pressure, which reduces the amount of water available for the plant. When the ability of the plant to acquire water is reduced a decrease in cell expansion is observed which slows shoot development. Moreover, impaired nutrient uptake mechanism and ion toxicity due to salinity negatively affect plant growth (Ashraf and Harris, 2004). Therefore, salt stress causes a decrease in the dry and fresh weights (Tuteja, 2007). Our results showed that Mg and Fe content decreased in plants grown under salinity stress (Figure 1), which might be the one of the underlying reasons for the significant decreases in chlorophyll a, chlorophyll b and total chlorophyll amounts in pepper seedlings (Table 2). Similarly, Marscher (2011) reported that Fe and Mg deficiencies cause a decrease in chlorophyll synthesis activity. Ion accumulation and irregularities in stomatal closure cause reductions in total chlorophyll at high salt levels (Kıran *et al*., 2018). Under salt stress conditions, chlorophyll is broken down by oxygen radicals in plants and chloroses occur (Jaleel *et al*., 2008). The decreases in chlorophyll a and b content with salt stress generally occur due to the damage of chloroplasts thylakoid membrane (De Pascale *et al*., 2003). It has been stated that salt stress causes cell death due to ion toxicity, cell damage, and deterioration in pigments (Suriyan and Chalermpol, 2009). This effect of salt has been attributed to the salt-induced attenuation of the protein pigment-lipid complex or increased chlorophyllase enzyme activity (Hand *et al*., 2017). Besides salt sensitive pepper varieties (Hand *et al*., 2017), earlier studies reported a decrease in chlorophyll content of other plants such as lettuce (Yildirim *et al*., 2015) and melon (Kusvuran *et al*., 2007).

Membrane permeability (MP) was found to increase in pepper seedlings under salt stress (Table 3). Similarly, salt stress has been reported to increase the MP rate in peppers in previous studies (Aktas *et al*., 2006; Houimli *et al*., 2008; Houimli *et al*., 2010). One of the harmful effects of salt stress is on the cell membrane. The cell membrane is a selectively permeable membrane consisting of a double phospholipid layer and proteins embedded in this layer. Salt stress initiates the change of lipid composition and causes membrane damage. Under salt stress conditions, the enzymes in the lipid composition that synthesize lipids change, and/or hydrolysis of the phospholipid types occur. This process affects the permeability, fluidity and protein activity of the membrane (Zhang *et al*., 2016). Thus, the tissue electrical conductivity of the plant begins to increase under stress conditions. Due to the increase in salt stress, there was a statistically significant decrease in the amount of LRWC in salt-stressed plants. In a previous study, pepper genotypes showed a different response to salinity, and the amount of LRWC in resistant varieties increased

Table 2. Plant height, stem diameter, chlorophyll reading value, Chlorophyll a, Chlorophyll b and total Chlorophyll of pepper seedlings in response to different PGPR treatments under salt stress.

Salt (mM NaCl)	Bacteria	Plant height (cm)	Stem diameter (mm)	Chlorophyll (SPAD)	Chlorophyll a (mg g^{-1})	Chlorophyll b (mg g^{-1})	Total Chlorophyll (mg g^{-1})
0	B0	29.83±1.13 a***	5.28±0.07 b***	52.50±2.01 a***	1.71±0,17 c***	2.62±0,03 a***	4.55±0,33 b***
	B1	28.89±1.52 a	5.29±0.02 b	53.77±1.59 a	2.98±0,07 a	2.73±0,21 a	5.25±0,36 a
	B2	29.52± 1.11 a	5.66±0.14 a	50.30± 2.14 a	2.67±0,35 a	3.06±0,81 a	5.29±0,02 a
100	B0	16.19±0.76 d	4.17±0.08 d	27.80±2.91 c	1.61±0,05 c	1.36±0,27 b	2.59±0,68 d
	B1	22.42±0.63 c	4.56±0.06 c	35.53±0.67 b	1.70±0,22 c	1.71±0,32 b	3.23±0,13 c
	B2	25.08±1.16 b	4.50±0.04 c	30.67±1.46 c	2.28±0,14 b	1.75±0,07 b	4.03±0,07 b
B		***	***	**	***	ns	***
S		***	***	***	***	***	***
B x S		***	***	*	*	ns	ns

*: p<0.05; **: p<0.01; ***: p<0.001; ns: p>0.05.
Data followed by a different letter were significantly different according to Duncan's Multiple Range Test.
Chlo-a: Chlorophyll a, Chlo-b: Chlorophyll b, Total Chlo: Total chlorophyll content, B0: No bacteria treatment, B1: *Bacillus pumilus* UG-41, B2: *Bacillus cereus* UG-50.

Table 3. Shoot fresh weight, root fresh weight, shoot dry weight, MP and LRWC of pepper seedlings in response to different PGPR treatments under salt stress.

Salt (mM NaCl)	Bacteria	Shoot fresh weight (g)	Root fresh weight (g)	Shoot dry weight (g)	Root dry weight (g)	MP (%)	LRWC (%)
0	B0	11.81±0.19 b***	9.56±0.10 b***	2.95±0.11 c***	0.90±0.02 b***	22.59±1.87 d***	77.99±2.59 a***
	B1	12.12±0.15 b	10.02±0.21 a	3.11±0.09 b	0.93±0.02 b	23.81±1.68 d	78.04±3.89 a
	B2	12.68±0.08 a	9.59±0.26 b	3.39±0.03 a	1.15±0.01 a	24.39±0.27 d	77.12±3.67 a
100	B0	5.67±0.31 e	5.22±0.14 d	1.11±0.06 e	0.53±0.02 e	86.37±1.80 a	45.87±4.04 c
	B1	6.56±0.23 d	6.64±0.32 c	1.32±0.03 d	0.59±0.01 d	72.34±3.17 c	66.81±0.86 b
	B2	7.29±0.09 c	6.84±0.10 c	1.42±0.04 d	0.65±0.02 c	78.52±1.17 b	76.89±3.99 a
B		***	***	***	***	***	***
S		***	***	***	***	***	***
B x S		**	***	*	***	***	***

*: p<0.05; ***: p<0.001.
Data followed by a different letter were significantly different according to Duncan's Multiple Range Test.
MP: Membrane permeability, LRWC: Leaf relative water content, B0: No bacteria treatment, B1: *Bacillus pumilus* UG–41, B2: *Bacillus cereus* UG–50

Table 4. Hormone content of pepper seedlings in response to different PGPR treatments under salt stress

Salt (mM NaCl)	Bacteria	Gibberellic acid (ng μg^{-1})	Salicylic acid (ng μg^{-1})	Abscisic acid (ng μg^{-1})	Indole acetic acid (ng μg^{-1})
0	B0	195.73±23.40 c***	69.77±5.19 b***	1.59±0.58 bc***	1.28±0.08 c***
	B1	239.65±23.24 b	78.48±6.74 b	1.19±0.50 c	2.40±0.12 b
	B2	271.65±8.94 a	96.71±2.50 a	1.12±0.19 c	4.46±0.13 a
100	B0	123.38±5.15 d	45.92±5.10 c	3.32±0.25 a	0.51±0.10 d
	B1	212.53±11.49 bc	70.22±5.75 b	2.06±0.21 b	1.12±0.06 c
	B2	233.12±17.32 b	76.77±3.42 b	1.24±0.07 c	2.23±0.03 b
B		***	***	***	***
S		***	***	***	***
B x S		ns	*	**	***

*: p<0.05; ***: p<0.001 ; ns: p>0.05.
Data followed by a different letter were significantly different according to Duncan's Multiple Range Test.
B0: No bacteria treatment, B1: *Bacillus pumilus* UG-41, B2: *Bacillus cereus* UG-50

Table 5. H_2O_2, MDA, proline and sucrose content of pepper seedlings in response to different PGPR treatments under salt stress.

Salt (mM NaCl)	Bacteria	H_2O_2 (mmol kg^{-1})	MDA (mmol kg^{-1})	Proline (mmol kg^{-1})	Sucrose (%)
0	B0	9.33±1.07 d***	5.40±0.14 d***	69.00±1.44 c***	20.56±2.77 d***
	B1	10.61±0.62 cd	5.16±0.09 d	34.48±0.89 e	37.69±1.72 b
	B2	9.94±0.23 d	5.03±0.33 d	17.06±0.90 f	45.94±1.45 a
100	B0	17.19±1.17 a	11.88±0.76 a	186.35±9.88 a	28.26±1.35 c
	B1	13.94±0.71 b	7.10±0.10 c	85.51±6.68 b	27.21±2.15 c
	B2	11.81±0.49 c	8.37±0.22 b	44.87±1.98 d	36.32±4.54 b
B		***	***	***	***
S		***	***	***	***
B x S		***	***	***	ns

***: p<0.001; ns: p>0.05.
Data followed by a different letter were significantly different according to Duncan's Multiple Range Test.
H_2O_2: Hydrogen peroxide, MDA: Malondialdehyde, B0: No bacteria treatment, B1: *Bacillus pumilus* UG-41, B2: *Bacillus cereus* UG-50

Table 6. Antioxidant activity of pepper seedlings in response to different PGPR treatments under salt stress

Salt (mM NaCl)	Bacteria	CAT (eu g leaf^{-1})	POD (eu g leaf^{-1})	SOD (eu g leaf^{-1})
0	B0	147.64±3.57 c***	8601.97±501.78 d***	524.71±66.59 c***
	B1	153.87±9.28 c	9151.52±570.02 cd	421.62±71.45 d
	B2	152.68±2.25 c	9150.21±87.23 cd	206.17±12.69 e
100	B0	375.06±4.23 a	15599.63±860.06 a	965.32±41.33 a
	B1	175.93±6.61 b	10451.94±599.19 b	672.62±61.01 b
	B2	170.28±3.51 b	9971.49±195.06 bc	676.08±14.15 b
B		***	***	***
S		***	***	***
B x S		***	***	**

**: p<0.01; ***: p<0.001; ns: p>0.05
Data followed by a different letter were significantly different according to Duncan's Multiple Range Test.
CAT: Catalase, POD: peroxidase, SOD: superoxide dismutase, B0: No bacteria treatment, B1: *Bacillus pumilus* UG-41, B2: *Bacillus cereus* UG-50.

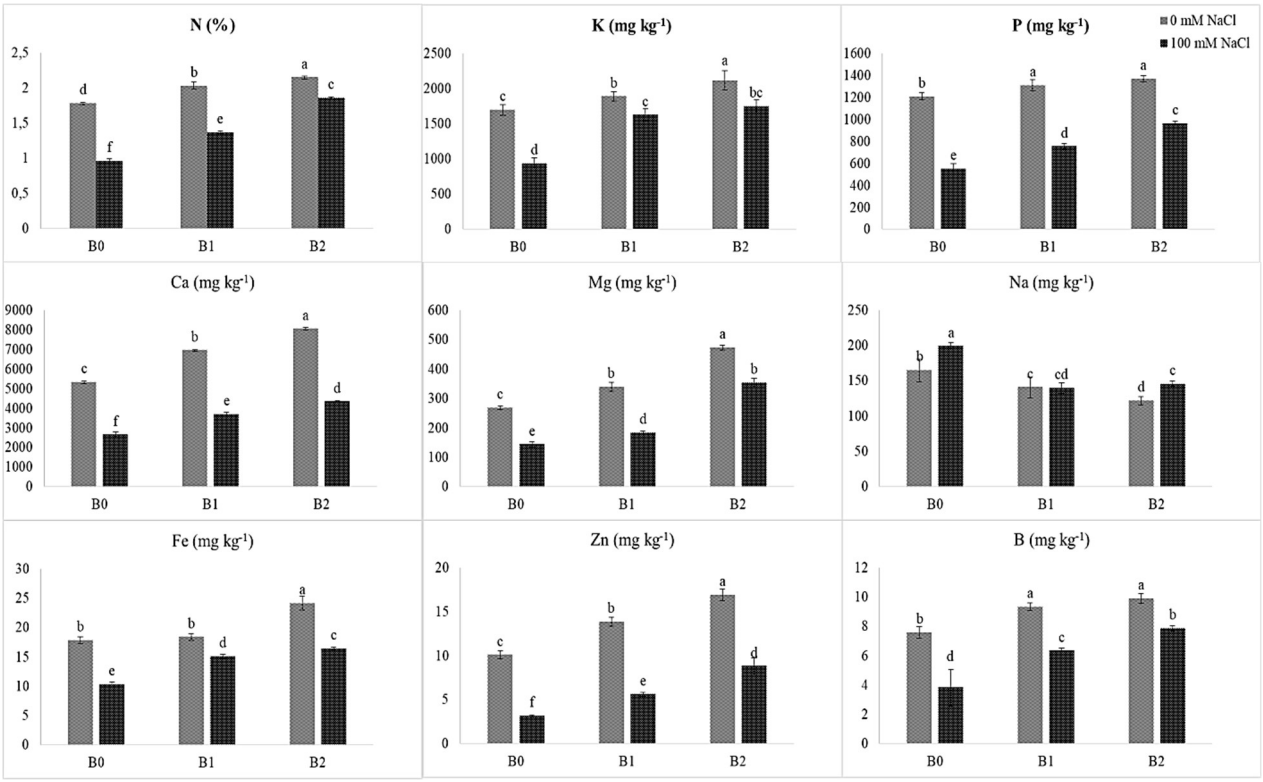

Fig. 1. Plant nutrient element content of pepper seedlings in response to different PGPR treatments under salt stress. Data followed by a different letter were significantly different according to Duncan's Multiple Range Test. B0: No bacteria treatment, B1: *Bacillus pumilus* UG-41, B2: *Bacillus cereus* UG-50

compared to other varieties (Arrowsmith *et al*., 2012). Hahm *et al* (2017) reported in their study that salt stress reduces the amount of LRWC in different pepper varieties. Hand *et al*. (2017) determined that the LRWC values of different pepper varieties grown under salt stress differ, and sensitive varieties have lower values. Salt stress causes a decrease in water content osmotically in plants. Thus, the decrease in the ratio of the dry and fresh matter of leaves and roots means an osmotic adjustment in the plant. However, decreased LRWC may result from dehydration of cell walls. The reason for this may be the increase in Na and Cl concentrations detected in the cell outer wall (Flowers, 1991). These results can be attributed to the accumulation of toxic ions such as Na and Cl, leading to a decrease in intracellular CO_2 partial pressure, reducing leaf expansion, and reducing stomatal closure (Hasegawa *et al*., 2000).

Salt stressed plants had less hormone content except for ABA than the non-stressed plants. Salt stress conditions increased ABA content in pepper seedlings (Table 4). Similarly, Piñero *et al*. (2014) reported that salt caused an increase in the amount of ABA in pepper. Response to chemical agents such as ABA in the plant is the closure of stomata and this is a mechanism of avoiding drought and salinity stress (Alscher and Cumming, 1990; Ghanem *et al*., 2008; Santner and Estelle, 2009). It has

been stated that ABA accumulation caused by salt stress may be caused by the decreased cell volume or changes in plasmalemma leading to ABA accumulation and an osmosensing mechanism (Jia *et al*., 2002).

In this study, an increase in MDA and H_2O_2 content was detected in pepper varieties grown under salt stress (Table 5). Oxidative damage occurred in the cell membranes due to the elevated levels of H_2O_2 resulted in an increase in the amount of MDA which ultimately led to an increase in the membrane permeability (MP). Similarly previous studies reported increased levels of MDA and H_2O_2 in peppers grown under salt stress (Azuma *et al*., 2010; Penella *et al*., 2016). MDA is formed by the peroxidation of the cell membrane. Changes in lipid peroxidation are considered to be an important factor in determining the degree of oxidative damage in living organisms, resulting in decreased membrane stability in living organisms under stress conditions. The most important cause of severe damage to the cell membrane, superoxide radicals, hydrogen peroxide, and radical hydroxyl exposure has been found to cause peroxidation of cell membrane lipids (Lim *et al*., 2009; Sairam *et al*., 2002). Our results showed that, proline and sugar levels increased with the increasing salt concentration in pepper seedlings (Table 5). Similar to our study, it was found that the amount of proline in peppers increased under salt stress (Kaouther *et al*., 2012). Proline is one of the most stable amino acids in plants that resist oxidative stress and has a little inhibitory effect on cell growth among all amino acid groups (Pérez-López *et al*., 2009; Sudhakar *et al*., 1993). Proline accumulation plays a role in maintaining the osmotic balance of the cell and proline accumulation in the plant increases the salt resistance (Kishor *et al*., 2005). Wang *et al*. (2018) reported that PGPR treatments increase the proline content in pepper seedlings which result in alleviation of the negative effects of salt stress. Likewise, sugars play a major role under stress as osmotic agents. In stress conditions, the increase in sugar is significantly associated with osmotic regulation and maintenance of inflammation, resulting in protein and membrane stability as an osmotic preservative. Soluble sugars and proline can be used to arrange osmotic potential in plant cells (Sánchez *et al*., 1998). In this study, it was found that the activities of CAT, SOD and POD enzymes were higher in pepper seedlings grown under salt stress (Table 6). Similar to our results, in a study by Lim *et al*. (2009), it was determined that the antioxidant enzyme activity of the cold-resistant pepper varieties was higher than the sensitive varieties.

In the pepper seedlings grown under salt stress conditions, a decrease was observed in the nutrient content of the plant, except for Na. Similarly, it has been reported in many studies that plant nutrient content decreases in plants grown in salty conditions (Cabañero *et al*., 2004; Cramer, 2002; Mansour, 2000; Marschner, 2012). Salt causes a decrease in water potential, disruption of the ion balance in the cell, and a negative effect on plant growth. An excessive amount of NaCl in the root environment causes an increase in Na and Cl levels in the cell and a decrease in the amount of Ca, K, Mg. Sodium ion (Na) entering the cells disrupts the membrane potential and causes the extracellular Cl to enter the cell passively via the anion channels.

In this context, in order to alleviate the negative effects resulted from salt stress, the use of tolerant varieties as well as cultural measures such as excessive fertilization and avoiding irrigation gain importance. In addition, the use of beneficial microorganisms (PGPR) in abiotic stress conditions has become an interesting subject in recent years. In this study, we have shown that PGPR treatments mitigated the negative impacts of salinity on the growth of pepper seedlings (Table 2 and Table 3). Phosphate solubilizing and nitrogen fixing bacteria can improve the N and P nutrition of plants and stimulate plant growth. Mayak *et al*. (2004) reported that the adverse effects of salt stress could be overcome by using bacteria such as *Achromobacter piechaudii*. These bacteria were isolated from the plant root surface and were capable of producing 1-Aminocyclopropane-1-Carboxylate (ACC) deaminase (enzyme) which contributed to the growth of tomato seedlings under salt stress conditions (172 mM NaCl). In a similar study, although the dry weight of pepper seedlings decreased by 1.3 times in salt stress environment, treatment with ACC deaminase-producing bacteria preserved the plant weight (Siddikee *et al*., 2011). Samancıoğlu and Yildirim (2015) also reported that PGPR can have a positive effect on plant growth and yield in plants grown under abiotic stress conditions by facilitating the intake of nutrients by the plant or by reducing the ethylene level. Our results showed that PGPR inoculated plants had more macro and micro mineral content compared to the non-inoculated plants under salt stress, except for Na (Figure 1). It was reported that bacterial inoculation could restrict Na and Cl uptake and increase the uptake of mineral matter such as N, P, K and Ca under salt stress (Yildirim *et al*., 2008). In a similar study, Mayak *et al*. (2004), found that root bacteria helped the plant in nutrient intake which alleviated the negative effects of salinity on the plant.

In another study, Han and Lee (2005), reported that under salt stress, PGPR application increased the P, K, and Ca intake compared to the control which decreased the adverse effects of .salinity. Altın and Bora (2005) and Samancıoğlu *et al*. (2016) also reported that bacteria that promote plant growth have mechanisms such as facilitating food intake. Ashraf and Harris (2004) determined that PGPR, exopolysaccharide -producing bacteria, could restrict Na influx into the roots. Furthermore, there are many studies showing that PGPR could increase the uptake of the minerals in the presence or absence of salt stress (Grichko and Glick, 2001;

Egamberdieva and Höflich, 2003; Mayak *et al*., 2004). Phosphate solubilizing and N-fixing bacteria (Table 1) can improve the N and P intake of plants and stimulate plant growth (Yildirim *et al*., 2008; Karlidag *et al*., 2011). Our data showed that higher nutrient uptake by PGPR inoculations significantly improved seedling growth.

In a study conducted on lettuce plants, the effect of root bacteria on salt stress was investigated, and it was reported that the dry weight of green parts was higher than the control group and that the root dry weight increased by 30%. In addition, in this study, it was concluded that the use of PGPR against salt stress can be used as an effective method in terms of the data obtained from antioxidative enzyme parameters (Kohler *et al*., 2009, 2010).

It has been previously reported that PGPR applications increase the chlorophyll content in peppers and other plants grown both under salt stress and under stress-free conditions. Jamal *et al*. (2018) investigated the effects of *Bacillus amyloliquefaciens* Y1 strain on soil properties, seedling development, and soil enzyme activity and found that PGPR increased the biomass in root and shoot in pepper, increased the total number of flowers, and improved chlorophyll content. Similarly, Wang *et al*. (2018) reported that strain WU-5 (Bacillus spp.) increased the growth parameters such as fresh weight, dry weight, shoot length and root length of pepper seedlings compared to the control under salt stress .

PGPR can directly affect plant growth through the production of phytohormones, indole-3-acetic acid and cytokinins. PGPR have also been reported to able to control ACC levels or block ethylene biosynthesis in plants, which stimulate the root growth and protect plants from the adverse effects of salt stress (Samancıoğlu and Yildirim, 2015). The positive effects of PGPR treatments on the yield and growth of plants can be attributed to the production of phytohormones such as indole-3-acetic acid and cytokinins, N_2-fixation ability, phosphate solubilizing capacity, and antimicrobial substance production. Under stress conditions, PGPR affect plant growth through mechanisms such as plant hormone synthesis and adjustment of plant hormone levels (Timmusk and Wagner, 1999; Lucy *et al*., 2004). PGPR application increased the organic acid, amino acid, enzyme, and hormone production of plants (Gunes *et al*., 2015). PGPR could help the growth of plants by mitigating the deleterious effects of salinity conditions by promoting the accumulation of proline and glutamate (Bashan and Holguin, 1998). It has been determined that PGPR stimulate the elongation and division of cells by producing auxin hormone; affect stem elongation by the production of gibberellin; and affect cell division, root development and yield by the production of cytokine. In addition, PGPR reduce the level of vegetable ethylene by preventing ethylene production (Glick *et al*., 1998; Gutierrez Mañero *et al*., 2001; Dobbelaere *et al*., 2003). The promoting effects of PGPR under salinity conditions can also be attributed to their ability to control ACC. By enhancing the production of 1-aminocyclopropane-1-carboxylate, PGPR promote root growth due to the decreased levels of ethylene and help alleviating the negative effects of the salinity stress conditions (Mayak *et al*., 2004). It has been noted that with the IAA produced by PGPR, it is able to balance the decline in IAA levels in the root and improve the growth and development of the plant under salt stress (Egamberdieva, 2013). Pieterse *et al*. (2003) suggested that PGPR can stimulate a PGPR-mediated induced systemic resistance and promote the accumulation of the signaling molecules such as salicylic acid and jasmonate, which modulate plant responses to abiotic stress conditions (Pieterse *et al*., 2003).

Our results showed that, PGPR inoculated plants had less electrolyte leakage compared to their respective non-inoculated controls. Bacterial inoculations significantly increased LRWC, which is a useful measure of the physiological water status of plants. Increased LRWC by PGPR has been reported for radish (Yildirim *et al*., 2008), lettuce (Yildirim *et al*., 2011), and strawberry (Karlidag *et al*., 2011) grown under salt stress. Mayak *et al*. (2004) reported that PGPR could facilitate the rooting and growth of plants grown under salt stress by improving water use efficiency.

In conclusion, our data suggest that PGPR inoculations could alleviate the adverse effects of soil salinity by increasing the level of antioxidant enzymes, phytohormones (indole-3-acetic acid and cytokinins), chlorophyll content, and by altering mineral uptake, therefore enhancing salt tolerance in pepper seedlings.

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