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Role of inoculation with multi-trait rhizobacteria on strawberries under water deficit stress

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Abstract

This study was conducted during 2011 and 2012 to evaluate the effect of 1-aminocyclopropane-1-carboxylate (ACC) deaminase-containing, N_2-fixing and P-solubilizing bacteria on the yield and morpho-physiological parameters of strawberry. A total of 8 applications at the trial set, with four water regimes were randomly distributed into the pots. The diminishing water supply caused a gradual decrease in the plant growth, chlorophyll content and berry yield, accompanied by increasing activities of drought stress markers such as total phenolics content (TPC), trolox equivalent antioxidant capacity (TEAC), malondialdehyde (MDA) content, hydrogen peroxide (H_2O_2), glutathione reductase (GR), glutathione S-transferase (GST), catalase (CAT), peroxidase (POD), superoxide dismutase (SOD) and ascorbate peroxidase (APX) in the leaves of strawberry. The multi-trait bacteria also increased plant growth and yield as well as TPC, TEAC, antioxidant enzymes (GR, GST, CAT, POD, SOD and APX) activity, phytohormone (GA, SA and IAA) and the contents of N, P, K, Ca, Fe, Mn, Zn and Cu, but decreased MDA and H_2O_2 contents which may contribute in part to activation of physiological and biochemical processes involved in the alleviation of the effect of drought stress.

Key words: drought stress, enzyme activity, *Fragaria* × *ananassa*, nutrient uptake, plant growth-promoting bacteria.

Introduction

Strawberry (*Fragaria* × *ananassa* Duch.) is a shallow-rooted crop very sensitive to soil water deficit. Strawberry plants are very sensitive to drought stress during flowering and fruit ripening. Drought stress constitutes a major threat for crop yield worldwide and water shortage considerably lowers plant dry matter production, and thus the final yield. On the other hand, to limit the amounts of water used for several horticultural crops, water deficit irrigation has been seen as a potential alternative for new cultivation systems (Bordonaba, Terry, 2010). In strawberry plants regulated deficit irrigation technique is generally associated with reduction in fruit size and yield; (Liu et al., 2007). Despite this fact, other attributes, related to fruit quality increased (Terry et al., 2007; Heiadari, Golpayegani, 2012).

Plant growth-promoting rhizobacteria (PGPR) generally improve the nutritional, biochemical, physiological and morphological responses of many plants and, thus, it enhances the plant resistance to biotic and abiotic stresses. Plants inoculated with PGPR strains and exposed to water stress showed a better water status than control plants, alleviated drought stress by using alternative mechanisms, and higher yields under drought conditions were obtained (Compant et al., 2010). Like many other environmental factors, drought also induces accelerated ethylene production in plant tissues which leads to abnormal growth of a plant (Saleem et al., 2007; Bresson et al., 2013). Inoculation of crops with ACC deaminase-containing PGPR may assist plant growth by alleviating deleterious effects of stress ethylene.

GST, GR, SOD, CAT and APX can protect cells from a wide variety of biotic and abiotic stresses (Gill, Tuteja, 2010), and several growth and development related events. Alleviation of the oxidative damage and sustaining of growth under stress was correlated with the enhancement of GR activities and GR activity increased under drought stress (Nikolaeva et al., 2010). Under drought stress, the activities of POD, SOD, CAT, APX and GR increased consistently (Wu et al., 2006). Recently, our studies demonstrated for the first time that PGPR could enhance GR and GST activities, together with the growth of plants (Çakmakçı et al., 2007; 2009). Malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) contents usually serve as physiological indices of plant stress response. As the intensity of drought increased, both H_2O_2 and MDA levels increased indicating the oxidative stress. Activities of SOD, POD and CAT antioxidant enzymes and MDA content are suitable indicators to evaluate the degree of drought tolerance in crop plants (Zhang et al., 2011).

The use of beneficial bacteria as agricultural inputs for increasing crop production needs the selection of competent rhizobacteria with plant growth-promoting attributes, irrigation water deficit has been seen as a potential alternative for considerably new cultivation systems which could not only reduce water usage but also increase the water use efficiency in crops. Another alternative strategy is to induce stress tolerance by using beneficial microorganisms. Also, a few studies have focused on the effects of free-living rhizospheric microorganisms on the amelioration of water stress in plants. However, there is still a lack of information about morpho-physiological behaviour of different strawberry cultivars under limited water availability. Therefore, this study was conducted in order to investigate the effect of different 1-aminocyclopropane-1-carboxylate (ACC) deaminase-containing, auxin (IAA)-producing, N_2-fixing and/or P-solubilizing bacterial species on the growth, yield, selected morphological and physiological parameters, indicative of oxidative stress (MDA and H_2O_2), and antioxidant enzymes (GR, GST, CAT, POD, SOD and APX) in the leaves of strawberry cultivars grown in a non-sterile soil, under well-watered and water-deficit stress conditions.

Materials and methods

Plant material and growth conditions. The trial was organized as one set for strawberry cultivar 'Aromas' and was carried out for two years (2011–2012) in a greenhouse of Ispir Vocational School in Erzurum, Turkey. Experiments were conducted to study the effect of irrigation regimes and plant growth-promoting rhizobacteria (PGPR) on growth and growth characters of strawberry. The experiment was conducted using a completely randomized factorial design. Treatments with four replicates were as follows: 1) control (without bacteria inoculation), 2) *Paenibacillus polymyxa* RC05, 3) *P. polymyxa* RC35, 4) *Pseudomonas fluorescens* RC77, 5) *P. fluorescens* RC86, 6) *Pseudomonas putida* RC06, 7) *P. putida* 29/2 and 8) *Rhodococcus erythropolis* RC9. There were eight treatments, four water regimes (25, 50, 75 and 100 % of water-holding capacity (WHC), and four replicates (each having five plants) totalling 640 plastic containers. For this experiment, pure cultures were grown in 50% strength tryptic soy broth (Merck, Germany) on a rotary shaker (120 rpm, 25°C) for 3 days. Bacteria were then harvested by centrifugation (ca. 3000 × g for 10 min), washed and re-suspended in a 10 mM sterile phosphate buffer (SPB), pH 7 to a density of 10^9 cfu mL^{-1} for the bacterial strains. Young rooted cuttings of uniform height were inoculated with each of the PGPR strains. The bacterial inoculation involved dipping the root system of the saplings into a suspension of each PGPR strain for 60 min, prior to planting. Control plants received 5 mL of diluted SPB with no bacteria.

Bacterial strains. We selected seven different potential PGPR from a pool of 460 rhizobacterial isolates based on their 1-aminocyclopropane-1-carboxylate (ACC) deaminase-containing, auxin (IAA)-producing, N_2-fixing and P-solubilizing strains (Table 1). They were simultaneously tested for their growth and yield increasing potential under greenhouse conditions by conducting pot experiments in two years. The bacterial strains *P. polymyxa* RC35, *P. fluorescens* RC77 and *R. erythropolis* RC9 were isolated from the rhizosphere of wild red raspberries (Çakmakçı et al., 2007; 2009), and *P. polymyxa* RC05 and *P. putida* RC06 were isolated from wheat, and the other two strains (*P. fluorescens* RC86 and *P. putida* 29/2) were isolated from the rhizosphere of tea (Çakmakçı et al., 2010).

Table 1. Biochemical characteristics of the bacterial strains tested

Bacterial strains	IAA-production µg mL^{-1} OD_{600} $unit^{-1}$	Nitrogenase activity nmol C_2H_4, 10^7 cfu h^{-1}	P-solubilization µg P mL^{-1} d^{-1}	ACC deaminase activity nmol α-ketobutyrate mg^{-1} protein h^{-1}
Paenibacillus polymyxa RC05	32.8 ± 2.6	0.68 ± 0.14	10.07 ± 0.9	682.1 ± 33.7
Paenibacillus polymyxa RC35	31.6 ± 2.4	0.65 ± 0.11	11.9 ± 1.1	441.3 ± 21.2
Pseudomonas fluorescens RC77	32.4 ± 2.9	0.79 ± 0.15	39.4 ± 1.7	364.4 ± 26.8
Pseudomonas fluorescens RC86	30.6 ± 1.9	0.48 ± 0.07	36.7 ± 1.8	245.4 ± 19.5
Pseudomonas putida RC06	26.8 ± 2.7	0.54 ± 0.08	17.6 ± 1.3	746.2 ± 47.8
Pseudomonas putida 29/2	16.4 ± 1.4	0.47 ± 0.12	28.9 ± 1.8	332.6 ± 17.4
Rhodococcus erythropolis RC9	22.6 ± 1.5	0.55 ± 0.11	27.8 ± 1.5	577.8 ± 26.7

Note. Data were means ± standard error of three replicates, IAA (auxin)-production in average 72 h pure cultures, ACC – 1-aminocyclopropane-1-carboxylate.

Pot experiments were conducted on strawberry (*Fragaria* × *ananassa* Duch. cv. 'Aromas') well supplied with water (100% water-holding capacity), under mild water stress (75% of WHC), under moderate water stress (50% of WHC) and severe water stress (25% of WHC). At the beginning of the experiments, pots were water saturated and allowed to drain freely until there was no change in the weight. The difference between this weight and soil dry weight was used to calculate 100% of WHC. Also, water regimes were defined as a percentage of WHC of the cultivation substrate which was initially determined gravimetrically in the laboratory. The various irrigation regimes were initiated during the first three weeks after planting to allow successful establishment of the PGPR growth at 90% of WHC. Thereafter, the water regimes were maintained gravimetrically by daily irrigation. The soil water content was daily measured with the ThetaProbe ML2 (Delta-T Devices, UK) before rewatering. The amount of water lost was added to each pot in order to keep the soil water content at the desired level of WHC. All plants were grown in a greenhouse under a day/night cycle of 16/8 h natural light, 25/18°C and 60/70% relative humidity.

Preparation of the homogenate, determination of enzyme activities and protein concentrations. Tissue samples were washed three times with 50 mM Tris-HCl + 0.1 M Na_2SO_4 (pH 8.0), each was homogenized by liquid nitrogen, transferred to 100 mM PVP + 10mM NaN_3 +

50 mM Tris-HCl + 0.1 M Na_2SO_4 (pH 8.0) buffer and centrifuged at 4°C, 15,000 g for 60 min (Çakmakçı et al., 2009). Glucose-6-phosphate dehydrogenase (G6PD, EC 1.1.1.49) and 6-phosphogluconate dehydrogenase (6PGD, EC 1.1.1.44) activities were determined according to the method of Minucci et al. (2009). The activities of glutathione reductase (GR; EC 1.8.1.7) and glutathione S-transferase (GST; EC 2.5.1.18) were assayed by the method of Chikezie et al. (2009) and Minucci et al. (2009), respectively. All reactions were initiated by the addition of the enzyme solution. All enzymatic activities were determined spectrophotometrically at 25°C using a spectrophotometer Shimadzu 1208 UV (Shimadzu Co., Japan). Protein concentrations were calculated from the measurements of absorbance at 595 nm according to the method of Song et al. (2015) with bovine serum albumin as a standard.

Determination of antioxidant enzyme activity (SOD, POD, CAT and APX). Plant sample (500 mg dry weight) was homogenized with a mortar and pestle by adding 3 mL of 50 mM phosphate buffer (pH 7). Homogenates were filtered through two layers of Miracloth (Calbiochem, USA) and the filtrate was centrifuged at 15 000 × g for 15 min at 4ºC. The resulting supernatant was stored at 80ºC. For antioxidant enzyme assays, frozen cell samples were ground to a fine powder under liquid nitrogen and extracted with ice-cold 0.1 mM phosphate buffer, pH 7.8, containing 1 mM ethylenediamine-tetra-acetic acid (EDTA), 1 mM phenylmethanesulphonylfluoride (PMSF) and 0.5% polyvinylpyrrolidone (PVP). Superoxide dismutase (SOD), peroxidase (POD), catalase (CAT) and ascorbate peroxidase (APX) enzyme activities in the apoplastic fractions were measured spectrophotometrically. The CAT activity was measured by monitoring the decrease in absorbance at 240 nm in 50 mM phosphate buffer (pH 7.5) containing 20 mM H_2O_2. One unit of CAT activity was defined as the amount of enzyme that used 1 µmol H_2O_2 min^{-1}. APX activity was determined by following the decrease in A290 (extinction coefficient 2.8 mM^{-1} cm^{-1}) for 1 min in 1 mL of a reaction mixture containing 50 mM potassium phosphate buffer (pH 7.0), 0.5 mM ascorbic acid, 0.1 mM H_2O_2 and 200 µl of enzyme extract (Guo et al., 2010). The reaction was started by adding enzyme extract. Correction was done for the low, non-enzymatic oxidation of ascorbic acid by H_2O_2. The POD activity was measured by monitoring the increase in absorbance at 470 nm in 50 mM phosphate buffer (pH 5.5) containing 1 mM guaiacol and 0.5 mM H_2O_2. One unit of POD activity was defined as the amount of enzyme that caused an increase in absorbance of 0.01 min^{-1}. The SOD activity was estimated by recording the decrease in optical density of nitro-blue tetrazolium dye by the enzyme (Guo et al., 2010). Three milliliters of the reaction mixture contained 2 µM riboflavine, 13 mM methionine, 75 µM nitroblue tetrazolium chloride, 0.1 mM EDTA, 50 mM phosphate buffer (pH 7.8), 50 mM sodium carbonate and 0.1 mL of the apoplastic fraction. Reactions were started by adding 60 µL from 100 µM riboflavine solution and placing the tubes under two 30 W fluorescent lamps for 15 min. A complete reaction mixture without enzyme, which gave the maximal colour, served as control. Reactions were stopped by switching off the light and putting the tubes into the dark, a non-irradiated complete reaction mixture served as a blank. The absorbance was recorded at 560 nm and one unit of enzyme, which reduced the absorbance reading to 50% in comparison with tubes lacking enzyme (Dai, Mumper, 2015).

Total phenolics content (TPC). The amount of TPC in extracts was determined according to the Folin-Ciocalteu's spectrophotometric 2501 PC (Shimadzu, Japan) procedure (Giannakoula et al., 2012) using gallic acid (GA) as a standard for the calibration curve. The linear reading of the curve was from 0 to 350 mg of GA mL^{-1}. Samples were mixed with 0.25 N Folin-Ciocalteu reagents and after 3 min 0.2 M sodium carbonate solution was added and incubated for 60 min. Results were read at 724 nm and expressed as mg of GA equivalents per g of fresh weight (mg eq GA g^{-1} fresh weight).

Trolox equivalent antioxidant capacity (TEAC). The hydrophilic antioxidant capacity was performed by using the $ABTS^+$ radical cation assay. In the presence of metmyoglobin and hydrogen peroxide, ABTS is oxidized to the durable radical cation $ABTS^+$ measured photometrically at 734 nm. Trolox was used as the standard, and the antioxidant capacity was expressed as trolox equivalent antioxidant capacity (Gündüz, Özdemir, 2014). The results were expressed as µmols trolox equivalent in g fresh weight (µmols TE g^{-1} fresh weight) basis.

Measurement of hydrogen peroxide (H_2O_2) and malondialdehyde (MDA). The content of H_2O_2 was determined according to Sairam and Srivastava (2002) method. The concentration of H_2O_2 was estimated by measuring the absorbance of the titanium-hydroperoxide complex and using a standard curve plotted with a known concentration of H_2O_2. Oxidative damage to lipids was determined by measuring the content of malondialdehyde (MDA), prepared in 10% trichloroacetic acid containing 0.65% 2-thiobarbituric acid (TBA) and heated at 95°C for 25 min, and then quickly cooled (Sun et al., 2015). MDA content was calculated by correcting for compounds other than MDA which absorb at 532 nm by subtracting the absorbance at 532 nm of a solution containing plant extract incubated without TBA from an identical solution containing TBA.

Plant analysis. Leaf samples were oven-dried at 68°C for 48 h and ground to pass 1 mm. The Kjeldahl method and a Vapodest 10 Rapid Kjeldahl Distillation Unit (G. Gerhardt GmbH, Germany) were used to determine total N of the strawberry leaves (Bremner, 1996). After extraction methods, tissue P, K, Ca, Fe, Mn, Zn and Cu were determined with an inductively coupled plasma spectrophotometer Perkin-Elmer Optima 2100 DV ICP/OES (Perkin-Elmer, USA).

Data collection and statistical analysis. The data were collected both in 2011 and 2012. From each plant, both of the secondary fruits from the primary truss were harvested according to developmental stage. All fruits were harvested at the red stage, which was considered as optimum ripeness. At each harvest, total fresh yield (g $plant^{-1}$) and number of berries as well as average fresh weight per berry (g $plant^{-1}$), and titratable acids (%) were determined. Chlorophyll contents of the top fourth and fifth leaves were measured using a chlorophyll meter SPAD-502 ("Minolta", Japan) which is used to measure leaf greenness of the plants. In addition, we measured the activities of antioxidant enzymes in the leaves of strawberry. Enzyme activities were determined on three samples from each replicate. All data were statistically

evaluated using analysis of variance (*ANOVA*), followed by means separation using the Duncan's multiple range-test at ($p \leq 0.05$). All calculations were performed with software package *STATISTICA 6.0* (StatSoft, USA).

Results

Water deficit irrigation experiments were conducted on strawberry plants well supplied with water (100% water-holding capacity), under mild water stress (75% of WHC), moderate water stress (50% of WHC) and severe water stress (25% of WHC). Overall, inoculation with the PGPR strains resulted in a significant increase in growth of all the plants (Table 2). Water deficit, particularly severe water stress (25% of WHC), increased berry number per plant and reduced the weight of berry at harvest. The results showed that by increasing water stress, leaf chlorophyll content decreases leading to less photosynthesis, growth and yield. Both the weight of berries and the average berry fresh weight (FW) per plant were reduced by mild water stress (MiWS), moderate water stress (MoWS) and severe water stress (SWS) treatments as compared to full irrigation (FI), even though the increase in berry number per plant was significant (Table 2).

Table 2. Effect of plant growth-promoting rhizobacteria (PGPR) and water deficit treatments on the average number of berries and fresh weight per berry, titratable acidity, chlorophyll contents (SPAD) and yield of strawberry cultivar 'Aromas' as an average of 2011 and 2012

Treatments	Water regimes	Weight of berries g plant^{-1}	Number of berries per plant	Titratable acidity %	SPAD value	Yield per plant g		
						2011	2012	average
Control	FI	10.48 cd*	39.0 ik	0.84 ab	39.5 l	344.4 bc	488.3 ac	416.3 bd
	MiWS	9.35 e	38.1 jk	0.81 ae	40.0 l	296.9 d	418.0 df	357.4 eg
	MoWS	7.10 g-j	42.5 fk	0.76 ch	39.6 l	247.3 g	360.5 fh	303.9 hi
	SWS	5.98 lm	43.3 ej	0.71 gh	39.7 l	187.4 h	327.3 h	257.3 j
	Average	8.23 c	40.3 d	0.78 bc	39.7 f	269.0 d	398.5 d	333.8 d
RC05	FI	11.61 a	42.0 fk	0.79 bf	50.9 a	410.9 a	515.8 a	463.3 a
	MiWS	10.36 cd	41.6 gk	0.76 dh	48.1 aj	354.2 b	514.7 a	434.4 ab
	MoWS	7.40 gi	41.4 b	0.74 fh	48.8 ah	297.5 d	464.7 ad	381.1 ce
	SWS	6.12 km	52.0 b	0.71 gh	47.6 dj	252.7 fg	408.3 dg	330.5 gh
	Average	8.87 ab	46.2 ac	0.75 ce	48.8 ac	328.8 a	475.9 a	402.3 a
RC35	FI	11.38 ab	39.8 ik	0.82 ac	50.5 ac	376.5 b	510.3 a	443.4 ab
	MiWS	9.82 de	38.5 jk	0.79 bf	50.6 ab	311.4 cd	445.7 be	378.5 ce
	MoWS	6.76 hl	50.4 bc	0.77 cg	49.6 ae	284.6 df	396.4 eg	340.5 eh
	SWS	6.17 km	48.5 bd	0.71 gh	45.5 jk	241.8 g	352.2 gh	297.0 hj
	Average	8.53 bc	44.3 ac	0.77 bd	49.1 ab	303.6 b	426.1 bd	364.9 b
RC77	FI	10.79 bc	40.3 ik	0.76 dh	49.2 ag	371.5 b	500.2 ab	435.9 ab
	MiWS	10.27 cd	37.4 k	0.76 dh	47.8 bj	311.7 cd	445.4 be	378.6 ce
	MoWS	7.47 gh	47.0 bf	0.73 fh	47.4 ek	288.1 de	419.7 df	353.9 eg
	SWS	6.89 hk	46.0 cg	0.70 h	46.2 hk	246.4 g	398.6 eg	322.5 gh
	Average	8.86 ab	42.3 cd	0.74 de	47.6 ce	304.4 b	441.0 ab	372.7 b
RC86	FI	10.37 cd	40.5 gk	0.85 a	48.6 ah	258.2 b	483.0 ac	420.7 ac
	MiWS	7.82 fg	45.5 ch	0.81 ae	48.8 ai	297.3 d	427.6 ce	362.5 eg
	MoWS	6.32 jm	48.6 bd	0.77 cg	46.6 fk	255.7 eg	363.9 fh	309.8 hi
	SWS	5.83 m	46.9 bf	0.74 fh	48.0 aj	195.8 h	349.5 gh	272.6 ij
	Average	7.58 d	45.5 ac	0.79 ab	47.9 bd	276.8 cd	406.0 cd	341.4 cd
RC06	FI	10.56 cd	39.0 ik	0.77 cg	50.4 ad	358.2 b	468.6 ad	413.4 bd
	MiWS	9.22 e	40.5 gk	0.75 eh	49.4 af	305.2 d	446.3 be	375.7 df
	MoWS	7.17 gi	46.0 cg	0.72 gh	49.3 ag	260.8 eg	405.9 dg	333.3 fh
	SWS	6.00 lm	49.0 bd	0.70 h	49.0 ah	205.5 h	396.3 eg	300.9 hi
	Average	8.24 c	44.0 bd	0.73 e	49.5 a	282.4 cd	429.3 bc	365.9 bc
29/2	FI	9.92 de	43.9 di	0.79 bf	48.5 ah	370.1 b	500.3 ab	435.2 ab
	MiWS	7.70 fg	47.9 be	0.75 dh	47.5 ej	308.8 d	441.4 be	375.1 df
	MoWS	6.66 il	50.0 bc	0.73 fh	45.6 ik	261.8 eg	411.2 dg	336.5 eh
	SWS	5.57 m	49.4 bc	0.70 h	44.7 k	203.0 h	353.7 gh	278.3 ij
	Average	7.46 d	48.2 a	0.74 de	46.5 e	285.9 c	426.6 bd	356.3 bc
RC9	FI	11.70 a	42.5 fk	0.85 a	50.9 a	433.0 a	491.0 ac	462.0 a
	MiWS	10.35 cd	42.5 fk	0.84 ab	47.7 cj	365.5 b	518.3 a	441.9 ab
	MoWS	8.32 f	45.5 ch	0.81 ae	44.7 k	312.5 cd	446.5 be	379.5 ce
	SWS	5.58 m	56.5 a	0.77 cg	46.4 gk	247.6 g	409.5 dg	328.5 gh
	Average	8.99 a	46.9 ab	0.82 a	47.4 de	339.7 a	466.3 a	403.0 a
Average	FI	10.85 a	40.0 b	0.81 a	48.5 a	377.9 a	494.7 a	436.3 a
	MiWS	9.36 b	41.5 b	0.78 b	47.4 b	318.9 b	457.2 b	388.0 b
	MoWS	7.15 c	47.9 a	0.75 c	46.4 c	276.0 c	408.6 c	342.3 c
	SWS	6.02 d	49.4 a	0.72 d	45.9 c	222.5 d	374.4 d	298.5 d

Note. FI – full irrigation (100% water-holding capacity), MiWS – mild water stress (75% of WHC), MoWS – moderate water stress (50% of WHC), SWS – severe water stress (25% of WHC); * – values followed by different lower-case letters in a column (each section separately) were significantly different ($P \leq 0.05$).

Except for RC86, all strains improved the plant growth and increased the yield. The water-stressed plants inoculated with the effective PGPR recorded improved plant growth in terms of number of berries per plant, chlorophyll contents and berry yield in comparison to the un-inoculated, water-stressed plants (Table 2). On average of both years and four water regimes, inoculation of PGPR increased the berry yield, except RC86. All the strains enhanced (up to 17.1–24.7%) chlorophyll contents as compared to the control. Of these seven bacteria, higher fresh berry weight, and berry yield were recorded in plants applied with RC05, RC9, RC35 and RC77. Thus, on average in four water regimes, in 2011, inoculation with RC05, RC35, RC77, RC86, RC06, 29/2 and RC9 increased berry yields over control by 22.2, 12.9, 13.2, 2.9, 5.0, 6.3 and 26.3 %, respectively. In the growth season of 2012 similar increases were obtained (Table 2). Thus, on average of both years and four water regimes, inoculation with RC05, RC35, RC77, RC86, RC06, 29/2 and RC9 increased the berry yield by 20.5, 9.3, 11.7, 2.3, 9.6, 6.7 and 20.7 %, respectively, compared with the control.

The data revealed that drought stress applied at 25% of WHC had the most negative effect on the fresh berry weight and yield of strawberry cv. 'Aromas'. However, inoculation with ACC deaminase-containing, IAA-producing, N_2-fixing, P-solubilizing PGPR reduced the effects of drought stress applied owing to low soil moisture and, in most of the cases, significantly increased the fresh weight and yield compared with their respective uninoculated control. On average of both years, maximum increase in fresh berry yield was recorded in the case of strawberry plants inoculated with RC05 under moderate and severe drought stress applied at 50% and 25% WHC, and it was 25.4% and 28.4% higher than the respective uninoculated control. At 100% of WHC, inoculation with RC05 caused maximum increase in the yield of berry that was 11.3% higher than the respective uninoculated control.

Drought stress decreased mineral uptake and the yield of strawberry cultivar 'Aromas', and generally, inoculation of the multi-trait bacteria under drought stress significantly improved the N, P, K, Ca, Fe, Mn, Zn and Cu uptake, but mineral uptake responses were strain-specific (Table 3). Three of the PGPR strains (RC35, RC86 and 29/2) did not change the N content of the strawberry plants. On the other hand, the other four strains significantly increased N concentrations. The maximum P and K concentration in the strawberry leaves was found after RC77 treatment, followed by RC05, RC9 and RC35 treatments. Except for RC35, the bacterial inoculation significantly increased the Ca concentration in strawberry, and strains RC05, RC77, RC86, RC06 and RC9 increased the Mn concentration (Table 3). *P. fluorescens* RC77 inoculants significantly increased the Fe content, while RC05, RC77, RC86 and RC35 inoculation increased the Zn concentration in the leaves of strawberry.

Table 3. Effect of plant growth-promoting rhizobacteria (PGPR) and water deficit treatments on macro- and micro-nutrient concentrations in strawberry leaves

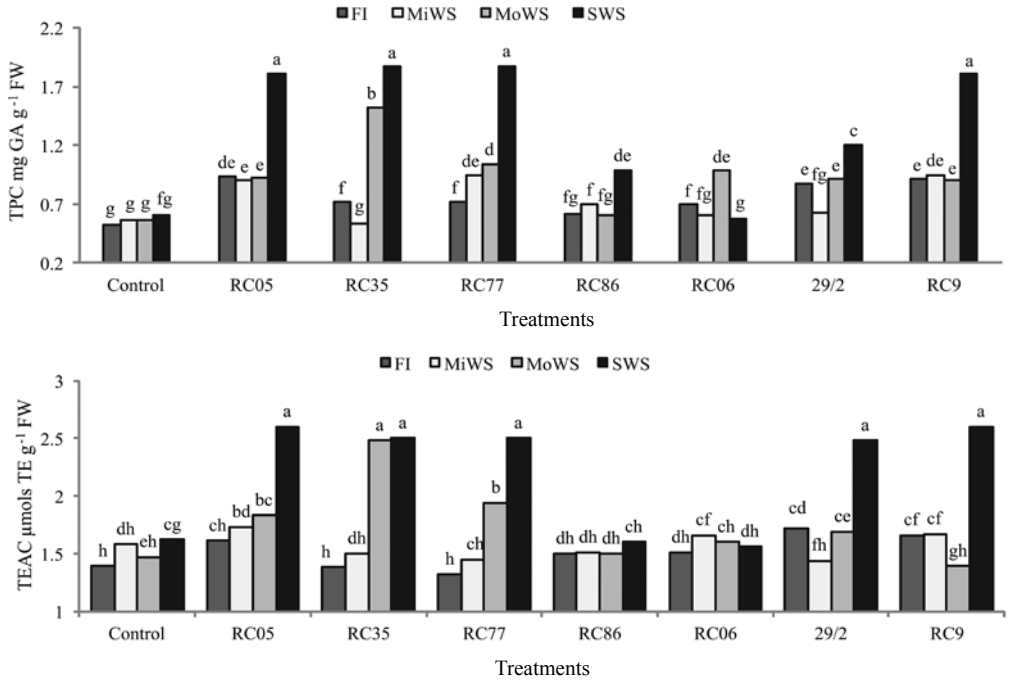
Treatments[1]	Water regimes[1]	N %	Macro-nutrients g kg^{-1} DW			Micro-nutrients mg kg^{-1} DW			
			P	K	Ca	Fe	Mn	Zn	Cu
1	2	3	4	5	6	7	8	9	10
Control	FI	2.84 cf[2]	2.42 d-f	25.42 ik	23.71 ij	20.15 af	15.46 gi	13.26 h	6.24 bg
	MiWS	2.80 df	2.31 f	25.10 jk	23.11 j	18.52 eh	13.97 hj	13.85 dh	5.47 g
	MoWS	2.81 cf	2.31 f	25.70 hk	23.69 ij	18.13 fh	13.29 j	12.74 h	5.47 g
	SWS	2.78 df	2.38 d-f	24.99 k	23.00 j	17.15 h	13.333 j	12.69 h	5.46 g
	Average	2.81 c	2.35 c	25.30 d	23.39 c	18.49 bc	14.01 b	13.13 c	5.66 d
RC05	FI	3.26 a	2.51 af	33.54 a	33.43 ab	21.65 a	17.93 be	15.27 ad	6.62 ae
	MiWS	3.10 ad	2.61 ae	30.27 af	31.84 bd	18.10 fh	17.37 cf	15.74 ab	6.44 ae
	MoWS	2.96 af	2.40 df	28.83 dh	28.74 ef	19.59 ag	15.41 gi	15.88 ab	6.09 eg
	SWS	2.82 cf	2.59 af	27.97 ek	25.89 fj	18.66 dh	13.88 hj	14.57 bf	6.02 dg
	Average	3.03 a	2.53 ab	30.15 ab	29.97 a	19.50 ab	16.15 a	15.36 a	6.29 b
RC35	FI	3.15 ac	2.75 ab	29.76 bg	29.56 ce	20.89 ad	17.39 cf	15.46 ac	6.29 bf
	MiWS	2.83 cf	2.32 ef	29.75 bg	29.56 ce	19.22 ch	15.66 fh	14.72 be	6.02 dg
	MoWS	2.89 bf	2.36 df	28.47 di	24.14 hj	20.09 af	14.20 hj	13.26 eh	5.47 g
	SWS	2.83 cf	2.62 a-d	27.05 fk	23.15 j	18.26 eh	13.62 ij	13.26 eh	5.46 g
	Average	2.92 ac	2.51 ab	29.06 bc	25.87 bc	19.61 ab	15.22 b	14.11 b	5.81 cd
RC77	FI	3.25 a	2.76 a	33.18 a	31.83 bd	20.24 af	18.01 be	15.90 ab	6.76 ad
	MiWS	3.07 ae	2.76 a	32.52 ab	33.44 ab	20.87 ad	19.16 ad	14.07 ch	6.51 ae
	MoWS	2.95 af	2.52 a-f	32.18 ac	24.59 gj	20.45 ae	14.09 hj	15.90 ab	5.86 eg
	SWS	2.84 cf	2.44 d-f	29.29 bg	24.77 gj	18.42 eh	14.19 hj	14.51 bg	5.57 fg
	Average	3.02 ab	2.62 a	31.80 a	28.66 ab	19.99 a	16.36 a	15.23 a	6.17 bc
RC86	FI	3.04 af	2.74 a-c	31.58 ad	34.55 ab	21.61 ab	20.36 a	16.48 a	6.20 bg
	MiWS	2.86 bf	2.40 d-f	28.12 ek	32.59 b	19.25 ch	19.20 ac	14.72 be	5.54 fg
	MoWS	2.77 df	2.35 d-f	24.78 k	23.26 j	17.33 gh	13.24 j	14.47 bg	5.45 g
	SWS	2.72 f	2.44 d-f	25.31 ik	23.97 ij	17.15 h	14.12 hj	14.15 ch	5.46 g
	Average	2.85 bc	2.48 a-c	27.45 c	28.59 ab	18.84 ac	16.73 a	14.95 a	5.66 d
RC06	FI	3.11 ad	2.55 af	31.27 ae	36.29 a	19.40 bh	19.99 a	14.10 ch	7.17 a
	MiWS	3.00 af	2.41 df	28.42 dj	36.21 a	21.67 a	19.41 ab	12.70 h	6.95 ab
	MoWS	2.93 af	2.45 cf	27.07 fk	27.54 eg	17.96 fh	14.76 gj	12.68 h	6.15 cg
	SWS	2.93 af	2.60 af	26.59 gk	25.50 gj	19.52 ag	13.67 ij	12.96 gh	5.58 fg
	Average	2.99 ab	2.50 ac	28.34 bc	31.38 a	19.64 ab	16.96 a	13.11 c	6.71 a
29/2	FI	3.11 ad	2.30 f	30.27 af	28.92 cf	18.66 dh	15.64 fh	12.65 h	7.20 a
	MiWS	2.90 bf	2.38 df	29.11 cg	25.37 gj	17.12 h	13.89 hj	12.87 h	6.87 ac

Table 3 continued

1	2	3	4	5	6	7	7	8	10
	MoWS	2.76 ef	2.47 af	28.54 di	25.93 fj	18.04 fh	14.20 hj	12.77 h	6.61 ae
	SWS	2.73 ef	2.40 df	26.89 fk	24.87 gj	17.69 gh	13.62 ij	13.27 eh	6.12 cg
	Average	2.88 ac	2.39 bc	28.70 bc	26.28 b	17.88 c	14.34 b	12.89 c	6.70 a
RC9	FI	3.26 a	2.73 ac	32.49 ab	27.20 eh	21.28 ac	16.53 dg	13.18 eh	6.24 bg
	MiWS	3.19 ab	2.36 df	29.09 cg	29.24 ce	18.10 fh	17.77 be	12.87 h	6.12 cg
	MoWS	2.91 bf	2.51 af	29.27 bg	26.65 ei	19.34 ch	16.20 dg	12.67 h	5.57 fg
	SWS	2.71 f	2.46 bf	26.93 fk	24.17 hj	18.42 eh	14.69 gj	12.69 h	5.46 g
	Average	3.02 ab	2.52 ab	29.45 b	26.82 b	19.28 ab	16.30 a	13.00 c	5.85 cd
Average	FI	3.13 a	2.59 a	30.94 a	30.69 a	20.49 a	17.66 a	14.54 a	6.59 a
	MiWS	2.97 b	2.44 b	29.05 b	29.81 a	19.11 ab	17.05 a	14.01 ab	6.24 ab
	MoWS	2.87 c	2.42 b	28.11 c	25.57 b	18.87 bc	14.42 b	13.83 ab	5.83 bc
	SWS	2.79 d	2.49 b	26.88 d	24.42 b	18.16 c	13.89 b	13.51 b	5.64 c

Note. [1] – bacterial strains and water regimes are explained in Table 1 and under Table 2; DW – dry weight; [2] – values followed by different lower-case letters in a column (each section separately) were significantly different ($P \leq 0.05$).

Various enzyme activities, total phenolic and trolox equivalent antioxidant capacity were positively influenced by the RC05, TC35, RC77, 29/2 and RC9 treatments, and were significantly higher than in the control plants under the stress conditions (Fig. 1).



Note. Values with different letters are significantly different at $p \leq 0.05$ (Duncan's test); FW – fresh weight; FI – full irrigation, MiWS – mild water stress, MoWS – moderate water stress, SWS – severe water stress.

Figure 1. Effect of rhizobacterial inoculations on the total phenolics content (TPC) and trolox equivalent antioxidant capacity (TEAC) of strawberry leaves under different irrigation regimes

Under drought stress, there was a significant increase in enzyme activity in both inoculated and uninoculated treatments. In general, enzyme activity in the uninoculated plants was lower than that in inoculated plants (Table 4). GR, CAT, POD, SOD and APX activities were greatest with the application of RC06, whereas the highest levels of GST activity were determined in treatments with RC77. Except for RC35, the bacterial inoculation significantly increased GST; RC06, RC08, RC77, RC86 and 29/2 strains increased GR. Of the bacterial inoculants, maximum CAT and POD in strawberry were measured in the RC06 followed by RC77, RC05 and RC9 treatments. In the case of increasing enzyme activities, RC06 and RC77 were the most effective, followed by RC05 and RC9.

The diminishing water supply caused a gradual decrease in the plant growth, accompanied by the increasing concentrations of drought stress markers (MDA and H_2O_2 content) in strawberry (Fig. 2). The MDA content was measured to determine the extent of lipid peroxidation. The oxidative damage to lipids increased as a consequence of drought as measured by the MDA content. After drought treatment, gradual increases of H_2O_2 and MDA contents were observed in all treatments. The MDA content was higher in control plants at all the stress levels. The highest MDA content under severe drought stress (25% of WHC) was observed in the control plants followed by RC86. As the intensity of drought increased, both H_2O_2 and MDA levels increased. Compared to well-watered plants, at 25% of RWC, H_2O_2 levels were increased by 74.8%,

Table 4. Effect of plant growth-promoting rhizobacteria (PGPR) and water deficit treatments on the activities of the antioxidant enzymes (GR, GST, CAT, POD, SOD and APX) and the pentose phosphate oxidative cycle enzymes (G6PD and 6PGD) in the leaves of strawberry cultivar 'Aromas'

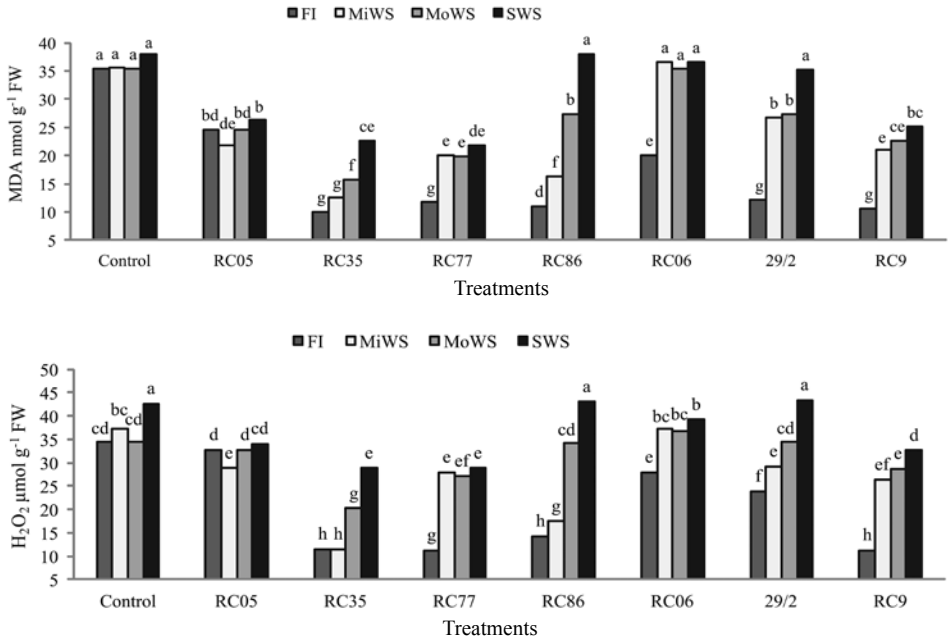
Treatments[1]	Water regimes[1]	GR	GST	G6PD	6GPD	CAT	POD	SOD	APX
		units mg^{-1} protein				units g^{-1} FW			
Control	FI	2.00 j[2]	0.93 h	1.50 f	3.60 fg	373 f	27.1 h	319 f	2.60 g
	MiWS	2.01 j	1.07 gh	2.40 df	3.94 eg	448 e	31.0 h	336 f	3.20 g
	MoWS	3.00 ej	1.28 eh	2.07 ef	5.68 dg	490 ce	36.2 g	487 a-c	10.36 e
	SWS	2.79 fj	1.21 fh	2.04 ef	5.94 df	516 cd	46.2 de	515 a	19.55 b
	Average	2.45 e	1.12 d	2.00 de	4.79 d	457 c	35.1 c	414 bc	8.93 c
RC05	FI	2.56gj	1.73 cg	1.78 f	5.88 df	566 bc	46.8 de	431 de	14.92 cd
	MiWS	3.00 ej	1.89 cf	2.41 df	6.00 df	583 ab	48.3 de	449 ce	15.14 cd
	MoWS	2.79 fj	1.93 ce	2.74 cf	6.61 bd	589 ab	50.1 d	463 be	20.68 ab
	SWS	2.87 ej	1.95 ce	3.62 bd	7.09 ad	496 ce	62.6 ac	522 a	22.27 a
	Average	2.80 de	1.91 b	2.64 c	6.39 bc	558 ab	51.94 ab	466 a	18.25 a
RC35	FI	2.13 ij	1.10 gh	1.58 f	3.83 eg	319 f	29.4 h	321 h	2.75 g
	MiWS	2.15 ij	0.92 h	2.52 df	3.48 g	369 f	29.2 h	343 f	3.10 g
	MoWS	2.73 fj	1.06 gh	4.54 ab	6.48 bd	373 f	29.6 h	366 f	9.48 e
	SWS	4.17 ae	1.57 ch	4.57 ab	8.47 ac	509 cd	61.1 bc	499 ab	19.57 b
	Average	2.80 de	1.16 d	3.30 b	5.57 cd	392 d	27.3 c	382 c	8.72 c
RC77	FI	3.16 cj	1.98 cd	3.75 bc	7.29 ad	594 ab	53.2 d	436 de	14.96 cd
	MiWS	4.41 ac	2.82 a	5.80 a	8.88 ab	594 ab	66.7 a	431 de	16.06 c
	MoWS	4.60 ab	2.65 ab	5.64 a	8.83 ab	589 ab	48.3 de	448 c-e	20.74 ab
	SWS	5.10 a	2.94 a	5.80 a	9.16 a	496 c-e	40.1 fg	481 a-d	20.90 ab
	Average	4.32 ab	2.60 a	5.25 a	8.54 a	568 ab	52.1 ab	449 ab	18.16 a
RC86	FI	2.26 hj	1.67 cg	2.02 ef	3.91 eg	370 f	29.4 h	321 f	2.75 g
	MiWS	3.94 af	1.83 cf	1.98 ef	7.24 ad	446 e	36.8 g	422 e	5.73 f
	MoWS	4.36 ad	1.99 cd	1.97 ef	7.65 ad	519 cd	48.6 de	426 e	14.84 cd
	SWS	5.11 a	1.96 ce	1.75 f	8.45 ac	541 bc	50.2 d	450 ce	14.87 cd
	Average	3.92 bc	1.86 b	1.93 de	6.31 bc	469 c	41.3 c	405 bc	9.55 c
RC06	FI	3.96 af	1.73 cg	1.81 ef	6.20 ce	589 ab	53.1 d	436 de	16.06 c
	MiWS	5.11 a	1.96 ce	2.47 df	7.60 ad	641 a	61.3 ac	449 ce	21.32 ab
	MoWS	5.15 a	2.06 bc	2.56 df	7.92 ad	616 a	64.5 ab	503 ab	22.29 a
	SWS	5.20 a	2.07 bc	3.86 bc	8.49 ac	595 ab	65.9 ab	518 a	22.11 a
	Average	4.85 a	1.95 b	2.67 c	7.55 ab	610 a	61.2 a	477 a	20.45 a
29/2	FI	3.52 bh	1.42 ch	1.97 cd	3.85 eg	319 f	31.0 h	337 f	3.21 g
	MiWS	3.19 cj	1.35 ch	1.52 f	3.88 eg	500 ce	40.4 fg	416 e	14.01 d
	MoWS	3.10 dj	1.42 ch	1.94 ef	4.08 eg	500 ce	48.7 de	431 de	14.56 cd
	SWS	3.44 bI	1.62 cg	1.97 ef	5.91 df	555 bc	49.3 d	447 ce	15.41 cd
	Average	3.31 cd	1.45 c	1.79 e	4.43 d	469 c	42.4 c	408 bc	11.80 bc
RC9	FI	2.48 gj	1.88 cf	1.57 f	5.76 dg	471 de	39.2 fg	416 e	6.40 f
	MiWS	2.35 hj	2.07 bc	1.69 f	6.20 ce	519 cd	43.2 ef	446 c-e	14.82 cd
	MoWS	2.56 gj	1.65 cg	3.07 ce	6.63 bd	599 ab	58.6 c	456 b-e	14.23 cd
	SWS	3.77 bg	1.67 cg	3.36 cd	6.62 bd	519 cd	60.7 bc	523 a	20.98 ab
	Average	2.79 de	1.82 b	2.42 cd	6.30 bc	529 b	50.4 b	460 a	14.11 b
Average	FI	2.76 c	1.57 b	2.00 c	5.04 d	450 b	38.7 c	377 d	7.96 d
	MiWS	3.27 bc	1.74 ab	2.60 bc	5.90 cd	514 a	44.6 b	411 c	11.67 c
	MoWS	3.54 ab	1.75 ab	3.06 ab	6.74 ab	524 a	48.1 b	448 b	15.90 b
	SWS	4.06 a	1.87 a	3.34 a	7.52 a	539 a	54.5 a	494 a	19.46 a

Notes. [1] – bacterial strains and water regimes are explained in Table 1 and under Table 2; GR – glutathione reductase, GST – glutathione S-transferase, G6PD – glucose-6-phosphate dehydrogenase, 6PGD – 6-phosphogluconate dehydrogenase; CAT – catalase, POD – peroxidase, SOD – superoxide dismutase, APX – ascorbate peroxidise; FW – fresh weight. [2] – values followed by different lower-case letters in a column (each section separately) were significantly different ($P \leq 0.05$).

while the corresponding increase in lipid peroxidation was 79.7%. The increase in the yield loss was nearly twofold in the control plants exposed to severe drought stress compared to the well-watered plants. However, under drought stress conditions, the presence of RC77, RC35 and RC9 reduced MDA levels, indicating that these strains imparted considerable protection against oxidative damage of lipids. The accumulation of MDA content was lowest in the treatment RC35 followed by RC77 revealing reduced accumulation of lipid peroxides under drought stress. PGPR inoculation has been shown to reduce the negative effects of drought stress. As MDA and H_2O_2 decreased, strawberry growth, yield and chlorophyll contents increased. Yield of strawberry negatively and significantly correlated ($p \leq 0.01$) with MDA ($r = -0.54$**) and H_2O_2 ($r = -0.53$**) contents. Also, yield ($r = 0.35$**) was positively correlated with chlorophyll contents.

Discussion

Under insufficient water supply, the weight of berries, titratable acidity, chlorophyll contents, and macro- and micro-nutrient concentrations were lower than under well-watered conditions. The results showed that by increasing water-deficit stress, chlorophyll contents



Note. Values with different letters are significantly different at $p \leq 0.05$ (Duncan's test); FW – fresh weight; water regimes and bacterial strains are explained under Table 2 and in Table 1.

Figure 2. Effect of different irrigation regimes and bacterial applications on malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) content in strawberry leaves

decrease, which leads to less yield and growth. Deficit irrigation in strawberry fruits is generally associated with reduction in berry size and yield; however, a recent study demonstrated that reducing water irrigation on strawberry can increase the concentration of some taste- and health-related compounds in fruits (Bordonaba, Terry, 2010).

Leaf chlorophyll, fresh berry yield, individual berry fresh weight, and titratable acidity were significantly lower in the plants that are under moderate and severe drought stress than those under full irrigation; whereas the total number of berry per plant was higher under severe drought stress. Previous studies also showed that fruits from strawberry plants that received full irrigation had a higher water content and greater berry fresh weight than fruits from plants grown under reduced irrigation (Liu et al., 2007; Terry et al., 2007; Bordonaba, Terry, 2010; Ipek et al., 2014). Water stress has a great influence on the plant photosynthetic capacity of strawberry (Mao et al., 2009). Other authors have also reported that smaller fruit resulted from reduced irrigation (Terry et al., 2007).

Decreasing water availability under drought generally results in the reduced total nutrient uptake and frequently reduced concentrations of mineral nutrients in crop plants. Drought stress also decreased macro- and micro-nutrient concentrations in strawberry leaves P, K, S and Ca uptake of strawberry cultivar 'Aromas', whereas application of PGPR increased the uptake of all of these elements. Reduced plant growth caused by drought may be attributed to a disturbance in the nutrients of plants, resulting from the decreased uptake of mineral nutrients. Strawberry plants inoculated with three PGPR strains (RC05, RC9 and RC77) generally grew better and had higher N, P, K, Fe and Mn uptake and berry yield than plants inoculated with other strains and the control (Tables 2–3). K nutrition can improve drought resistance (Wang et al., 2013). Results of several studies indicate that application of PGPR increased the growth, nutrient element content, and yield of strawberry plants (Esitken et al., 2010; Ipek et al., 2014).

The activities of the anti-oxidative enzymes such as GR, GST, CAT, POD, SOD and APX increased under water-deficit stress in the plants. These results are in agreement with those of other researchers (Wu et al., 2006), who reported that the activities of SOD, POD, CAT, APX and GR increased under drought stress. Plant cells stimulate different antioxidant enzymes such as CAT, POD, SOD and APX that eliminate these reactive free radicals or suppress their formation (Simova-Stoilova et al., 2008). These results suggest that the activities of SOD, POD and CAT, and contents of H_2O_2 and MDA are the most important traits for plants' ability to survive under drought stress (Zhang et al., 2011). Increase in SOD, POD, CAT and APX activities in plant leaves under drought conditions has also been reported by Patel and Hemantaranjan (2012).

In the present study the CAT, POD, SOD and APX activity as well as the MDA content and H_2O_2 levels increased with the increasing levels of water deficit in both the PGPR inoculated and the un-inoculated plants. Thus, increased stress tolerance in PGPR inoculated plants could be correlated with the higher total phenolics content, antioxidant capacity and antioxidant enzyme activity. It has been found that strawberry plants inoculated with multi-traits PGPR strains showed high antioxidant enzymes activity which contributed to enhance the plant protection against drought stress. In addition, plants inoculated with ACC deaminase-containing PGPR significantly lowered the level of ACC in the stressed plants, thereby lowering the amount of stress ethylene synthesis and hence damage to the plant (Zahir et al., 2008). Reduction of oxidative stress is correlated with drought stress tolerance induced by plant-beneficial bacteria (Compant et al., 2010).

Water deficit treatment significantly increased MDA and H_2O_2 accumulation, which indicated the extent of oxidative injury posed by stress conditions. MDA and H_2O_2 levels were increased by drought stress both in inoculated and in non-inoculated plants. Four of the PGPR strains (RC05, RC35, RC77 and RC9) exhibiting

better performance under water deficit conditions have been observed to have lower levels of MDA content in the shoot which correlated well with their decreased H_2O_2 content (Fig. 2) and enhanced total phenolics and antioxidant capacity (Fig. 1), thus protecting the plants from lipid peroxidation of membrane systems as compared to the other bacteria and control which had higher levels of MDA content. These results indicated that water-stressed RC05, RC35, RC77 and RC9 plants showed much less oxidative damage (reduced MDA and H_2O_2 content) compared with water-stressed control plants. Drought stress and bacterial application increased enzyme activities, and TPC content, whereas effective bacterial strains such as RC35, RC77 and RC9 decreased MDA and H_2O_2 content. It induced the activity of enzymes, alleviated membrane lipid peroxidation as well as membrane system damage, thus improving the drought resistance of strawberry (Sun et al., 2013). Our findings showed an increase in MDA and H_2O_2 in both well-watered and drought-stressed plants though increase was less evident in the PGPR-treated strawberry plants. The PGPR could induce plant growth and development, reduce stress susceptibility, and may contribute to the concept of biotechnology application in agriculture.

Conclusions

1. Bacterial inoculation minimized the drought stress-imposed effects significantly increasing the fresh berry yield, individual berry fresh weight, and titratable acidity, chlorophyll content, and macro- and micro-nutrient concentrations in strawberry leaves. Considering all the results together, it was observed that the strawberry cultivar 'Aromas' which showed better seedling growth accompanied by increased activities of both the enzymes and decreased contents of malondialdehyde (MDA) and hydrogen peroxide (H_2O_2), under water deficit conditions, performed much better and thus exhibited higher stress resistance.

2. Changes in plant total phenolics content (TPC), trolox equivalent antioxidant capacity (TEAC), MDA and H_2O_2 content, CAT, POD, SOD, APX, GST and GR activities as a result of inoculant application would be useful markers for the bacterial effect on the strategies of drought tolerance in these plants. Plant growth-promoting rhizobacteria (PGPR) has played critical roles in strawberry responses to stress and alleviated drought-induced oxidative stress.

3. Our results provide strong evidence that the role of PGPR in the performance of strawberry plants in stressful environment of soils.

4. In spite of the evident relation among plant growth, chlorophyll contents and drought tolerance, the influence of PGPR on plant drought tolerance was also based on mechanisms independent of multiple plant growth-promotion traits.

5. The selected ACC deaminase-containing, IAA-producing, N_2-fixing and P-solubilizing PGPR strains, such as RC05, RC9, RC35 and RC77 could play an important role in understanding plant tolerance to stress, adaptation to stress and mechanisms that develop in plants under stress conditions, and could be practical and effective application in protecting different plant species against drought stress.

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Augimą skatinančiomis rizobakterijomis inokuliavimo įtaka braškėms esant vandens stygiaus stresui

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Santrauka

Tyrimas atliktas 2011 ir 2012 m. Vegetaciniuose induose įvertinta bakterijų, turinčių 1-aminociklopropano-1-karboksilato (ACC) deaminazės, fiksuojančių N_2 ir tirpinančių P junginius įtaka braškių derliui ir morfofiziologiniams rodikliams. Aštuoni inokuliavimo bakterijomis variantai su keturiais vandens režimais buvo išdėstyti atsitiktine tvarka. Dėl mažėjančio aprūpinimo vandeniu palaipsniui mažėjo augalų augimas, chlorofilo kiekis bei uogų derlius ir braškių lapuose didėjo sausros streso žymeklių bendras fenolių kiekis (TPC), trolokso ekvivalento antioksidacinė geba (TEAC), malondialdehido (MDA) kiekis, vandenilio peroksido (H_2O_2), glutationo reductazės (GR), glutationo S-transferazės (GST), katalazės (CAT), peroksidazės (POD), superoksidazės dismutazės (SOD) ir askorbato peroksidazės (APX) aktyvumas. Bakterijos taip pat padidino augalų augimą ir TPC, TEAC, antioksidacinių fermentų (GR, GST, CAT, POD, SOD ir APX) aktyvumą, fitohormonų (GA, SA ir IAA) ir N, P, K, Ca, Fe, Mn, Zn bei Cu kiekius, bet sumažino MDA ir H_2O_2 kiekius, kurie iš dalies galėjo suaktyvinti fiziologinius ir biocheminius procesus, mažinančius sausros streso poveikį.

Reikšminiai žodžiai: augalų augimą skatinančios bakterijos, fermentų veikla, *Fragaria* × *ananassa*, maisto medžiagų įsisavinimas, sausros stresas.

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