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ORIGINAL RESEARCH

Compost as an eco-friendly alternative to mitigate salt-induced effects on growth, nutritional, physiological and biochemical responses of date palm

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Abstract

Purpose In this study, the role of compost application in alleviating salt stress effects on date palm seedlings growth and development was investigated.

Method The experiment was set in a randomized design, with or without green waste-based compost, and under two salinity levels (0 and 240 mM NaCl). Growth, mineral uptake, photosynthetic pigments content, oxidative stress markers' accumulation and antioxidant activity were assessed.

Results Plants grown under saline condition showed low values of growth attributes while the application of compost increased these attributes under 240 mM NaCl. Salinity increased sodium (Na^+) and chlorine (Cl^-) ions concentration in plants and reduced phosphorus (P), nitrogen (N), potassium (K^+) and calcium (Ca^{2+}) uptake. The presence of compost mitigated these effects by improving the concentrations of the essential elements (P, K^+, N and Ca^{2+}) in both plant shoots and roots and by limiting salt ion (Na^+ and Cl^-) toxicity and thereby induced higher K/Na and Ca/Na ratios. Furthermore, leaf water status, stomatal conductance and photosynthetic efficiency were increased and were coupled with high chlorophyll and protein concentrations in plants amended with compost under salt stress. NaCl stress induced high lipid peroxidation and H_2O_2 accumulation; however, the application of compost lowered these two parameters in stressed plants through stimulation of the antioxidant enzymes activity and increasing soluble sugars and proline accumulation.

Conclusion Results suggest that the green waste-based compost can boost date palm seedlings tolerance in salt-affected soils by mitigating the different adverse effects of salinity stress.

Keywords Salinity, Compost, Mineral uptake, Antioxidant system, Salt tolerance, Date palm

Introduction

In arid and semi-arid regions, soil salinity is one of the most damaging environmental constraint for plants' growth and development (Yaish and Kumar 2015; Ait-El-Mokhtar et al. 2020b). It has been estimated that around one billion hectares of earth surface suffers from excess salinity with a clear increasing trend (Shahid et al. 2018). This issue is further aggravated by climate change, irrigation with salty water and excessive treatments with chemical inputs (Munns 2005; Trenberth et al. 2014). In addition, salt accumulation in soil is a major cause to land degradation and considerably reduces crop production by over 20% (Setia et al. 2013). Excess salt in soil solution disrupts all aspects of plant physiological and biochemical functions such as respiration process, nutrients homeostasis, osmotic adjustment and photosynthesis (Ben-Laouane et al. 2019; Rekaby et al. 2020). High salinity levels induce osmotic stress and specific ion effects, which produce an additional stress on plants known as oxidative stress

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(Yaish and Kumar 2015). Oxidative stress leads to the accumulation of reactive oxygen species (ROS) like superoxide, hydroxyl and peroxide radicals in plant tissue. ROS disrupt metabolism by damaging biomolecules, including DNA, lipids, and proteins could trigger programmed cell death pathway (Gill and Tuteja 2010; Howell 2013). To mitigate the osmotic and oxidative stresses, plants have established different defense mechanisms to protect cell's integrity and keep ROS at tolerable levels (Miller et al. 2010; Kamiab 2020). Plentiful evidence points out the role of the antioxidant enzyme's system in scavenging ROS, especially H_2O_2. This system contains many enzymes such as: catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX), peroxidase (POD), glutathione reductase (GR) and polyphenoloxidase (PPO) that scavenge ROS and preserve cell components from various damages (Foyer 2018; Moradbeygi et al. 2020). Osmotic regulation is another protection strategy that helps plants to cope with both the effects of osmotic and ionic toxicity of salt stress by elimination of salts and Na^+ ions sequestration in the apoplast or vacuole (Apse and Blumwald 2007). Furthermore, salt tolerance also occurs through osmolytes compounds' production including proline, soluble sugars and glycine- betaine (Zhu 2003).

In the last decades, applying organic fertilizers to soil became a common practice in areas suffering from excess salinity and it is considered as a promising environmental strategy for soil regeneration and fertility restoration especially in arid and semi-arid zones (Scotti et al. 2016; Boutasknit et al. 2020a). Compost is an organic material which decomposes and improves physicochemical properties of soil (Meena et al. 2016; Anli et al. 2020a, b; Boutasknit et al. 2020b; Demir 2020). Many recent studies have focused on the use of compost in alleviating the negative effects of salinity (Oo et al. 2015; Chaichi et al. 2017; Guangming et al. 2017; Mbarki et al. 2018, 2020). The addition of compost to salt-affected soils might accelerate Na^+ leaching, increase water infiltration, cation-exchange and water-holding capacity, aggregate stability, and decrease electrical conductivity and exchangeable sodium percentage (Wang et al. 2014; Oo et al. 2015; Manirakiza and Şeker 2020; Hasini et al. 2020). In addition, the organic input can have a potential effect on plant growth along with stress tolerance thanks to soil enrichment of humic substances, nutrients and beneficial microorganisms as well as improvement of soil enzymatic activities (Wright et al. 2008; Mora et al. 2010; Alromian 2020). Furthermore, composted organic matter could stimulate plant enzymatic- and nonenzymatic-antioxidant system (Lakhdar et al. 2011; Tartoura and Youssef 2011; Youssef and Tartoura 2013), which play a key role in plant tolerance to different stress conditions.

Date palm (*Phoenix dactylifera* L.) is an important common crop in areas characterized by arid and semi-arid climate including the Middle East and North Africa where it plays nutritional, socio-economic and environmental roles (Chao and Krueger 2007). Dates constitute a quality food due to their richness in essential nutrients like proteins, sugars, minerals, fibers, vitamins and antioxidants (Vayalil 2012; Kamal-Eldin and Ghnimi 2018). Most studies involving compost amendment were more focused on its effects in improving soil traits and crop productivity. However, limited studies (Tartoura et al. 2014; Rady et al. 2016; Ramzani et al. 2017; Mbarki et al. 2018, 2020) have reported on the compost mitigating effects on plants under salt stress and the involved mechanisms. Thus, this study aims to investigate the effects of compost application on growth, mineral uptake, photosynthesis, water status and antioxidant system of date palm in the presence of salinity. We hypothesize that compost application to soil would mitigate the adverse effects of salt stress through regulation and/or stimulation of different aspects of plant functioning such as growth, water and nutrient uptake, photosynthesis and ROS scavenging system.

Material and methods

Plant and compost materials and treatments

For surface-sterilization, date palm seeds (Boufeggous cv) were immersed in 10% sodium hypochlorite for 10 min, followed by five washings with sterilized distilled water. They were then sown in plastic basins filled with sterilized sand and were incubated at 38 °C in obscurity for 21 days. Date palm seedlings of one leaf stage were transferred to plastic pots of 2.3 kg of previously sterilized sand (for 3 h at 180 °C during three consecutive days) which had the following characteristics: electrical conductivity (EC): 0.29 dS cm^{-1}, pH: 9.31, 0.001% Phosphorus (P), 0.001% Potassium (K), 0.006% Magnesium (Mg), 0.012% Iron (Fe), 0.01% Calcium (Ca), 0.002% Sodium (Na), 0.01% Aluminum (Al) and 0.002% Silicon (Si).

Green wastes were used for compost preparation according to Meddich et al. (2016). The prepared compost has the following characteristics: pH 6.87, organic carbon (C) (306.5 g kg^{-1}), organic matter (OM) (527.2 g kg^{-1}), total nitrogen (N) (21.9 g kg^{-1}), C/N ratio (14.00), available P (0.27 mg g^{-1}), ashes (490 g kg^{-1}), NH_4^+ (0.03 10^{-3} mg g^{-1}), NO_3^- (0.07 10^{-3} mg g^{-1}), NH_4^+/ NO_3^- ratio (0.44), fungal population (9.75 10^4 cfu g^{-1}), and bacterial population (2.12 10^5 cfu g^{-1}). The supplementation of compost was performed during seedlings' transplantation, with a 5% (w/w) ratio (Meddich et al. 2015; Anli et al. 2020b).

Date palm transplants were regularly watered with fresh water for 150 days, and then they were divided and subjected to two concentrations of NaCl (0 and 240 mM NaCl) (Ait-El-Mokhtar et al. 2019). Salinity treatments were progressively applied on alternative days to reach the desired NaCl concentration (240 mM NaCl) and to ovoid osmotic damage. Each pot was placed on a plastic bag for drained water recuperation. The collected water was reapplied to the respective pots. Date palm transplants were grown for 300 days without any chemical fertilization. At the end of the experiment, electrical conductivity of non-salt treated pots and salt treated pots was 0.73 and 24.6 mS cm^{-1}, respectively.

Experimental design and plant growth conditions

The study consisted of a factorial arrangement of two compost levels and two NaCl levels resulting in four treatments: untreated plants under 0 mM NaCl (Control), compost treated plants under 0 mM NaCl (C), untreated plants under 240 mM NaCl (S) and compost treated plants under 240 mM NaCl (CS). The pots were placed in a completely randomized design with 10 replicates for each treatment (a total of 40 pots). Transplants were kept for 300 days under greenhouse semi-controlled conditions, at an average temperature of 25.5 °C, 69% average relative humidity, 16/8 h day/night period and light intensity of 410 μmol^{-2} s^{-1}.

Evaluation of plant growth traits

After 300 days, transplants were harvested and rinsed with tap water then with distilled water. Roots were separated from shoots and plant length, leaf area, leaf number and fresh and dry weights were measured.

Nutrient content evaluation

Oven-dried roots and leaves were ground and total N content was measured using Kjeldahl method and P content was assessed according to Olsen method (Olsen and Dean 1965). Na^+, K^+, and Ca^{2+} levels in the transplants were measured as described by Wolf (1982) using flame photometry (JENWAY, PFP7) while the silver nitrate ($AgNO_3$) titration protocol was used for chlorine (Cl^-) content measurement.

Stomatal conductance and photosynthetic efficiency evaluation

Before the harvest, stomatal conductance (gs) was measured at a sunny day (between 09:30–11:00 a.m.) using a porometer (Leaf Porometer LP1989, Decagon Device, Inc., Washington, USA) on five replicates (the second youngest leaf) per treatment following the instructions in the user manual.

Photosynthetic efficiency was measured on the leaves from the third rank with five replicates per treatment. Measurements were performed using a portable fluorometer (Opti-sciences OSI 30p) according to Baker (2008). Photosynthetic efficiency was recorded as F_v/F_m ratio where: $F_v=F_m–F_0$, F_0: initial fluorescence and F_m: maximum fluorescence.

Leaf water potential and leaf relative water content evaluation

The pressure chamber method was used for leaf water potential (LWP) measurement (Scholander et al. 1965) performed on freshly developed leaves from five plants per treatment.

Fresh weight (FW), dry weight (DW) and turgid weight (TW) were measured using portions taken on the third youngest leaf. To determine leaf relative water content (LRWC), FW, TW and DW values were used according to the following formula (Barrs and Weatherly 1962):

$$\text{LRWC (\%)} = \frac{\text{FW} - \text{DW}}{\text{TW} - \text{DW}} \text{x100}$$

Photosynthetic pigment's content determination

Photosynthetic pigment's extraction was performed as described by Arnon (1949). Fresh leaf samples were ground in 80% acetone and the extract was centrifuged at 10,000 g for 10 min. The supernatant absorbance was measured at three wavelengths: 480, 645, and 663 nm with a spectrophotometer (UV-3100PC spectrophotometer). The photosynthetic pigment contents were calculated based on the recorded absorbance values. 80% acetone was used as a blank.

Hydrogen peroxide content and lipid peroxidation evaluation

Hydrogen peroxide contents in roots and leaves were determined according to Velikova et al. (2000) method. Fresh material (0.25 g) was homogenized in 5 mL of 10% (w/v) trichloroacetic acid (TCA) and then centrifuged at 15,000 g for 15 min. The recovered supernatant was used to assess hydrogen peroxide content. 0.5 mL of the supernatant was added to 0.5 mL potassium phosphate buffer (10 mM, pH 7) and 1 mL iodic potassium (1 M). After 1 h incubation in dark, the absorbance was recorded at 390 nm. 10% TCA was used as blank. Malondialdehyde (MDA) content was used to assess lipid peroxidation according to Dhindsa et al. (1981) method. Roots and leaves fresh samples (0.25 g) were ground in 10 mL of 0.1% TCA and centrifuged at 18,000 g for 10 min at 4 °C. 2 mL of the supernatant were mixed with 2 mL of 20% TCA solution containing 0.5% thiobarbituric acid (TBA). The mixture was boiled for 30 min at 100 °C, cooled rapidly and then centrifuged at 10,000 g for 10 min for clearing. The absorbance of the supernatant was recorded at 532 and 600 nm to measure the MDA concentration.

Soluble sugars and proline contents evaluation

Roots and leaf frozen material (0.1 g) was ground in 4 mL of 80% ethanol and the extract was centrifuged at 5000 rpm for 10 min. After collecting the supernatant, the pellet was re-suspended in 2 mL of ethanol and re-centrifuged. Both supernatants served to quantify soluble sugars using Dubois et al. (1956) method. 1 mL of supernatant was added to 5 mL of concentrated sulfuric acid and 1 mL of 5% phenol solution. The absorbance was recorded after 5 min at 485 nm with a spectrophotometer (UV-3100PC). Glucose was used as a standard.

Date palm root and leaf proline content was extracted using Bates et al. (1973) method. Frozen roots and leaf samples (0.1 g) were ground in 5 mL of 3% (w/v) aqueous sulphosalicylic acid and the mixture was centrifuged at 12,000 g for 15 min. 2 mL of glacial acetic acid and 2 mL of acid ninhydrin reagent were added to 2 mL of the supernatant and incubated for 1 h at 100 °C water bath. The reaction was stopped using an ice bath, followed by extraction with toluene. The proline concentration was calculated based on the absorbance values recorded at 520 nm and on pure proline as standard.

Enzymatic antioxidant activities' evaluation

Enzymes extraction was achieved according to the optimized protocol (Ait-El-Mokhtar et al. 2019). Fresh roots and leaf material (0.5 g) were frozen and ground using liquid nitrogen at 4 °C in 5 mL solution containing potassium phosphate buffer (0.1 M, pH 7.0), 0.1 g polyvinylpolypyrrolidone (PVPP), and 0.1 mmol ethylenediaminetetraacetic acid (EDTA). The mixture was centrifuged at 18,000 g for 10 min at 4 °C, and the supernatant was preserved at −20 °C for the following enzyme assay.

Estimation of the activity of superoxide dismutase (SOD) is based on the ability of this enzyme to inhibit the nitro blue tetrazolium (NBT) photochemical reduction. It was measured using Beyer and Fridovich (1987) method. The required enzyme amount to induce a 50% NBT reduction inhibition at 25 °C is defined as one unit of SOD. The SOD activity was measured in unit min^{-1} mg^{-1} protein. Catalase (CAT) activity was measured by following the absorbance decrease for 3 min at 240 nm resulting from H_2O_2 decomposition (Aebi 1984). The reaction solution (2 mL) contained 100 μL of enzyme extract, potassium phosphate buffer (0.1 M, pH 7.0), 20 mM H_2O_2 and 0.1 mM EDTA. Peroxidase (POD) activity was determined according to Polle et al. (1994) by monitoring the absorbance variation for 3 min at 470 nm. The reaction solution (3 mL) contained 0.1 mL enzyme extract, potassium phosphate buffer (0.1 M, pH 7.0), 20 mM guaiacol and 10 mM H_2O_2. The activity of the ascorbate peroxidase (APX) was assessed using Amako et al. (1994) method. APX activity was measured as an absorbance decrease for 1 min at 290 nm. The reaction mixture consisted of potassium phosphate buffer (50 mM, pH 7.0), 0.5 mM H_2O_2, 0.1 mM ascorbate and 100 μL of enzyme extract. Polyphenoloxidase (PPO) activity was measured at 410 nm by monitoring catechol oxidation according to Hori et al. (1997) method. 600 μL of 0.1 M catechol and 100 μL enzyme extract were added to 3 mL of potassium phosphate buffer (0.1 M, pH 7.0). Enzyme activity was measured in μmol of catechol min^{-1} mg^{-1} of protein. The concentration of protein was measured using Bradford (1976) protocol, with bovine serum albumin (BSA) as a standard.

Statistical analysis

To perform the statistical analysis, SPSS 22.0 software for Windows was used. One-way analysis of variance (ANOVA) was carried out to assess the significance of the treatments, and means comparisons were done using Duncan's test at $p<0.05$. Heat map analysis was performed using Microsoft Office Excel 2016, to visualize the interactions between variables and applied treatments.

Results and discussion

Growth traits

Salt stress had a significant negative impact on date palm seedlings growth. It reduced plants height, leaf number, leaf area and root and shoot fresh and dry mass both in the presence and the absence of compost (Table 1). Salinity affected roots more than shoots as root dry weight was decreased by 41% while shoot dry matter was decreased by 30% compared to the control plants. The decline in date palm growth could be attributed to the negative effects of salinity on some basic physiological and biochemical processes such as nutrients uptake, photosynthesis and antioxidant enzymes activity (Tartoura et al. 2014; Al Kharusi et al. 2019; Toubali et al. 2020). Many researches have reported the same adverse impact of salt stress on date palm performances (Yaish et al. 2015; Meddich et al. 2018; Ait-El-Mokhtar et al. 2019, 2020a; Al Kharusi et al. 2019; Toubali et al. 2020). In contrast, compost application improved all plant growth traits reduced by salinity compared to S treated plants. Under 240 mM NaCl and in the presence of compost, shoot dry matter recorded the maximum increase of 135% while plant height showed the lowest increase of 10% in comparison to S treated plants. The positive effect of green waste compost application on growth under salinity may be explained by the fact that organic amendment might improve soil physico-chemical and biological attributes including the improvement of soil water holding capacity and providing more available nutrients to the plant by increasing their release from compost (Weber et al. 2014; Akhzari et al. 2015; Oo et al. 2015; Meddich et al. 2019; Zaman et al. 2020).

Table 1 Effect of salinity and compost on plant height, leaves number, leaf area and fresh and dry weight of date palm plants after five months of exposure to salinity

NaCl treatment	Compost	Plant Height (cm)	Leaves number	Leaf area (cm^2)	Shoot fresh weight (g $plant^{-1}$)	Shoot dry weight (g $plant^{-1}$)	Root fresh weight (g $plant^{-1}$)	Root dry weight (g $plant^{-1}$)
0 mM	- compost	29.9 ± 0.4^{b}	3.1 ± 0.4^{c}	19.1 ± 0.7^{b}	4.3 ± 0.1^{c}	1.6 ± 0.1^{c}	5.0 ± 0.2^{c}	1.2 ± 0.1^{b}
	+ compost	33.7 ± 0.4^{a}	4.9 ± 0.3^{a}	31.7 ± 0.3^{a}	10.4 ± 1.4^{a}	3.6 ± 0.4^{a}	9.2 ± 0.2^{a}	2.0 ± 0.1^{a}
240 mM	- compost	26.9 ± 0.5^{c}	3.0 ± 0.3^{c}	11.3 ± 1.0^{d}	2.8 ± 0.4^{d}	1.0 ± 0.1^{d}	3.6 ± 0.3^{d}	0.8 ± 0.1^{c}
	+ compost	30.1 ± 0.6^{b}	4.1 ± 0.3^{b}	17.0 ± 0.5^{c}	5.9 ± 0.7^{b}	2.6 ± 0.5^{b}	7.3 ± 0.6^{b}	1.3 ± 0.3^{b}

The values of each parameter labeled by different letters indicate significant differences assessed by Duncan's test ($p<0.05$).

Nutrient contents

As shown in Table 2, N, P, K^{+} and Ca^{2+} contents were significantly decreased under salinity compared to the control plants. P root concentration was the most reduced with a decrease of 74% while Ca^{2+} root content was less affected by salinity with a decrease of 11%.

The same negative effect was observed for C treated plants. In contrast, Na^+ and Cl^- concentrations were significantly increased in S treated palms. At the same time, K^+/Na^+ and Ca^{2+}/Na^+ ratios showed a significant decrease with NaCl application (Table 2). This nutrient imbalance may disrupt cellular metabolic processes including photosynthesis and consequently plant's growth (Ait-El-Mokhtar et al. 2020a). CS treated plants had considerably increased N, P, K^+ and Ca^{2+} content and K^+/Na^+ and Ca^{2+}/Na^+ ratios in both leaves (89, 216, 48, 44, 88 and 83%, respectively) and roots (41, 445, 132, 25, 149 and 34%, respectively) compared to S treated plants. Furthermore, compost application decreased Na^+ and Cl^- uptakes under 240 mM NaCl. The improvement of plant nutrient uptake through compost application seems to be one of the main explanations of growth improvement under salinity stress since compost is considered as an important source of mineral elements in the soil. The abundance of saprophytic bacterial and fungal populations in the used compost could improve the availability of mineral elements for the plant after mineralization of organic matter. Under saline condition, compost application has been reported to positively affect plant physiological traits such as mineral nutrient uptake (Ramzani et al. 2017; Mbarki et al. 2018). A recent study (Mbarki et al. 2020) showed that alfalfa plants growing in the presence of compost showed an increase in N, P and K^+ content under 100 mM NaCl salt regime. Similar improvement in mineral uptake (N, P, K^+, Ca^{2+}, Mg^{2+} and Mn) was recorded in plants grown in salty soils with the application of organic amendments (Mbarki et al. 2018; Ben-Laouane et al. 2020). The increase of P uptake could be related to its high release from compost and its high uptake by plant. This could contribute to the improvement of date palm salinity tolerance since P uptake can be involved in preserving cell membranes integrity and facilitating the mobilization of Na^+ and Cl^- ions into the vacuoles (Yaish et al. 2015). Moreover, the inhibition of Na^+ uptake through Na^+ mobility decrease in compost amended soil could be considered as an alternative strategy to improve plant tolerance to salt stress (Mbarki et al. 2018). Furthermore, compost amendment has been reported to be closely linked to soil Na adsorption and Na leaching ratio resulting in Na removal from the root contact area (Chaganti and Crohn 2015). On the other hand, the increase in K^+/Na^+ and Ca^{2+}/Na^+ ratio in compost treated plants in the presence of salinity was commonly related to the salt stress effects mitigation

Table 2 Effect of salinity and compost on mineral content and K/Na and Ca/Na ratio in the leaves and the roots of date palm plants after five months of exposure to salinity

NaCl treatment	Compost	Na ($mg\ g^{-1}$ DW)	Cl ($mg\ g^{-1}$ DW)	N ($mg\ g^{-1}$ DW)	P ($mg\ g^{-1}$ DW)	K ($mg\ g^{-1}$ DW)	Ca ($mg\ g^{-1}$ DW)	K/Na	Ca/Na
Leaves									
0 mM	-compost	5.99±0.36^{d}	20.44±1.75^{d}	1.54±0.03^{c}	2.79±0.38^{c}	11.64±0.49^{b}	7.58±0.51^{b}	1.61±0.03^{b}	1.23±0.20^{a}
	+ compost	8.24±0.56^{c}	22.58±0.67^{c}	3.33±0.03^{a}	7.83±0.79^{a}	16.32±0.47^{a}	8.44±0.18^{a}	1.98±0.08^{a}	1.03±0.05^{b}
240 mM	- compost	36.60±0.70^{a}	37.67±1.46^{a}	1.14±0.02^{d}	1.64±0.17^{d}	6.04±0.55^{d}	5.23±0.12^{c}	0.18±0.01^{d}	0.13±0.01^{d}
	+ compost	28.75±0.24^{b}	31.73±0.34^{b}	2.16±0.03^{b}	5.19±1.06^{b}	8.92±0.96^{c}	7.52±0.38^{b}	0.31±0.03^{c}	0.26±0.01^{c}
Roots									
0 mM	- compost	23.28±0.95^{d}	22.49±0.76^{d}	1.14±0.03^{b}	0.18±0.04^{c}	5.44±0.17^{c}	8.48±0.59^{c}	0.21±0.01^{b}	0.35±0.10^{b}
	+ compost	27.97±0.88^{c}	27.14±0.89^{c}	2.15±0.03^{a}	0.33±0.03^{a}	13.23±1.86^{a}	11.68±0.11^{a}	0.47±0.05^{a}	0.42±0.02^{a}
240 mM	- compost	54.43±1.36^{a}	52.08±2.35^{a}	0.81±0.02^{c}	0.06±0.01^{d}	3.42±0.36^{d}	7.57±0.72^{d}	0.08±0.01^{d}	0.15±0.01^{d}
	+ compost	50.68±0.88^{b}	48.84±1.62^{b}	1.15±0.02^{b}	0.25±0.01^{b}	7.95±0.67^{b}	9.45±0.61^{b}	0.16±0.01^{c}	0.19±0.01^{c}

The values of each parameter labeled by different letters indicate significant differences assessed by Duncan's test ($p<0.05$).

in plants by enhancing selectivity of K^+ and Ca^{2+} to plasmalemma mobilization sites instead of Na^+ ions (Ayub et al. 2020). Sustaining greater K^+/Na^+ and Ca^{2+}/Na^+ ratios inside the plant cell under salt stress provides better environment for a different metabolic process (Ahanger et al. 2015). Higher values of these two parameters enhance Ca^{2+} signaling pathways and hydraulic conductivity (Lovelock and Ball 2002) and preserve photosynthetic apparatus from salinity adverse effect by preventing Na^+ entry into its tissues (Cuin et al. 2011).

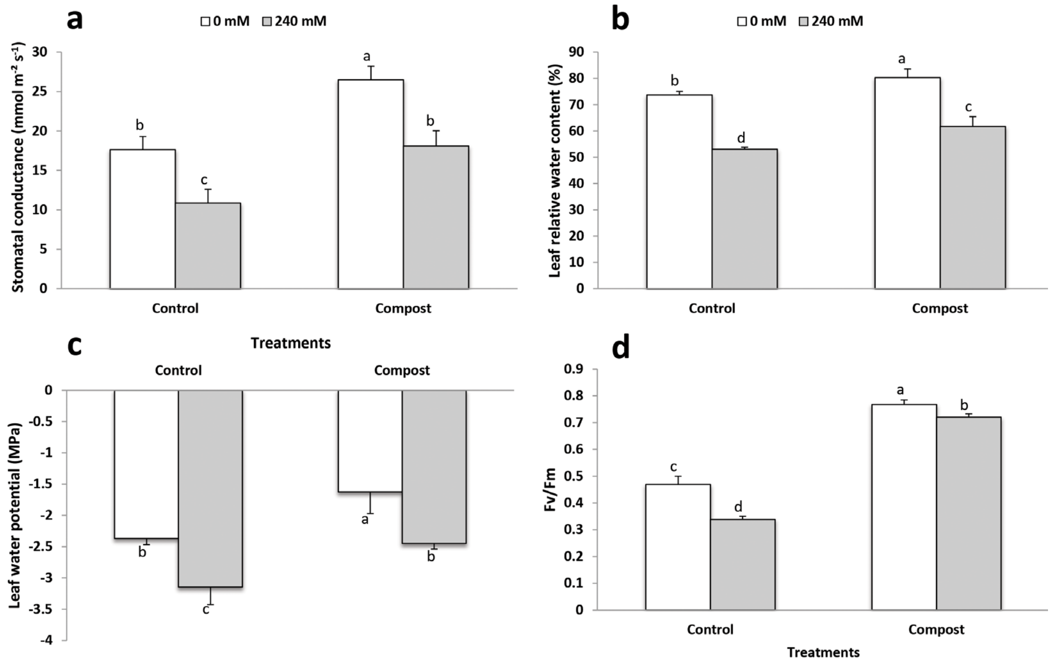

Fig. 1 Effect of salinity and compost on physiological traits and water status (a: stomatal conductance, b: leaf relative water content, c: leaf water potential and d: Fv/Fm) of date palm plants after five months of exposure to salinity

The values of each parameter labeled by different letters indicate significant differences assessed by Duncan's test ($p<0.05$)

Physiological parameters and water status

Salinity and compost application impact on physiological variables and water status is shown in Fig. 1. The application of 240 mM NaCl decreased all the parameters, notably stomatal conductance and leaf water potential which decreased by 38 and 33%, respectively in S treated plants. Similar adverse effect of salinity application was recorded on these parameters in C treated plants. Salinity stress disrupts photosynthesis apparatus and damages its components. Under saline condition, the osmotic stress causes a decrease in CO_2 availability and assimilation which is due to a decrease in stomatal conductance (Chaves et al. 2009; Asgari and Diyanat 2020). Stomata play a crucial role in regulating the uptake of CO_2 for photosynthesis against the loss of water via transpiration. Furthermore, salt stress disrupts the photochemical reactions of photosynthesis, in particular PSII efficiency (Ait-El-Mokhtar et al. 2019, 2020a). In contrast, CS treated plants showed significantly improved water and physiological traits compared to S treated plants. The maximum increase was noticed for photosynthetic efficiency which recorded an increase of 113% compared to S treatment. The positive effect of compost application on these attributes could be related to the increase in N uptake since N is a key component in different photosynthetic enzymes such as RuBisCO (Ahanger et al. 2015). The beneficial effect of compost application could also be related to glycine betaine and proline accumulation in amended seedlings that ensures the stabilization of many enzymes involved in the fixation of CO_2 including RuBisCO and carbonic anhydrase and the protection of PSII pigment-protein complexes (Tartoura et al. 2014).. Salt stress not only impacts photosynthetic attributes, but also plant water status. In fact, salt-affected date palms recorded lower LWP and LRWC values. The decrease in the water status in plants irrigated with saline solution might be attributed to the osmotic stress caused by salt which restrains water molecules and makes them unavailable for the plant roots (Arif et al. 2019). However, compost amendment significantly enhanced the water status of date palms under salinity treatment, as showed by the increase in LRWC values coupled with the decrease in LWP values. This positive effect could be explained by the improvement in soil structure by forming aggregates which increase water availability in the rhizospheric soil (Medina and Azcón 2010; Wang et al. 2014; Oo et al. 2015).

Photosynthetic pigments

As presented in Table 3, salt stress significantly decreased photosynthetic pigments' content with a 54% decrease for chlorophyll a (chl a), 43% decrease for chlorophyll b (chl b), 50% decrease for total chlorophyll and 37% decrease for carotenoids in comparison to the control plants. The same negative impact of salt stress was noticed in C treated plants. This effect is related to the different negative effects of salt stress on photosynthesis functioning such as chloroplast damage due to the salinity toxicity (Zörb et al. 2009), the chlorophyll degradation and the alteration of the functioning of enzymes involved in the photosynthetic pigments synthesis (Murkute et al. 2006). Moreover, the lower chlorophyll content values, in S treated date palms, could be explained by the reduced nutrient uptake, especially magnesium, under salt stress (Ayub et al. 2020). In contrast, the compost application significantly enhanced different photosynthetic pigment contents under 240 mM NaCl condition. CS treated seedlings positively counteracted the negative salinity effects by showing great increase in photosynthetic pigments content (97% for chl a, 79% for chl b, 89% for total chlorophyll and 58% for carotenoids) compared to S treated plants. The improvement of chlorophyll synthesis is linked directly to the mineral elements absorption, efficiency and transport; as they are necessary for heme, chlorophyll synthesis, and as co-factors for several critical cellular processes, including the photosynthesis (Ayub et al. 2020). Rao and Chaitanya (2016) reported that an increase in Mg^{2+} availability for the plant due to the compost addition and an increase in its absorption might be possible reasons for stimulating chlorophyll pigments synthesis and therefore for boosting photosynthetic capacity.

Table 3 Effect of salinity and compost on the concentrations of photosynthetic pigments of date palm plants after five months of exposure to salinity

NaCl treatment	Compost	Chl a (mg g^{-1} FW)	Chl b (mg g^{-1} FW)	Chl T (mg g^{-1} FW)	Carot (mg g^{-1} FW)
0 mM	-compost	11.8 ± 0.9^b	6.8 ± 1.0^b	18.6 ± 1.8^b	60.0 ± 4.9^b
	+compost	19.3 ± 2.0^a	12.7 ± 1.0^a	32.0 ± 3.0^a	113.9 ± 11.9^a
240 mM	-compost	5.5 ± 0.5^c	3.9 ± 0.5^c	9.3 ± 0.8^c	37.8 ± 4.2^c
	+compost	10.7 ± 0.7^b	6.9 ± 0.5^b	17.7 ± 1.2^b	59.9 ± 4.3^b

Chl a: chlorophyll a, Chl b: chlorophyll b, Chl T: total chlorophyll, Carot: carotenoids.
The values of each parameter labeled by different letters indicate significant differences assessed by Duncan's test ($p<0.05$).

Hydrogen peroxide and malondialdehyde content

Results in Table 4 show a clear significant improvement in H_2O_2 and MDA contents (in both roots and leaves) with salt application in the presence and the absence of compost. The most increased content was the root H_2O_2 content which was enhanced by 39% and the less affected was the root MDA content which recorded an increase of 18%. The decline in date palm biomass accumulation in the presence of salinity was combined with a high H_2O_2 and MDA accumulation. Salt stress induced more oxidative damage (high ROS accumulation) to root tissues than shoot ones since roots are the first to experience high salt levels in soil solution. Persistent salinity-induced ROS accumulation -resulting from an imbalance between ROS production and its removal by enzymatic and non-enzymatic detoxification mechanisms- causes oxidative stress-associated injuries, including lipid peroxidation measured as MDA accumulation. The same findings are reported by recent researches on three cultivars (Umsila, Zabad and Boufeggous) of *Phoenix dactylifera* L. (Ait-El-Mokhtar et al. 2019; Al Kharusi et al. 2019), *Pistacia vera* L. (Kamiab 2020), and *Medicago sativa* L. (Ben-Laouane et al. 2020). In contrast, compost application showed a significant decrease in those parameters in both salt-affected and non-salt affected date palms. The maximum decline (37%) was recorded for leaf MDA concentration compared to S treated plants. This effect could be attributed to the improvement of antioxidant enzymes efficiency that scavenges the ROS before damaging membrane lipids which results in limited lipids peroxidation and H_2O_2 accumulation. Our findings are supported by the results obtained by Ramzani et al. (2017) who reported a reduced accumulation of MDA and H_2O_2 in quinoa plants in the presence of compost under salt stress. Furthermore, Tartoura et al. (2014) found a decrease in H_2O_2 concentration in salt-affected tomato plants grown in compost amended soil.

Table 4 Effect of salinity and compost on the concentrations of hydrogen peroxide, MDA, proline and soluble sugars of date palm plants after five months of exposure to salinity

NaCl treatment	Compost	H_2O_2 (µmol g^{-1} FW)	MDA (nmol g^{-1} FW)	Proline (µmol g^{-1} FW)	Soluble sugars (µg mg^{-1} FW)
Leaves					
0 mM	-compost	18.01±0.37^{bc}	11.97±0.39^{b}	11.61±0.82^{d}	386.31±15.15^{c}
	+ compost	16.27±0.90^{c}	8.60±0.30^{d}	13.08±0.41^{c}	443.61±38.47^{b}
240 mM	- compost	24.78±2.14^{a}	14.95±0.86^{a}	19.13±1.14^{b}	435.89±33.71^{b}
	+ compost	19.18±0.83^{b}	9.46±0.30^{c}	23.35±0.85^{a}	563.30±43.87^{a}
Roots					
0 mM	- compost	37.04±1.82^{c}	23.57±1.45^{b}	34.53±4.02^{d}	78.85±6.65^{c}
	+ compost	26.54±1.28^{d}	17.89±1.19^{c}	51.27±4.43^{c}	92.73±3.38^{b}
240 mM	- compost	53.03±2.45^{a}	26.91±0.28^{a}	65.19±3.65^{b}	96.75±3.41^{b}
	+ compost	43.41±0.68^{b}	23.91±0.79^{b}	79.25±1.30^{a}	118.22±1.74^{a}

MDA: malondialdehyde

The values of each parameter labeled by different letters indicate significant differences assessed by Duncan's test ($p<0.05$).

Proline and soluble sugars content

Data presented in Table 4 also show that proline and soluble sugar concentrations were significantly improved under salinity in both control and C treated plants. Plants under salt stress recorded significant high values of these organic osmolytes in comparison with the control plants. Proline and soluble sugars are considered as inert compatible osmolytes that could play a key role in regulating the osmotic potential in plant cell and are commonly used to evaluate the level of plant adaptation to salinity stress (Ashraf and Foolad 2007; Zamani et al. 2020). Under salt stress, compost application showed an increase of soluble sugars and proline content in roots (22 and 21%, respectively) and in leaves (29 and 22%, respectively). This effect might be one of the initiated plant mechanisms to mitigate salinity impacts by promoting the osmotic adjustment and scavenging the free radicals (Yaish and Kumar 2015). Our results showing increment in proline and soluble sugars content due to compost application in salt-affect soils support the findings of Chinsamy et al. (2013).

Antioxidant enzymes activity

The effect of salt stress and compost on antioxidant enzymes activity in date palm seedlings' results are shown in Figs 2 and 3. Plants under NaCl stress showed a significant increment in enzymatic antioxidant activity (SOD, PPO, POD, APX, and CAT), in both leaves and roots, in the presence and the absence of compost. The activity of PPO was the most sensitive to NaCl stress and showed a maximum augmentation of 287% in roots compared to the control plants. Plants adopt several strategies to improve their tolerance to salinity stress. The antioxidant enzyme system induction is concidered as the most efficient mechanism to scavenge oxidative damage. The activities of antioxidant enzymes were further enhanced in stressed plants grown in compost amended soil. SOD is the first enzyme of antioxidant defense and permits the conversion of superoxide radicals into oxygen and H_2O_2 (Mittler 2002). The obtained H_2O_2 is trasformed to H_2O, thanks to APX, CAT and POD enzymes (Mittler 2002). In this study, SOD activity improvement confirms the increase in the activity of H_2O_2 detoxifying enzymes (POD, CAT and APX). On the other hand, PPO catalyzes phenolic compounds oxidation to quinones using oxygen molecules as electron acceptors (Strack and Schliemann 2001) and an increment in its activity is considered as one of the indicators of improvement of saline stress tolerance (Kamiab 2020; Zamani et al. 2020). The stimulation of enzymatic antioxidant activity in compost treated plants compared with non-amended plants was coupled to low oxidative markers (MDA and H_2O_2) levels showing efficient ROS scavenging system via a diminution in oxidative damages in the amended plants. Moreover, date palm proteins content was reduced under saline condition which indicates that their synthesis is sensitive to salt effects. However, the organic amendment had significant and positive effect on protein concentration and showed 33 and 26% greater protein respectively in leaves and roots of CS plants as compared to S plants. This improvement could be attributed to the increase of nutrients uptake observed in this study, particularly N uptake. Previous reports have shown that the strength of the cell membrane is enhanced by proteins, which helps in reducing the unsaturation of membranes under stressful conditions (Zamani et al. 2020). Our result is in agreement with the findings of Saeed et al. (2016) which reported that protein concentration was improved in salt-affected *Cyamopsis tetragonoloba* L. plants by the application of tea leaf compost.

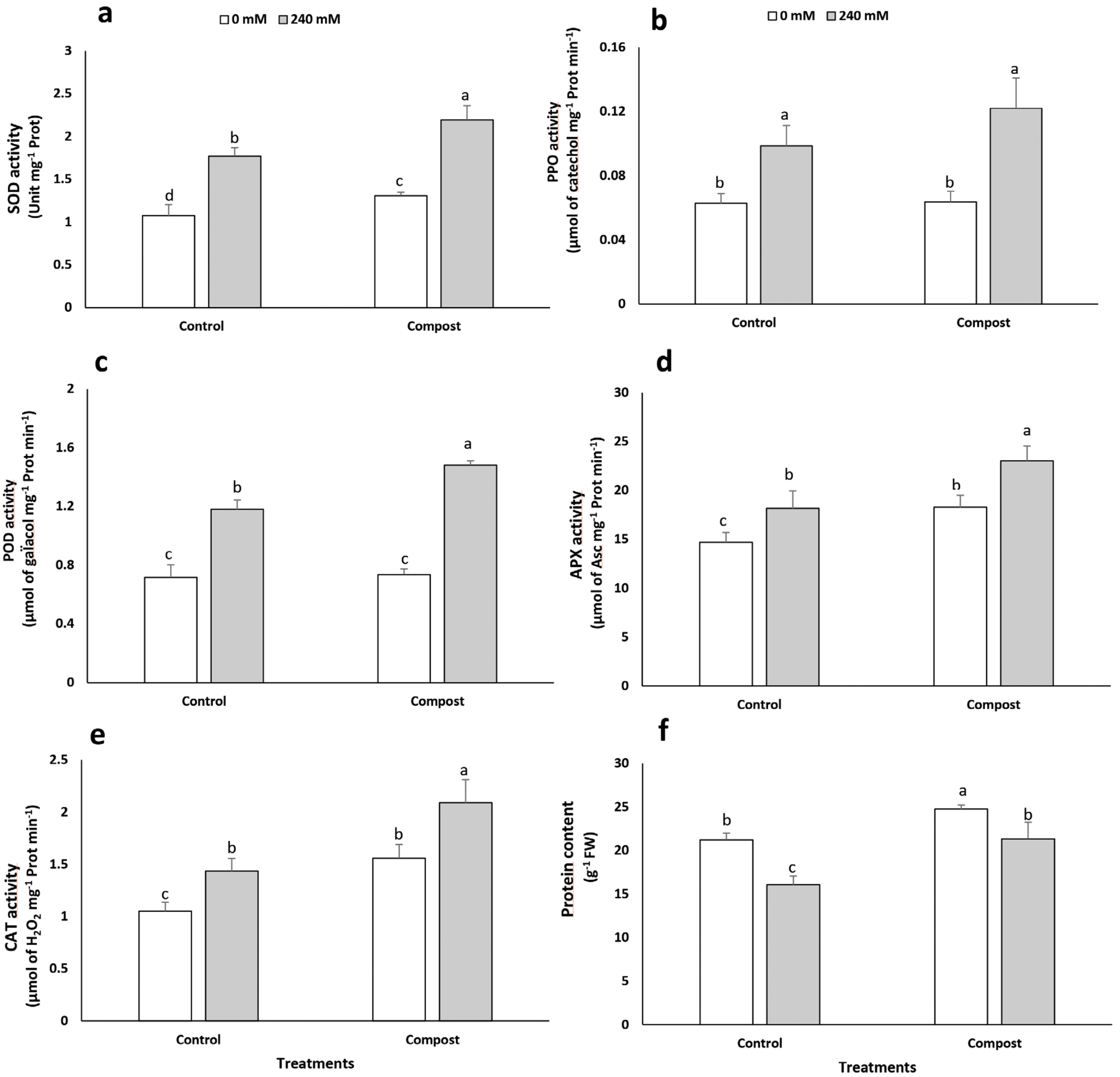

Fig. 2 Effect of salinity and compost on the specific activity of superoxide dismutase (SOD)(a), polyphenoloxidase (PPO)(b), peroxidase (POD)(c), ascorbate peroxidase (APX)(d), catalase (CAT)(e) and concentration of protein (f) in the leaves of date palm plants after five months of exposure to salinity

The values of each parameter labeled by different letters indicate significant differences assessed by Duncan's test ($p<0.05$)

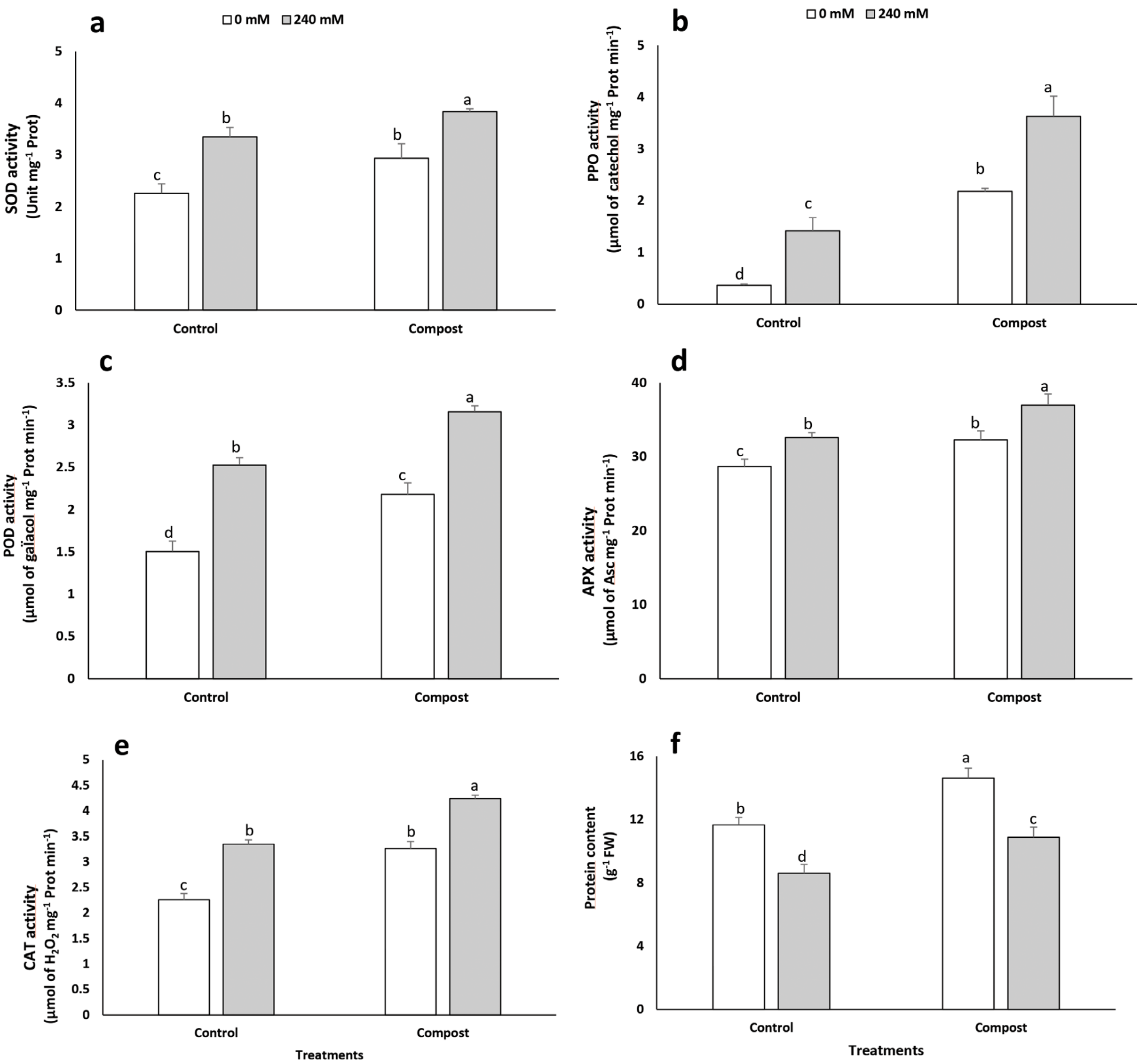

Fig. 3 Effect of salinity and compost on the specific activity of superoxide dismutase (SOD)(a), polyphenol oxidase (PPO)(b), peroxidase (POD)(c), ascorbate peroxidase (APX)(d), catalase (CAT)(e) and concentration of protein (f) in the roots of date palm plants after five months of exposure to salinity

The values of each parameter labeled by different letters indicate significant differences assessed by Duncan's test ($p<0.05$)

Heat map analysis

Heat map revealed the interactions between the applied treatments and the measured variables in date palm (Fig. 4). The analysis indicates that the highest values of growth (PH, NL, LA, SFW, SDM, RFW and RDM), physiological (gs, LWP, Fv/Fm, LRWC and photosynthetic pigments content) and nutritional (P,N, K, Ca, K/Na, Ca/Na) traits and protein content were recorded in C treated date palms except for L-Ca/Na which showed the greatest value in the control plants. The lowest values of these parameters were recorded in S treated palms. In contrast, the toxic ions (Na^+ and Cl^-) and the oxidative markers (H_2O_2 and MDA) present the highest accumulation under S treatment. On the other hand, the antioxidant system defense (sugar and proline content and SOD, CAT, APX, PPO and POD activities) seems to be more efficient in CS treated plants. Our investigation demonstrates that compost addition to soil mitigated salt stress effects through regulation and/or activation of biochemical and physiological strategies. The Heat map analysis highlights the different mechanisms initiated by compost application to improve plant performance under saline environment. Date palms growing in salt-affected soil presented a disrupted nutrient balance, water deficiency, oxidative damage and low photosynthetic activity, which leads to reduced biomass accumulation. Under the same condition, compost amendment improves plant water and nutrient status through increasing water and nutrient absorption as it is considered a mineral elements source (N, P, K and Ca) for both soil and plant. In addition, compost can improve soil water holding capacity and aggregate stability and thereby improve water absorption. Compost application also alleviate the ions toxicity (Na^+ and Cl^-) by removing these ions from the rhizospheric area and thus minimizing their effect on the plant root system. Furthermore, compost application promotes tolerance of date palm seedlings by improving the activity of antioxidant enzymes and accumulating organic osmolytes which reduce the oxidative markers' (H_2O_2 and MDA) levels and thus prevent the oxidative damages. The improvement of nutrient uptake and antioxidant system stimulate the photosynthetic apparatus functioning which increase plant biomass production under saline condition.

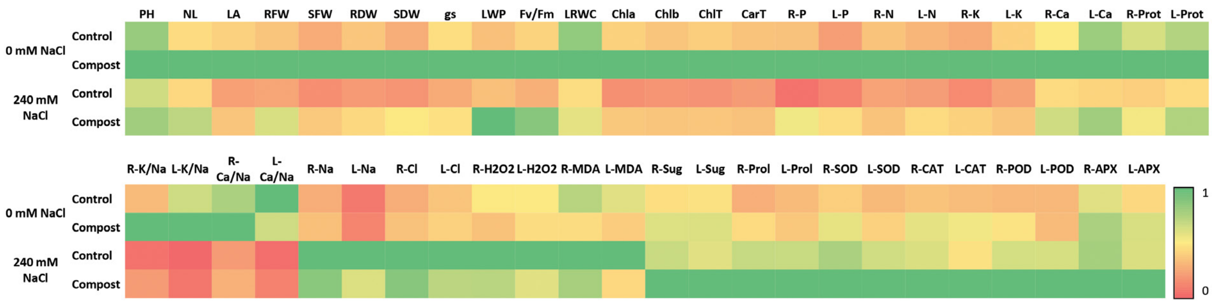

Fig. 4 Heat map analysis of the studied traits in date palms growing in the absence or the presence of the compost under saline and non saline conditions

PH: plant height, NL: number of leaves, LA: leaf area, SFW: shoot fresh weight, SDW: shoot dry weight, RFW: root fresh weight, RDW: root dry weight, , L-Na: leaf sodium content, R-Na: root sodium content, L-Cl: leaf chloride content, R-Cl: root chloride content, L-P: leaf phosphorous content, R-P: root phosphorous content, L-N: leaf nitrogen content, R-N: root nitrogen content, L-K: leaf potassium content, R-K: root potassium content, L-Ca: leaf calcium content, R-Ca: root calcium content, LRWC: leaf relative water content, LWP: leaf water potential, gs: stomatal conductance, Fv/Fm: photosynthetic efficiency, Chl a: chlorophyll a content, Chl b: chlorophyll b content, Chl T: total chlorophyll content, Carot: carotenoids content, L-K/Na: leaf K/Na ratio, R-K/Na: root K/Na ratio, L-Ca/Na: leaf Ca/Na ratio, R-Ca/Na: root Ca/Na ratio, L-H_2O_2: leaf H_2O_2 content, R-H_2O_2: root H_2O_2 content, L-MDA: leaf MDA content, R-MDA: root MDA content, L-Prol: leaf proline content, R-Prol: root proline content, L-Sug: leaf sugar content, R-Sug: root sugar content, L-APX: leaf ascorbate peroxidase activity, R-APX: root ascorbate peroxidase activity, L-CAT: leaf catalase activity, R-CAT: root catalase activity, L-POD: leaf peroxidase activity, R-POD: root peroxidase activity, L-SOD: leaf superoxide dismutase activity, R-SOD: root superoxide dismutase activity, L-PPO: leaf polyphenoloxidase activity, R-PPO: root polyphenoloxidase activity, L-Prot: leaf protein content, R-Prot: root protein content

Conclusion

Salt stress induced significant adverse effects on growth, physiological and biochemical attributes of date palm plants. The application of compost amendment alleviated these effects by improving the aforementioned traits. Date palms grown in compost amended soil recorded greater values of photosynthetic efficiency, water status and the photosynthetic pigments concentration under NaCl stress by improving N, P, K^+, and Ca^{2+} content and decreasing Na^+ and Cl^- uptake. In addition, compost application mitigated salt-induced oxidative stress through boosting antioxidant enzymes system and increasing osmolytes compounds accumulation which induced a decline in lipid peroxidation and hydrogen peroxide levels. All these changes preserve the membrane integrity and cells apparatus from oxidative damage and promote date palms tolerance to salinity stress. The application of compost could be recommended as an efficient agro-technological asset to alleviate the adverse effects of salinity and to improve crop production in salty soils in arid and semi-arid regions.

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Compliance with ethical standards

Conflict of interest The authors declare that there are no conflicts of interest associated with this study.

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