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Research Article

Effect of salicylic acid on salt tolerance of *Aloe vera* plants under both salt-acclimated and non-acclimated conditions

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Abstract

Since the role of salicylic acid (SA) in *Aloe vera* plants under salt stress is not yet clarified, this experiment was conducted to investigate the role of SA (100 and 500 µM) in photosynthesis, antioxidative capacity and ion homeostasis in salt acclimated (EC 5 dS/m) and non-acclimated *Aloe* plants against subsequent salt stress (EC 21 dS/m). Salinity exerted an adverse effect on the leaf dry weight, whereas foliar spray of 100 µM SA mitigated the salt-induced inhibitory effects on the plant growth, especially under acclimated conditions. While salt stress caused a significant increase in Na accumulation and a considerable decrease in K and Ca, higher levels of K/Na ratio were observed after SA treatment. SA application (100 µM) also alleviated the damage to PSII function induced by salt, contributing to the improvement of electron trapping under salinity. Furthermore, *Aloe* plants exposed to EC 21 dS/m exhibited an oxidative damage, determined by increased content of oxidants (hydrogen peroxide and malondialdehyde). In contrast, foliar spray of 100 µM SA increased CAT activity as well as carotenoids content, whereas reduced content of oxidants under salt stress. Consequently, under both salt-acclimated and non-acclimated conditions, SA at concentration of 100 µM was more effective in alleviation of salt stress in *Aloe* plants via the enhancement of photochemical activity of photosynthesis, the activities of antioxidant enzymes and the ratio of K and Na under salinity.

Keywords: *Aloe vera*, antioxidant status, Ion homeostasis, Quantum yield of electron transport, Photochemistry activity, Salinity

Introduction

Among abiotic stresses, salt stress induces osmotic and ionic changes in plants that seriously limit plant growth and crop productivity by causing oxidative stress and enhancing the excessive production of reactive oxygen species (ROS) (Jiang *et al*., 2017). Under these conditions, excessive ROS affect photosynthesis (Munns and Tester, 2008), mainly because of the inhibition of the photosynthetic electron transport activities, degradation of chlorophylls (Habibi, 2017), and deterioration of membrane integrity and proteins linked with photosynthetic apparatus (Miller *et al*., 2010).

Reports have shown that exogenous application of SA can ameliorate toxicity symptoms caused by salinity stress in many plant species (Hayat *et al*., 2010; Jayakannan *et al*., 2015). However, earlier studies have revealed the effects of SA on photochemical efficiency of photosystem II (PSII) and the antioxidative defense system were dependent on the concentration used and the method of application (Chen *et al*., 2016; Habibi, 2018). SA at high concentration increases the accumulation of ROS in the leaves accompanied with the oxidative damage to cell membranes (Chen *et al*., 2016), while at appropriate concentrations, SA may act as a potential growth regulator to improve salinity stress resistance of plants (Bastam *et al*., 2013; Shaki *et al*., 2019). The enhanced salt-stress protection by SA is associated with increased activities of antioxidative enzymes, accumulated osmotic adjustment solutes (e.g., proline and sugars), regulated ions homeostasis as well as modulated quantum yield of PSII photochemistry (Hayat *et al*., 2010; Youssef *et al*., 2018; Bukhat *et al*., 2019).

Aloe vera L., a succulent species with crassulacean acid metabolism (CAM) pathway, grows well on moderate saline soils, however, its growth and yield is diminished at high salinity (Silva *et al*., 2014; Hazrati *et al*., 2017). The present study was undertaken to explore the role of exogenous SA application in mitigating the negative effects of salt stress, which may be of great help in understanding the roles and mechanisms of exogenous SA in promoting the salt stress tolerance of plants. To this date, no study has focused on the role of SA in salt-acclimated *Aloe* plants under stress conditions. In addition, fewer studies have analyzed the role of salt acclimation in the up-regulation of photochemical activity in salt acclimated plants against subsequent salt stress. Hence, these results will provide evidence to determine whether the mitigation of salinity stress may be contributed to the improvement of photochemical functioning by exogenous SA under both

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salt-acclimated and non-acclimated conditions. To address this issue, we examined to some detail the biochemical mechanisms by which SA affects the plant growth, PSII functioning, antioxidative system and phenolic metabolism in salt-treated *Aloe* plants.

Materials and methods

Plant material and treatments: The 15–20 cm pups of *Aloe vera* L. plants were planted in top of the cylindrical plastic pots (20 cm in diameter and 30 cm in depth) containing humus-fine sand-perlite mixture (pH 7.4, soil organic matter (SOM) 22.8 g/kg) for five months, and irrigated with distilled water every 10 days. Plants were grown in a growth room under the following conditions: day/night temperature of 30-35/18-22ºC, 16/8 hrs. day/night cycle, relative humidity of 30-35 % and daily photon flux density of about 400-420 µmol m^{-2} s^{-1}. The salinity level for the acclimation experiment was chosen according to Pandolfi *et al*. (2016) method. Salicylic acid was dissolved in absolute ethanol and then added drop-wise to water (ethanol:water, 1:1000, v/v) (Li *et al.*, 2014), and then was sprayed on the leaves at concentrations of 0.1 or 0.5 mM with a hand sprayer twice every 7 days. After the acclimation period (21 days at salinity levels of 6 dS/m), NaCl was added to the pots to obtain the electric conductivity (EC) of 21 dS/m according to the method described by Hajiboland *et al*. (2010). Accordingly, saline solutions of 0.2–1.0 g NaCl were added to the soil. After providing saturated extracts of soil, the regression equation was used to evaluate the amount of NaCl to obtain salinity levels of 21 dS/m. Treatments were termed as control (non-acclimated, non-stressed), salinity (non-acclimated, stressed) and Ac + salinity (acclimated, stressed). The EC of control pots was 1.88 dS m^{-1}. Fully expanded and mature leaves were used for measurement of enzymatic analysis after 60 days after treatment with EC 21 dS/m. Then leaves were separated and washed with distilled water, blotted dry on filter paper and after determination of fresh weight (FW) they were dried for 48 hrs. at 70°C for determination of dry weight (DW). Leaf samples were frozen immediately in liquid N_2 and were stored until assay.

Determination of proline, soluble sugars, and starch: Proline was determined as described by Bates *et al.* (1973). Leaf samples from each group were homogenized in 3% (w/v) sulphosalycylic acid at 4°C and the homogenate was centrifuged at 3,000g for 20 min. About 2 mL of extract was taken in test tube and 2 mL of glacial acetic acid and 2 mL of ninhydrin reagent were added. The tube was cooled over crushed ice, and then absorbance of red color developed was read at 520 nm against toluene black on UV-visible spectrophotometer. Standard curve was created using proline (Sigma). Soluble sugars concentrations were determined according to the method of Quentin *et al.* (2015). Leaf tissues were homogenized with 2.5 mL 80% ethanol in a water bath for 2 hrs. at 30ºC. After centrifugation at 3,000 g for 10 min, the supernatants were subjected to soluble sugars analysis by anthrone-sulfuric reagent at 630 nm. Glucose (Sigma) was used for production of a standard curve. The pellets were kept for starch analysis by following the method of Magne *et al*. (2006). Starch was dissolved after resuspendation in a 4:1 (v/v) mixture of 8 N HCl / dimethylsulfoxide, and the supernatant was mixed with iodine–HCl solution and the absorbance was read at 600 nm. Starch (Merck) was used for the production of standard curve.

Determination of chlorophyll *a* fluorescence, total carotenoids, and chlorophyll *a* and *b*: Chlorophyll *a* fluorescence transient (OJIP test) was estimated with a Packet-PEA chlorophyll fluorimeter (Plant Efficiency Analyser, Hansatech Instruments Ltd., King's Lynn, Norfolk, PE 32 1JL, England) in dark-adapted leaves for at least 25 min. We used the JIP-test to analyse chlorophyll a fluorescence rises (table 1). Some groups of measured and calculated parameters using the JIP-test (Strasser *et al*., 2004) were represented in the following section.

For determination of chlorophyll and carotenoids, samples were homogenized in the methanol according to Lichtenthaler and Wellburn (1983). After centrifugation at 1000 rpm for one minute, supernatants were used for determination of photosynthetic pigments, and the absorbance was read at 400-700 nm on spectrophotometer.

Determination of Na, K and Ca contents: All samples were dry-ashed at 550°C for 8 hrs., and dry powders of samples were mixed with 0.5 M HCl and made up to volume by double-distilled water. Then, the concentrations of Na and K were determined by an Inductively-Coupled Plasma-Atomic Emission Spectrometry (ICP-AES, INTEGRA XL2, GBC; Australia).

Assay of antioxidative enzymes activity and related metabolites: The activities of superoxide dismutase (SOD) and catalase (CAT) were determined according to methods described elsewhere (Habibi, 2017). Lipid peroxidation was monitored from the amount of malondialdehyde (MDA) formed in a reaction mixture containing thiobarbituric acid (Sigma) at 532 nm. MDA levels were quantified from a 1, 1, 3, 3-tetraethoxypropane (Sigma) standard curve. The hydrogen peroxide (H_2O_2) content in the leaves was evaluated according to the method of Velikova *et al*. (2000). The content of H_2O_2 was given on a standard curve.

Statistical analysis: Experiments were under taken in completely randomized design with 4 independent replications. Significant differences between means were concluded by Tukey test ($P < 0.05$) using Sigma Stat (4.0) software.

Results and discussion

SA pretreatment ameliorated leaf growth inhibition during salt stress: Under non-saline conditions, leaf biomass of plants was decreased by foliar application of

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Table 1. Information selected from the fast OJIP fluorescence induction

$F_v/F_m = (F_m - F_o)/F_{max}$	the maximum PSII photochemical efficiency, namely the maximum quantum yield of primary photochemistry
$F_v/F_o = (F_m - F_o)/F_o$	the efficiency of the water-splitting complex on the donor side of PSII
$PI_{abs} = (RC/ABS) \times (\varphi_{Po}/(1-\varphi_{Po})) \times (\psi_o/(1-\psi_o)$	the performance index
Φ_{Eo}	the quantum yield of electron transport

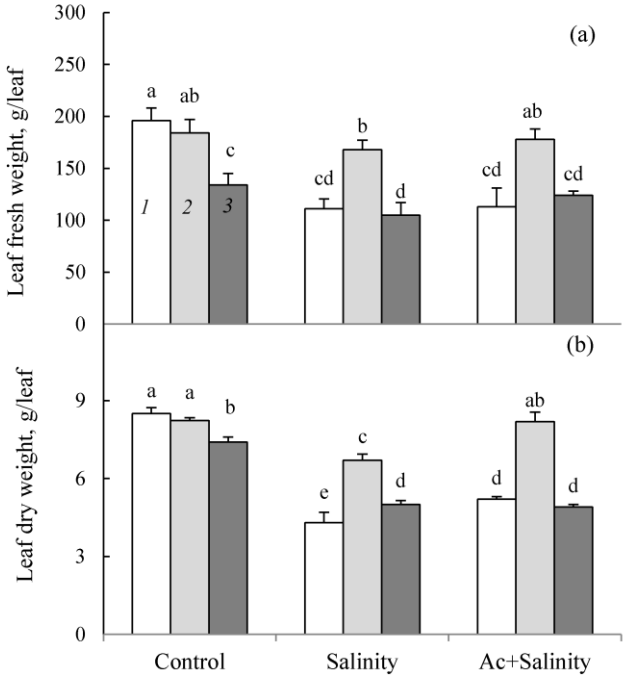

Fig. 1. Effects of salt stress on leaf fresh (a) and dry weight (b) of *Aloe vera* plants exposed to exogenous SA under acclimated and non-acclimated conditions. Bars indicated with the same letter are not significantly different (P < 0.05). Values are the mean ± standard deviation (SD) (n = 4). *1* – 0 µM SA, *2* – 100 µM SA and *3* – 500 µM SA.

SA at 0.5 mM (Fig. 1). Also, the inhibition effect of SA at high concentration on plant biomass was reported in many previously studies (Lee *et al*., 2010; Miura and Tada, 2014; Habibi, 2018). Salt-stressed plants had relatively lower leaf dry weight compared with the control plants; however, this inhibition of leaf dry weight was mitigated by exogenously applied SA at the concentration of 0.1 mM. Our results were in agreement with the findings of Poor *et al*. (2011) in tomato plants, and with the results of Bukhat *et al*. (2019) in *Raphanus sativus*, who reported that exogenous SA alleviated salt stress-induced growth inhibition. Thus, our results demonstrated that a foliar spray of SA at 0.1 mM could mitigate negative effects of salt stress on *Aloe* leaves growth, especially under acclimated conditions.

Exogenous SA altered solute content under salt stress: Many plants accumulate proline when exposed to salinity stress, as ROS scavenger and osmotic regulator (Ma *et al*., 2016). Similarly, a significant increase in proline content was found in leaves of salt-stressed *Aloe* plants (Fig. 2). While exogenous SA application did not significantly affect soluble sugars and starch concentrations in salt-stressed *Aloe* leaves, it raised endogenous proline contents under both acclimated and non-acclimated conditions (Fig. 2). Similar results were observed by Liu *et al*. (2016), who found that SA application further increased the contents of proline in the leaves of NaCl-treated *Nitraria tangutorum* seedlings.

Exogenous SA changed ionic homeostasis of *Aloe* leaves during salt stress: Under salt stress conditions, a significant increase in Na content was observed in leaves (Fig. 3). Also, a significant decrease of K and Ca contents was detected in plants under salt stress. The present results are in agreement with the findings of Jiang *et al*. (2017), which revealed that salt stress caused a significant increase in Na accumulation and a considerable decrease in K. In this study, under salt stress, the application of SA caused substantial increases in the Ca and K contents while decreasing Na in leaves. The same effect of SA was reported by Shaki *et al*. (2019) in salt-stressed safflower plants. These results suggested that exogenous SA had a positive effect on K and Ca contents, but reduced Na content.

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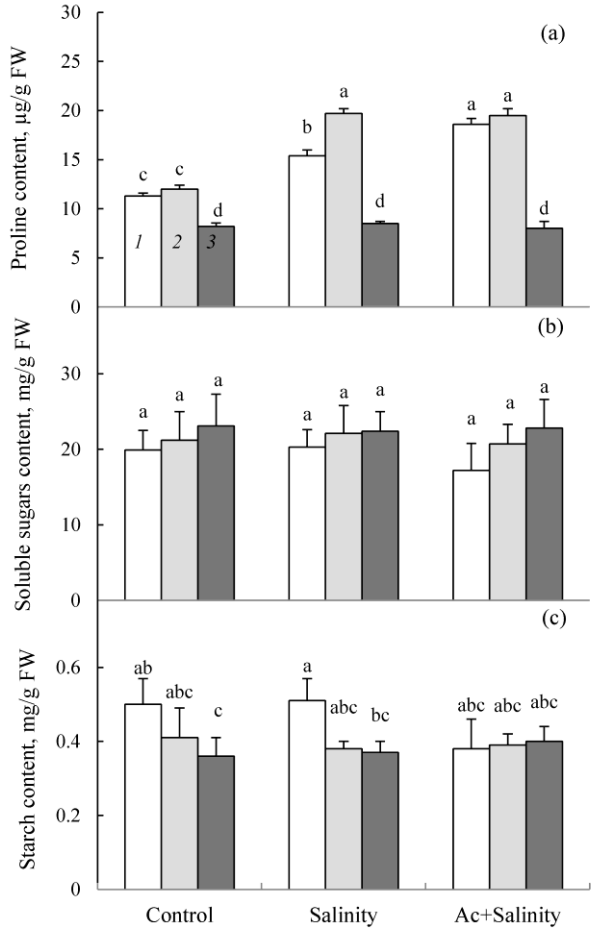

Fig. 2. Effects of salt stress on soluble sugars, starch and proline content of *Aloe vera* plants pretreated with exogenous SA under acclimated and non-acclimated conditions. Bars indicated with the same letter are not significantly different (P < 0.05). Values are the mean ± SD (n = 4). *1* – 0 µM SA, *2* – 100 µM SA and *3* – 500 µM SA.

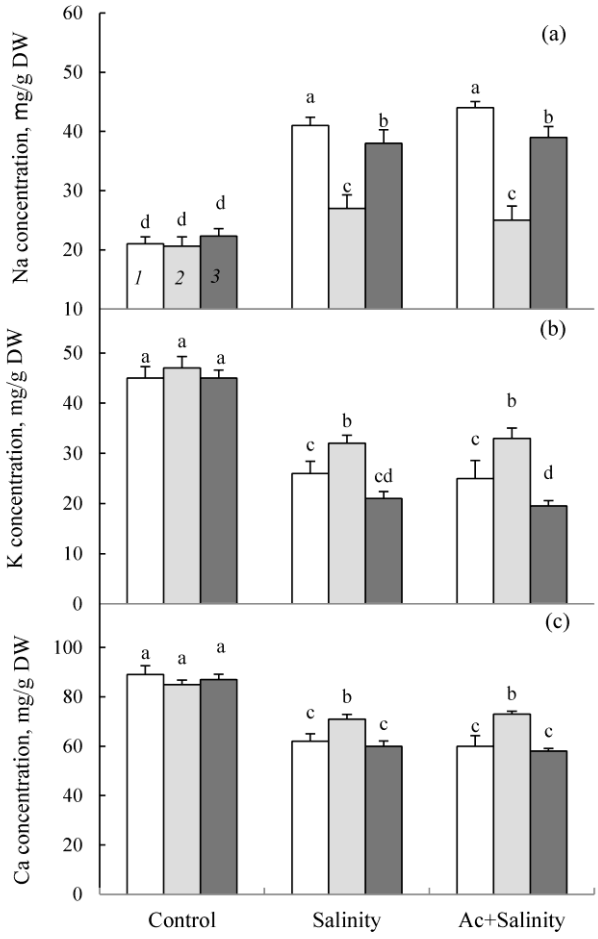

Fig. 3. Effects of salt stress on leaf Na, K and Ca content of *Aloe vera* plants exposed to exogenous SA under acclimated and non-acclimated conditions. Bars indicated with the same letter are not significantly different (P < 0.05). Values are the mean ± SD (n = 4). *1* – 0 µM SA, *2* – 100 µM SA and *3* – 500 µM SA.

SA pretreatment mitigated the adverse effects of salt stress on the PSII function: In this study, chlorophyll *a* and carotenoids concentrations were significantly decreased by salt stress (Fig. 4). However, the decreases in pigment contents in the leaves of salt-treated plants were significantly inhibited by SA application. This higher carotenoids accumulation can exhibit a mechanism that enhances the non-enzymatic antioxidant capacity as well as alleviates the impact of excessive excitation energy on PSII (Samadi *et al*., 2019) to prevent inhibition of photosynthetic primary reactions of *Aloe* leaves under salt stress. The maximum quantum yield of photosystem II (F_v/F_m) was not influenced in plants grown with or without SA treatment under non-salt stress conditions (Fig. 5). Under control conditions, the oxygen-evolving complex efficiency of PSII (F_v/F_o) and the performance index of photosystems (PI_{abs}) were diminished by SA at 0.5 mM; however, SA treatment at 0.1 mM promoted a strong increase in PI_{abs}. The quantum yield of electron transport (Φ_{Eo}) in plant leaves was reduced by salinity only in non-acclimated plants. Salt stress greatly decreased PI_{abs} and F_v/F_o in acclimated and non-acclimated plants, whereas the pretreatments with exogenous SA at 0.1 mM raised these parameters. The improvement of photochemistry and photosynthesis in response to SA has also been reported in *Dianthus superbus* (Ma *et al*., 2016) and in *Raphanus sativus* (Bukhat *et al*., 2019) under salt stress. While the maximum quantum yield of PSII (F_v/F_m) was not influenced by salt stress alone, it exhibited a significant decrease in response to combined treatments of 0.5 mM SA + salinity, suggesting that the negative effect of 0.5 mM SA resulted in defective photochemical functioning. This observation was consistent with the findings of Habibi (2018), who showed that the negative effect of exogenously applied SA on photosynthetic parameters of maize plants was dependent on doses of SA used.

The JIP-test (Strasser *et al*., 2004) was used to analyse each OJIP transient (a sequence of phases have been named as O, J, I, P from the initial (F_0) to the maximal (F_m) fluorescence value). Under control

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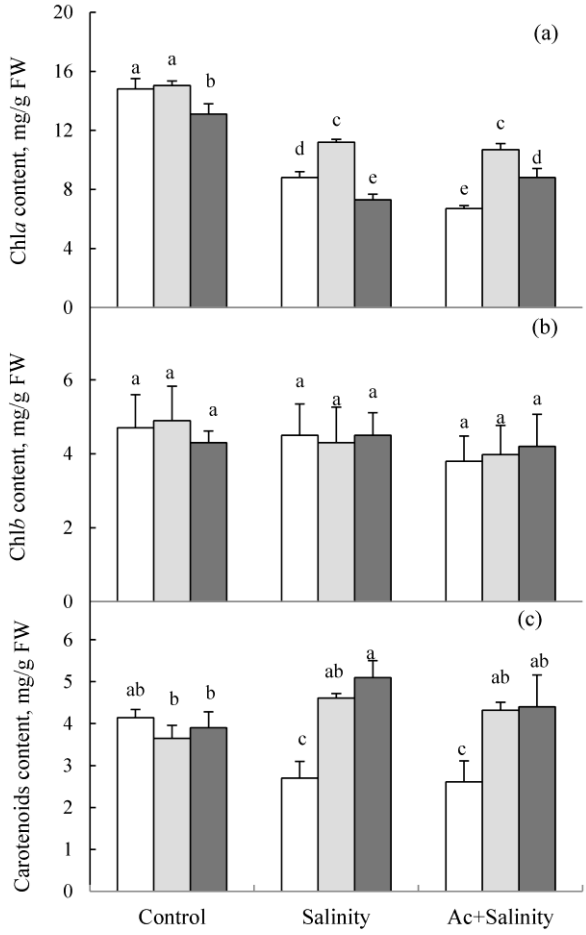

Fig. 4. Effects of salt stress on the content of chlorophyll *a, b* and total carotenoids in *Aloe vera* plants exposed to exogenous SA under acclimated and non-acclimated conditions. Bars indicated with the same letter are not significantly different (P < 0.05). Values are the mean ± SD (n = 4). *1* – 0 µM SA, *2* – 100 µM SA and *3* – 500 µM SA.

conditions, a quicker fluorescence rise in the O-J part of the induction phases was observed in response to 0.5 mM SA, which was connected to deactivation of the reaction center leading to drastic reduction in photochemistry through a blockage of electron flow (Kalaji *et al*., 2016). Under saline conditions, a general decrease in the I–P part of the induction curve of salt-stressed plants was observed (Fig. 7), which may be related to the damage to the electron trapping leading to drastic reduction in primary photochemistry (Kalaji *et al*., 2016). However, the application of SA at 0.1 mM caused a clear increase in the I-P parts of the fluorescence rise and diminished the adverse effects of salt stress on the PSII functioning. Thus, exogenous SA at 0.1 mM significantly increased the photochemical activity of leaves grown under salt stress. This increased ability was correlated with an increase in carotenoids level, which ameliorates the impact of excessive excitation energy on PSII (Gururani *et al*., 2015). Thus, the application of exogenous SA significantly increased the photochemical activity of *Aloe* leaves under salt stress, which was correlated with the increase of carotenoids levels.

SA at 0.1 mM was an alleviant for the oxidative stress effects caused by salinity: The activity of SOD was not significantly affected by salt; however, the activity of CAT in salt-stressed *Aloe* leaves was enhanced under acclimated and non- acclimated conditions (Fig. 6). Under salt stress, SA at 0.1 mM improved CAT activity levels in SA-treated plants compared with non-SA-treated plants. These observations were consistent with the findings of Liu *et al*. (2016), who showed that SA application significantly increased the activities of SOD and CAT of *Nitraria tangutorum* plants under NaCl stress. Since CAT is predominantly involved in scavenging excess ROS (Feng *et al*., 2013), an increase in this enzyme activity corresponded with a significant decrease in the damage to the cell membranes in SA-treated plants compared with the non-SA-treated plants under salt stress. It is well confirmed that salt stress causes accumulation of reactive oxygen species (ROS) in plants, resulting in membrane lipid peroxidation ion leakage (Jiang *et al*., 2017). In this study, prolonged salt stress resulted in severe damage to the *Aloe* plants, determined by the H_2O_2 and MDA accumulation. Interestingly, plants supplemented by SA at a concentration of 0.5 mM exhibited an extreme stress for

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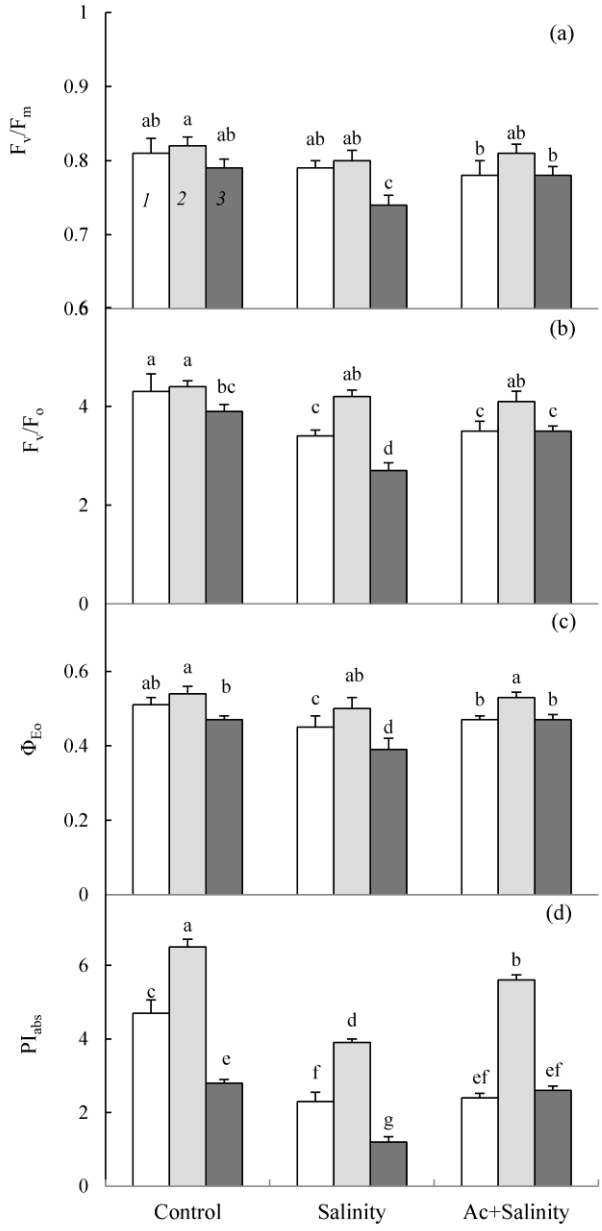

Fig. 5. Effects of salt stress on the maximum quantum yield (F_v/F_m), the performance index (PI_{abs}), the oxygen-evolving complex efficiency of PSII (F_v/F_o) and the quantum yield of electron transport (Φ_{Eo}) of *Aloe vera* leaves exposed to exogenous SA under acclimated and non-acclimated conditions. Bars indicated with the same letter are not significantly different (P < 0.05). Values are the mean ± SD (n = 4). *1* – 0 µM SA, *2* – 100 µM SA and *3* – 500 µM SA.

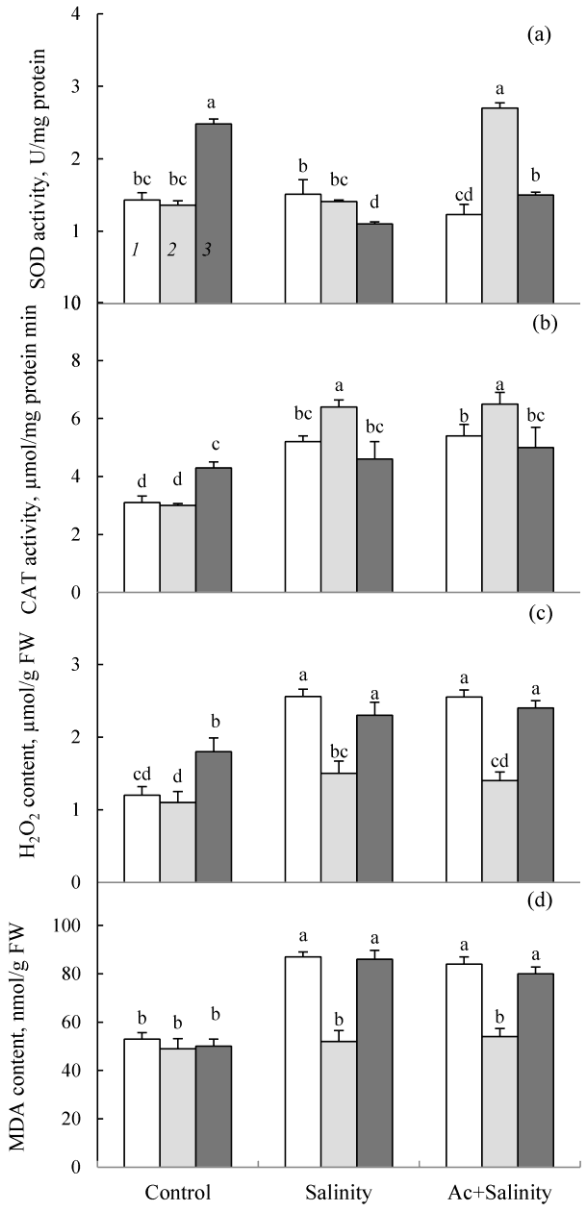

Fig. 6. Effects of salt stress on the activity of superoxide dismutase (SOD), catalase (CAT), and the concentration of hydrogen peroxide (H_2O_2) and maloendialdehyde (MDA) in *Aloe vera* plants exposed to exogenous SA under acclimated and non-acclimated conditions. Bars indicated with the same letter are not significantly different (P < 0.05). Values are the mean ± SD (n = 4). *1* – 0 µM SA, *2* – 100 µM SA and *3* – 500 µM SA.

Aloe plants, as demonstrated by accumulation of H_2O_2 was similar to that observed in salinity treatment (Fig. 7). The increases in MDA content in the leaves of salt-treated *Aloe* plants were markedly inhibited by SA application at 0.1 mM. In agreement with our results, Bukhat *et al*. (2019) found that SA application resulted in lower membrane damage in salt-stressed radish plant. Therefore, exogenous SA at appropriate concentrations (0.1 mM) could effectively promote antioxidant enzyme activity, and counteracted salt stress-induced growth inhibition in *Aloe* plants.

conclusion

the growth and photosynthesis of *Aloe* leaves were decreased under salt stress; however, the application of low levels of SA (100 µM) had a different ameliorating

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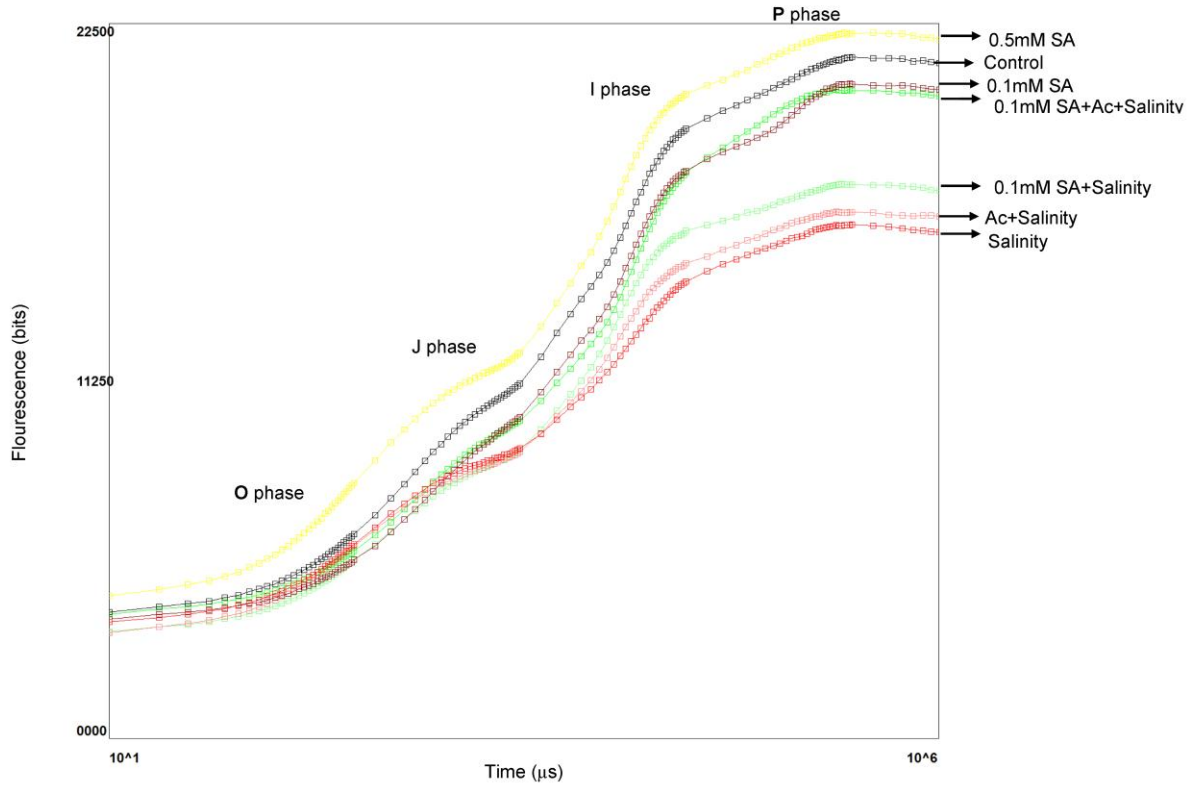

Fig. 7. Effects of salt stress on the chlorophyll *a* fluorescence induction curve of *Aloe vera* leaves exposed to exogenous SA under acclimated and non-acclimated conditions. Bars indicated with the same letter are not significantly different (P < 0.05). Values are the mean ± SD.

effect, contributing to the improvement in photosynthetic capacity by the preservation of oxygen-evolving complex efficiency of PSII (F_v/F_o) and the quantum yield of electron transport (Φ_{Eo}), the activation of the antioxidant defense system to prevent ROS damage, and the amendment of ion homeostasis under salinity stress. Furthermore, in SA-supplied plants, the degree of reduction in PI_{abs} was smaller than the SA-untreated plants suggesting that the pretreatment with SA increases the salt tolerance of *Aloe vera* by improvement of PSII photochemical efficiency. Based on the present results, we concluded that exogenous SA application at concentration of 100 µM was an effective regulator for enhancing the salt tolerance of *Aloe vera* plants under both salt-acclimated and non-acclimated conditions.

References

Bastam N, Baninasab B, Ghobadi C (2013) Improving salt tolerance by exogenous application of salicylic acid in seedlings of pistachio. Plant Growth Regulation 69(3):275-84.

Bates LS, Waldren RP, Teare ID (1973) Rapid determination of free proline for water-stress studies. Plant Soil 39(1):205-7.

Bukhat S, Manzoor H, Zafar ZU, Azeem F, Rasul S (2019) Salicylic Acid Induced Photosynthetic Adaptability of *Raphanus sativus* to Salt Stress is Associated with Antioxidant Capacity. J Plant Growth Regulation 1-4.

Chen YE, Cui JM, Li GX, Yuan M, Zhang ZW, Yuan S, Zhang HY (2016) Effect of salicylic acid on the antioxidant system and photosystem II in wheat seedlings. Biol Planta 60(1): 139-147.

Feng R, Wei C, Tu S (2013) The roles of selenium in protecting plants against abiotic stresses. Environ Exp Bot 87:58–68.

Gururani MA, Venkatesh J, Tran LSP (2015) Regulation of photosynthesis during abiotic stress-induced photoinhibition. Mol Plant 8(9):1304–1320

Habibi G (2018) Antioxidant metabolism and performance index of photosystem II in maize seedlings exposed to high concentration of salicylic acid. Indian J Plant Physiol 23(2):360-8.

Habibi G (2017) Physiological, photochemical and ionic responses of sunflower seedlings to exogenous selenium supply under salt stress. Acta Physiol Plant 39(10), 213.

[DOR: 20.1001.1.23222727.1400.10.43.2.6]

Hajiboland R, Aliasgharzadeh N, Laiegh SF, Poschenrieder C (2010) Colonization with arbuscular mycorrhizal fungi improves salinity tolerance of tomato (*Solanum lycopersicum* L.) plants. Plant Soil 331:313-27.

Hayat Q, Hayat S, Irfan M, Ahmad A (2010) Effect of exogenous salicylic acid under changing environment: a review. Environ Exp Bot 68(1):14-25.

Hazrati S, Tahmasebi-Sarvestani Z, Mokhtassi-Bidgoli A, Modarres-Sanavy SA, Mohammadi H, Nicola S (2017) Effects of zeolite and water stress on growth, yield and chemical compositions of Aloe vera L. Agr Water Manag 181:66-72.

Jayakannan M, Bose J, Babourina O, Rengel Z, Shabala S. (2015) Salicylic acid in plant salinity stress signalling and tolerance. Plant Growth Regul 76(1):25-40.

Jiang C, Zu C, Lu D, Zheng Q, Shen J, Wang H, Li D (2017) Effect of exogenous selenium supply on photosynthesis, Na^+ accumulation and antioxidative capacity of maize (*Zea mays* L.) under salinity stress. Sci Rep 7:42039.

Kalaji HM, Jajoo A, Oukarroum A, Brestic M, Zivcak M, Samborska IA, Cetner MD, Łukasik I, Goltsev V, Ladle RJ (2016) Chlorophyll *a* fluorescence as a tool to monitor physiological status of plants under abiotic stress conditions. Acta Physiol Plant 38:102

Lee, S., Kim, S. G., & Park, C. M. (2010). Salicylic acid promotes seed germination under high salinity by modulating antioxidant activity in Arabidopsis. *New Phytologist*, *188*(2), 626-637.

Li XM, Ma LJ, Bu N, Li YY, Zhang LH (2014) Effects of salicylic acid pre-treatment on cadmium and/or UV-B stress in soybean seedlings. Biologia Plantarum 58(1):195-9.

Lichtenthaler, H. K., & Wellburn, A. R. (1983). Determinations of total carotenoids and chlorophylls a and b of leaf extracts in different solvents. Biochemical Society Transactions, 11(5), 591–592.

Liu W, Zhang Y, Yuan X, Xuan Y, Gao Y, Yan Y (2016) Exogenous salicylic acid improves salinity tolerance of *Nitraria tangutorum*. Russian J Plant Physiol 63(1):132-42.

Magne´ C, Saladin G, Cle´ment C (2006) Transient effect of the herbicide flazasulfuron on carbohydrate physiology in *Vitis vinifera*. Chemosphere 62:650-657.

Ma X, Ou YB, Gao YF, Lutts S, Li TT, Wang Y, Chen YF, Sun YF, Yao YA (2016) Moderate salt treatment alleviates ultraviolet–B radiation caused impairment in poplar plants. Sci Rep 6:32890.

Miller GA, Suzuki N, Ciftci SU, Mittler RO (2010) Reactive oxygen species homeostasis and signalling during drought and salinity stresses. Plant Cell Environ 33:453-467.

Miura, K., & Tada, Y. (2014). Regulation of water, salinity, and cold stress responses by salicylic acid. *Frontiers in Plant Science*, *5*, 4.

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Annu Rev Plant Biol 59:651-681.

Pandolfi C, Azzarello E, Mancuso S, Shabala S (2016) Acclimation improves salt stress tolerance in Zea mays plants. J Plant Physiol 201:1-8.

Poór P, Gémes K, Horváth F, Szepesi A, Simon ML, Tari I (2011) Salicylic acid treatment via the rooting medium interferes with stomatal response, CO_2 fixation rate and carbohydrate metabolism in tomato, and decreases harmful effects of subsequent salt stress. Plant Biology 13(1):105-14.

Quentin AG, Pinkard EA, Ryan MG, Tissue DT, Baggett LS, Adams HD, Maillard P, Marchand J, Landhäusser SM, Lacointe A, Gibon Y (2015) Non-structural carbohydrates in woody plants compared among laboratories. Tree Physiol 35(11):1146-6

Samadi S, Habibi G, Vaziri A (2019) Exogenous trehaloese alleviates the inhibitory effects of salt stress in strawberry plants. Acta Physiol Plant 41(7):112.

Shaki F, Maboud HE, Niknam V (2019) Effects of salicylic acid on hormonal cross talk, fatty acids profile, and ions homeostasis from salt-stressed safflower. Journal of Plant Interactions 14(1):340-346.

Silva H, Sagardia S, Ortiz M, Franck N, Opazo M, Quiroz M, Baginsky C, Tapia C (2014) Relationships between leaf anatomy, morphology, and water use efficiency in *Aloe vera* (L) Burm f. as a function of water availability. Revista chilena de historia natural 87(1):13.

Strasser RJ, Tsimilli-Michael M, Srivastava A (2004) Analysis of the chlorophyll a fluorescence transient. In: Papageorgiou G, Govindjee (eds) Advances in photosynthesis and respiration. chlorophyll a fluorescence: a signature of photosynthesis. Springer, Dordrecht, pp 321–362

Velikova V, Yordanov I, Edreva A (2000) Oxidative stress and some antioxidant systems in acid rain-treated bean plants: protective role of exogenous polyamines. Plant Sci 151:59-66.

Youssef SM, Abd Elhady SA, Aref RM, Riad GS (2018) Salicylic acid attenuates the adverse effects of salinity on growth and yield and enhances peroxidase isozymes expression more competently than proline and glycine betaine in cucumber plants. Gesunde Pflanzen 70:75–90.

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