Exogenous Salicylic Acid Mitigates Adverse Effects of Salinity on some Photosynthesis-Related Parameters of Almond

H. Mohammadi¹, A. Imani¹*, V. Abdosi¹, M. R. Asghari³, and A. R. Talaei⁴

ABSTRACT

Effects of salinity (0, 2, 6, and 8 dS m⁻¹) on some photosynthetic parameters and morphological characteristics of 3 almond cultivars (‘Tuono’, ‘Shoukofeh’ and ‘Sahand’), with or without Salicylic Acid (SA) treatment (at 0, 1 and 2 mM), were studied in a factorial experiment using the completely randomized design with 3 replications, in a greenhouse experiment. Results revealed that while SA at 1 mM significantly improved morphological and photosynthetic properties of salinized plants, its relatively higher concentration (2 mM) impaired growth and photosynthetic attributes. Of the tested cultivars, Shokoufeh grafted on the GF677 rootstock showed higher salt tolerance than the others. This study provides convincing evidence with regard to the potential of SA in improving almond plant growth under salt stress; suitable concentrations of SA when added to saline situations helped the plants in osmotic adjustment for alleviating the harmful effects of salinity. Efficacy of SA may be tested under field conditions before recommending it as a practical tool to enhance almond plant performance in saline soils.

Keywords: Chlorophyll fluorescence, Gas exchange, Prunus amygdalus L., Stomatal conductance.

INTRODUCTION

Almond (Prunus amygdalus L. from the family Rosaceae) is one of the major fruit trees grown in several temperate zones of the world. Almond grows profusely in areas with moderate winters and hot dry summers where the salinity of the soil and groundwater may sometimes exceed tolerable levels, causing damage to the almond trees. Estimates show that over 800 million hectares of soils in the world are salt-affected (Munns and Tester, 2008) and it is expected to increase further in the coming decades due to factors like irrigation expansion, use of poor quality salty waters in irrigation, and climate change impacts (Sharma and Singh, 2017a). It has also been shown that adverse impacts of salinization may especially be severe in irrigated arid and semi-arid regions reeling under adverse impacts of fresh water shortages and climate change-induced alterations in crop growing conditions (Sharma and Singh, 2017b). Although plant growth and productivity in salt-affected soils are negatively affected by a complex interplay among plant, soil, and environmental variables (Sharma and Singh, 2017a), ionic imbalances and toxicities coupled with osmotic stress-induced cellular abnormalities are the major causes of poor plant performance in saline soils (Munns and Tester, 2008). Although several agronomic options are available for improving the crop productivity in salt-affected soils, they suffer from cost and technical constraints, enhancing the interest in plant-based solutions. Use of salt tolerant cultivars, with or without the aid of other management practices, is considered one of the

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reliable techniques to cope up with salinity problem (Ashraf and Harris, 2013).

Majority of the fruit crops grown commercially show high sensitivity to salinity and associated problems like drought or waterlogging. Like other crops, negative effects of excess salts on fruit trees are manifested as stunted growth, small leaves, foliar injury symptoms and, in extreme cases, plant mortality. Even crops considered to be fairly tolerant of salinity (e.g., olive and dates) exhibit marked declines in tree growth and fruit yield after prolonged exposure to salinity. In saline soils, fruit tree growth is hampered by osmotic, ionic and oxidative stresses. Fruit plants respond to these stresses by restricting the salt uptake, modulating the endogenous hormonal balance, accumulating organic and inorganic osmolytes, maintaining photosynthesis and up-regulating enzymatic and non-enzymatic antioxidant defense systems (Singh and Sharma, 2018; Li et al., 2013). Many studies suggest that almond is relatively sensitive to salinity (Ranjbarfordoei et al., 2006; Dejampour et al., 2012; Momenpour et al., 2018).

Physiological, biochemical, and molecular processes in plants undergo dramatic changes under abiotic stresses like salinity, soil drying, and high temperature. Photosynthesis, a vital and complex physiological process in green plants, is strongly affected by such stresses. The photosynthesis in plants consists of various components and pathways including light-harvesting pigments and photochemical systems, electron transfer chain, gas exchange systems, and CO₂ reduction and fixation pathways. Evidently, any injury to any such component will diminish the overall photosynthetic ability of a green plant (Zhang and Shi, 2013). Abiotic stresses negatively influence photosynthesis in plants by affecting leaf pigments, photosynthetic systems, components of the electron transport processes, and by altering the functions of many key enzymes. While such effects have been investigated in detail in a few plant species, there are many economically important plants where little is known about the effects of stress conditions on key metabolic processes and gas exchange characteristics (Ashraf and Harris, 2013).

There is evidence that the growth of almond trees and rootstocks is adversely affected by salt stress (Dejampour et al., 2012). It is known that surplus ions in saline soils enhance the osmotic capacity of the soil, altering the plant transpiration and photosynthesis processes (Gupta and Huang, 2014). Reports reveal that salt stress affects water potential, homoeostasis and ion diffusion at both cellular and whole plant levels, causing the osmotic stress. Osmotic stress causes stomatal closing, diminishes intercellular CO₂ partial pressure, increases active electrons, leads to the generation of free radicals like hydrogen superoxide, hydroxide and oxygen active species, and impairs the light-harvesting systems and thus resulting in reduced photosynthetic efficiency. Photosynthesis efficiency can be assayed by calculating the enhanced number of electron carriers and, finally, the safety of the photosynthetic electron transfer system using the chlorophyll fluorescence (Mehta et al., 2010). According to Massai et al. (2004), gas exchange of peach plants decreases as salinity increases.

Salinity, in addition to its adverse effects on plant morphological traits, also alters several physiological processes. Ranjbarfordoei et al. (2006) reported that salinity reduced the leaf water content and osmotic potential in the leaves of almond. Variations in Photosynthesis rate (Pₚ), stomatal conductance (gₛ), mesophyll conductance (gₘᵢₙ), transpiration (T), internal Concentration of CO₂ (Cᵢ), and leaf surface Temperature (ΔT) in drought-stressed almond plants have also been reported: certain genotypes outperform others reflecting that genotypic differences need to be considered for selecting the stress tolerant types for potential applications (Rouhi et al., 2007; Karimi et al., 2015). Evidently, the selection of tolerant cultivars/rootstocks could be a major way of diminishing the detrimental consequences of salinity in almond, especially in dry regions. For example, it has been revealed that the ‘GF677’ rootstock has more tolerance to salinity than P. persica×P. davidiana (Munns and Tester, 2008; Dejampour et al., 2012).

Recently, the role that phytohormones can play in enhancing plants’ endurance against environmental stresses is also increasingly being realized. SA is one of the phytohormones known to enhance the tolerance of several plant species against different stresses (Asghari and Zahedipour, 2016). There are different opinions
about this phytohormone. Hayat et al. (2010) reported that SA, like a non-enzymatic antioxidant, is a major growth regulator with a phenolic nature that associates in numerous physiological actions and supports the plants against biotic and abiotic stresses. SA affects plant growth and development as well as performance in a dose-dependent mode; depending on the concentration used plant growth and yield may increase or decrease in response to SA application. For example, in Matricaria chamomilla, it was revealed that 50 and 250 μM of SA promote and inhibit the plant growth, respectively (Kovacik et al., 2009).

There is a little or no reliable information about the influence of SA on grafted almond cultivars under salt stress situations. Therefore, it is necessary to study the influence of this phytohormone on various almond cultivars and screening the tolerant and sensitive cultivars. In this backdrop, this study was carried out to assess the impact of exogenous SA on some photosynthetic parameters of three almond cultivars grafted on GF677 rootstock.

MATERIALS AND METHODS

Plant Materials and Treatments

In order to estimate the tolerance of three almond cultivars to irrigation water salinity in response to SA application, a factorial experiment was conducted according to the Completely Randomized Design (CRD) with 4 sodium chloride solutions (0, 2, 6 and 8 dS m⁻¹) and 3 SA levels (0, 1 and 2 mM) having 3 replications, during 2016 growing season. One-year-old plants of GF-677 obtained from Ita-Sadra Tissue Culture Company (Fars Province, Iran), were planted in pots filled with 25 kg soil of fine loam in early March, 2016. Some physicochemical characteristics of the soil mixture used were: Texture= Loamy, Electrical Conductivity (EC)= 1.28 dS m⁻¹, pH= 7.4 and Organic carbon= 1.43 %. Pots were placed in a greenhouse at Temperate Fruit Research Center, Horticultural Research Institute, Karaj, Iran (Temperature: 25±2°C; Photoperiod: 16/8 hours light/dark; Light intensity: 500-700 μmol m⁻² s⁻¹). After six months when rootstocks were sufficiently developed, cultivars were grafted by shield budding in mid-May 2017 and, after the establishment and sufficient growth of the scions (10 weeks after budding), salinity treatments were started in late July, 2017 and continued for 12 weeks. To avoid sudden shock and plasmolysis, mixed salt with water was gradually added to the growing medium until it reached the final concentration within a week by 2 irrigations. Field Capacity (FC) of soil in pots was measured by weighing method before transferring plants. To determine FC, some pots containing the tested beds were saturated with water so that water drains out from the bottom of the pots. To prevent evaporation, the pot surface was covered with aluminum foil. The weight of pots was evaluated each day until it reached a stable level, then, the soil of each pot was mixed to make a uniform mixture and then some soil was removed to record its wet weight. To determine the soil dry weight, it was placed in the oven for 24 hours at 72°C. Then the field capacity was calculated (Khan et al., 2008) according to the following equation: FC= (WW-DW/DW) ×100 Where, FC is Field Capacity, WW is the soil Wet Weight and DW is the soil Dry Weight.

The pot's water was maintained by weighing the pots and replenishing the water lost by evapotranspiration with a precision scale. Irrigation of pots was done according to changes in their weight and leaching requirement. Before applying the salinity treatments, plants were treated with SA at 0 (control), 1 and 2 mM at two stages at a 1-week interval. In order to prepare the solutions, the needed amount of SA (Sigma, Germany) was dissolved in 5 mM ethanol and then made into a final volume using distilled water. Salts were added to water to obtain solutions with EC of 0, 2, 6, and 8 dS m⁻¹. Initiation of saline treatments was done one week after the last stage of SA treatment. EC of irrigation water was measured for each salinity treatment. To avoid a sudden shock to the plants, different concentrations of salt were applied to irrigation water gradually in two steps. For this purpose, in the first stage, water with salinity of 2 dS m⁻¹ was added to all pots,
except the control pots. At each irrigation, each treatment received its own concentrations. Sixty days after applying the salt treatment, signs of salinity stress appeared in the plants and different parameters were measured.

Measurement of Photosynthesis-Related Parameters

The photosynthesis-related parameters including stomatal conductance ($g_s$), mesophyll conductance ($g_m$), sub-stomata $CO_2$ ($C_i$) content, transpiration rate (T), leaf surface Temperature ($\Delta_T$), quantum efficiency of the photosystem II (Fv/Fm) and Photosynthesis rate ($PN$) were determined in young fully expanded leaves at the top of the branch between 9:00 am to 11:00 am using a portable photosynthesis vector (LCi model 32648, ADC BioScientific Ltd, UK) (Bastam et al., 2013). The conditions for determining photosynthetic parameters were as follows: The amount of Photosynthetic Active Radiation (PAR) was 1,895-1,425 µmol m$^{-2}$ s$^{-1}$, ambient temperature was 32.8±1.2°C, atmospheric pressure was 101.45 KPa, daily average relative humidity was 27% ±1.9%, air $CO_2$ content was 387±1.9 ppm and the leaf area contained within the chamber was 6.25 cm$^2$. Chlorophyll fluorescence in each plant was measured by sampling the 10th leaf developed from the top of the shoots between 9:00 am to 11:00 am. For instance, chlorophyll fluorescence meter (Model Hansatech) was attached to the leaves so that a portion of the leaf was placed under the clip and in the darkness for 30 minutes, then, we used a fluorescence measuring apparatus. The light was applied to the leaf and minimal Fluorescence ($F_{0}$) and maximum Fluorescence ($F_{m}$) values were read. The variable Fluorescence ($F_{v}$), value of the difference between $F_{m}$ and $F_{0}$ and the $F_{v}/F_{m}$ ratio were also calculated (Maxwell and Johnson, 2000).

Measurement of Some Morphological Characteristics

In order to study the effects of salt stress, SA treatment, and also almond cultivars on rootstock growth and development, some morphological characteristics including plant height, rootstock diameter, scion diameter, index shoot length, shoot number and leaves number were also determined sixty days after applying the salt treatment.

Statistical analysis

The data were analyzed using SAS 9.4 software. The comparison of the means was done by Duncan’s multiple range test (P<0.05) with MSTAT-C software and the graphs were drawn using the Minitab software (version 17.3).

RESULTS

Stomatal Conductance ($g_s$)

The $g_s$ rates of different cultivars in normal (unstressed) and salinity stress conditions were different and SA significantly enhanced the $g_s$ rate of the plants under salt stress (Table 1). According to Figure 1-A, in all cultivars, the highest $g_s$ was recorded in unstressed conditions (control) and $g_s$ rate decreased in all cultivars with the increasing salinity. However, this reduction was amended by SA treatment in a dose-dependent manner, such that with a rise in concentration from 1 to 2 mM, the positive influences of SA in retaining $g_s$ rates increased. Under normal conditions, the highest $g_s$ content was obtained by Shokoufeh, Tuono, and Sahand cultivars, respectively. At 2 dS m$^{-1}$ level, the highest and lowest decrement in $g_s$ was found in Sahand (0.228 mol $CO_2$ m$^{-2}$ s$^{-1}$) and Shokoufeh (0.288 mol $CO_2$ m$^{-2}$ s$^{-1}$) cultivars, respectively. Also, under moderate (6 dS m$^{-1}$) and severe (8 dS m$^{-1}$) salt stresses, the highest $g_s$ was obtained in Shokoufeh cultivar, which showed it to be the most tolerant cultivar in our study (Figure 1-B).
Table 1. Analysis of variance of different concentrations of SA and salinity on some photosynthetic parameters of selected almond cultivars.

<table>
<thead>
<tr>
<th>SOV</th>
<th>df</th>
<th>$g_n$</th>
<th>$g_m$</th>
<th>$T$</th>
<th>$C_t$</th>
<th>$\Delta t$</th>
<th>Fv/Fm</th>
<th>P$_N$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cultivar</td>
<td>2</td>
<td>0.04796**</td>
<td>0.000318**</td>
<td>21.49**</td>
<td>3328.4**</td>
<td>45.14**</td>
<td>0.00067**</td>
<td>9.517**</td>
</tr>
<tr>
<td>SA</td>
<td>2</td>
<td>0.00011**</td>
<td>0.000724**</td>
<td>0.99**</td>
<td>2765.8**</td>
<td>35.13**</td>
<td>0.00058**</td>
<td>39.364**</td>
</tr>
<tr>
<td>Salinity</td>
<td>3</td>
<td>0.39426**</td>
<td>0.008593**</td>
<td>165.37**</td>
<td>13453.5**</td>
<td>336.62**</td>
<td>0.05890**</td>
<td>367.910**</td>
</tr>
<tr>
<td>Cultivar x SA</td>
<td>4</td>
<td>0.00367*</td>
<td>0.000596**</td>
<td>0.75*</td>
<td>197.6**</td>
<td>3.46*</td>
<td>0.00018**</td>
<td>25.573**</td>
</tr>
<tr>
<td>Cultivar x Salinity</td>
<td>6</td>
<td>0.01071**</td>
<td>0.000287**</td>
<td>4.15**</td>
<td>557.3**</td>
<td>9.75*</td>
<td>0.00055**</td>
<td>15.399**</td>
</tr>
<tr>
<td>SA x Salinity</td>
<td>6</td>
<td>0.00483**</td>
<td>0.000329**</td>
<td>2.10**</td>
<td>205.9**</td>
<td>2.29*</td>
<td>0.00099**</td>
<td>11.302**</td>
</tr>
<tr>
<td>Cultivar x SA x Salinity</td>
<td>12</td>
<td>0.00156**</td>
<td>0.000315**</td>
<td>0.77**</td>
<td>116.9**</td>
<td>3.49*</td>
<td>0.00028**</td>
<td>11.412**</td>
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<td>Error</td>
<td>72</td>
<td>0.00126</td>
<td>0.000045</td>
<td>0.54</td>
<td>40.7</td>
<td>1.33</td>
<td>0.00008</td>
<td>2.072</td>
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<td>CV%</td>
<td></td>
<td>10.78</td>
<td>11.67</td>
<td>18.45</td>
<td>9.90</td>
<td>3.67</td>
<td>5.78</td>
<td>7.56</td>
</tr>
</tbody>
</table>

* Significant (P ≤ 0.05); ** Significant (P ≤ 0.01); ns Non significant (P > 0.05).
The highest reduction in $g_s$ was obtained in Sahand cultivar in severe salinity stress with $g_s$ of 0.024 mol CO$_2$ m$^{-2}$ s$^{-1}$. Contrarily, Shokoufeh cultivar with 0.099 mol CO$_2$ m$^{-2}$ s$^{-1}$ had the maximum stomatal conductance at this stress level. It has been shown that the decline in $g_s$ in salt-treated plants suggests a major role for stomatal factors in photosynthetic inhibitions (Singh et al., 2016). Under some conditions, cultivars tolerant of saline stress can maintain their $g_s$ in stress situations, thereby increasing their photosynthesis levels.

Almond cultivars showed a differential response to the SA application in normal and stress conditions (Figure 1-C). In salt-free soils, the highest and the lowest $g_s$ were found in Shokoufeh (0.225 mol CO$_2$ m$^{-2}$ s$^{-1}$) and Tuono (0.177 mol CO$_2$ m$^{-2}$ s$^{-1}$), respectively. In Shokoufeh cultivar treated with 1 mM SA, the $g_s$ was (0.245 mol CO$_2$ m$^{-2}$ s$^{-1}$), but it was 0.220 mol CO$_2$ m$^{-2}$ s$^{-1}$ in plants treated with 2 mM SA. A similar pattern was seen in Sahand cultivar indicating that SA may adversely affect the plants at 2 mM SA.

**Mesophyll Conductance ($g_m$)**

There were significant differences in the $g_m$ under different treatments (Table 1). Among the cultivars, the highest $g_m$ amount was found in Shokoufeh treated with SA at 1 mM. As shown in Table 2, the highest $g_m$ was found in the control plants treated with SA. In normal conditions, Sahand cultivar had the lowest $g_m$ (0.0029 mol CO$_2$ m$^{-2}$ s$^{-1}$), while plants of Sahand cultivar treated with 1 mM SA showed the highest $g_m$ (0.0428 mol CO$_2$ m$^{-2}$ s$^{-1}$). At 2 dS m$^{-1}$ salinity, Shokoufeh plants treated with 1 mM SA showed the highest $g_m$ (0.0492 mol CO$_2$ m$^{-2}$ s$^{-1}$). The maximum decline in $g_m$ (0.0029 mol CO$_2$ m$^{-2}$ s$^{-1}$) at 8 dS m$^{-1}$ was recorded in the control plants of Sahand ($P< 0.01$). On the other hand, the highest $g_m$ (0.0443 mol CO$_2$ m$^{-2}$ s$^{-1}$) at this level of salinity was obtained in Shokoufeh plants receiving 1 mM SA. Different cultivars showed different responses to severe salinity stress, such that Shokoufeh, Tuono and Sahand had the highest $g_m$ respectively. Severe salinity stress caused by 8 dS m$^{-1}$ NaCl significantly reduced the $g_m$ rate of all cultivars, but SA was effective in decreasing the adverse effects of salinity on $g_m$ rates in different cultivars.

**Transpiration Rate (T)**

The highest and the lowest T rates were observed in Shokoufeh (3.77 mmol m$^{-2}$ s$^{-1}$) and Sahand (2.123 mmol m$^{-2}$ s$^{-1}$) cultivars, respectively. Additionally, 1 mM SA significantly enhanced the T rates of all cultivars in both unstressed and saline conditions (Figure 2).

**Sub-Stomata CO$_2$ (C$_i$) Content**

Data for the influences of salinity stress and SA on C$_i$ in different cultivars are shown in Tables 1 and 2. Salinity stress induced a rise in C$_i$ content and the reaction of each cultivar was different. SA decreased the C$_i$ in all treated plants. Under salinity level of 8 dS m$^{-1}$, the highest and lowest C$_i$ was obtained in Sahand and Shokoufeh cultivars, respectively. At this level of salinity stress, the lowest C$_i$ (231 μmol mol$^{-1}$) was noted in Shokoufeh cultivar treated with SA at 1 mM.

**Leaf Surface Temperature ($\Delta T$)**

Data reported in Table 2 show that $\Delta T$ for different cultivars did not differ under non-stressed situations while it increased during salinity stress (Table 2). With the increase in salinity level, the $\Delta T$ was increased such that the highest amount was found in plants treated with 8 dS m$^{-1}$ NaCl. Samples from Shokoufeh cultivar showed the lowest $\Delta T$ and 1 mM SA significantly decreased the $\Delta T$ in all cultivars.

**Quantum Efficiency of the Photosystem II ($F_v/F_m$)**

The quantum efficiency of the photosystem II in all cultivars showed an indirect relationship with salinity stress such that with increasing salinity stress (8 dS m$^{-1}$), the $F_v/F_m$ was decreased. SA at 1 mM enhanced the $F_v/F_m$ in all the cultivars under stress and normal conditions.
Table 2. The interaction effects of cultivar, salinity stress, and Salicylic Acid (SA) treatment on some photosynthetic parameters of selected almond cultivars.\textsuperscript{a}

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Salinity stress (dS m\textsuperscript{-1})</th>
<th>S (mM)</th>
<th>g\textsubscript{m} (mol CO\textsubscript{2} m\textsuperscript{-2} s\textsuperscript{-1})</th>
<th>C\textsubscript{i} (µmol mol\textsuperscript{-1})</th>
<th>\Delta T (°C)</th>
<th>F\textsubscript{v}/F\textsubscript{m}</th>
<th>P\textsubscript{N} (µmol m\textsuperscript{-2} s\textsuperscript{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tuono</td>
<td>0</td>
<td>0</td>
<td>0.0379d</td>
<td>215.3h</td>
<td>27.8d</td>
<td>0.762ab</td>
<td>8.18c</td>
</tr>
<tr>
<td>Tuono</td>
<td>2</td>
<td>0</td>
<td>0.0243f</td>
<td>222.6f</td>
<td>28.5d</td>
<td>0.728b</td>
<td>5.41d</td>
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<tr>
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<td>6</td>
<td>0</td>
<td>0.0085e</td>
<td>262.3c</td>
<td>32.1bc</td>
<td>0.693c</td>
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<td>8</td>
<td>0</td>
<td>0.0051h</td>
<td>272.6b</td>
<td>34.5b</td>
<td>0.635d</td>
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<td>Tuono</td>
<td>0</td>
<td>1</td>
<td>0.0534c</td>
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<td>11.21ab</td>
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<td>0.665cd</td>
<td>2.89e</td>
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<td>Shoukofeh</td>
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<td>0.005h</td>
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<td>0.642d</td>
<td>1.51f</td>
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<td>0.0611a</td>
<td>200.3h</td>
<td>25.1e</td>
<td>0.782a</td>
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<td>Shoukofeh</td>
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<td>0.0492b</td>
<td>205.6h</td>
<td>26.3de</td>
<td>0.751ab</td>
<td>10.13b</td>
</tr>
<tr>
<td>Shoukofeh</td>
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<td>222.6fg</td>
<td>27.1d</td>
<td>0.701bc</td>
<td>4.22de</td>
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<tr>
<td>Shoukofeh</td>
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\textsuperscript{a} Similar letters in each column indicate that there is no significant difference based on the Duncan multi-thread test.
During severe salinity stress (8 dS m⁻¹), in all cultivars, a significant decline was obtained in F₅/F₇m compared to the control. The highest reduction in F₅/F₇m (0.632) was found in Sahand cultivar. Shokoufeh plants treated with 1 mM SA had the highest F₅/F₇m at this stress level. In our study, F₅/F₇m declined with increasing severity of salinity along with high or without SA application, such that the amount of F₅/F₇m in the high concentrations of SA (2 mM) or without SA (0 mM) under severe salinity stress decreased as compared with to the low concentration (1 mM) of SA.

**Photosynthesis Rate (P₅)**

According to results in Table 1, the effects of all three factors, as well as the interaction effects of SA×salinity, cultivar×salinity, and SA×cultivar and triple SA×cultivar×salinity stress were significant on P₅ (P< 0.01). The highest P₅ (12.24 μmol m⁻² s⁻¹) was found in the control plants of Shokoufeh cultivar. At 6 dS m⁻¹ salinity stress, the highest and the lowest P₅ were found in Shokoufeh treated with 1 mM SA (4.22 μmol m⁻² s⁻¹) and the control plants of Sahand (1.43 μmol m⁻² s⁻¹), respectively. Under 8 dS m⁻¹ salinity stress, the highest P₅ was obtained in Shokoufeh (3.26 μmol m⁻² s⁻¹) and Tuono cultivars (2.89 μmol m⁻² s⁻¹) treated with 1 mM of SA, which were significantly higher than the control plants (P < 0.01). Sahand was the most sensitive cultivar showing significantly decreased P₅ (2.69 μmol m⁻² s⁻¹) even after treatment with SA. At the salinity level of 8 dS m⁻¹, all cultivars showed a significant decline in P₅ as compared with the control. At this level of

Figure 2. Interaction effects of cultivar and SA (A) and salinity and SA (B) on transpiration rate (T). Similar letters in each column indicate that there is no significant difference based on the Duncan’s multiple range test.
Salicylic Acid Mitigates Effects of Salinity

Salinity, the tolerance of cultivars was higher at 1 mM of SA.

Morphological Characteristics

Generally, all studied morphological characteristics were significantly affected by the simple and the interaction effects of salt stress, SA treatment and almond cultivars (Table 3). As shown in Table 4, the highest plant height (138.83 cm) was obtained in Tuono cultivar under non-salinity conditions and treatment with 1 mM of SA, while Sahand cultivar under 8 dS m$^{-1}$ of salinity stress and treatment with 2 mM of SA showed the lowest plant height (38.33 cm). Tuono cultivar under 2 dS m$^{-1}$ of salinity stress and treated with 2 mM of SA had the highest rootstock diameter (1.66 cm), whereas the lowest rootstock diameter (0.93 cm) was observed in Sahand cultivar under similar conditions. Furthermore, Tuono cultivar treated with 2 mM of SA under non-salinity condition and 2 dS m$^{-1}$ of salinity stress had the highest scion diameter, while the lowest scion diameter (0.58 cm) was found in Sahand cultivar under 2 dS m$^{-1}$ of salinity stress and treatment with 1 mM of SA (Table 4).

The results indicated that Tuono cultivar treated with 1 mM of SA under 8 dS m$^{-1}$ of salinity stress had the highest shoot length (51.33 cm) although it had no significant differences with some other treatments (Table 4). On the other hand, Sahand cultivar under 2 dS m$^{-1}$ of salinity stress treated with 2 mM of SA showed the lowest shoot length (8.16 cm). It was found that the Shoukofeh cultivar, especially under 6 dS m$^{-1}$ of salinity stress treated with 1 mM of SA, had the highest shoot number as compared with other cultivars. The lowest shoot number was observed in Sahand cultivar, especially under 2 dS m$^{-1}$ of salinity stress and treatment with 1 mM of SA. However, this treatment (Sahand cultivar under 2 dS m$^{-1}$ of salinity stress and treatment with 1 mM of SA) showed the highest number of leaves. Moreover, it was revealed that the lowest number of leaves was found in Sahand cultivar under 2 dS m$^{-1}$ of salinity stress and treatment with 2 mM of SA (Table 4).
Table 4. The interaction effects of cultivar, salinity stress and Salicylic Acid (SA) treatment on some morphological characteristics of selected almond cultivars. 

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>SA (mM)</th>
<th>Salinity stress (dS m⁻¹)</th>
<th>Plant height (cm)</th>
<th>Rootstock diameter (cm)</th>
<th>Scion diameter (cm)</th>
<th>Shoot length index (cm)</th>
<th>Shoot number</th>
<th>Leaves number of index shoot</th>
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<td>0</td>
<td>0</td>
<td>60.33±mm</td>
<td>1.24±op</td>
<td>1.00±jk</td>
<td>14.83±q</td>
<td>5.00hijj</td>
<td>23.00mnno</td>
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<td>1.31±klnn</td>
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<td>1.34±ijklm</td>
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<td>2.33±l</td>
<td>42.00±b</td>
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* Similar letters in each column indicate that there is no significant difference based on the Duncan multi-thread test.
DISCUSSION

Salt stress caused stomatal closure; therefore, it reduced partial CO\(_2\) pressure and thus \(C_i\) and \(g_s\) (Ali et al., 2008). Moreover, stomatal closure under stress situations to reduce water loss can result in reduced photosynthesis by limiting CO\(_2\) entrance (Ashraf and Harris, 2004). The antioxidant activity prevents the oxidative burst and prompts the synthesis of protective proteins under stress and normal conditions. Delavari et al. (2010) showed that SA induced increase in ABA might contribute to a preadaptation of plants to stress. Besides the SA amount, the interval and term of the SA application, plant species, age, and treated plant tissue can also affect the SA-influences in plants (Shi et al., 2009; Miura and Tada, 2014).

Many studies mentioned the effects of salinity on \(g_m\) in various plants. Lower amounts of photosynthesis and CO\(_2\) processing are at high sub-stomata CO\(_2\) levels (Volpe et al., 2011). If \(g_m\) is high, CO\(_2\) in mesophyll cells is used in photosynthesis, which is characteristic of plants tolerant to salinity stress. Therefore, in this study, Shokoufeh cultivar treated with 1 mM SA showed a higher \(g_m\) under salinity, indicating that it was able to tolerate salinity stress. This difference can be related to the differences in the anatomy of mesophyll cells in different almond cultivars (Rahimi-Eichi et al., 2014), which was enhanced by the capacity of the GF-677 rootstock to better tolerate salinity stress conditions (Karimi et al., 2015; Gholami and Rahemi, 2009). The subsequent use of SA was beneficial to maintain the \(g_m\) and diminish the harmful influences of salt stress. It has been reported that SA partially enhances mesophyll conductivity in plants, SA as one of the main plant growth regulator acts in controlling stomatal opening, net photosynthesis, and other physiological traits, such as transpiration, glycolysis, absorption and transport of nutrients, membrane permeability, flowering and thermogenesis, and growth rate (Ashraf et al., 2010).

Our results confirm the reports of Tattini et al. (1997) who reported decreased gas exchange properties in two olive varieties differing in stress tolerance. They reported that transpiration and gas exchange reduction in sensitive cultivars were faster than the tolerant ones. Salinity stress increases the soil osmotic potential, causing the decline of plant water absorption and, consequently, transpiration and plant growth. The continuity of saline stress causes destruction of the plant because of the increment of sodium and chlorine ions in leaves (Sivritepe et al., 2010).

The decline in transpiration rate attributed in response to salinity stress has also been mentioned (Wani et al., 2016). Reasons for the reduction in gas-exchange traits under NaCl stress are the faster senescence and variations in enzyme activities caused by dysfunction of proteins and adverse feedback by declined sink potential (Iyengar and Reddy, 1996). Saline conditions adversely affect plant photosynthesis process by stomatal closure and decreasing intracellular CO\(_2\), which results in accumulation of extra energy electron carriers, the creation of free radicals, and alterations in light absorbing compounds (Ranjbarfordoei et al., 2006). Furthermore, SA has been shown to mitigate the harmful influences of different stresses including saline stress on stomatal closing and gas exchange (Khoshbakht and Asghari, 2015). Belkadhi et al. (2014) reported that treating plants with SA induced the generation of antioxidant enzymes that increased sunflower salt tolerance. It has been mentioned that SA amends the detrimental influences of salinity by enhancing growth hormones such as IAA and cytokinins (Shakirova et al., 2003), decreasing the absorption of toxic ions and preserving the cellular membrane integrity (Gupta and Huang, 2014).

SA not only acts as one of the antioxidants located in the chloroplast but also enhances the production and accumulation of different antioxidants resulting in preserving the photosynthetic system under stress conditions by detoxifying the ROS (Sreenivasulu et al., 2000).

SA acts as one of the antioxidant materials located in the chloroplast and preserves the photosynthetic system when a plant is exposed to numerous stresses by detoxifying the ROS (Sreenivasulu et al., 2000).

The structure of mesophilic cells and the CO\(_2\) consumption rate or its conductance to processing centers may differ in different cultivars. Salt stress damages the photosynthetic mechanisms at various concentrations, like pigment content, anatomy and performance of...
transpiration for cooling and
hyll fluorescence increases
nts a CO$_2$
other parameters, can be used to
2
thylakoids, electron transport and enzymes,
stomatal performance, and gas exchange
(Geissler et al., 2009). Higher concentrations of
salt might cause stomatal closure, thereby
reducing the partial CO$_2$ pressure and internal
CO$_2$ level and, consequently, resulting in a
decided photosynthetic yield (Khoshbakht and
Asghari, 2015). In sunflower, salinity treatment
was reported to decrease the $g_s$, without altering
sub-stomatal CO$_2$ levels (Rivelli et al., 2002). It
appears that, during salinity stress, rapid stomatal
closure results in a reduction of CO$_2$ entry that is
related to a decrement in photosynthesis and $g_{m}$,
but in tolerant cultivars, the stress-relief
mechanism, such as delay in closure of the
stomata and partial closure, prevents a CO$_2$
shortage. SA at low amounts is able to delay the
stomatal closure and enhance the CO$_2$ entry rate
(Khoshbakht and Asghari, 2015).

Temperature is a vital environmental factor in
regulating most of the plant physiological
processes, but the influences of temperature on $g_s$
are not completely understood yet (Teskey et al.,
2015). Plant stomata act as a vital key in water
absorption and carbon cycles. Furthermore,
the largest water flowing from soil toward the
atmosphere moves via plants and its precise rate
is controlled by stomata (Schlesinger and
the stable situation of the leaf temperatures by
low and high stomata amounts and revealed that
high stomatal density is necessary to permit for
adequate evapotranspiration for cooling and
prevent harmful leaf temperatures (about 45-
55 °C) in heavy irradiance conditions. The
increment in $\Delta T$ can be attributed to the lower $g_s$
and higher transpiration rates (Karimi et al.,
2015). In most stresses, the $g_s$ is decreased due to
transpiration and considered as a cooling
mechanism in plants. Evapotranspiration as a
main cooling mechanism leads to a decrease in
temperature. The different response of cultivars
to salinity stress linked with the changes in leaf
temperature is related to these traits (Nazar et al.,
increment of leaf temperature caused stomatal
closure and reduced photosynthesis in
Pinus taeda and Populus deltoidsx nigra.

From a physiologist perspective, the $F_{v}/F_{m}$
along with other parameters, can be used to
estimate the tolerable levels of stress by the
plants. Therefore, the $F_{v}/F_{m}$ relation is an index
of salinity stress. In the process may be by
reducing the consumption of electron transport
system products (NADPH and ATP), increase in
the reduction of ferredoxin and free radicals,
resulting in degradation of the thylakoid
membrane and, subsequently, in the transfer
of electrons from the receptive site of photosystem
II and yield maximum of photosystem II reduce
and chlorophyll fluorescence increases
(Chaparzadeh and Hosseinzad-Behboud, 2015).

The $F_{v}/F_{m}$ is linked to the performance of leaf
photosynthesis. The decrease of $F_{v}/F_{m}$ indicates
an index of photo-inhibitory injury induced by
the occurrence of photon flux density when
plants are exposed to numerous abiotic stresses.
Maintenance of $F_{v}/F_{m}$ ratio in SA-treated plants
during salinity stress has been reported on
tomato plants by Szepesi et al. (2005). Similar
reports show that $F_{v}/F_{m}$ depends on the transfer
of photosynthetic intermediaries between cell
components and these reactions are affected by
salinity (Ghaderi et al., 2015), as well as low and
high concentrations of SA (Kovacik et al., 2009).

Several reports have mentioned the effects of
drought and salinity stress on $P_{N}$ in various
plants, including almond (Gholami and Rahemi,
2009), which are in accordance with our results.
Salinity stress negatively affects the
photosynthesis performance by decreasing the
cell integrity, CO$_2$ enhacement, accumulation of
Na and Cl ions, stomatal conductance, ROS
accumulation, modification of cytoplasm
structural and production of assimilates
(Sharma and Dubey, 2005). Reduction of photosynthetic
function during saline stress is often related to
the formation of ROS (Noreen et al., 2010).
Salinity stress inhibits photosynthesis at several
levels, for example, by interfering in pigment
biosynthesis and function, stomatal performance,
gaseous exchange, formation and performance of
thylakoid membrane, electron transport, and
enzyme activities. (Sudhir and Murthy, 2004). It
has been confirmed that under different stress
conditions, SA enhances plant antioxidant
activity, CO$_2$ enrichment, chlorophyll
maintenance and Rubisco activity resulting in the
retention of photosynthesis capacity
(Chaparzadeh and Hosseinzad- Behboud, 2015).
Moreover, it was found that SA at 0.1 and 0.5
mM promoted the photosynthesis rate in Vigna
radiate, whereas decreased the plant growth at 1
mM SA (Nazar et al., 2011).
Shi et al. (2006) reported that the SA treatment improved photosynthesis function via promoting the performance of the photosynthetic system in plants either by the mobilization of nitrate inside the tissues or by chlorophyll production. Additionally, SA has been indicated to enhance photosynthetic capacity in maize through stimulation of Rubisco activity (Moussa and Khodary, 2004). This higher photosynthetic activity induced sap formation, which caused the maintenance of relative water content in leaf and improved growth rate. It was showed SA by enhancing the antioxidant system of the cells (Sreenivasulu et al., 2000). However, the genetic variation between plants causes differences in photosynthesis capacity. Moreover, SA content, plant species, plant growth stage, and plant tissue can also affect the efficiency of SA (Miura and Tada, 2014).

In our study, the simple and the interaction effects of salt stress, SA treatment, and almond cultivars significantly influenced the plant growth, as we evaluated according to morphological characteristics (Tables 3 and 4). These results are in agreement with Momenpour et al. (2018), who reported that various almond genotypes showed different growth response under salinity stress.

Plant growth and development is greatly dependent on environmental factors. For example, the osmotic impacts of salinity can be recognized directly after salt application and are believed to continue for the exposure time, inhibiting cell expansion and cell division (Munns and Tester, 2008). Furthermore, under salinity stress, the loss of water availability, the toxicity of Na⁺, and ion imbalance reduce plant growth (Momenpour et al., 2018). Similar to our results, Delavari et al. (2010) and Ghaderi et al. (2015) indicated that SA treatment at an appropriate concentration significantly mitigated the negative effects of abiotic stress. This effect of SA could be related to its role in enhancing the salinity tolerance by improving the photosynthetic functions of different almond cultivars.

CONCLUSIONS

SA can mitigate the harmful influences of salt stress on the photosynthetic process as well as morphological characteristics of almond trees. However, the efficiency of SA in alleviating the detrimental influences of salinity stress is dependent on the intensity of salt stress. The appropriate concentration of SA application can improve the performance of some almond cultivars under saline conditions.

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کاهش اثرات مضر شوری بر برخی پارامترهای مرتبط با فتوسنتز بادام با استفاده از کاربرد اسید سالیسیلیک

چکیده

اثر شوری آب آبیاری (۰، ۲، ۴ و ۶ دسی‌گرم بر متر مربع) بر برخی پارامترهای فتوسنتزی و وزن‌گیری های مورفولوژیکی ۳ رنگ باران "نو"، "شکوفه" و "سختی" با و بدون تیمار اسید سالیسیلیک (صفر و ۲ میلی‌متر باران) در قبلاً آزمایش‌فکوریل بر باهی اثر کامل تصادفی با ۳ نفره در گل‌خانه‌های مورد مطالعه قرار گرفت. نتایج نشان داد که تیمار اسید سالیسیلیک با غلظت ۱ المیلی‌متر باران لیتر بطور قابل توجهی خواص مورفولوژیکی و فتوسنتزی گیاهان تحت تاثیر شوری را بهبود می‌بخشد. در حالی که غلظت نسبتاً بالاتر (۲ المیلی‌متر باران) باعث بهبود رشد و وزن‌گیری های فتوسنتزی نمی‌شود. از میان رقم‌های مورد آزمایش "شکوفه" روز پایه ۶۷۷ به‌طور کامل نمک بالاتر تأثیر سیار در نشان داد. این مطالعه شواهد قطع کننده ای در رابطه با پاتالیس اسید سالیسیلیک در بهبود رشد بادام تحت تاثیر شوری را فراهم نمود. غلظت مناسب اسید سالیسیلیک هنگام افزودن به شرایط شوری گیاهان را در تنظیم اسمزیری برای کاهش اثرات مضر شوری کمک کرد. الیخنی اسید سالیسیلیک را می‌توان در شرایط مزروعه آزمایش کرد. در نتیجه این که آن را با عوامل یک اثر عمیق برای افزایش کارایی بادام در خاک‌های شور توصیف نمود.