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

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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 CO_2 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 CO_2 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 (P_N), stomatal conductance (g_s), mesophyll conductance (g_m), transpiration (T), internal Concentration of CO_2 (C_i), and leaf surface Temperature (Δ_T) 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

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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 soli 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,

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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 Pparameters

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 (Δ_T), quantum efficiency of the photosystem II (Fv/Fm) and Photosynthesis rate (P_N) 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 an 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).

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Table 1. Analysis of variance of different concentrations of SA and salinity on some photosynthetic parameters of selected almond cultivars.

SOV	df	Mean square					
		g_s	g_m	T	C_i	Δ_T	Fv/Fm	P_N
Cultivar	2	0.04796**	0.000318 **	21.49**	3328.4**	45.14**	0.00067**	9.517*
SA	2	0.00011^{ns}	0.000724**	0.99^{ns}	2765.8**	35.13**	0.00858**	39.364**
Salinity	3	0.39426**	0.008593**	165.37**	13453.5**	336.62**	0.05899**	367.910**
Cultivar×SA	4	0.00367*	0.000596**	0.75^{ns}	197.6**	3.46*	0.00018^{ns}	25.573**
Cultivar×Salinity	6	0.01071**	0.000287**	4.15**	557.3**	9.75**	0.00005**	15.399**
SA× Salinity	6	0.00483**	0.000329**	2.10**	205.9**	2.29 ^{ns}	0.00099**	11.302**
Cultivar×SA× Salinity	12	0.00156 ^{ns}	0.000315**	0.77 ^{ns}	116.9**	3.49**	0.00028**	11.412**
Error	72	0.00126	0.000045	0.54	40.7	1.33	0.00008	2.072
CV%	-	10.78	11.67	18.45	9.90	3.67	5.78	7.56

* Significant (P≤ 0.05); ** Significant (P≤ 0.01), ^{ns} Non significant (P> 0.05).

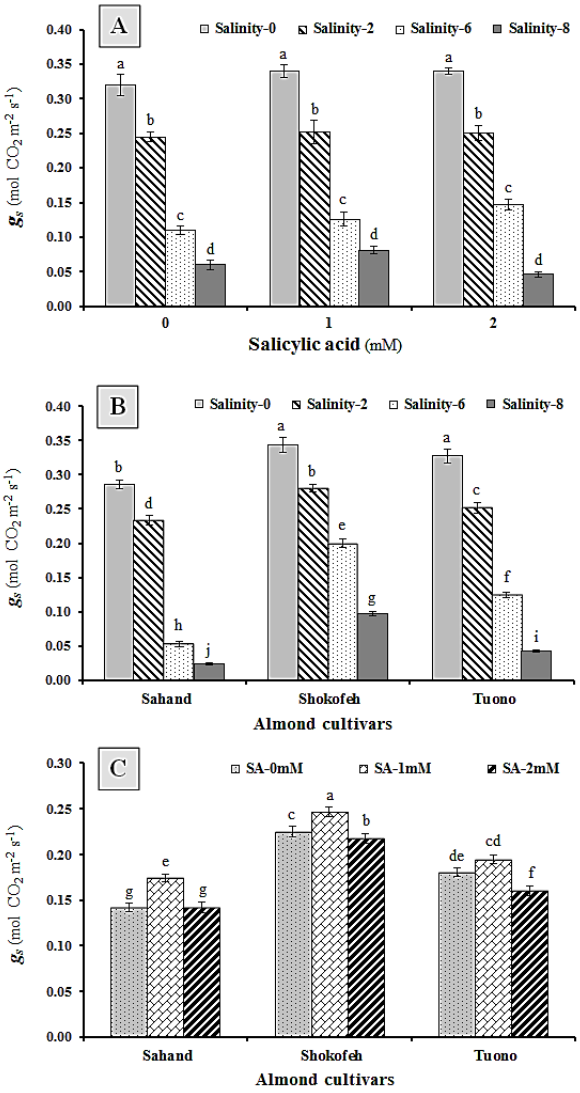

Figure 1. Interaction effects of SA and salinity stress (A), salinity stress and cultivars (B) and cultivar and SA (C) on g_s content in selected almond cultivars. Similar letters in each column indicate that there is no significant difference based on the Duncan's multiple range test.

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 gs 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 (Δ_T)

Data reported in Table 2 show that Δ_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 Δ_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 Δ_T and 1 mM SA significantly decreased the Δ_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.

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Table 2. The interaction effects of cultivar, salinity stress, and Salicylic Acid (SA) treatment on some photosynthetic parameters of selected almond cultivars.[a]

Cultivar	Salinity stress (dS m^{-1})	S (mM)	g_m (mol CO_2 m^{-2} s^{-1})	C_i (µmol mol^{-1})	Δ_T (°C)	F_v/F_m	P_N (µmol m^{-2} s^{-1})
Tuono	0	0	0.0379d*	215.3h	27.8d	0.762ab	8.18c
Tuono	2	0	0.0243f	222.6f	28.5d	0.728b	5.41d
Tuono	6	0	0.0085e	262.3c	32.1bc	0.693c	2.25e
Tuono	8	0	0.0051h	272.6b	34.5b	0.635d	1.43f
Tuono	0	1	0.0534c	209.6h	25.9e	0.777a	11.21ab
Tuono	2	1	0.0443d	217.6fh	26.4de	0.761ab	9.64b
Tuono	6	1	0.0156f	237.3e	28.7d	0.709bc	3.72de
Tuono	8	1	0.0118g	244.6d	31.2c	0.665cd	2.89e
Tuono	0	2	0.0400cd	214.0g	26.3de	0.769a	8.58c
Tuono	2	2	0.0354ef	219.6fg	27.4d	0.757ab	7.78c
Tuono	6	2	0.0100e	250.2d	30.2c	0.698c	2.51e
Tuono	8	2	0.0056h	265.1c	33.2bc	0.660cd	1.49f
Shoukofeh	0	0	0.0455c	208.3g	26.5de	0.767a	9.49b
Shoukofeh	2	0	0.0293ef	220.3fg	27.4d	0.729b	6.46cd
Shoukofeh	6	0	0.0091f	253.3d	31.1c	0.699bc	2.33e
Shoukofeh	8	0	0.005h	265.5c	34.4b	0.642d	1.51f
Shoukofeh	0	1	0.0611a	200.3h	25.1e	0.782a	12.24a
Shoukofeh	2	1	0.0492b	205.6h	26.3de	0.751ab	10.13b
Shoukofeh	6	1	0.0189d	222.6fg	27.1d	0.701bc	4.22de
Shoukofeh	8	1	0.0141e	231.3de	30.5c	0.692bc	3.26de
Shoukofeh	0	2	0.0493b	210.6gh	26.1de	0.770a	10.39b
Shoukofeh	2	2	0.0367e	217.6fh	26.7de	0.731b	7.99c
Shoukofeh	6	2	0.0163f	233.2de	29.3cd	0.697bc	3.81de
Shoukofeh	8	2	0.0095g	238.3d	31.2c	0.670cd	2.27e
Sahand	0	0	0.0251f	216.3h	29.3c	0.758a	5.44d
Sahand	2	0	0.0185g	232.2de	30.3c	0.722b	4.31de
Sahand	6	0	0.0052h	272.1b	35.6b	0.690bc	1.43f
Sahand	8	0	0.0029i	277.6ab	37.7a	0.632d	0.82g
Sahand	0	1	0.0428ef	219.6fg	26.9de	0.768a	9.41b
Sahand	2	1	0.0329f	229.3f	27.7d	0.733b	7.55c
Sahand	6	1	0.0172h	241.6e	29.5cd	0.688bc	4.17de
Sahand	8	1	0.0102h	262.6c	34.9b	0.655d	2.69e
Sahand	0	2	0.0323ef	224.3f	27.8d	0.765a	7.25c
Sahand	2	2	0.0285f	239.3e	28.3cd	0.756ab	6.84cd
Sahand	6	2	0.0092g	273.1b	30.6c	0.696bc	2.53e
Sahand	8	2	0.0033g	280.3a	35.7b	0.650d	0.94g

[a] Similar letters in each column indicate that there is no significant difference based on the Duncan multi-thread test.

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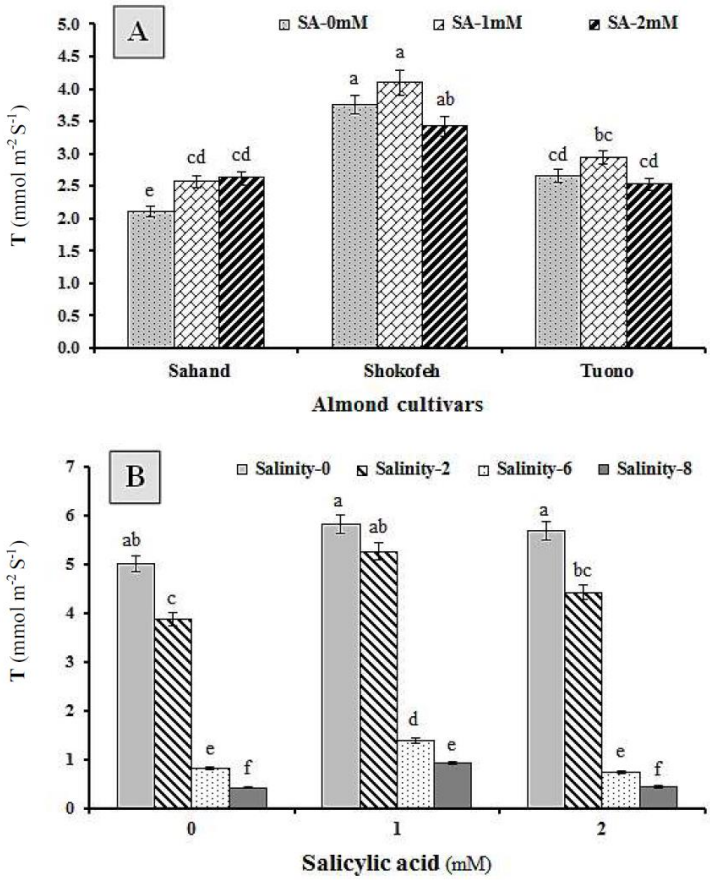

Figure 2. Interaction effects of cultivar and SA (A) and salinity and SA (B) on transpiration rate (T). Similar letters in each column indicate that there is no significant difference based on the Duncan's multiple range test.

During severe salinity stress (8 dS m^{-1}), in all cultivars, a significant decline was obtained in F_v/F_m compared to the control. The highest reduction in F_v/F_m (0.632) was found in Sahand cultivar. Shokoufeh plants treated with 1 mM SA had the highest F_v/F_m at this stress level. In our study, F_v/F_m declined with increasing severity of salinity along with high or without SA application, such that the amount of F_v/F_m 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 (P_N)

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 P_N ($P< 0.01$). The highest P_N (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 P_N 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 P_N 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 P_N (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 P_N as compared with the control. At this level of

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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 3. Analysis of variance of different concentrations of SA and salinity on some morphological characteristics of selected almond cultivars.

SOV	df	Mean Square					
		Plant height	Rootstock diameter	Scion diameter	Shoot length index (cm)	Shoot number	Leaves number of index shoot
Cultivar	2	7868.35**	0.635**	1.0441**	1153.59**	252.23**	598.12**
SA	2	1877.66**	0.036**	0.0235**	840.89**	7.12*	457.40**
Salinity	3	2064.69**	0.090**	0.1082**	657.84**	54.18**	18.77**
Cultivar×SA	4	1182.03**	0.084**	0.0787**	409.23**	8.31*	189.61**
Cultivar×Salinity	6	1115.02**	0.162**	0.0685**	216.06**	1.22^{ns}	100.11**
SA× Salinity	6	439.19**	0.025**	0.0317**	345.60**	4.37^{ns}	389.13**
Cultivar×SA× Salinity	12	404.05**	0.042**	0.0305**	382.22**	12.04**	332.45**
Error	72	7.60	0.001	0.0004	3.34	2.39	4.57
CV%	-	4.10	3.14	1.99	5.86	12.28	7.95

* Significant (P≤ 0.05); ** Significant (P≤ 0.01), ^{ns} Non significant (P> 0.05).

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Table 4. The interaction effects of cultivar, salinity stress and Salicylic Acid (SA) treatment on some morphological characteristics of selected almond cultivars.[a]

Cultivar	SA (mM)	Salinity stress (dS m^{-1})	Plant height (cm)	Rootstock diameter (cm)	Scion diameter (cm)	Shoot length index (cm)	Shoot number	Leaves number of index shoot
Tuono	0	0	60.33lmn	1.24op	1.00jk	14.83q	5.00hijk	23.00mno
Tuono	0	2	51.33qr	1.31klmn	0.97k	13.16q	4.33ijkl	18.00qr
Tuono	0	6	77.16f	1.38ghij	1.11fg	32.33fgh	8.00defg	33.00ef
Tuono	0	8	93.00c	1.43defg	1.20bcde	30.00hij	5.00hijk	21.66nop
Tuono	1	0	138.83a	1.34ijklm	1.17e	13.83q	6.00ghij	25.66jklm
Tuono	1	2	70.83gh	1.47cde	0.99jk	48.33b	6.00ghij	25.00klmn
Tuono	1	6	102.50b	1.38ghij	1.19cde	32.16fgh	8.33cdefg	27.33hijkl
Tuono	1	8	102.83b	1.26nop	1.10fg	51.33a	6.33fghij	33.33ef
Tuono	2	0	77.00f	1.46cdef	1.32a	18.50op	4.00jkl	19.66opq
Tuono	2	2	62.16klm	1.66a	1.32a	37.33e	5.00hijk	27.00ijkl
Tuono	2	6	15.17fg	1.40fghi	1.18de	31.66fghi	7.33efgh	18.33pqr
Tuono	2	8	99.17b	1.48cd	1.22bc	31.16ghi	8.33cdefg	18.00qr
Shoukofeh	0	0	59.16mn	1.45cdef	1.23b	42.50c	9.66abcde	28.00hijk
Shoukofeh	0	2	48.33rs	1.30lmn	1.20bcde	50.83ab	5.33hijk	36.66cd
Shoukofeh	0	6	58.33mno	1.32jklmn	1.13f	49.50ab	11.00ab	37.00c
Shoukofeh	0	8	69.00hi	1.49cd	1.22bc	29.16ij	11.33a	15.00rs
Shoukofeh	1	0	58.83mn	1.23p	1.01j	42.33cd	6.33fghij	30.66fgh
Shoukofeh	1	2	58.00mno	1.40fghi	1.19cde	26.16kl	8.66bcdef	18.00qr
Shoukofeh	1	6	50.00qrs	1.30lmn	1.20bcde	43.16c	12.00a	17.33qrs
Shoukofeh	1	8	65.33ijk	1.28mnop	1.05hi	42.16cd	11.33a	25.66jklm
Shoukofeh	2	0	57.17nop	1.50c	1.20bcde	21.33no	10.00abcd	22.33mno
Shoukofeh	2	2	57.33nop	1.12q	1.08gh	24.66lm	11.00ab	16.00rs
Shoukofeh	2	6	59.50mn	1.35hijkl	1.21bcd	34.16f	11.33a	24.00lmn
Shoukofeh	2	8	83.00e	1.41efgh	1.17e	43.50c	10.66abc	28.66ghij
Sahand	0	0	59.00mn	1.03rs	0.80m	22.16mn	2.33l	32.00efg
Sahand	0	2	40.33t	1.32jklmn	0.88l	15.66pq	5.00hijk	23.00mno
Sahand	0	6	57.17nop	1.57b	1.10fg	39.50ed	5.00hijk	37.00c
Sahand	0	8	64.16jkl	1.05r	0.90l	28.16jk	6.00ghij	34.33cde
Sahand	1	0	67.00hij	1.12q	1.00jk	31.16ghi	5.33hijk	44.33b
Sahand	1	2	54.17opq	0.98st	0.58o	50.00ab	2.00l	60.66a
Sahand	1	6	88.17d	1.44cdefg	1.13f	20.16no	6.66fghi	17.33qrs
Sahand	1	8	47.33rs	0.97st	0.69n	34.00fg	9.66abcde	30.00fghi
Sahand	2	0	53.50pq	0.99rst	0.78m	14.50q	3.00kl	22.33mno
Sahand	2	2	46.17s	0.93t	0.71n	8.16r	4.00jkl	14.00s
Sahand	2	6	70.36h	1.32jklmn	1.02ij	20.16no	6.00ghij	22.00no
Sahand	2	8	38.33t	1.05r	0.70n	34.16f	2.33l	42.00b

[a] Similar letters in each column indicate that there is no significant difference based on the Duncan multi-thread test.

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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 CO2 processing are at high sub-stomata CO2 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

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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 declined 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 Jasechko, 2014). Beerling *et al.* (2001) simulated 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 Δ_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.*, 2011). According to Urban *et al.* (2017) increment of leaf temperature caused stomatal closure and reduced photosynthesis in *Pinustaeda* and *Populus deltoids*×*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 enhancement, 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).

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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

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چکیده

اثر شوری آب آبیاری (۰، ۲، ۶ و ۸ دسی زمنس بر متر) بر برخی پارامترهای فتوسنتزی و ویژگی های مورفولوژیکی ۳ رقم بادام "تونو"، شکوفه" و "سهند "با و بدون تیمار اسید سالیسیلیک (صفر، ۱ و ۲ میلی مولار بر لیتر) در قالب آزمایش فاکتوریل بر پایه طرح کاملا تصادفی با ۳ تکرار در گلخانه مورد مطالعه قرار گرفت. نتایج نشان داد که تیمار اسید سالیسیلیک با غلظت ۱ میلی مولار بر لیتر به طور قابل توجهی خواص مورفولوژیکی و فتوسنتزی گیاهان تحت تنش شوری را بهبود می بخشد، در حالی که غلظت نسبتا بالاتر آن (۲ میلی مولار بر لیتر) باعث بهبود رشد و ویژگی های فتوسنتز نمی شود. از میان رقم های مورد آزمایش،"شکوفه" روی پایه GF677 تحمل به نمک بالاتر از سایرین نشان داد. این مطالعه شواهد قانع کننده ای در رابطه با پتانسیل اسید سالیسیلیک در بهبود رشد بادام تحت تنش شور را فراهم نمود. غلظت مناسب اسید سالیسیلیک هنگام افزودن به شرایط شوری، گیاهان را در تنظیم اسمزی برای کاهش اثرات مضر شوری کمک کرد. اثربخشی اسید سالیسیلیک را می توان در شرایط مزرعه آزمایش کرد تا قبل از این که آن را به عنوان یک ابزار عملی برای افزایش کارایی بادام در خاک های شور توصیف نمود.

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