

Salicylic acid and iron-oxide nanoparticles improved the growth and productivity of ajowan under salt stress

K. Ghassemi-Golezani (*), S. Abdoli

Department of Plant Ecophysiology, Faculty of Agriculture, University of Tabriz, Tabriz, Iran.

Key words: Foliar application, root growth, salinity, seed filling, yield parameters.



(*) Corresponding author:
golezani@gmail.com

Citation:

GHASSEMI-GOLEZANI K., ABDOLI S., 2024 - Salicylic acid and iron-oxide nanoparticles improved the growth and productivity of ajowan under salt stress. - Adv. Hort. Sci., 38(2): 129-139.

Copyright:

© 2024 Ghassemi-Golezani K., Abdoli S. This is an open access, peer reviewed article published by Firenze University Press (<http://www.fupress.net/index.php/ahs/>) and distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement:

All relevant data are within the paper and its Supporting Information files.

Competing Interests:

The authors declare no competing interests.

Received for publication 9 January 2024
Accepted for publication 10 March 2024

Abstract: Two factorial experiments with randomized complete block design in three replicates were conducted in a greenhouse at the University of Tabriz to investigate the individual and combined effects of SA and Fe₂O₃-NPs spray (1 mM and 3 mM, respectively) on cations contents, root and shoot growth, seed filling and yield parameters of salt-stressed ajowan plants (0, 4, 8 and 12 dS m⁻¹ NaCl; as non-saline and low, moderate and high salinities, respectively). Salt stress enhanced Na⁺ contents and reduced K⁺ and Ca²⁺ contents, and K⁺/Na⁺ and Ca²⁺/Na⁺ ratios, leading to a reduction in root and shoot growth, particularly under high salinity. Reduction in plant growth parameters under salt stress had a negative impact on yield components and seed yield of ajowan. These deleterious impacts of salinity on plants were largely overcome by foliar treatments, particularly by SA + Fe₂O₃-NPs. The improvement of seed yield by these treatments was highly correlated with enhanced root and shoot growth, seeds per plant, and 1000-seed weight, especially under moderate and high salinities. Thus, the simultaneous application of SA and Fe₂O₃-NPs was the best foliar treatment for enhancing the growth and productivity of ajowan plants under normal and saline conditions.

1. Introduction

Growth and development of plants are constantly influenced by various environmental stresses including salinity (Sarker and Oba, 2019). Salt stress triggers many cellular events, causing physiological, biochemical and eventually morphological alterations. This stress chiefly causes ionic toxicity by enhancing Na⁺ concentration in plant cells, which ultimately prevents the acquisition of essential nutrients, ionic homeostasis and cell metabolism (Nikpour-Rashidabad *et al.*, 2022). Salinity not only causes cellular water imbalance, osmotic stress and abscission, but also significantly influences different photosynthetic enzymes and gas exchange parameters (Lotfi *et al.*, 2020; Rasheed *et al.*, 2020). Salt toxicity may also lead to oxidative stress due to the physiological imbalance between the generation and scavenging of

reactive oxygen species (ROS) (Ghassemi-Golezani and Abdoli, 2022 a). Elevated ROS may cause the oxidation of proteins and membrane lipids and also impair cellular redox homeostasis. A stress-induced decline in plant growth and productivity is a common phenomenon in many plant species, which is most likely attributed to the changes in plant physiology, and metabolism (Ghassemi-Golezani *et al.*, 2021; Ghassemi-Golezani and Rahimzadeh, 2022) and phenology attributes (Kazan and Lyons, 2016). The major negative impacts of salinity on root growth have been formerly confirmed in *Portulaca oleracea* (Kafi and Rahimi, 2011), *Mentha spicata* (Chrysargyris *et al.*, 2019), *Oryza sativa* (Chang *et al.*, 2019) and *Jatropha curcas* (Abrar *et al.*, 2020), *Brassica napus* (Ghassemi-Golezani and Abdoli, 2022 b) plants. Therefore, salt toxicity is an escalating problem in different agricultural systems worldwide.

The emerging roles of plant hormones and nanoparticles in modulating various abiotic stresses have been extensively evaluated (Ghassemi-Golezani and Abdoli, 2021; Singh *et al.*, 2021 b). Salicylic acid (SA) as a naturally phenolic hormone has effectual roles in numerous metabolic processes and regulates photosynthesis and antioxidant activities, redox and osmotic hemostasis, ionic uptake and secondary metabolite synthesis in plants exposed to salinity (Abdoli and Ghassemi-Golezani, 2021; Hussain *et al.*, 2021). Salicylic acid can reverse the ethylene-induced detrimental impacts via modulating the transcription of *ACS*, *NHX*, *sos1*, *HKT1* and *HKT2* genes, and improving antioxidants capacity, leading to an increase in shoot and root growth, leaves per plant, leaf area and plant productivity (Rao *et al.*, 2021). Simultaneous application of SA and nanoparticles can be more effective in augmenting the ameliorative effects of SA under salt stress (Mozafari *et al.*, 2018; Ghassemi-Golezani and Abdoli, 2021). Nanoparticles (NPs) rapidly penetrate the plant cell due to their small size and high solubility, thereby compensating the nutrient deficiencies. Through phloem vessels and plasmodesmata, foliar applied nanoparticles can be transferred into the cells (Knoblauch and Oparka, 2012). The bond between carrier proteins and nanoparticles facilitates the entry of nanoparticles into the cells through ion channels, aquaporin, and endocytosis (Nair *et al.*, 2010). Since the uptake of most micronutrients is reduced under salinity, supplying nano-forms of these elements not only reduces nutritional imbalance, but also helps the

plants to cope with stress through various physiological and metabolic changes. For instance, silica NPs boost salt tolerance by regulating ion homeostasis, osmotic adjustment and chlorophyll content, which recover plant growth and productivity (Alsaeedi *et al.*, 2019). Iron oxide NPs may have critical roles in different biochemical synthesis, antioxidant activity and genes expression (Moradbeygi *et al.*, 2020). The Fe_2O_3 -NPs induced salt tolerance in *Moldavian balm* plants was due to augmenting DPPH radical scavenging activity, biochemical compounds accumulation and stimulating expression of genes involved in the biosynthesis pathway of important phenolic acids such as rosmarinic acid (Moradbeygi *et al.*, 2020). Recent investigations indicated that foliar spray of Fe_2O_3 -NPs on plants under salt stress notably increased chlorophyll concentration, carbohydrate content (i.e., sugars), and enzymatic defense capacity. Moreover, it decreased lipid peroxidation and ROS generation (Singh *et al.*, 2021 a). According to Dola *et al.* (2022) application of 200 ppm iron-oxide nanoparticles resulted in an improvement of plant growth, relative water content chlorophyll content, 100-seed weight, seed yield, and protein and oil contents of soybean. Adding Fe_2O_3 -NPs to the soil enhanced leaf area, leaf number per plant, shoot length, and shoot and root weights of tomatoes (El-Desouky *et al.*, 2021). Improving plant growth by iron oxide nanoparticles was also observed by several studies on wheat (Rizwan *et al.*, 2019; Manzoor *et al.*, 2021; El-Saber *et al.*, 2021).

Ajowan (*Trachyspermum ammi* L.) is a medicinal plant belonging to the Apiaceae family. It is well known for its essential oil (up to 5%), particularly in seeds (Minija and Thoppil, 2002). Due to numerous pharmacological properties of ajowan essential oil including stimulant, antiseptic, anesthetic, antimicrobial, antiviral, antiulcer, antihypertensive, antitussive, antihyperlipidemic and bronchodilatory, this plant is widely employed (Bhadra, 2020). In our previous reports (Abdoli *et al.*, 2020; Ghassemi-Golezani and Abdoli, 2021) the mechanisms of improving salt tolerance in ajowan plants by salicylic acid and iron oxide nanoparticles were discussed in details. In addition to the reported results, this research aimed at evaluating the growth responses of ajowan to these treatments focusing on root and shoot growth, and yield-related traits under salt stress.

2. Materials and Methods

Experimental conditions and treatments

Two pot experiments with a factorial arrangement based on a randomized complete block design in three replicates were set up in a greenhouse at the University of Tabriz, Iran, to investigate the effects of individual and simultaneous application of SA (1 mM) and Fe₂O₃-NPs (3 mM) on sodium, potassium and calcium contents, root and shoot growth, seed filling and yield parameters of salt-stressed (0, 4, 8 and 12 dS m⁻¹ NaCl; as non-saline and low, moderate and high salinities, respectively) ajowan plants. The salinity (Nikpour-Rashidabad *et al.*, 2022) and foliar spray (Hussain *et al.*, 2019; Ghassemi-Golezani and Farhadi, 2022) levels were selected according to previous reports. The average temperatures of day and night, relative humidity and light intensity in the greenhouse were 29°C, 25°C, 35-40%, and 141 Wm⁻² (about 780 μmol m⁻²s⁻¹), respectively.

This research was performed with 52 pots (48 pots for sowing and 4 unsown pots for checking the water status). Ajowan seeds (30 seeds per pot) were sown in each pot in 1 cm depth of a mixture of perlite and cocopeat to keep long-term moisture in the substrate. The tested salt solutions were added to the substrate of the pots up to 100% field capacity (FC). The emerged seedlings were reduced to keep 10 plants per pot. The water loss from the pots was compensated by tap water or Hoagland solution (EC=1.3 dS m⁻¹, pH=6.7-7.2) up to 100% FC. To prevent excess increment of EC in the substrate due to Hoagland addition, the perlite + cocopeat within all pots were washed slowly every 30 days by pouring water into the pots and draining from the lower holes of the pots. The EC of draining water was measured frequently and when the pouring and draining waters showed similar ECs, washing was stopped and then re-treated with salt solutions. The SA, Fe₂O₃-NPs and tap water were sprayed on plants at two different stages (7 leaves and flowering), by a two-liter manual sprayer.

Estimation of Na⁺, K⁺ and Ca²⁺ contents

The sodium, potassium and calcium contents in plant tissues were determined by a flame photometer (Corning flame photometer, 410). The samples of ajowan plants were reduced to dry ashes in an electric furnace at 500°C for 7 h, and the carbon-free residue was then dissolved in 1 N HCl. The Na⁺, K⁺ and Ca²⁺ contents were determined as

milligrams per gram dry weight.

Measurement of root and shoot parameters

Two plants from each pot were removed at maturity. The roots were cut from the crown and thoroughly washed and air-dried. Then, the root and shoot lengths, root diameter, branches per plant and leaves per plant were recorded. Subsequently, the samples of roots and shoots were separately dried at 75°C for 48 h and weighed.

Seed filling

During seed filling in 2018, two plants from each pot were harvested at 10 days intervals, beginning 20 days after flowering and then seeds were removed from the plants and weighed at five stages.

Yield parameters

The seeds of two plants from each pot were separated and then the number of umbels per plant, seeds per umbel, seeds per plant, 1000-seed weight and seed yield were determined. The harvest index was calculated as:

$$\text{Harvest index} = (\text{Seed yield/shoot} + \text{seed mass}) \times 100$$

Statistical analysis

All collected data in this study were subjected to a two-way analysis of variance (ANOVA) using MSTAT-C, and means were compared by Duncan's multiple range test at $p \leq 0.05$. The mean data were presented as means \pm standard error. Pearson correlation coefficient was used to analyze the relations between morphological and yield-related traits of ajowan plants, using SPSS 16.

3. Results

The Na⁺, K⁺ and Ca²⁺ contents

The Na⁺, K⁺ and Ca²⁺ contents and K⁺/Na⁺ and Ca²⁺/Na⁺ ratios were significantly affected by salt stress and foliar treatments ($p \leq 0.01$). The K⁺ and Ca²⁺ contents and K⁺/Na⁺ and Ca²⁺/Na⁺ ratios were decreased, while the Na⁺ content was increased by the increment of salt toxicity. The 4 dS m⁻¹ NaCl had no significant impact on Ca²⁺ content. Foliar treatments, particularly SA + Fe₂O₃-NPs, reduced Na⁺ content and enhanced K⁺ and Ca²⁺ contents and K⁺/Na⁺ and Ca²⁺/Na⁺ ratios. Differences between SA and SA + Fe₂O₃-NPs treatments in Na⁺ and Ca²⁺

contents and Ca^{2+}/Na^{+} ratio were not statistically significant. All of these parameters (except K^{+}/Na^{+} ratio) were similarly affected by SA and Fe_2O_3 -NPs treatments (Table 1).

Root growth

Significant interaction of salt stress and foliar treatments were observed for root growth parameters ($p \leq 0.01$). The length, weight and diameter of ajowan roots were decreased as salinity increased. No differences among foliar treatments in root parameters were recorded under low salinity. Nonetheless, foliar sprays significantly promoted root growth of plants at different saline conditions, especially under moderate and high salinities. The SA and SA + Fe_2O_3 -NPs treatments were the superior treatments in improving root growth (Table 2). In most cases, the differences between hormonal and nutritional treatments were not statistically significant (Table 2).

Shoot parameters

A significant interaction of salinity and foliar applications was observed for shoot mass and length, branches and leaves per plant (Table 3). Increasing salinity significantly decreased shoot parameters. The shoot length of treated and untreated plants was not significantly varied under non-saline conditions. However, foliar treatments significantly increased shoot length under all salinity levels. The shoot mass, and branches and leaves per plant were enhanced by

different foliar treatments, especially by SA + Fe_2O_3 -NPs, under saline and non-saline conditions. The differences among SA, Fe_2O_3 -NPs and SA + Fe_2O_3 -NPs treatments in shoot mass under 4 dS m^{-1} NaCl, in shoot length under 4 and 8 dS m^{-1} NaCl and in branches per plant under 8 dS m^{-1} NaCl were not significant (Table 3).

Seed filling

The dry weight of ajowan seeds was gradually enhanced with seed development up to about 50 days after flowering and afterwards no significant changes occurred. Seed dry weight was not significantly affected by low salinity (4 dS m^{-1} NaCl), but further increment of salt stress, particularly high salinity, caused a significant decrease in the dry weight of ajowan seeds at later stages of seed development under all foliar treatments. Application of SA, Fe_2O_3 -NPs individually and in combination form increased seed weight under moderate and high salinities. This improvement was mainly due to increasing seed filling rate rather than seed filling duration (Fig. 1).

Yield components

The interaction of salinity and foliar treatments was significant for umbels per plant, seeds per plant, 1000-seed weight, seed yield and harvest index (Table 4). Seeds per umbel were only affected by salt stress. Low salinity had no significant effect on seeds per umbel. However, further increment in salinity

Table 1 - The Na^{+} , K^{+} and Ca^{2+} contents (mg g^{-1} dry weight) of ajowan plants affected by foliar treatments under saline and non-saline conditions

Treatments	Na^{+}	K^{+}	Ca^{2+}	K^{+}/Na^{+}	Ca^{2+}/Na^{+}
<i>Salinity conditions</i>					
Non-Saline	9.29 ± 0.45 d	45.17 ± 1.8 a	13.94 ± 0.24 a	5.05 ± 0.38 a	1.53 ± 0.06 a
4 dS m^{-1} NaCl	15.14 ± 1.17 c	40.86 ± 1.8 b	13.19 ± 0.43 a	2.86 ± 0.23 b	0.92 ± 0.08 b
8 dS m^{-1} NaCl	27.57 ± 0.99 b	30.72 ± 1.3 c	10.63 ± 0.55 b	1.15 ± 0.08 c	0.40 ± 0.03 c
12 dS m^{-1} NaCl	32.35 ± 1.51 a	28.01 ± 1.2 d	7.82 ± 0.72 c	0.90 ± 0.07 d	0.25 ± 0.03 d
<i>F test</i>	479.64 **	220.88 **	60.57 **	679.22 **	369.80 **
<i>Foliar treatment</i>					
Water	26.39 ± 3.52 a	28.36 ± 1.74 c	9.91 ± 1.19 c	1.53 ± 0.33 d	0.57 ± 0.14 c
SA	19.53 ± 2.72 b	37.97 ± 2.49 b	11.86 ± 0.64 ab	2.82 ± 0.61 b	0.86 ± 0.17 ab
Fe_2O_3 -NPs	19.30 ± 2.47 b	37.16 ± 2.22 b	11.23 ± 0.81 b	2.56 ± 0.46 c	0.78 ± 0.15 b
SA+ Fe_2O_3 -NPs	19.14 ± 2.60 b	41.28 ± 2.29 a	12.58 ± 0.58 a	3.04 ± 0.63 a	0.89 ± 0.16 a
<i>F test</i>	52.44 **	101.29 **	10.15 **	82.99 **	22.85 **

Different letters in each column indicate significant differences at $p \leq 0.05$; ** = significant at $p \leq 0.01$.

Fe_2O_3 -NPs= Iron-oxide nanoparticles; SA= Salicylic acid.

Table 2 - Combined analysis of variance of the data for root growth parameters of ajowan affected by foliar treatments under saline and non-saline conditions in 2018 and 2019

Salinity	Foliar treatments	Root mass (g)	Root length (cm)	Root diameter (mm)
Non-Saline	Water	1.88 ± 0.02 abc	32.98 ± 0.05 abc	2.63 ± 0.17 a
	SA	1.97 ± 0.04 a	34.28 ± 0.6 ab	2.51 ± 0.11 a
	Fe ₂ O ₃ -NPs	1.94 ± 0.05 ab	34.48 ± 0.5 a	2.37 ± 0.11 ab
	SA+ Fe ₂ O ₃ -NPs	1.99 ± 0.05 a	34.23 ± 0.4 ab	2.57 ± 0.12a
4 dS m ⁻¹ NaCl	Water	1.74 ± 0.05 ef	28.95 ± 0.6 d	2.41 ± 0.08 ab
	SA	1.85 ± 0.03 bcd	32.95 ± 0.5 abc	2.43 ± 0.08 ab
	Fe ₂ O ₃ -NPs	1.83 ± 0.04 cde	31.83 ± 0.8 c	2.38 ± 0.7 ab
	SA+ Fe ₂ O ₃ -NPs	1.90 ± 0.04 abc	32.20 ± 0.8 bc	2.48 ± 0.08 a
8 dS m ⁻¹ NaCl	Water	1.23 ± 0.05 h	17.12 ± 0.7 hi	1.88 ± 0.06 def
	SA	1.76 ± 0.02 de	24.02 ± 0.8 ef	2.13 ± 0.06 bcd
	Fe ₂ O ₃ -NPs	1.64 ± 0.03 f	22.47 ± 0.8 f	2.31 ± 0.05 abc
	SA+ Fe ₂ O ₃ -NPs	1.80 ± 0.03 cde	25.75 ± 1.0 e	2.32 ± 0.10 abc
12 dS m ⁻¹ NaCl	Water	0.83 ± 0.06 i	14.37 ± 0.6 j	1.62 ± 0.06 f
	SA	1.50 ± 0.04 g	19.03 ± 0.4 gh	2.05 ± 0.07 cd
	Fe ₂ O ₃ -NPs	1.21 ± 0.06 h	16.48 ± 0.5 i	1.72 ± 0.09 ef
	SA+ Fe ₂ O ₃ -NPs	1.48 ± 0.02 g	19.90 ± 0.6 g	2.00 ± 0.06 de
Source of variation				
Year (Y)		NS	NS	NS
Salinity (S)		**	**	**
Foliar treatments (F)		**	**	*
Y x S		*	*	NS
Y x F		NS	NS	NS
S x F		**	**	*
Y x SxF		NS	NS	NS
F test		17.14**	4.39**	2.36*

Different letters in each column indicate significant differences at $p \leq 0.05$; NS, *, **= No significant and significant at $p \leq 0.05$ and $p \leq 0.01$, respectively. Fe₂O₃-NPs= Iron-oxide nanoparticles; SA= Salicylic acid.

considerably reduced this parameter. The plants grown under high salinity had the lowest seeds per umbel compared to unstressed plants (Fig. 2).

Rising salinity significantly reduced the other yield parameters and harvest index. Foliar treatments had no significant effects on 1000-seed weight under non-saline conditions and on umbels per plant, seeds per plant and harvest index under non-saline and low salinity. However, hormonal and nutritional treatments enhanced these parameters under saline conditions. This improvement was more evident under moderate and high salinities. In these levels of salinities, the SA and SA + Fe₂O₃-NPs were the best treatments for improving yield parameters, followed by Fe₂O₃-NPs (Table 4).

Correlations

All morphological and yield parameters of ajowan had as significant positive correlation with each other

(Table 5). Root and shoot masses and lengths were highly related to each other and with leaves per plant ($r \geq 0.85^{**}$). The root and shoot parameters as well as yield components and harvest index were positively and significantly correlated with seed yield per plant. However, the highest relations with seed yield were recorded for shoot mass and seeds per plant, followed by shoot and root lengths, leaves per plant and 1000-seed weight (Table 5).

4. Discussion and Conclusions

The Na⁺ toxicity negatively influenced different aspects of plant growth such as root and shoot parameters, resulting in less seed production. The salt-treated ajowan plants responded to foliar applications, particularly to SA and SA + Fe₂O₃-NPs treatments, as demonstrated by higher K⁺ and Ca²⁺

Table 3 - Combined analysis of variance of the data for shoot mass, shoot length, brunches and leaves of ajowan plants affected by foliar treatments under saline and non-saline conditions in 2018 and 2019

Salinity	Foliar treatments	Shoot mass (g)	Shoot length (cm)	Branches per plant	Leaves per plant
Non-Saline	Water	15.48 ± 0.18 b	99.87 ± 0.72 abc	11.85 ± 0.74 d	58.47 ± 1.10 ab
	SA	16.08 ± 0.20 a	101.1 ± 0.78 ab	13.82 ± 0.29 ab	57.33 ± 0.88 b
	Fe ₂ O ₃ -NPs	15.97 ± 0.22 a	99.93 ± 0.70 abc	12.33 ± 0.48 cd	59.10 ± 0.53 ab
	SA+Fe ₂ O ₃ -NPs	16.17 ± 0.22 a	101.7 ± 0.96 a	14.62 ± 0.44 a	60.78 ± 0.91 a
4 dS m ⁻¹ NaCl	Water	14.22 ± 0.15 d	95.22 ± 0.70 e	10.50 ± 0.36 e	45.00 ± 0.86 de
	SA	14.73 ± 0.22 c	96.93 ± 0.99 de	13.40 ± 0.43 bc	51.33 ± 0.95 c
	Fe ₂ O ₃ -NPs	14.70 ± 0.20 c	99.03 ± 0.64 bcd	12.40 ± 0.34 cd	47.10 ± 0.80 d
	SA+Fe ₂ O ₃ -NPs	14.90 ± 0.21 c	97.78 ± 0.61 cd	14.17 ± 0.37 ab	50.77 ± 0.68 c
8 dS m ⁻¹ NaCl	Water	8.63 ± 0.27 g	68.67 ± 0.71 gh	8.85 ± 0.31 fg	31.67 ± 0.80 i
	SA	12.42 ± 0.27 e	79.22 ± 0.67 f	11.72 ± 0.37 d	41.57 ± 0.69 fg
	Fe ₂ O ₃ -NPs	11.35 ± 0.34 f	78.82 ± 0.66 f	11.75 ± 0.45 d	39.47 ± 0.46 g
	SA+Fe ₂ O ₃ -NPs	12.49 ± 0.25 e	80.87 ± 0.68 f	11.67 ± 0.37 d	42.67 ± 0.56 ef
12 dS m ⁻¹ NaCl	Water	4.52 ± 0.27 j	61.23 ± 0.61 i	8.17 ± 0.42 g	24.00 ± 0.89 j
	SA	7.54 ± 0.12 h	69.03 ± 0.79 g	9.05 ± 0.28 fg	35.33 ± 0.84 h
	Fe ₂ O ₃ -NPs	6.25 ± 0.23 i	66.27 ± 0.60 h	8.48 ± 0.38 g	30.70 ± 0.63 i
	SA+Fe ₂ O ₃ -NPs	7.73 ± 0.09 h	68.80 ± 0.98 g	9.72 ± 0.33 ef	34.67 ± 0.92 h
<i>Source of variation</i>					
Year (Y)		NS	NS	*	ns
Salinity (S)		**	**	**	**
Foliar treatments (F)		**	**	**	**
Y × S		NS	NS	*	NS
Y × F		NS	NS	NS	NS
S × F		**	**	**	**
Y × S × F		NS	NS	NS	NS
<i>F test</i>		21.99**	11.64**	3.05**	7.81**

Different letters in each column indicate significant differences at p≤0.05; NS, *, **= No significant and significant at p≤0.05 and p≤0.01, respectively. Fe₂O₃-NPs= Iron-oxide nanoparticles; SA= Salicylic acid.

contents in plant tissues, root and shoot growth and yield-related traits. A high concentration of Na⁺ ions in the substrate led to an increase in Na⁺ uptake and accumulation in plant tissues and a decline in K⁺ and Ca²⁺ uptake, and K⁺/Na⁺ and Ca²⁺/Na⁺ ratios (Table 1). This imbalance in the nutrient status of tissues might be due to an injury in the cell membrane and specific ion channels (Jayakannan *et al.*, 2013). However, the reduction of Na⁺ accumulation by foliar spray, particularly by SA + Fe₂O₃-NPs, enhanced the uptake of essential nutrients. This improvement could be related to the activation of H⁺-ATPase and H⁺-PPase pumps by SA and Fe₂O₃-NPs treatments that induces

Na⁺ secretion in vacuoles (Ghassemi-Golezani and Abdoli, 2021) and helps plants cope with salt toxicity. Our results suggest that the enhancement of root growth by these treatments (Table 2) is effective in improving nutrient availability to the plants. The manganese-iron nanoparticles have been reported to increase the efflux of H⁺ and influx of K⁺, leading to high K⁺/Na⁺ ratio (Wang *et al.*, 2022).

The roots play an imperative part in plant establishment in the soil and water and nutrient absorptions. A comprehensive understanding of root response to the foliar spray of SA and Fe₂O₃-NPs can more likely provide useful information for improving

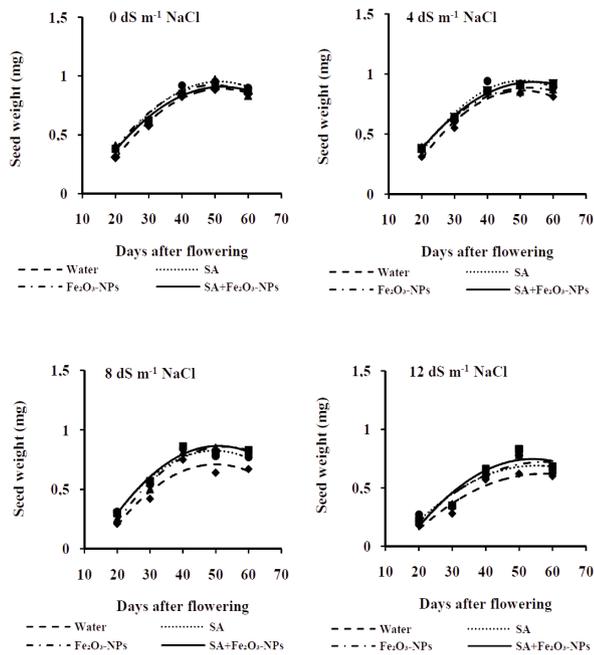


Fig. 1 - Changes in mean seed weight during seed development in response to salinity and foliar treatments. Fe₂O₃-NPs= Iron oxide nanoparticles, SA= Salicylic acid.

crop productivity in saline soils. The length, mass and diameter of roots in salt-stressed plants, especially under moderate and high salinities, were limited due to nutritional (Table 1) and hormonal imbalances (Zhang *et al.*, 2018), that limit cell elongation and division (Yang *et al.*, 2019). The GiA Roots analysis also revealed a decrease in the penetration and distribution of plant roots under different levels of salinities, particularly under high saline conditions (Ghassemi-Golezani and Abdoli, 2022 b). These negative impacts of salinity on root growth were relieved by foliar treatments of SA and Fe₂O₃-NPs (Table 2). The cross-talk of SA with auxins, cytokinins and gibberellins (Shakirova *et al.*, 2003; Agami and Mohamed, 2013; Miura *et al.*, 2013) can potentially promote cell elongation and division. In addition, the expression of auxin biosynthesis genes might be regulated by Fe status of cells (Sun *et al.*, 2017). Iron-NPs may enhance root growth by inducing OH radical generation and demolition of cell wall polysaccharides (Kim *et al.*, 2014). Stimulation of SA synthesis in plants by Fe₂O₃-NPs related treatments (Abdoli *et al.*, 2020) is also effective in improving plant growth.

Reduction in shoot mass and length, and branches and leaves per plant due to salinity (Table 3) is

related to Na⁺ toxicity and competition of plants for nutrients (Table 1) and water (Abdoli *et al.*, 2020). This is a mechanism for minimizing energy losses and maintaining plant survival chance under stress conditions. It has been confirmed that salt stress leads to growth reduction, which is more pronounced in leaf area (Acosta-Motos *et al.*, 2015), branches and leaves per plant and shoot length and mass (Table 3). Foliar treatments promoted shoot growth by enhancing root growth (Table 2), and improving K⁺ and Ca²⁺ contents in plant tissues by limiting Na⁺ absorption by the plants (Table 1). The effectiveness of salicylic acid in promoting cell division and enlargement is also supported by a previous report on wheat plants (Agami and Mohamed, 2013). Inhibition of ethylene synthesis by SA (Khan *et al.*, 2014) can enhance the plant growth duration. A decline in abscisic acid content due to iron nanoparticles may also promote growth and retard the senescence of plants (Rui *et al.*, 2016). Moreover, iron nanoparticles are involved in protein synthesis and enzymes activation, which can promote the plant growth and reduce the senescence especially under stressful conditions (Sheykhbaglou *et al.*, 2018). Wang *et al.* (2022) suggested that cytokinin level, SCFTIR1/AFB-AUX/IAA signaling pathway, ATP synthesis, cell elongation and plant biomass could be enhanced by iron nanoparticles.

Decreasing root- and shoot-related traits (Tables 2 and 3) due to salt stress reduced yield parameters including seed filling rate (Fig. 1), seeds per plant, 1000-seed weight and seed yield (Table 4; Fig. 2). These reductions are most likely attributed to the enhanced vegetative and reduced reproductive periods under salinity (Ghassemi-Golezani and Farhangi-Abri, 2021). Retarding flowering due to salinity reduced umbels and seeds per plant, 1000-seed weight, and consequently seed yield (Table 4). The reduction in photosynthetic efficiency (Ghassemi-Golezani *et al.*, 2021) and allocation of assimilates to the seeds (Kafi *et al.*, 2013) might be the main reasons for yield losses under moderate and high salinities. The SA + Fe₂O₃-NPs treatment alleviated these detrimental impacts of salinity on plant productivity through the improvement of nutrient availability (Table 1), root (Table 2) and shoot (Table 3) growth, photosynthetic potential (Ghassemi-Golezani and Farhadi, 2022) and stimulation of flower-inducing factor (Hayat *et al.*, 2007). In a study on salt-stressed pennyroyal plants, the SA application enhanced Rubisco activity, a

Table 4 - Combined analysis of variance of the data for yield parameters of ajowan affected by salinity and foliar treatments in 2018 and 2019

Salinity	Foliar treatments	Umbels per plant	Seeds per plant	1000-seed weight (mg)	Seed yield (g plant ⁻¹)	Harvest index (%)
Non-Saline	Water	50.67 ± 0.42 a	6367.9 ± 56.7 a	865.7 ± 3.7 ab	5.51 ± 0.07 b	35.63 ± 0.06 a
	SA	51.00 ± 1.24 a	6498.5 ± 110.0 a	888.3 ± 6.0 a	5.77 ± 0.07 a	35.88 ± 0.19 a
	Fe ₂ O ₃ -NPs	52.00 ± 0.36 a	6577.6 ± 30.5 a	870.0 ± 6.8 ab	5.72 ± 0.07 a	35.84 ± 0.16 a
	SA + Fe ₂ O ₃ -NPs	51.18 ± 0.76 a	6527.8 ± 119.1 a	882.2 ± 7.0 a	5.75 ± 0.07 a	35.59 ± 0.14 a
4 dS m ⁻¹ NaCl	Water	45.68 ± 0.92 b	5760.1 ± 47.0 b	829.3 ± 9.2 cd	4.78 ± 0.08 d	33.60 ± 0.28 b
	SA	45.22 ± 0.23 b	5751.6 ± 89.0 b	881.7 ± 4.7 a	5.07 ± 0.07 c	34.43 ± 0.17 b
	Fe ₂ O ₃ -NPs	45.83 ± 0.54 b	5874.3 ± 71.0 b	854.3 ± 8.2 bc	5.02 ± 0.07 c	34.14 ± 0.17 b
	SA + Fe ₂ O ₃ -NPs	46.83 ± 0.31 b	5919.4 ± 85.5 b	866.0 ± 3.6 ab	5.12 ± 0.06 c	34.40 ± 0.24 b
8 dS m ⁻¹ NaCl	Water	33.72 ± 0.77 e	3953.6 ± 144.3 e	669.3 ± 9.6 f	2.64 ± 0.06 g	30.63 ± 0.45 d
	SA	39.35 ± 0.83 c	4789.9 ± 97.4 c	827.5 ± 7.0 d	3.96 ± 0.07 e	31.92 ± 0.31 c
	Fe ₂ O ₃ -NPs	36.65 ± 0.78 d	4437.6 ± 106.2 d	780.3 ± 6.9 e	3.46 ± 0.06 f	30.55 ± 0.53 d
	SA + Fe ₂ O ₃ -NPs	39.78 ± 1.00 c	4852.7 ± 120.6 c	836.2 ± 12.8 cd	4.05 ± 0.08 e	32.45 ± 0.30 c
12 dS m ⁻¹ NaCl	Water	19.57 ± 0.72 g	1946.3 ± 108.7 h	605.0 ± 2.2 h	1.18 ± 0.07 j	26.10 ± 0.51 f
	SA	31.75 ± 0.37 e	3326.2 ± 117.0 f	687.7 ± 12.8 f	2.27 ± 0.03 h	30.19 ± 0.18 d
	Fe ₂ O ₃ -NPs	27.18 ± 1.04 f	2820.9 ± 87.3 g	630.0 ± 2.6 g	1.78 ± 0.05 i	28.47 ± 0.30 e
	SA + Fe ₂ O ₃ -NPs	33.32 ± 0.44 e	3471.7 ± 102.6 f	686.7 ± 8.8 f	2.38 ± 0.05 h	30.79 ± 0.42 d
<i>Source of variation</i>						
Year (Y)		NS	NS	NS	NS	NS
Salinity (S)		**	**	**	**	**
Foliar treatments (F)		**	**	**	**	**
Y × S		NS	NS	NS	**	NS
Y × F		NS	NS	NS	NS	NS
S × F		**	**	**	**	**
Y × S × F		NS	NS	NS	NS	NS
<i>F test</i>		13.19**	12.73**	12.92**	32.35**	9.78**

Different letters in each column indicate significant differences at p≤0.05;

NS, **= No significant and significant at p≤0.01, respectively.

Fe₂O₃-NPs= Iron-oxide nanoparticles; SA= Salicylic acid.

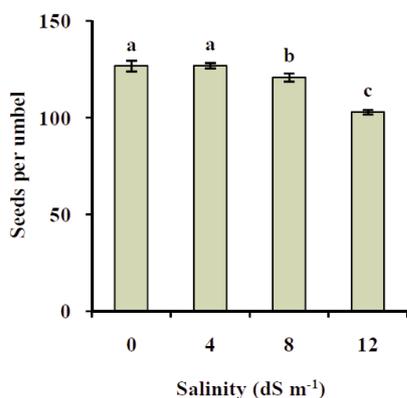


Fig. 2 - Changes in seeds per umbel of ajowan in response to salinity. The data represents the average of three replicates in two years ± standard errors. Different letters indicate significant differences at p≤0.05.

critical enzyme in photosynthetic machinery. The enhanced seed-filling rate (Fig. 1) by simultaneous application of SA and Fe₂O₃-NPs under moderate and high salinities resulted in the production of larger seeds (Table 4). The high correlation of root and shoot parameters, seeds per plant and 1000-seed weight with seed yield (Table 5) suggests that improving these traits by breeding or foliar treatments can potentially increase crop productivity under normal and stressful conditions. Our results indicated that foliar spray of SA and SA + Fe₂O₃-NPs often similarly improves salt tolerance and seed yield of ajowan, so application of SA and/or SA + Fe₂O₃-NPs treatments can be cost-effective in reducing salinity-induced losses in large-scale production systems.

Salinity remarkably limited the root and shoot

Table 5 - Correlations of morphological and yield parameters of ajowan with each other

Parameters	Root mass	Root length	Shoot mass	Shoot length	Branches per plant	Leaves per plant	Seeds per plant	1000 seed weight	Seed yield	Harvest index
Root mass	1									
Root length	0.86 **	1								
Shoot mass	0.91 **	0.94 **	1							
Shoot length	0.85 **	0.96 **	0.96 **	1						
Branches per plant	0.77 **	0.80 **	0.82 **	0.81 **	1					
Leaves per plant	0.87 **	0.94 **	0.93 **	0.93 **	0.79 **	1				
Seeds per plant	0.90 **	0.94 **	0.99 **	0.95 **	0.79 **	0.94 **	1			
1000-seed weight	0.90 *	0.91 **	0.95 **	0.92 **	0.83 **	0.89 **	0.92 **	1		
Seed yield	0.90 *	0.96 **	0.99 **	0.97 **	0.82 **	0.95 **	0.99 **	0.95 **	1	
Harvest index	0.86 **	0.92 **	0.92 **	0.92 **	0.75 **	0.94 **	0.94 **	0.91 **	0.94 **	1

** Significant at $p \leq 0.01$.

growth of ajowan, leading to lower seed yield. Negative impacts of salt stress on plant growth and productivity could be considerably alleviated by exogenous salicylic acid and Fe_2O_3 nanoparticles, particularly in combined form. These beneficial effects were more pronounced under severe salinity. The ameliorative effects of SA and SA+ Fe_2O_3 -NPs on seed yield of salt-subjected ajowan plants were mostly related to enhancing root and shoot growth, seeds per plant, seed filling rate, and 1000-seed weight. Future works may reveal other beneficial effects of different hormones and/or nanoparticles on crops under various environmental conditions.

Acknowledgements

We appreciate the financial support of this research by the University of Tabriz and the Iran National Science Foundation.

References

- ABDOLI S., GHASSEMI-GOLEZANI K., 2021 - *Salicylic acid: an effective growth regulator for mitigating salt toxicity in plants*. - J. Plant Physiol. Breeding, 11: 1-15.
- ABDOLI S., GHASSEMI-GOLEZANI K., ALIZADEH-SALTEH S., 2020 - *Responses of ajowan (Trachyspermum ammi L.) to exogenous salicylic acid and iron oxide nanoparticles under salt stress*. - Environ. Sci. Pollut. Res. Int., 27(29): 36939-36953.
- ABRAR M.M., SAQIB M., ABBAS G., ATIQU-UR-RAHMAN M., MUSTAFA A., SHAH S.A., MEHMOOD K., MAITLO A.A., SUN N., XU M., 2020 - *Evaluating the contribution of growth, physiological, and ionic components towards salinity and drought stress tolerance in Jatropha curcas*. - Plants, 9: 1574.
- ACOSTA-MOTOS J.R., DÍAZ-VIVANCOS P., ÁLVAREZ S., FERNÁNDEZ-GARCÍA N., SÁNCHEZ-BLANCO M.J., HERNÁNDEZ J.A., 2015 - *Physiological and biochemical mechanisms of the ornamental Eugenia myrtifolia L. plants for coping with NaCl stress and recovery*. - Planta, 242: 829-846.
- AGAMI R.A., MOHAMED G.F., 2013 - *Exogenous treatment with indole-3-acetic acid and salicylic acid alleviates cadmium toxicity in wheat seedlings*. - Ecotox. Environ. Safe., 94: 164-171.
- ALSAEEDI A., EL-RAMADY H., ALSHAAL T., EL-GARAWANY M., ELHAWAT N., AL-OTAIBI A., 2019 - *Silica nanoparticles boost growth and productivity of cucumber under water deficit and salinity stresses by balancing nutrients uptake*. - Plant Physiol. Bioch., 139: 1-10.
- BHADRA P., 2020 - *An overview of ajwain (Trachyspermum ammi)*. - Indian J. Nat. Sci., 10: 18466-182474.
- CHANG J., CHEONG B.E., NATERA S., ROESSNER U., 2019 - *Morphological and metabolic responses to salt stress of rice (Oryza sativa L.) cultivars which differ in salinity tolerance*. - Plant Physiol. Bioch., 144: 427-435.
- CHRYSARGYRIS A., PAPAKYRIAKOU E., PETROPOULOS S.A., TZORTZAKIS N., 2019 - *The combined and single effect of salinity and copper stress on growth and quality of Mentha spicata plants*. - J. Hazard. Mater., 368: 584-593.

- DOLA D.B., MANNAN M.A., SARKER U., MAMUN M.A.A., ISLAM T., ERCISLI S., SALEEM M.H., ALI B., POP O.L., MARC R.A., 2022 - *Nano-iron oxide accelerates growth, yield, and quality of Glycine max seed in water deficits*. - Front. Plant Sci., 13: 992535.
- EL-DESOUKY H.S., ISLAM K.R., BERGEFURD B., GAO G., HARKER T., ABD-EL-DAYEM H., ISMAIL F., MADY M., ZEWAİL R.M., 2021 - *Nano iron fertilization significantly increases tomato yield by increasing plants' vegetable growth and photosynthetic efficiency*. - J. Plant Nutr., 44: 1649-1663.
- EL-SABER M.M., MAHDI A.A., HASSAN A.H., FARROH K.Y., OSMAN A., 2021 - *Effects of magnetite nanoparticles on physiological processes to alleviate salinity induced oxidative damage in wheat*. - J. Sci. Food Agr., 101: 550-5562.
- GHASSEMI-GOLEZANI K., ABDOLI S., 2021 - *Improving ATPase and PPase activities, nutrient uptake and growth of salt stressed ajowan plants by salicylic acid and iron-oxide nanoparticles*. - Plant Cell Rep., 40: 559-573.
- GHASSEMI-GOLEZANI K., ABDOLI S., 2022 a - *Physiological and biochemical responses of medicinal plants to salt stress*, pp. 153-181. - In: AFTAB T. (ed.). *Environmental challenges and medicinal plants: sustainable production solutions under adverse condition*. Springer, Cham, Switzerland, pp. 512.
- GHASSEMI-GOLEZANI K., ABDOLI S., 2022 b - *Alleviation of salt stress in rapeseed (Brassica napus L.) plants by biochar-based rhizobacteria: new insights into the mechanisms regulating nutrient uptake, antioxidant activity, root growth and productivity*. - Arch. Agron. Soil Sci., 68: 1-18.
- GHASSEMI-GOLEZANI K., FARHADI N., 2022 - *The efficacy of salicylic acid levels on photosynthetic activity, growth, and essential oil content and composition of pennyroyal plants under salt stress*. - J. Plant Growth Regul., 41: 1953-1965.
- GHASSEMI-GOLEZANI K., FARHANGI-ABRIZ S., 2021 - *Biochar-based metal oxide nanocomposites of magnesium and manganese improved root development and productivity of safflower (Carthamus tinctorius L.) under salt stress*. - Rhizosphere, 19: 100416.
- GHASSEMI-GOLEZANI K., FARHANGI-ABRIZ S., ABDOLI S., 2021 - *How can biochar-based metal oxide nanocomposites counter salt toxicity in plants?* - Environ. Geochem. Health, 43: 2007-2023.
- GHASSEMI-GOLEZANI K., RAHIMZADEH S., 2022 - *Biochar-based nutritional nanocomposites: a superior treatment for alleviating salt toxicity and improving physiological performance of dill (Anethum graveolens)*. - Environ. Geochem. Health, 45: 3089-3111.
- HAYAT S., ALI B., AHMAD A., 2007 - *Salicylic acid: biosynthesis, metabolism and physiological role in plants*, pp. 1-14. - In: HAYAT S., and A. AHMAD (eds.). *Salicylic acid: a plant hormone*. Springer, Dordrecht, The Netherlands, pp. 401.
- HUSSAIN A., ALI S., RIZWAN M., REHMAN M.Z.U., QAYYUM M.F., WANG H., RINKLEBE J., 2019 - *Responses of wheat (Triticum aestivum) plants grown in a Cd contaminated soil to the application of iron oxide nanoparticles*. - Ecotoxicol. Environ. Saf., 173: 156-164.
- HUSSAIN S.J., KHAN N.A., ANJUM N.A., MASOOD A., KHAN M.I.R., 2021 - *Mechanistic elucidation of salicylic acid and sulphur-induced defence systems, nitrogen metabolism, photosynthetic, and growth potential of mung-bean (Vigna radiata) under salt stress*. - J. Plant Growth Regul., 40: 1000-1016.
- JAYAKANNAN M., BOSE J., BABOURINA O., RENGEL Z., SHABALA S., 2013 - *Salicylic acid improves salinity tolerance in Arabidopsis by restoring membrane potential and preventing salt-induced K⁺ loss via a GORK channel*. - J. Exp. Bot., 64: 2255-2268.
- KAFI M., RAHIMI Z., 2011 - *Effect of salinity and silicon on root characteristics, growth, water status, proline content and ion accumulation of purslane (Portulaca oleracea L.)*. - Soil Sci. Plant Nutr., 57: 341-347.
- KAFI M., SHARIAT-JAFARI M.H., MOAYEDI A., 2013 - *The sensitivity of grain sorghum (Sorghum bicolor L.) developmental stages to salinity stress: an integrated approach*. - J. Agr. Sci. Technol., 15: 723-736.
- KAZAN K., LYONS R., 2016 - *The link between flowering time and stress tolerance*. - J. Exp. Bot., 67:47-60.
- KHAN M.I.R., ASGHER M., KHAN N.A., 2014 - *Alleviation of salt-induced photosynthesis and growth inhibition by salicylic acid involves glycine betaine and ethylene in mung bean (Vigna radiata L.)*. - Plant Physiol.Bioch., 80:67-74.
- KIM J.H., LEE Y., KIM E.J., GU S., SOHN E.J., SEO Y.S., AN H.J., CHANG Y.S., 2014 - *Exposure of iron nanoparticles to Arabidopsis thaliana enhances root elongation by triggering cell wall loosening*. - Environ. Sci. Technol., 48: 3477-3485.
- KNOBLAUCH M., OPARKA K., 2012 - *The structure of the phloem - still more questions than answers*. - Plant J., 70: 147-156.
- LOTFI R., GHASSEMI-GOLEZANI K., PESSARAKLI M., 2020 - *Salicylic acid regulates photosynthetic electron transfer and stomatal conductance of mung bean (Vigna radiata L.) under salinity stress*. - Biocatal. Agr. Biotech, 26: 101635.
- MANZOOR N., AHMED T., NOMAN M., SHAHID M., NAZIR M.M., ALI L., ALNUSAIRE T.S., LI B., SCHULIN R., WANG G., 2021 - *Iron oxide nanoparticles ameliorated the cadmium and salinity stresses in wheat plants, facilitating photosynthetic pigments and restricting cadmium uptake*. - Sci. Total Environ., 769: 145221.
- MINIJA J., THOPPIL J.E., 2002 - *Essential oil composition of Trachyspermum ammi (L.) Sprague from South India*. - Indian J. Pharmaceut. Sci., 64: 250-251.

- MIURA K., OKAMOTO H., OKUMA E., SHIBA H., KAMADA H., HASEGAWA P.M., MURATA Y., 2013 - *SIZ1 deficiency causes reduced stomatal aperture and enhanced drought tolerance via controlling salicylic acid induced accumulation of reactive oxygen species in Arabidopsis*. - Plant J., 49:79-90.
- MORADBEGI H., JAMEI R., HEIDARI R., DARVISHZADEH R., 2020 - *Fe₂O₃ nanoparticles induced biochemical responses and expression of genes involved in rosmarinic acid biosynthesis pathway in Moldavian balm under salinity stress*. - Physiol. Plantarum, 169: 555-570.
- MOZAFARI A.A., DEDEJANI S., GHADERI N., 2018 - *Positive responses of strawberry (Fragaria × ananassa Duch.) explants to salicylic and iron nanoparticle application under salinity conditions*. - Plant Cell Tiss. Org., 134: 267-275.
- NAIR R., VARGHESE S.H., NAIR B.G., MAEKAWA T., YOSHIDA Y., KUMAR D.S., 2010 - *Nanoparticulate material delivery to plants*. - Plant Sci., 179: 154-163.
- NIKPOUR-RASHIDABAD N., GHASSEMI-GOLEZANI K., SAMEA-ANDABJADID S., 2022 - *Physiological performance of dill plants affected by seed pretreatments under salt stress*. - Gesunde Pflanzen, 75: 1833-1842.
- RAO Y.R., ANSARI M.W., SAHOO R.K., WATTAL R.K., TUTEJA N., KUMAR V.R., 2021 - *Salicylic acid modulates ACS, NHX1, sos1 and HKT1;2 expression to regulate ethylene overproduction and Na⁺ ions toxicity that leads to improved physiological status and enhanced salinity stress tolerance in tomato plants cv. Pusa Ruby*. - Plant Signal. Behav., 16: 1950888.
- RASHEED F., ANJUM N.A., MASOOD A., SOFO A., KHAN N.A., 2020 - *The key roles of salicylic acid and sulfur in plant salinity stress tolerance*. - J. Plant Growth Regul., 41: 1891-1904.
- RIZWAN M., ALI S., ALI B., ADREES M., ARSHAD M., HUSSAIN A., UR-REHMAN M.Z., WARIS A.A., 2019 - *Zinc and iron oxide nanoparticles improved the plant growth and reduced the oxidative stress and cadmium concentration in wheat*. - Chemosphere, 214: 269-277.
- RUI M., MA C., HAO Y., GUO J., RUI Y., TANG X., ZHAO Q., FAN X., ZHANG Z., HOU T., ZHU S., 2016 - *Iron oxide nanoparticles as a potential iron fertilizer for peanut (Arachis hypogaea)*. - Front. Plant Sci., 7: 815.
- SARKER U., OBA S., 2019 - *Salinity stress enhances color parameters, bioactive leaf pigments, vitamins, polyphenols, flavonoids and antioxidant activity in selected Amaranthus leafy vegetables*. - J. Sci. Food Agric., 99: 2275-2284.
- SHAKIROVA F.M., SAKHABUTDINOVA A.R., BEZRUKOVA M.V., FATKHUTDINOVA R.A., FATKHUTDINOVA D.R., 2003 - *Changes in the hormonal status of wheat seedlings induced by salicylic acid and salinity*. - Plant Sci., 164: 317-322.
- SHEYKHBAGLOU R., SEDGHI M., FATHI-ACHACHLOUIE B., 2018 - *The effect of ferrous nano-oxide particles on physiological traits and nutritional compounds of soybean (Glycine max L.) seed*. - Ann. Acad. Bras. Ciênc., 90: 485-494.
- SINGH P., ARIF Y., SIDDIQUI H., SAMI F., ZAIDI R., AZAM A., ALAM P., HAYAT S., 2021 a - *Nanoparticles enhances the salinity toxicity tolerance in Linum usitatissimum L. by modulating the antioxidative enzymes, photosynthetic efficiency, redox status and cellular damage*. - Ecotox. Environ. Safe., 213: 112020.
- SINGH S., PRAKASH P., SINGH A.K., 2021 b - *Salicylic acid and hydrogen peroxide improve antioxidant response and compatible osmolytes in wheat (Triticum aestivum L.) under water deficit*. - Agr. Res., 10: 175-186.
- SUN H., FENG F., LIU J., ZHAO Q., 2017 - *The interaction between auxin and nitric oxide regulates root growth in response to iron deficiency in rice*. - Front. Plant Sci., 8: 2169.
- WANG Z., TANG J., ZHU L., FENG Y., YUE L., WANG C., XIAO Z., CHEN F., 2022 - *Nanomaterial-induced modulation of hormonal pathways enhances plant cell growth*. - Environ. Sci.: Nano, 9: 1578-1590.
- YANG L., WANG X., CHANG N., NAN W., WANG S., RUAN M., SUN L., LI S., BI Y., 2019 - *Cytosolic glucose-6-phosphate dehydrogenase is involved in seed germination and root growth under salinity in Arabidopsis*. - Front. Plant Sci., 10: 182.
- ZHANG X., WU W., ERVIN E.H., SHANG C., HARICH K., 2018 - *Salt stress-induced injury is associated with hormonal alteration in Kentucky bluegrass*. - HortSci., 53: 97-101.

