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Hormonal and Physiological Changes in Miniature Roses (*Rosa chinensis* Jacq. var. *minima* Rehd.) Exposed to Water Deficit and Salinity Stress Conditions

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Abstract

Abiotic stresses are the most harmful factors for plant growth and production. Drought and salinity are two major abiotic stresses that severely damage plant cells. They also change plant hormones like IAA, Zea, GA, and ABA. An investigation was conducted to examine the performance of miniature rose plants as landscape cultivars under salinity and water management. Three cultivars ('Little Buckaroo', 'Sourati Local Cultivar' and 'Little Flirt') received water deficit irrigation, with intervals of 2, 4, and 6 days, and 2 and 4dS/m NaCl salinity. The results showed that severe water deficit and salinity stress reduced indoleacetic acid (IAA) and zeatin content in all cultivars, and the lowest IAA was observed in 'Sourati Local Cultivar'. The 'Little Flirt' had the highest IAA at all salinity levels. The interaction of 6-day irrigation interval and 4dS/m salinity reduced gibberellic acid (GA) in all cultivars. ABA was increased with the highest salinity level, regardless of the irrigation interval. Overall, in most water deficit and salinity stress levels, zeatin and IAA were the highest in 'Little Flirt' and the lowest in 'Sourati Local Cultivar'. In the highest level of salinity, 'Sourati Local Cultivar' had the most electrolyte leakage and the least relative water content. In addition, 'Sourati Local Cultivar' showed the least flower diameter, chlorophyll content and chlorophyll fluorescence in interaction of 4-day irrigation intervals and 4dS/m salinity. For all cultivars, 4dS/m salinity in all irrigation treatments, reduced shoot fresh and dry weights. Therefore, it may be concluded that 'Little Flirt' was the most tolerant and 'Sourati Local Cultivar' was the most sensitive cultivars to drought and salinity stresses.

Keywords Abiotic stress · Abscisic acid · Gibberellic acid · Indoleacetic acid · Rose · Zeatin

Introduction

Abiotic stresses are the most detrimental factors to crop growth and production (Rao et al. 2016; Umar et al. 2019). Drought and salinity are expanding in many regions, and over half of the arable lands of the world will have become salinized by 2050 (Shrivastava and Kumar 2015; Wang et al. 2003). Salinity and water deficiency stresses act individually or in combination, causing morphological, physiological, biochemical, and molecular changes, thereby adversely affecting or reducing plant growth and yield in arid and semi-arid regions (Bhanuprakash and Yogeesha 2016; Rao et al. 2016). Plants respond to abiotic stresses by physiological changes and hormonal activities (Liu et al. 2019). Physiological responses of plants to survive drought stress include leaf wilting, leaf area reduction, leaf falling, and root growth stimulation by transferring nutrients to underground parts (Ahmed et al. 2015). Salt and drought stress induces primary stresses, including osmotic and ionic stress then lead to various physiological and molecular changes and impede plant growth by inhibiting photosynthesis, thus reducing the available resources and repressing cell division and expansion (Zelm et al. 2020). As water deficit progresses and leaf water content declines, stomatal conductance to water vapor and net photosynthesis tends to decrease (Chaves et al. 2009; Chastain et al. 2014). Under

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salt stress, ion imbalance and water deficiency in the plant cell cause osmotic stress. This results in multiple transient biophysical changes, such as the reduction in cell turgor pressure, shrinkage of the plasma membrane, and physical alteration of the cell wall (Park et al. 2016).

Different signaling molecules, such as plant phytohormones, play important roles in plants to abiotic stresses to resistance or survive stressful conditions (Liu et al. 2019). Plant growth regulators (PGR) greatly influence the growth and differentiation of cells, tissues, and organs of plants and their functions as chemical signal carriers in intercellular communications (Upreti and Sharma 2016). Auxins especially abscisic acid (ABA) are involved in various growth processes and responses to abiotic stresses. ABA is a phytohormone, which regulates different physiological activities from stomatal opening to protein accumulation and causes adaptation to drought and salt stress by decreasing transpiration and protecting photosynthesis (Ahmed et al. 2015; Sah et al. 2016; Yang et al. 2019). For example, in plant cells, abscisic acid (ABA) activates Ca2+ signaling, which leads to the control of the S-type anion channel, SLAC1, for the regulation of stomatal closure (Brandt et al. 2015).

Cytokinins are important growth-promoting compounds that play roles in the regulation of the functioning of stomata and in the communication between roots and shoots in plants that are suffering from stresses. Plants that perceive abiotic stress tend to decrease their cytokinin contents. By decreasing cytokinin synthesis or increasing its decomposition, or even both, cytokinin content keeps decreasing (Upreti and Sharma 2016).

Roses are among the most popular flowering plants in the world, which are cultivated for different reasons including for their flower color and form, growth habit, and good adaptation in different environments (Cai et al. 2014). China rose (Rosa chinensis) is a common salinity-susceptible species yet it is good for landscape (Li et al. 2015). It is of crucial importance to grow salinity-tolerant garden roses in urban landscapes of arid and semi-arid regions where soils are saline due to the low quality of the irrigation water (Cai et al. 2014). As miniature roses are conventional landscape flower plants and considering the fact that the limitation of water resources and salinity increases, it is necessary to reduce water use, manage irrigation, use non-drinking water with a higher electrical conductivity in landscape irrigations. Due to the inherent limitations of studying the real responses to a combination of two or several stress factors in landscape roses, the present study aimed to explore hormonal and physiological changes in three cultivars when exposed to water deficit and salinity stresses and their interaction.

Materials and Methods

Plant Material and Growing Conditions

The research was conducted during 2016–2017 in a research greenhouse, College of Agriculture and Natural Resources, University of Tehran, Karaj (Lat. $35^{\circ}56'$ N., Long. $50^{\circ}58'$ E., Elevation 1316 m.). The maximum and minimum average temperatures and relative humidity were 28, 23 °C, 58, and 30%, respectively. The plants were grown in 7L plastic pots ($20.5 \text{ cm} \times 21 \text{ cm}$). The substrate was a 3:1:1 mixture of soil, peat moss, and sand. The concentrations of the main elements as well as EC and pH of the soil was evaluated (Table 1). Three cultivars of miniature roses (*Rosa chinensis* Jacq. var. *minima* Rehd.) were purchased from a flower farm in Mahallat, Markazi, Iran. All plants were propagated from stem cuttings and they were all two years old at the flowering stage.

All plants were pruned to the same height to obtain uniformly sized plants, and their places on the tables were swapped weekly in order to reduce the microclimatic differences. The plants were fertigated with a commercial 20-20-20 NPK fertilizer to prevent nutrient deficiency and make uniformity in growth and over irrigated once every two weeks for leaching to prevent salt excessive accumulation. During the experiment, whiteflies and powdery mildew were controlled by using yellow sticky cards and Topaz[®] fungicide, respectively.

Water Deficit and Salinity Treatments

The treatments included (1) water deficit stress at three levels (irrigation intervals of 2, 4, and 6 days); (2) NaCl salinity at three levels (control (greenhouse water with an EC of 0.9 dS/m), 2 dS/m and 4 dS/m); and (3) three cultivars (cv. 'Little Buckaroo' with red flowers, 'Sourati Local Cultivar' with pink flowers, and 'Little Flirt' with yellow flowers).

Irrigation regimes were scheduled after permanent wilting point (PWP) of the substrate was estimated (Kirkham 2005). Pots reached the PWP after eight days, so the irrigation interval was set at 2, 4, or 6 days. During the experiment, soil water content was kept near the field capacity (FC) by daily monitoring plants pots. The water requirement was determined when all the pots were weighed and supplied with enough water to maintain the desired humidity levels (Kirkham 2005). For salinity treatments the NaCl salt was added to irrigation water. In order to avoid salt accumulation in the root zone 15% (v/v) of irrigation water was allowed to leach (Álvarez and Sánchez-Blanco 2015). After 65 days of growth, sampling in triplicate, was carried out to determine the effect of water deficit and salinity stress on physiological parameters in plants.

Table I	Thysical and chemical characteristics of substrate was used in this study									
SAR Meq/l	Mg ⁺	Ca ⁺	Na ⁺	K ⁺	Cl⁻	Organic material (%)	PWP	FC	EC (dS/m)	pН
2.7	6.3	15.2	8.9	0.41	8.4	1.84	12.5	22.2	2.68	8.4

Table 1 Physical and chemical characteristics of substrate was used in this study

Fresh and Dry Weight of Shoots, Flower Diameter

At the end of study, three plants in each treatment were selected for shoot and dry weight measurement. Then the shoot were detached from the roots and after washing the roots, they were weighted by a digital scale as shoot fresh weight. They were put in individual paper pocket and moved to oven 80 °C for 48h. After that, they were weighted by a digital scale for shoot dry weight. After about two months from starting the study, Flower diameter was measured by digital caliper (Insize 1108–200 model) as mm (Momenpour et al. 2015).

Relative Water Content

Relative water content (RWC, %) of leaves was determined as (FW-DM) / (TW-DM)×100, where FW is the fresh weight, DM is the dry matter after being dried in an oven at 60 °C until a constant weight was reached, and TW is the turgid weight of the leaf after equilibration in distilled water for 24h at 4 °C (Barrs and Weatherley 1962).

Ion Leakage Determination

In order to determine ion leakage, the leaves were cut into small discs (total 1.5 g fresh mass) and placed in beakers (50 cm^3) with 40 cm^3 of deionized water. After incubation at 25 °C for 12 h in darkness, the electrical conductivity in the bathing solution was determined (first EC) with a conductivity meter (DDSJ-308A, Shanghai Science Instrument Ltd, Shanghai, China). Then the samples were heated at 85 °C for 2 h, and the conductivity was read again in the bathing solution (final EC). Electrolyte leakage was defined as EC (%) = (first EC/final EC) * 100.

Chlorophyll Content and Chlorophyll Fluorescence

The chlorophyll content in the youngest expanded leaves was determined according to (Arnon 1949). 1 gr fresh leaves were dried in liquid nitrogen and ground in 80% acetone. Then the extraction was poured in centrifuge tube. After doing centrifuge, supernatant was discarded and 10 ml 80% acetone was added it. Quantification was done by a spectrophotometry (UV-Vis Analyst Version 5,11 Unico (Shanghai) Instruments Co., Ltd.,) in 663 and 645 nm. The chlorophyll content was calculated by following formula.

Chlorophyll (mg/gF.W.) = $\frac{[20.2(A645) + 8.02(A663) \times V]}{W \times 1000}$

V: Volume of extraction and acetone.

W: Leaves fresh weight.

Four leaves from the central parts of plants were used for the measurement of chlorophyll fluorescence using a Plant Efficiency Analyzer, Handy PEA (Hansatech Instruments Ltd., Norfolk, UK). Leaves were maintained in darkness for 15 min before taking the data on chlorophyll fluorescence, and the maximal quantum yield of photosystem II (PSII) photochemistry (Fv/Fm) was measured.

Abscisic Acid (ABA)

About two months after the treatments were applied, two plants were randomly taken from each treatment, and their leaves were used to measure the ABA content following (Li et al. 2010)'s method with some modified. In this method, 1g of fresh leaf sample was mixed with 10mL of 80% methanol and 0.1 g of polyvinylpyrrolidone, and the solution was homogenized at 4 °C. Then, it was centrifuged at 4000 rpm for 15 min, the supernatant was separated, and its pH was adjusted to 8. Then, methanol was evaporated under vacuum, and 5mL of deionized water was added to the remaining part. This process was repeated twice. In the second time, ethyl acetate was added, which was evaporated later. One mL of a solution containing 3% methanol and 0.1 M acetic acid was added to and solved in the precipitation. Then, it was passed through a 0.45-mm filter and injected into a reverse-phase column (Diamonsic, C18, $5\,\mu\text{m}$) with a length of 25 cm and a diameter of 4.6 mm in an HPLC Unicam (Crystal-200, England). The mobile phase of the methanol-acetic acid gradient at the rate of 4 mL/min was used with a diode-array detector. The retention time for ABA was 36.4 min. ABA standard with 99.97% purity made by the Sigma company was employed to use the output calibrated peak for the measurement of the extracted sample. The extracted sample was measured on the basis of the area under the curve and its success in the output peaks.

 Table 2
 Analysis of variance

 of shoot fresh weight, shoot
 dry weight, flower diameter of

 miniature rose
 miniature

S.O.V	Df	Mean Square			
		Shoot fresh weight	Shoot dry weight	Flower diameter	
Water Deficit (D)	2	259.85 **	34.31 **	41.74 *	
Salinity (S)	2	2326.17 **	181.78 **	173.39 **	
Cultivar (C)	2	964.46 **	13.83 ^{ns}	681.54 **	
D×S	4	161.51 **	19.07 *	116.7 **	
D×C	4	16.13 ^{ns}	4.68 ^{ns}	59.24 **	
S×C	4	120.54 *	13.13 ^{ns}	64.88 **	
D×S×C	8	73.36 ^{ns}	10.13 ^{ns}	31.17 **	
Error	54	37.91	5.58	10.33	
CV	-	13.38	12.93	8.88	

*, **, ns were shown significance in 5%, 1% and insignificance difference, respectively

Indoleacetic Acid (IAA), Zeatin, and Gibberellic Acid (GA)

IAA, Zeatin, and GA contents were measured by (Ma et al. 2008) and (Ge et al. 2004)'s methods. The extract was prepared from 2g of fresh leaf sample. Cold aqueous 80% methanol (<0°C) was used: it was homogenized with 30 mL of this methanol at 4 °C in darkness. The extract was, then, centrifuged at 5000rpm for 15 min, and the supernatant was collected, which was infiltrated. Then, the suspended particles were washed with methanol-acetic acid (1:100 v/v), methanol-water-acetic acid (1:50:50 v/v/v), methanol-water-acetic acid (1:70:30 v/v/v), and finally water. Then, 100 mL of it was poured into a C18 column. The column was washed with 10 mL of acidic water (pH 3). Plant hormones were washed with 5 ml of ethanol-wateracetic acid (1:20:80 v/v/v). Then, the components were evaporated under vacuum at room temperature and dissolved in 1 mL of methanol. Then, they were infiltrated with a 0.45-µm filter.

Measurements were made by an HPLC Unicam (Crystal 200, England). Additionally, 10μ L of the extract was injected into a C₁₈ reverse-phase column (2.1 mm diameter, 150 mm length, 3.5μ m, Zorbax SB-C₁₈ 100A°). The thermostat of the column was set at 25 °C. The retention time was 14.1 for zeatin, 19.5 min for GA, and 24 min for IAA. After every analysis, the column was rinsed with methanolformic acid (95:5 v/v) buffer for 5 min, and then formic acid-methanol 10:90 buffer was employed for 30 min. The peak of the standard region was used to measure the concentration of the samples.

Statistical Analysis of Data

The study was conducted as a factorial trial in a completely randomized design with three factors: Salinity, water deficit, and cultivar with seven replications for each treatment. Data were subjected to the analysis of variance with SAS Version 9.4 (Institute 2013) and to mean comparisons following the LSD test at $p \le 0.05$. Graphs were drawn in the MS-Excel (2016) software.

Results and Discussion

Fresh and Dry Weight of Shoot and Flower Diameter

Shoot fresh and dry weight was affected by the interaction of water deficit and salinity stress ($p \le 0.01$) and the interaction of salinity stress and cultivar ($p \le 0.05$) (Table 2). With the increase of water deficit and salinity stress, the shoot fresh weight decreased, so that the highest shoot fresh (58.64g) and dry (21.71g) weight were in 2-day irrigation intervals whithout salinity stress and the lowest fresh (32.04g) and dry (13.83g) weight were observed in 2-day irrigation intervals and 4 dS/m salinity (Fig. 1a,b). With increasing of salinity stress, the shoot fresh weight of all cultivars decreased, so that the highest shoot fresh weight were in greenhouse water and 'Sourati Local Cultivar' (61.05 gr) and the lowest (32.30 gr) in 4 dS/m salinity and 'Little Buckaroo'. 4dS/m salinity decreased all cultivars fresh weight significantly. In severe salinity stress compared to control, the shoot fresh weight reduction was 39.72%, 35.36% and 23.30% for 'Little Buckaroo', 'Sourati Local Cultivar' and 'Little Flirt', respectively. So, the fresh weight loss of shoots in 'Little Flirt' was less than other Fig. 1 Mean comparisons for the interaction between salinity stress, water deficit and cultivar on total chlorophylls of miniature rose leaves. *C1*: red, *C2*: pink and *C3*: yellow rose. *D1*: Irrigation interval 2 days, *D2*: Irrigation interval 4 days and *D3*: Irrigation interval 6 days. *S1*: Greenhouse water, *S2*: Salinity 2 dS/m and *S3*: Slinity 4 dS/m. Columns with similar letters show statistically insignificant differences based on the LSD test ($p \le 0.05$)



cultivars (Fig. 2). Therefore, the effect of salinity stress in reducing shoot fresh weight was more than water deficit. In 2–4 and 6 days irrigation intervals, using 4 dS/m salinity decreased the shoot fresh weight by 45.36%, 30.61% and 21.57% compared to control. It can be concluded that in the lowest irrigation intervals, the effect of severe salinity stress was greater than other irrigation intervals (Figs. 1 and 2). The highest flower diameter (52.12mm) was obtained in 2-day irrigation intervals, greenhouse water and 'Little Flirt', and the lowest (23.79mm) in 4-day irrigation intervals, 4 dS/m salinity and 'Sourati Local Cultivar', which didn't have difference significantly with 2-day irrigation intervals and 4 dS/m salinity. In 6-day irrigation intervals and severe salinity stress simultaneously, the highest and lowest flower diameter were observed in 'Little Flirt' and 'Sourati Local Cultivar', respectively. In the absence of salinity, severe water deficit led to decreasing of all cultivars diameter in comparison of control (Fig. 3).

Both stresses led to a decrease in shoot fresh weight, but salinity stress had more impact and at all irrigation levels, severe salinity stress significantly reduced shoot fresh and dry weight. Plant drought responses depend on the duration and severity level of the water deficitand vary within species and at different stages of plant development (Farooq et al. 2009). Abiotic stresses such as drought and salinity are recurrent causes of reduced crop yield and quality in arid and semiarid regions (De Pascale et al. 2007). The impact of water stress on leaf growth can be explained as a method of adaptation to the conditions of water shortage to limit the rate of transpiration (Lu and Neumann 1998). Physiological responses to abiotic stresses aremediated by ABA, which accumulates and/or mobilizes todifferent tissues and Fig. 2 Mean comparisons for the interaction between salinity stress and water deficit on electrical conductivity of drainage. *S1*: Greenhouse water, *S2*: Salinity 2 dS/m and *S3*: Slinity 4 dS/m. *D1*: Irrigation interval 2 days, *D2*: Irrigation interval 4 days and *D3*: Irrigation interval 6 days. Columns with similar letters show statistically insignificant differences based on the LSD test ($p \le 0.05$)



Fig. 3 Mean comparisons for the interaction between salinity stress and cultivar on leaf electrolyte leakage of miniature rose. *C1*: red, *C2*: pink and *C3*: yellow rose. *S1*: Greenhouse water, *S2*: Salinity 2 dS/m and *S3*: Slinity 4 dS/m. Columns with similar letters show statistically insignificant differences based on the LSD test ($p \le 0.05$)

organs to activate functional metabolic components essential for plant adaptation to different developmental stages, including germination and vegetative growth (Verslues and Zhu 2005). The high osmotic potential around the roots, it is possible for the roots to absorb less water, and as a result growth retardation may occurred (Bandeoğlu et al. 2004). Álvarez et al. (2013) noticed a decrease in growth and biomass traits in potted geranium when exposed to regulated deficit irrigation regimes. The reduction in fresh weight under water deficit may be due to the considerable decrease in plant growth, net photosynthetic rate and low turgor pressure (Idrees et al. 2010). Research on roses has shown that with increasing level and duration of the salinity, the FW and DW of plant decreases (Omidi et al. 2022; Ali et al. 2014). Similar to this study, Katsoulas et al. (2006) reported that irrigation frequency influenced fresh and dry weights of cut roses because the total fresh and dry weights of cut flower shoots were about 33% higher under high irrigation frequency as compared to low.

Electrolyte Leakage (EC)

With increasing the salinity treatment, the electrical conductivity increased. The lowest EC of drainage were observed in green house irrigation and the highest was found in 4ds/m in all treatments (Fig. 4). According to the results, the interaction between salinity and genotype affected electrolyte leakege in plant leaf (Table 3). At all Fig. 4 Mean comparisons for the interaction between salinity stress and cultivar on leaf RWC of miniature rose. *C1*: red, *C2*: pink and *C3*: yellow rose. *S1*: Greenhouse water, *S2*: Salinity 2dS/m and *S3*: Slinity 4dS/m. Columns with similar letters show statistically insignificant differences based on the LSD test ($p \le 0.05$)



salinity levels, 'Little Flirt' cultivar showed the lowest EC (18.27%) and the 'Sourati Local Cultivar'showed the highest EC (49.11%). In other words, the 'Sourati Local Cultivar' genotype was the most sensitive (Fig. 5). One of the serious harms of salinity stress is damage to the membrane and release of ions from the cell into the intercellular space, which is measured by measuring ionic leakage (Farooq et al. 2009). As this research numerous studies on roses have shown that ionic leakage also increases with increasing salinity (Ali et al. 2014; Omidi et al. 2022).

Relative Water Content (RWC)

The results in Fig. 6 show that RWC decreased by increasing salinity stress. Moreover, in the pink genotype, RWC was lowest. This means that this cultivar is more sensitive to salinity stress (Fig. 6). Relative water content is considered a measure of plant water status, can be used to screen for plants drought tolerance. Root water uptake decreases upon exposure to salt stress. This decrease can be caused by both osmotic and toxic effects, depending on the salt concentration present (Idrees et al. 2010). RWC of leaves is higher in the initial stages of leaf development and declines as the dry matter accumulates and leaf matures. RWC related to water uptake by the roots as well as water loss by transpiration. A decrease in the relative water content (RWC) in response to drought stress has been noted in wide variety of plants as reported by (Nayyar and Gupta 2006; Salehi and Aghdam 2016). Drought-tolerant plant species keep high RWC compared with drought-sensitive species in cultivars of sugarcane (Zhang et al. 2019). The decreased RWC under water deficit stress observed in this study is consistent with the previous studies (Idrees et al. 2010, Faghih et al. 2021).

Total Chlorophyll Content and Chlorophyll Fluorescence

Water deficit stress had a significant effect on chlorophyllous content ($p \le 0.01$) (Table 3). Salinity negetively affected chlorophyll content in all genotypegenotypes and treatments. The highest and lowest chlorophyll contents were found in 4 ds/m salinity and control in all water deficit, respectively (Fig. 7).

The effect of salinity stress and water deficit on fluorescence activity indicated that three genotypes showed different responses. With increasing salinity stress, fluorescence activity was decreased (Fig. 8.). 'Sourati Local Cultivar' showed the lowest chlorophyll fluorescence in 2-day and 4-day irrigation intervals at 4 ds/m. Results show that the pink genotype shows the lowest fluorescence in D1 and D2 at 4 ds/m. Photosynthetic parameters are good indicators for detecting effects of stress on plants because photosynthesis and growth/yield are closely related (Chastain et al. 2014; Rivero et al. 2014). Chlorophyll fluorescence is a non-invasive, effective, and reliable technique for detecting photosystem II (PSII) damage in plants exposed to abiotic stress (Baker and Rosenqvist 2004). Cultivar differences in Fv/Fm correlate with dry matter accumulation in wheat under heat stress (Sharma et al. 2014) and tomato cultivars during cold and heat stress, but these changes varied depending on genotype, stress level, and stress duration (Zhou et al. 2017). Reduction in Fv/Fm and chlorophyll content was reported in drought stressed cotton (Massacci et al. 2008), olive seedlings (Guerfel et al. 2009), sunflower plants (Kiani et al. 2008) and tomato cultivar 'Hybrid 61' (Nankishore and Farrell 2016) compared with control. It has been reported that under water deficits con-

S.O.V	Df	Mean Square					
		Total chlorophylls	RWC	Electrolyte leak- age	Electrical conductivity of drainage	Chlorophyll fluores- cence	
Water Deficit (D)	2	0.1042**	330.01**	14.21 ^{ns}	4.52 ^{ns}	0.0003 ^{ns}	
Salinity (S)	2	1.50**	540.08**	2954.52**	469.35**	0.0018**	
Cultivar (C)	2	0.0978**	1414.20**	1939.17**	1.70 ^{ns}	0.0008**	
D×S	4	0.0221 ns	5.94 ^{ns}	18.08 ns	6.94**	0.0001 ^{ns}	
D×C	4	0.0275 *	2.01 ^{ns}	20.86 ns	3.24 ^{ns}	0.0003^{*}	
S×C	4	0.1665**	41.25*	156.64**	1.14 ^{ns}	0.0002 ^{ns}	
D×S×C	8	0.0588^{**}	20.51 ^{ns}	19.60 ^{ns}	2.65 ^{ns}	0.0003^{*}	
Error	54	0.0102	11.19	20.68	1.47	0.0001	
CV (%)	-	9.12	4.24	14.02	14.68	1.31	

 Table 3
 Analysis of variance of total chlorophylls, RWC, Electrolyte leakage, electrical conductivity of drainage and chlorophyll fluorescence of miniature rose leaves

*, **, ns were shown significance in 5%, 1% and insignificance difference, respectively

ditions, the Fv/Fm ratio would be reduced (Maxwell and Johnson 2000; Arji et al. 2003).

Indoleacetic Acid (IAA)

Effects of water deficit, salinity, cultivar, water deficit × cultivar, and salinity × cultivar were significant ($p \le 0.01$) on leaf IAA content. Severe water deficit reduced IAA in all cultivars (Table 4). The highest IAA content (35.8 ngg⁻¹ leaf fresh weight [FW]) was obtained from 'Little Buckaroo' under 4-day irrigation intervals, while 'Sourati Local Cultivar' under 6-day irrigation intervals produced the lowest IAA content (12.49 ng/g leaf FW) (Fig. 9a).

The interaction of salinity and cultivar indicated that the highest leaf IAA content, 34.03 ng/g leaf FW, was obtained from 'Little Flirt' under no salinity conditions, and the lowest leaf IAA content, 13.15 ng/g leaf FW, was observed in 'Sourati Local Cultivar' exposed to 4 dS/m salinity. Increasing salinity to 2 and 4 dS/m reduced IAA content of 'Little Flirt' cultivar. 'Sourati Local Cultivar' showed a higher IAA content at 2 dS/m salinity and a lower IAA content at 4 dS/m salinity. Overall, the severe salinity stress significantly reduced IAA content in all cultivars (Fig. 9b).

The main centers of auxin synthesis are the terminal meristem tissues like opening buds, young leaves, root tips, and flowers or influorescences on flowering stems. Plants exposed to stress lose their ability to grow meristem tissues, which may be a reason for the decline of this hormone under stressful conditions. IAA plays a critical role in plant growth. For example, it regulates vascular tissues, cell elongation, and apical dominance (Wang et al. 2001). When plants are exposed to stresses, their IAA content changes via two mechanisms. One is the change in the expression of polar auxin transporter genes and the other is the inhibition of their polar translocation by means of specific compounds that are accumulated in response to the stresses. Furthermore, under abiotic stresses, IAA is metabolized by its oxidative decomposition through an increase in peroxidases and the synthesis of reactive oxygen species (ROS) (Upreti and Sharma 2016). In a study on salinity stress, ABA increased, but auxin decreased (Wang et al. 2001). which corroborates our findings of the increase in ABA (Fig. 3.) and the decline in IAA under salinity stress (Fig. 6.). Salinity reduced auxin content of tomato roots by 75% (Dunlap and Binzel 1996). In the present study, the results show that IAA content of 'Little Flirt' was higher than those of the other two cultivars under moderate and severe salinity. However, this cultivar exhibited a lower Na content in its leaves when exposed to salinity stress (data not shown), which can be an evidence for its higher tolerance to salinity stress (Niu and Rodriguez 2008). Under severe water deficit and salinity stresses, the lowest IAA content was observed in 'Sourati Local Cultivar' (Figs. 6 and 7), implying the lower tolerance of this cultivar against drought and salinity stresses.

Gibberellic Acid (GA)

Leaf GA content was significantly influenced by the interaction of water deficit, salinity and cultivar ($p \le 0.05$) (Table 4). In all cultivars, with increasing irrigation intervals to 4 and 6 days, in the absence of salinity, the GA content decreased. This reduction of GA was the highest in 'Little Buckaroo' irrigated every four days and in 'Sourati Local Cultivar' and 'Little Flirt' irrigated every six days. Overall, the highest leaf GA content (45.62 ng/g leaf FW)

Fig. 5 Mean comparisons for the interaction between salinity stress, water deficit and cultivar on total chlorophylls of miniature rose leaves. C1: red, C2: pink and C3: yellow rose. D1: Irrigation interval 2 days, D2: Irrigation interval 4 days and D3: Irrigation interval 6 days. S1: Greenhouse water, S2: Salinity 2dS/m and S3: Slinity 4dS/m. Columns with similar letters show statistically insignificant differences based on the LSD test ($p \le 0.05$)



2 dS/m

10 0 control Salinity stress was obtained from 'Little Buckaroo' exposed to the interaction of 2-day irrigation interval and greenhouse water, and the lowest leaf GA content (20.15 ng/g leaf FW) was found in 'Sourati Local Cultivar' exposed to the interaction of 6-day irrigation interval and 4 dS/m salinity. although there wasn't significant difference between 'Sourati Local Cultivar' and 'Little Flirt' in 6-day irrigation interval and 4 dS/m salinity Severe salinity stress at all irrigation intervals reduced GA content of 'Little Buckaroo' and 'Sourati Local

Cultivar', and only 'Little Flirt' displayed a slight increase

under the 4-day irrigation intervals, albeit not significantly

compared to the control (Fig. 10).

> Gibberellins are terpenoid compounds that are built from isoprene units. Gibberellins promote cell elongation and division. They are also involved in plant cell growth (Magome et al. 2004). The mechanism that links gibberellins to stress tolerance has not been precisely understood yet. One possible mechanism is the interaction of gibberellins with other plant hormones (Upreti and Sharma 2016). The other one is acting through changing gibberellin metabolism: osmotic stress contributes to the stability of Della proteins and the increase in endoreduplication (Claeys et al. 2012). (Zawaski and Busov 2014) found that in response to drought, gibberellin decomposition and the inhibition of signaling hin-

4 dS/m

Fig. 6 Mean comparisons for the interaction of water deficit and cultivar for indole-acetic acid (IAA) of miniature rose leaves. (The columns with similar letters show statistically insignificant differences based on the LSD test at $p \le 0.05$)

Fig. 7 Mean comparisons for the interaction of salinity stress and cultivar for indole-acetic acid (IAA) of miniature rose leaves. Bars with similar letters show statistically insignificant differences based on the LSD test ($p \le 0.05$)



der the growth of shoots and plant physiological adaptation. However, drought stress leads to the activity of a group of GA2-oxidase encoding genes and the genes related to Della proteins (Upreti and Sharma 2016). Salinity stress reduces cytokinin, auxin, gibberellin, and salicylic acid hormones and increases ABA (Ali et al. 2014; Javid et al. 2011). In our study, water deficit and salinity stresses reduced leaf GA, which is consistent with those studies.

Zeatin

The results revealed that the effect of water deficit, salinity stress, cultivar, interaction of water deficit and cultivar, and interaction of salinity stress and cultivar were significant ($p \le 0.01$) on leaf zeatin content (Table 4). Severe water deficit significantly reduced leaf zeatin in all cultivars. The highest zeatin content, 13.61 ng/g leaf FW, was obtained from 'Little Flirt' under 4-day irrigation intervals and the

lowest (3.37 ng/g leaf FW) from 'Little Buckaroo' under 4-day irrigation intervals (Fig. 11a).

Cytokinins are important growth compounds that are involved in seed germination, morphogenesis, chloroplast formation, fruit and leaf shedding, stomatal role regulation, and the connection between roots and shoots during stresses. These compounds are first synthesized in roots and apical buds and then in other tissues (Upreti and Sharma 2016). Zeatin, which is one of the most active cytokinins, is mainly involved in cell division. Leaf stomata play a major role in the adjustment of water transpiration and gas exchanges, and cytokinins are important for keeping the stomata open by ABA adjustment (Veselova et al. 2006).

Drought stress causes leaf senescence, which is associated with the reduction of cytokinin and the suppression of cytokinin signaling. Resistant lines show that if cytokinin levels are manipulated appropriately, drought tolerance might be improved (Le et al. 2012). In other words, the decline of cytokinin content increases the elongation of Fig. 8 Mean comparisons for the interaction of water deficit, salinity stress, and cultivar for gibberellic acid (GA) of miniature rose leaves. Columns with similar letters show statistically insignificant differences based on the LSD test ($p \le 0.05$)



Salinity stress

initial roots and root branches by increasing the expression of cytokinin oxidase genes. Consequently, root biomass increases, which improves the drought tolerance of the transgenic plants (Werner et al. 2010). Some studies have indicated that water stress reduces cytokinin in plant cells (Masia et al. 1994; Pillay and Beyl 1990; Satisha et al. 2005), and bioactive CKs concentrations of plants have decreased when under salinity and drought stresses (Sade et al. 2018).

The decline of cytokinin content is due to either the loss of its biosynthesis, the rise of its decomposition, or both of them (Murti and Upreti 2007). In our study, severe water deficit reduced cytokinin content of all cultivars whereas moderate stress reduced it in 'Little Buckaroo' and 'Sourati Local Cultivar' but resulted in its buildup in 'Little Flirt'.

The interaction of salinity stress and cultivar revealed that as the salinity was intensified, leaf zeatin content was significantly reduced in all cultivars. Under the severe salinity stress, zeatin was declined by 19.22% in 'Little Buckaroo', 31.85% in 'Sourati Local Cultivar', and 35.58% in 'Little Flirt'. In 'Little Buckaroo', when the salinity level increased, zeatin first decreased and then slightly increased. There was not a significant difference between the salinity levels of 2 and 4 dS/m. In 'Sourati Local Cultivar', the increase in salinity to 2 dS/m increased zeatin, but then it

Table 4 Analysis of variance of IAA, GA, Zeatin and ABA of miniature rose leaves

S.O.V	Df	Mean Square					
		IAA	GA	Zeatin	ABA		
Water Deficit (D)	2	148.83**	193.97 **	** 41/23 23.41 **	253.61 **		
Salinity (S)	2	130.56 **	95.64 **	40.76 **	179.18 **		
Cultivar (C)	2	876.76 **	486.85 **	240.69 **	777.89 **		
D×S	4	4.33 ^{ns}	8.9 ^{ns}	0.39 ^{ns}	5.6 ^{ns}		
D×C	4	136.48 **	93.13 **	10.3 **	153.3 **		
S×C	4	64.41 **	65.54 **	11.82 **	77.13 **		
D×S×C	8	3.67 ^{ns}	8.83 *	0.61 ^{ns}	11.48 *		
Error	27	1.85	3.41	0.48	4.5		
CV (%)	-	6.43	5.62	8.79	7.38		

*, **, ns were shown significance in 5%, 1% and insignificance difference, respectively

Fig. 9 Mean comparisons for the interaction of water deficit and cultivar for Zeatin of miniature rose leaves. (The columns with similar letters show statistically insignificant differences based on the LSD test at $p \le 0.05$)



reduced at the salinity level of 4dS/m. In 'Little Flirt', as salinity was increased to 2 and 4dS/m, zeatin content decreased. Overall, the highest leaf zeatin content (14.11 ng/g leaf FW) was observed in 'Little Flirt' when not exposed to salinity, and the lowest, 4.09 ng/g leaf FW, was observed in 'Little Buckaroo' treated with 2dS/m salinity (Fig. 11b).

Cytokinin decline induced by stress may be associated with the loss of its mobilization from roots and/or the increased level of its breakdown (Havlov et al. 2008; Werner et al. 2006). Cytokinin is incompatible with ABA in most physiological processes, including stomatal closure, growth and development, and leaf senescence. This antagonistic effect between ABA and cytokinin may be related to metabolic interactions with cytokinins that are made from a biosynthesis source that is common with ABA (Brault and Maldiney 1999). Similar to the results of IAA and GA, the water deficit and severe salinity reduced leaf zeatin content in all studied cultivars.

Abscisic Acid (ABA)

Leaf ABA content was significantly affected by the interaction between water deficit, salinity stress, and cultivar $(p \le 0.05)$. Water deficit and severe salinity increased ABA in all cultivars. In most studied treatments, the lowest ABA was found in 'Sourati Local Cultivar'. The lowest content (15.9 ng/g LFW) was observed in 'Sourati Local Cultivar' treated with water deficit and moderate salinity, but there was no significant difference between this treatment and that where 'Sourati Local Cultivar' was exposed to 2-day irrigation intervals and greenhouse water or 2-day irrigation intervals and 2 dS/m salinity. Fig. 10 Mean comparisons for the interaction of salinity stress and cultivar for Zeatin of miniature rose leaves. Bars with similar letters show statistically insignificant differences based on the LSD test ($p \le 0.05$)



Overall, the highest ABA content (46.66 ng/g LFW) was observed in 'Little Flirt' exposed to severe water deficit and salinity stress, simultaneously. At the 2-day irrigation intervals, the increase in salinity to 4dS/m was accompanied by an increase in the ABA content of 'Little Buckaroo', 'Sourati Local Cultivar', and 'Little Flirt' by 6.42, 14.24, and 29.47%, respectively. The highest ABA was observed in 4ds/m and in 6-day irrigation interval (Fig. 11).

ABA is a stress hormone with a lot of functions, e.g. increasing the expression of genes that are involved in enhancing osmotic stress tolerance (Dar et al. 2017). ABA can also influence the accumulation of proline by regulating the expression of P5 CS and P5CR in plants during

abiotic stress (Verslues and Bray 2006). Among the nine plant phytohormones, ABA is the most important hormone regulating stress responses. ABA functions as an important secondary signaling molecule to activate a kinase cascade and mediate gene expression during the salt stress response. Under stress conditions, ABA synthesis is induced quickly leading to rapid increases in ABA levels (Jia et al. 2002). The increase of ABA biosynthesis in the roots and the reduction of cytokinin synthesis in the roots, branches and buds in deficit irrigation affects the vegetative growth (Dodd 2005).

ABA can increase water permeability and escalate the genes responsible for the biosynthesis of late-embryogen-

Fig. 11 Mean comparisons for the interaction of water deficit, salinity stress, and cultivar for Abscisic acid (ABA) of miniature rose leaves. Columns with similar letters show statistically insignificant differences based on the LSD test ($p \le 0.05$)



esis abundant (LEA) protein, which in turn increases the amount of osmoprotectants and osmotic compounds such as proline and glysine betaine, which results in osmotic adjustment and an increase in water uptake (Fricke et al. 2004; Murti and Upreti 2007; Wang et al. 2001). However, a high ABA content causes stomatal closure, the loss of gas exchanges, reducing water loss and improving plant water status (Kim et al. 2010; Upreti and Sharma 2016).

The inhibition of ABA decomposition is also effective in its accumulation in stressful conditions. The extent of accumulation depends on such parameters as stress intensity, genetics, plant tissue, and development stage (Murti and Upreti 2007). The increase in ABA concentration under salinity stress has been reported in tomatoes (Ghanem et al. 2008) and maize (Zörb et al. 2013). Salinity stress increased ABA in *Iris hexagona* (Wang et al. 2001).

Drought stress increased ABA in five drought-tolerant genotypes of *Panicum virgatum* L. (Liu et al. 2015). In this study, it was revealed that at all salinity levels, the highest ABA content under moderate water deficit was found in 'Little Buckaroo'. At severe water deficit and all salinity levels, 'Little Flirt' showed the highest ABA. Therefore, these two cultivars were more tolerant than 'Sourati Local Cultivar'.

Conclusions

Abiotic stresses such as water-deficit and salinity stress caused damage to some physiological and hormonal characteristics. Drought is a worldwide problem, constraining global crop production and quality seriously, and recent global climate change has made this situation more serious. Drought stress affects the growth, dry matter and harvestable yield in plants. In this research salinity stress had negative effects on morpho-physiological characteristics of miniature roses. In addition, the decrease in RWC and chlorophyll at decreasing leaf water potentials can be attributed to the sensitivity of this pigment to increasing environmental stresses, especially to salinity and water deficit. Phytohormones play an important role in countering environmental stresses in addition to performing their functions in the growth and development of plants. The lowest RWC and the highest electrolyte leakage was observed in 'Sourati Local Cultivar' was irrigated by 4 dS/m. For the interaction of 4-day irrigation intervals and 4 dS/m, 'Sourati Local Cultivar' had the least of flower diameter, chlorophyll content and chlorophyll fluorescence. On the one hand, 'Sourati Local Cultivar' represented the lowest flower diameter, chlorophyll content and chlorophyll fluorescence, RWC, IAA and the highest electrolyte leakage and the other hand, 'Little Flirt' showed the most RWC, IAA, zeatin, ABA and the least electrolyte leakage.

There were differences between the varieties studied. Water deficit and severe salinity stress reduced IAA in all cultivars as compared to control. At all salinity stress levels, 'Little Flirt' exhibited the highest IAA and zeatin contents. The interaction between 6-day irrigation intervals and 4 dS/m salinity reduced GA in all cultivars. Severe water deficit, as well as salinity stress, decreased zeatin in all cultivars. At all irrigation intervals, the increase in salinity to 4dS/m resulted in a higher ABA in all cultivars. The highest ABA content was observed in 'Little Flirt' exposed to 6-day irrigation intervals and 4 dS/m salinity. Given the increasing rate of growth hormones like IAA, zeatin, and ABA in 'Little Flirt' exposed to water deficit and salinity stress and the role of these hormones in improving stress tolerance and their reduction in 'Sourati Local Cultivar' it can be inferred that 'Little Flirt' was the most tolerant and 'Sourati Local Cultivar' was the most susceptible to

the studied stresses. The results of the study indicated that PGRs could help Roses plants in different ways reducing the effects of water-deficit stress.

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Conflict of interest Z. Shahbani, M. Kosh-Khui, H. Salehi, M. Kafi, A.A.K. Haghighi, S. Eshghi and M. Omidi declare that they have no competing interests.

References

- Ahmed IM, Nadira UA, Bibi N, Zhang G, Wu F (2015) Tolerance to combined stress of drought and salinity in barley. Combined stresses in plants. Springer, pp 93–121
- Ali EF, Bazaid SA, Hassan FAS (2014) Salinity tolerance of Taif roses by gibberellic acid (GA3). Int J Sci Res 3(11):184–192
- Álvarez S, Sánchez-Blanco MJ (2015) Comparison of individual and combined effects of salinity and deficit irrigation on physiological, nutritional and ornamental aspects of tolerance in Callistemon laevis plants. J Plant Physiol 185:65–74
- Álvarez S, Bañón S, Sánchez-Blanco MJ (2013) Regulated deficit irrigation in different phenological stages of potted geranium plants: water consumption water relations and ornamental quality. Acta Physiol Plant 35(4):1257–1267. https://doi.org/10.1007/s11738-012-1165-x
- Arji I, Arzani K, Ebrahimzadeh H, Asghari R (2003) Effect of drought stress on physiological, morphological and biochemical characteristics of some olive cultivars. Doctoral dissertation, Tarbiat Modares University
- Arnon DI (1949) Copper enzymes in isolated chloroplasts. Polyphenoloxidase in Beta vulgaris. Plant Physiol 24:1–15
- Baker NR, Rosenqvist E (2004) Applications of chlorophyll fluorescence can improve crop production strategies: an examination of future possibilities. J Exp Bot 55:1607–1621
- Bandeoğlu E, Eyidoğan F, Yücel M, Avni Öktem H (2004) Antioxidant responses of shoots and roots of lentil to NaCl-salinity stress. Plant Growth Regul 42(1):69–77
- Barrs HD, Weatherley PE (1962) A re-examination of the relative turgidity technique for estimating water deficits in leaves. Aust J Biol Sci 15(3):413–428
- Bhanuprakash K, Yogeesha H (2016) Seed priming for abiotic stress tolerance: an overview. In: Abiotic stress physiology of horticultural crops, pp 103–117
- Brandt B, Munemasa S, Wang C, Nguyen D, Yong T, Yang PG, Schroeder JI (2015) Calcium specificity signaling mechanisms in abscisic acid signal transduction in Arabidopsis guard cells. elife 4:1–25
- Brault M, Maldiney R (1999) Mechanisms of cytokinin action. Plant Physiol Biochem 37:403–412
- Cai X, Niu G, Starman T, Hall C (2014) Response of six garden roses (Rosax hybrida L.) to salt stress. Sci Hortic 168:27–32
- Chastain DR, Snider JL, Collins GD, Perry CD, Whitaker J, Byrd SA (2014) Water deficit in field-grown Gossypium hirsutum primarily limits net photosynthesis by decreasing stomatal conductance, increasing photorespiration, and increasing the ratio of dark respiration to gross photosynthesis. J Plant Physiol 171(17):1576–1585
- Chaves MM, Flexas J, Pinheiro C (2009) Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. Ann Bot 103(4):551–560
- Claeys H, Skirycz A, Maleux K, Inzé D (2012) DELLA signaling mediates stress-induced cell differentiation in Arabidopsis leaves

through modulation of anaphase-promoting complex/cyclosome activity. Plant Physiol 159:739-747

- Dar NA, Amin I, Wani W, Wani SA, Shikari AB, Wani SH, Masoodi KZ (2017) Abscisic acid: A key regulator of abiotic stress tolerance in plants. Plant Gene 11:106–111
- De Pascale S, Martino A, Raimondi G, Maggio A (2007) Comparative analysis of water and salt stress-induced modifications of quality parameters in cherry tomatoes. J Hortic Sci Biotechnol 82(2):283–289
- Dodd IC (2005) Root-to-shoot signalling: assessing the roles of 'up'in the up and down world of long-distance signalling in planta. Plant Soil 274(1):251–270
- Dunlap JR, Binzel ML (1996) NaCI reduces indole-3-acetic acid levels in the roots of tomato plants independent of stress-induced abscisic acid. Plant Physiol 112:379–384
- Faghih S, Zamani Z, Fatahi R, Omidi M (2021) Infuence of kaolin application on most important fruit and leaf characteristics of two apple cultivars under sustained defcit irrigation. Biol Res 54(1):1–15
- Farooq M, Wahid A, Kobayashi MA, Fujita MA, Basra SMA (2009) Plant drought stress: effects, mechanisms and management. In: Sustainable agriculture. Springer, Dordrecht, pp 153–188
- Fricke W, Akhiyarova G, Veselov D, Kudoyarova G (2004) Rapid and tissue-specific changes in ABA and in growth rate in response to salinity in barley leaves. J Exp Bot 55:1115–1123
- Ge L, Yong JWH, Tan SN, Yang XH, Ong ES (2004) Analysis of some cytokinins in coconut (Cocos nucifera L.) water by micellar electrokinetic capillary chromatography after solid-phase extraction. J Chromatogr A 1048:119–126
- Ghanem ME, Albacete A, Martínez-Andújar C, Acosta M, Romero-Aranda R, Dodd IC, Lutts S, Pérez-Alfocea F (2008) Hormonal changes during salinity-induced leaf senescence in tomato (Solanum lycopersicum L.). J Exp Bot 59:3039–3050
- Guerfel M, Ouni Y, Boujnah D, Zarrouk M (2009) Photosynthesis parameters and activities of enzymes of oxidative stress in two young 'Chemlali' and 'Chetoui' olive trees under water deficit. Photosynt 47(3):340–346. https://doi.org/10.1007/s11099-009-0054-z
- Havlov AM, Dobrev PI, Motyka V, Štorchová H, Libus J, Dobr AJ, Malbeck J, Gaudinov AA, Vankov AR (2008) The role of cytokinins in responses to water deficit in tobacco plants overexpressing trans-zeatin O-glucosyltransferase gene under 35S or SAG12 promoters. Plant Cell Environ 31:341–353
- Idrees M, Khan MMA, Aftab T, Naeem M, Hashmi N (2010) Salicylic acid-induced physiological and biochemical changes in lemongrass varieties under water stress. J Plant Interact 5(4):293–303
- Institute S 2013 SAS Institute Inc. Using JMP 11, SAS Institute Inc, Cary, NC
- Javid MG, Sorooshzadeh A, Moradi F, Modarres Sanavy SAM, Allahdadi I (2011) The role of phytohormones in alleviating salt stress in crop plants. Aust J Crop Sci 5:726–734
- Jia W, Wang Y, Zhang S, Zhang J (2002) Salt-stress-induced ABA accumulation is more sensitively triggered in roots than in shoots. J Exp Bot 53(378):2201–2206
- Katsoulas N, Kittas C, Dimokas G, Lykas C (2006) Effect of irrigation frequency on rose flower production and quality. Biosyst Eng 93(2):237–244
- Kiani SP, Maury P, Sarrafi A, Grieu P (2008) QTL analysis of chlorophyll fluorescence parameters in sunflower (Helianthus annuus L.) under well-watered and water-stressed conditions. Plant Sci 175(4):565–573
- Kim T-H, Böhmer M, Hu H, Nishimura N, Schroeder JI (2010) Guard cell signal transduction network: advances in understanding abscisic acid, CO2, and Ca2+ signaling. Annu Rev Plant Biol 61:561–591
- Kirkham MB (2005) Principles of soil and plant water relations. Elsevier, Burlington, p 555

- Le DT, Nishiyama R, Watanabe Y, Vankova R, Tanaka M, Seki M, Yamaguchi-Shinozaki K, Shinozaki K, Tran L-SP (2012) Identification and expression analysis of cytokinin metabolic genes in soybean under normal and drought conditions in relation to cytokinin levels. PLoS ONE 7:e42411
- Li X, Kang Y, Wan S, Chen X, Xu J (2015) Effect of drip-irrigation with saline water on Chinese rose (Rosa chinensis) during reclamation of very heavy coastal saline soil in a field trial. Sci Hortic 186:163–171
- Li X-J, Yang M-F, Chen H, Qu L-Q, Chen F, Shen S-H (2010) Abscisic acid pretreatment enhances salt tolerance of rice seedlings: proteomic evidence. Biochimica et Biophysica Acta (BBA)-Proteins and. Proteomics 1804:929–940
- Liu Y, Zhang X, Tran H, Shan L, Kim J, Childs K, Ervin EH, Frazier T, Zhao B (2015) Assessment of drought tolerance of 49 switchgrass (Panicum virgatum) genotypes using physiological and morphological parameters. Biotechnol Biofuels 8:1–18
- Liu Y, Ji D, Turgeon R, Chen J, Lin T, Huang J, Luo J, Zhu Y, Zhang C, Lv Z (2019) Physiological and proteomic responses of Mulberry Trees (Morus alba. L.) to combined salt and drought stress. Int J Mol Sci 20:2486
- Lu Z, Neumann PM (1998) Water-stressed maize, barley and rice seedlings show species diversity in mechanisms of leaf growth inhibition. J Exp Bot 49(329):1945–1952
- Ma Z, Ge L, Lee AS, Yong JWH, Tan SN, Ong ES (2008) Simultaneous analysis of different classes of phytohormones in coconut (Cocos nucifera L.) water using high-performance liquid chromatography and liquid chromatography—tandem mass spectrometry after solid-phase extraction. Anal Chim Acta 610:274–281
- Magome H, Yamaguchi S, Hanada A, Kamiya Y, Oda K (2004) Dwarf and delayed-flowering 1, a novel Arabidopsis mutant deficient in gibberellin biosynthesis because of overexpression of a putative AP2 transcription factor. Plant J 37(5):720–729
- Masia A, Pitacco A, Braggio L, Giulivo C (1994) Hormonal responses to partial drying of the root system of Helianthus annuus. J Exp Bot 45:69–76
- Massacci A, Nabiev SM, Pietrosanti L, Nematov SK, Chernikova TN, Thor K, Leipner J (2008) Response of the photosynthetic apparatus of cotton (Gossypium hirsutum) to the onset of drought stress under field conditions studied by gas-exchange analysis and chlorophyll fluorescence imaging. Plant Physiol Biochem 46(2):189–195
- Maxwell K, Johnson GN (2000) Chlorophyll fluorescence—A practical guide. EXBOTJ 51(345):659–668
- Momenpour A, Imani A, Bakhshi D, Rezaei H (2015) Evaluation of salinity tolerance in some almond genotypes grafted on GF677 rootstock base on morphological characteristic and chlorophyll fluorescence. J Plant Process Funct 3(10):9–28
- Murti G, Upreti K (2007) Plant growth regulators in water stress tolerance. J Hortic Sci 2:73–93
- Nankishore A, Farrell AD (2016) The response of contrasting tomato genotypes to combined heat and drought stress. J Plant Physiol 202:75–82
- Nayyar H, Gupta D (2006) Differential sensitivity of C3 and C4 plants to water deficit stress: Association with oxidative stress and antioxidants. Environ Exp Bot 58(1–3):106–113. https://doi.org/10. 1016/j.envexpbot.2005.06.021
- Niu G, Rodriguez DS (2008) Responses of growth and ion uptake of four rose rootstocks to chloride-or sulfate-dominated salinity. J Am Soc Hortic Sci 133:663–669
- Omidi M, Khandan-Mirkohi A, Kafi M, Zamani Z, Ajdanian L, Babaei M (2022) Biochemical and molecular responses of Rosa damascena mill. cv. Kashan to salicylic acid under salinity stress. BMC Plant Biol 22(1):1–20
- Park HJ, Kim WY, Yun DJ (2016) A new insight of salt stress signaling in plant. Mol Cells 39(6):447

- Pillay I, Beyl C (1990) Early responses of drought-resistant and-susceptible tomato plants subjected to water stress. J Plant Growth Regul 9:213–219
- Rao NS, Laxman R, Shivashankara K (2016) Physiological and morphological responses of horticultural crops to abiotic stresses. In: Abiotic stress physiology of horticultural crops. Springer, pp 3–17
- Rivero RM, Mestre TC, Mittler R, Rubio F, Garcia-Sanchez F, Martinez V (2014) The combined effect of salinity and heat reveals a specific physiological, biochemical and molecular response in tomato plants. Plant Cell Environ 37:1059–1073
- Sade N, del Mar Rubio-Wilhelmi M, Umnajkitikorn K, Blumwald E (2018) Stress-induced senescence and plant tolerance to abiotic stress. J Exp Bot 69:845–853
- Sah SK, Reddy KR, Li J (2016) Abscisic acid and abiotic stress tolerance in crop plants. Front Plant Sci 7:571
- Salehi-Lisar SY, Bakhshayeshan-Agdam H (2016) Drought stress in plant: Causes, consequences and tolerance. In: Drought stress tolerance in plants, vol 1, pp 1–16
- Satisha J, Prakash G, Murti G, Upreti K (2005) Response of grape genotypes to water deficit: Root, shoot, growth and endogenous hormones. Indian J Plant Physiol 10:225
- Sharma DK, Andersen SB, Ottosen CO, Rosenqvist E (2014) Wheat cultivars selected for high Fv/Fm under heat stress maintain high photosynthesis, total chlorophyll, stomatal conductance, transpiration and dry matter. Physiol Planta 153:284–298
- Shrivastava P, Kumar R (2015) Soil salinity: A serious environmental issue and plant growth promoting bacteria as one of the tools for its alleviation. Saudi J Biol Sci 22:123–131
- Umar M, Uddin Z, Siddiqui Z (2019) Responses of photosynthetic apparatus in sunflower cultivars to combined drought and salt stress. Photosynthetica 57:627–639
- Upreti K, Sharma M (2016) Role of plant growth regulators in abiotic stress tolerance. Abiotic stress physiology of horticultural crops. Springer, Heidelberg, Berlin, pp 19–46
- Van Zelm E, Zhang Y, Testerink C (2020) Salt tolerance mechanisms of plants. Annu Rev Plant Biol 71:403–433
- Verslues PE, Bray EA (2006) Role of abscisic acid (ABA) and Arabidopsis thaliana ABA-insensitive loci in low water potential-induced ABA and proline accumulation. J Exp Bot 57(1):201–212
- Verslues PE, Zhu J-K (2005) (2005) Before and beyond ABA: upstream sensing and internal signals that determine ABA accumulation and response under abiotic stress. Biochem Soc Transact 33(2):375–379. https://doi.org/10.1042/BST0330375
- Veselova S, Farkhutdinov R, Veselov D, Kudoyarova G (2006) Role of cytokinins in the regulation of stomatal conductance of wheat seedlings under conditions of rapidly changing local temperature. Russ J Plant Physiol 53:756–761
- Wang W, Vinocur B, Altman A (2003) Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. Planta 218:1–14
- Wang Y, Mopper S, Hasenstein KH (2001) Effects of salinity on endogenous ABA, IAA, JA, and SA in Iris hexagona. J Chem Ecol 27:327–342
- Werner T, Köllmer I, Bartrina I, Holst K, Schmülling T (2006) New insights into the biology of cytokinin degradation. Plant Biol 8:371–381
- Werner T, Nehnevajova E, Köllmer I, Novák O, Strnad M, Krämer U, Schmülling T (2010) Root-specific reduction of cytokinin causes enhanced root growth, drought tolerance, and leaf mineral enrichment in Arabidopsis and tobacco. Plant Cell 22:3905–3920
- Yang Z, Liu J, Poree F, Schaeufele R, Helmke H, Frackenpohl J, Lehr S, von Koskull-Döring P, Christmann A, Schnyder H (2019) Abscisic acid receptors and coreceptors modulate plant water use efficiency and water productivity. Plant Physiol 180:1066–1080
- Zawaski C, Busov VB (2014) Roles of gibberellin catabolism and signaling in growth and physiological response to drought and shortday photoperiods in Populus trees. PLoS ONE 9:e86217

- Zhang YJ, Gao H, Li YH, Wang L, Kong DS, Guo YY, Lu YL (2019) Effect of water stress on photosynthesis, chlorophyll fluorescence parameters and water use efficiency of common reed in the Hexi Corridor. Russ J Plant Physiol 66(4):556–563
- Zhou R, Yu X, Ottosen CO, Rosenqvist E, Zhao L, Wang Y, Yu W, Zhao T (2017) Drought stress had a predominant effect over heat stress on three tomato cultivars subjected to combined stress. BMC Plant Biol 17:24
- Zörb C, Geilfus C-M, Mühling KH, Ludwig-Müller J (2013) The influence of salt stress on ABA and auxin concentrations in two maize cultivars differing in salt resistance. J Plant Physiol 170:220–224

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