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INTERACTION OF SALINITY AND PHYTOHORMONES ON WHEAT PHOTOSYNTHETIC TRAITS AND MEMBRANE STABILITY

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To evaluate phytohormones effects on stomatal conductance, chlorophyll fluorescence, membrane stability, relative water content and chlorophyll content under salinity, a factorial experiment with 4 replicates was conducted. Treatments were salinity (0, 3.5 and 7 dS/m), phytohormones (control, gibberellic acid and abscisic acid) and wheat cultivars (Gascogen, Zagros, and Kuhdasht). Results showed that a high level of salinity increased chlorophyll fluorescence and relative water content, while membrane stability, chlorophyll content, and stomatal conductance were decreased. Abscisic acid treatment had more effective role in membrane stability. Although membrane stability was much more under gibberellic acid treatment, restoration of membrane stability was considerable under abscisic acid treatment for Gascogen and Kuhdasht cultivars. Spraying of gibberellic acid induced the highest chlorophyll content in the three salinity levels and all of the cultivars. The maximum amount of stomatal conductance was achieved under gibberellic acid treatment. Abscisic acid caused less chlorophyll fluorescence in comparison to gibberellic acid. About relative water content, abscisic acid was effective in high salinity levels so that it caused stomatal closure, which reduced water loss and maintained turgor in plants.

Key words: *Triticum aestivum*, NaCl, gibberellic acid, abscisic acid, chlorophyll fluorescence, stomatal conductance

Salinity is one of the major abiotic stresses affecting plant growth, development and productivity (Rahnama & Ebrahimzadeh 2004). Salinity is a complex environmental constraint that presents two main components: i) osmotic component due to decrease in the external osmotic potential of the soil solution and ii) ionic component linked to the accumulation of ions which become toxic at high concentrations (mainly Na^+ and Cl^-) (El-Bassiouny & Bekheta 2004). It is estimated that over 800 million hectares of land in the world are affected by both salinity and sodicity (Munns 2005). Plants exposed to salt stress must undergo changes in their metabolism in order to survive in the deleterious condition of the stress (Rahnama & Ebrahimzadeh 2004). These changes include stomatal conductance (SC), photosynthetic efficiency, water and nutrients availability (Munns & Termaat 1986). Chlorophyll content (CC), relative water content (RWC) and SC are affected by increasing salinity (Adnan Shahid *et al*. 2008).

RWC represents a useful indicator of the state of plant water balance, because it expresses the absolute amount of water, which plant requires reaching full saturation (González & González-Vilar 2001). Leaf RWC is a useful trait for selection of tolerant plants in saline condition (Schonfeld *et al*. 1988) and is significantly reduced under salinity stress (El-Tayeb 2005). Furthermore, salinity stress also reduces RWC in sensitive wheat cultivars seedlings (Aldesuquy & Gaber 1993).

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Chlorophyll (Chl) is one of the most important pigments, and is responsible for green colour in plants. Changes in photosynthetic parameters could potentially be used as a screening method for salinity tolerance in plants, because more tolerant cultivars are expected to exhibit less disturbances in photosynthetic processes (Belkhodja *et al.* 1999). Generally, Chl content is reduced under salinity conditions (Iqbal *et al*. 2006).

One of the leading parameters for the estimation of salinity stress effects is chlorophyll fluorescence (CF). CF is a subtle reflection of primary reactions of photosynthesis (Sayed 2003). The ratio of F_v/F_m is proportional in order to show maximum amount of photosystem II (PSII), and this ratio is sensitive to environmental changes (Sayed 2003). Krishnaraj *et al*. (1993) used measurement of CF for screening of tolerant wheat genotypes (Krishnaraj *et al*. 1993). Various stress conditions may reduce the rate of photosynthesis, and disturb the light-driven photosynthetic electron transport *via* CF fluorescence (Allahverdiev *et al*. 1998). The inverse relationship between *in vivo* CF and photosynthetic activity can be used to study the potential photosynthetic activity of leaves and detect stress effects on green plants. There are several parameters of the *in vivo* CF which can be applied for detecting stress and damages to the photosynthetic apparatus. Variable fluorescence (F_v) and initial fluorescence (F_o) ratio are two of these parameters, and they show the efficiency of photosynthesis (Allahverdiev *et al*. 1998).

The decline in productivity in many plant species subjected to excess salinity is often associated with a reduction in photosynthetic capacity (Belkhodja *et al*. 1999). The reduction in photosynthetic capacity due to salt stress is associated with reduced SC (Belkhodja *et al*. 1999). Measurement of cell membrane stability (CMS) has often been used for screening for drought and salinity tolerance in various plants such as sorghum, maize, rice and wheat (Jyothsnakumari *et al*. 2009). The decreased gibberellic acid (GA_3) and increased abscisic acid (ABA) contents were reported in salt-stressed plants, which led to the suggestion that salt stress induces changes in RWC and membrane permeability (Kaya *et al*. 2009). Therefore, an alternative strategy to ameliorate salt stress could be exogenous application of plant growth regulators (Levent Tuna *et al*. 2008). So, focusing on using of phytohormones such as GA_3 (which has important effects on regulation of plant reaction to environment and control of some induced genes in stress condition) is necessary (Nagvi 1999). It has been reported that GA_3 treatment reduces the adverse effects of salt stress (Chakrabarti & Mukherji 2003). Phytohormones have also a control role in RWC and membrane permeability (Kaya *et al*. 2009). It was found that GA_3 increases plant growth and pigment content of salinized plants (Aldesuquy & Gaber 1993). Prakash and Prathapasenan (1990) observed a significant decrease in the levels of gibberellins and cytokinins and an abrupt rise in ABA content in salt-stressed plants (Prakash & Prathapasenan 1990). ABA has an important function in the ability of rice cultivars to tolerate conditions of stress (Abdel-Haleem & Tanimoto 2008), so ABA spraying increases expression of numerous reactive genes in salt-stressed rice cultivars (Gupta *et al*. 1998).

Wheat (*Triticum aestivum* L.) is one of the most important crops in Iran and throughout the world, which has a special importance in human nutrition (Esfandiari *et al*. 2007). Thus, this experiment was carried out to evaluate the effects of ABA and GA_3 on some physiological traits of wheat cultivars including membrane stability (MS), chlorophyll content (CC), chlorophyll fluorescence (CF), stomatal conductance (SC), relative water content (RWC) under saline conditions in order to evaluate inhibitory or stimulatory effects and importance of the hormones on above-mentioned parameters in the three Iranian indigenous wheat cultivars in saline conditions.

MATERIALS AND METHODS

This study was carried out using a factorial experiment based on a completely randomized design with 4 replicates in a greenhouse at The University of Mohaghegh Ardabili, Ardabil, Iran. Treatments were salinity [Control : 0 ($Ctrl_s$), 3.5 and 7 dS/m, phytohormones (GA_3 : 50 mg/l, ABA : 100 mg/l, and control ($Ctrl_h$)], and 3 wheat (*Triticum aestivum*) cultivars [Gascogen (G), Zagros (Z) and Kuhdasht (K)]. The seeds were sterilized for 4 minutes in sodium hypochlorite 0.5%, rinsed in distilled water and were placed at 23 ± 1°C in a germinator. Then,

germinated seeds were sown in pots (34 cm length, 25 cm width, and 18 cm height), which had sandy clay loam soil. Salt solutions (2.08 and 4.17 g/l NaCl, respectively) were poured on pots one week before planting, to reach 3.5 and 7 dS/m salinity levels. The initial salinity level (EC) of the soils in the pots was 3.93 dS/m. The phytohormones were foliarly sprayed in three stages, including tillering, shooting and flag leaf appearance stage (FLAS).

Membrane Stability (MS)

MS was measured once before hormone spraying and another time at FLAS. For MS determination, the procedures of Khandan Bejandi et al. (2009) that is briefly mentioned here was followed, the fully expanded leaves at each stage were selected and one-centimetre pieces were cut from the middle of the leaves. Then, 0.3 g of the leaf samples were weighed and rinsed in distilled water. These pieces were put in tubes with 25 ml distilled water and 25 ml polyethylene glycol 40% (PEG 6000) and then were put in an incubator for 24 hours (10°C). After that time, the solution of tubes was poured out, and the pieces were rinsed. Then, control and treatment samples were put in 25 ml distilled water for 24 hours. After a certain time, electrical conductivity of solutions was measured, and the samples were autoclaved for 15 min, cooled down to room temperature and then measured once more. MS is defined as Eq. (1) according to Khandan Bejandi *et al*. (2009):

$$CMS\ [\%] = 1 - (1 - T_1 / T_2) / (1 - C_1 / C_2) \times 100 \quad (1)$$

In the above equation, C and T are the electrical conductivity for control and PEG treatment, respectively. Indices 1 and 2 are the first and second conductance, respectively.

Chlorophyll Content (CC)

CC was estimated at two stages, once before hormone spraying (4 leaves stage) and another time at FLAS by hand-held chlorophyll meter (SPAD-502, Minolta, Japan).

Chlorophyll Fluorescence (CF)

CF was measured after hormone spraying at FLAS by a chlorophyll fluorometer (Optiscience, USA).

Stomatal Conductance (SC)

SC was measured after hormone spraying at FLAS by porometer (Decagon, USA).

Relative Water Content (RWC)

RWC was estimated according to Khandan Bejandi et al. (2009) using the following equation:

$$RWC = (F_W - D_W) / (T_W - D_W) \times 100 \quad (2)$$

where F_W, D_W and T_W are the fresh, dry and turgid weight of leaves, respectively. Samples were taken from newly expanded leaves. Leaves were immediately weighed and then immersed in distilled water for 5 hours. Thereafter, turgid weight was obtained and finally, dry weight was measured 24 hours after being put at 75°C oven.

Statistical Analysis

After normalization test, the data were analyzed by SAS 9.1 and SPSS 16.0 software. Means were compared by Slice command in SAS at 1% statistical probability level.

RESULTS AND DISCUSSION

The results showed that interactions among cultivars, salinity, and hormones on the evaluated traits were significant (Table 1). Based on the interaction between hormones and salinity, GA_3 decreased more inhibitory effects of salinity as compared to ABA (Table 2).

Before the hormone spraying, the highest MS was achieved in K and $Ctrl_s$ and the lowest value was obtained in G at 7 dS/m salinity level (Figure 1).

After the hormone spraying, the highest MS (about 20%) was achieved in K, without salinity and under GA_3 treatment and the lowest MS was observed in G, without salinity and under ABA treatment. By spraying of GA_3, MS was increased under control (0) and both salinity levels (3.5 and 7 dS/m). Also, spraying of ABA in interaction with salinity levels increased MS as compared to $Ctrl_s$ and $Ctrl_h$, but this increase was less than the content resulted from spraying of GA_3 (Table 2).

Tellingly, GA_3 as compared to ABA showed more MS. However, interestingly enough, GA_3 treatment under $Ctrl_s$ did not increase MS. By contrast, in G, GA_3 treatment at 3.5 and 7 dS/m salinity levels, in

comparison to Ctrls caused more decrease in MS as compared to the same condition for ABA. In K like G and contrary to Z, ABA in 3.5 and 7 dS/m salinity as compared to $Ctrl_s$ was better than GA_3 treatment. Ashraf *et al*. (2005) stated that membrane lipids stability under saline condition seldom remains intact. A major impact of environmental stress on plants is cellular membrane modification due to salt stress, expressed in increased permeability and leakage of ions (Khandan Bejandi *et al*. 2009). Studies showed that abiotic stresses, including salinity generated reactive oxygen species and membrane lipid peroxidation in leaves and ears of wheat (Beltrano *et al*. 1997), caused decrease in MS. Khandan Bejandi *et*

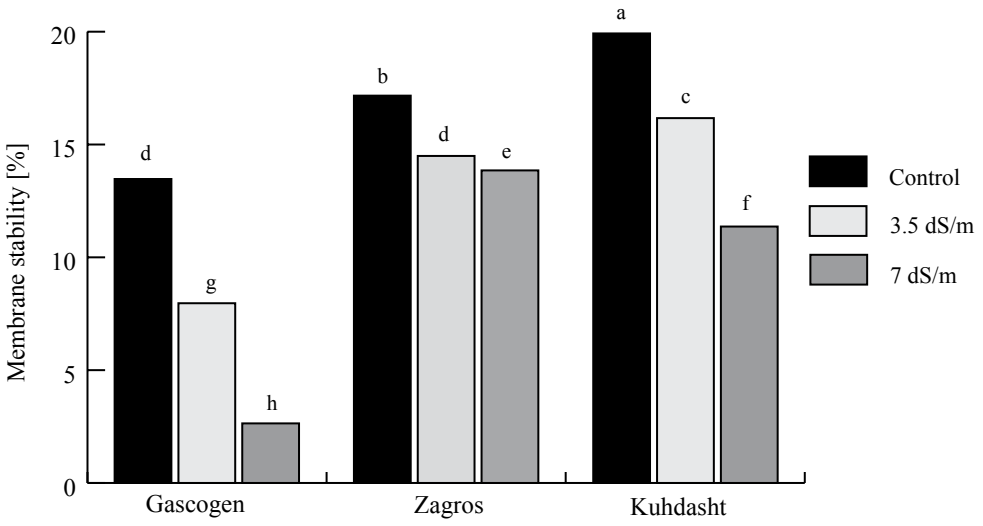

Figure 1. Membrane stability [%] under salinity stress in the three wheat cultivars

T a b l e 1

Analysis of variance for effects of cultivar, salinity and phytohormones on evaluated traits in wheat

S.O.V	df	MS				
		Membrane stability	Chlorophyll content	Stomatal conductance	Chlorophyll fluorescence	Relative water content
Cultivar (C)	2	2,638.021^{++}	862.156^{++}	576.411^{++}	0.001^{++}	2,839.828^{++}
Salinity (S)	2	123.486^{++}	162.443^{++}	1,518.478^{++}	0.001^{++}	594.008^{++}
Hormone (H)	2	109.446^{++}	58.609^{++}	1,789.296^{++}	0.035^{++}	816.332^{++}
C × S	4	39.406^{++}	12.108^{++}	851.088^{++}	0.001^{++}	246.715^{++}
C × H	4	15.156^{++}	0.191^{+}	215.310^{++}	0.002^{++}	23.098^{++}
H × S	4	18.542^{++}	0.074^{ns}	142.363^{++}	0.001^{++}	34.226^{++}
C × S × H	8	13.668^{++}	0.192^{++}	40.494^{++}	0.0001^{ns}	22.056^{++}
Error	81	0.062	0.060	0.066	0.0001	0.333
CV [%]		0.32	0.55	0.53	0.88	1.28

$^{+}$ and $^{++}$: Significant at 5% and 1% of probability levels, respectively; ^{ns}: Non-significant

al. (2009) stated that the accumulation of reactive oxygen species under stress conditions may damage many cell components, such as lipids, proteins, carbohydrates and nucleic acids as a result of cell membrane lipids peroxidation. The excess of NaCl leads to the loss of potassium due to membrane depolarization by sodium ions (Turan *et al*. 2009). Bhutta investigation (2011) showed that MS increased under the non-saline environment in the leaves of wheat seedlings, in so far as under low saline levels, MS decreased 22% and 29% after 20 and 40 days treatments, respectively. MS showed more decrease (27%) under high saline levels (160 n*M* NaCl) after 40 days. In other words, MS in wheat leaves reached the lowest levels in both wheat genotypes (S24 and DN-27).

T a b l e 2

Mean comparison of interaction among variety × salinity × hormone with evaluated traits in wheat

Treatment			Membrane stability [%]	Chlorophyll content	Stomatal conduct [mmol/m^2/s]	Chlorophyll fluorescence	Relative water content
S1	G	H1	85.65^{b}	53.79^{b}	40.57^{e}	0.7100^{b}	84.97^{c}
		H2	93.79^{a}	52.03^{c}	33.43^{f}	0.6733^{e}	83.50^{d}
		H3	74.37^{e}	54.67^{a}	60.98^{a}	0.6900^{c}	87.49^{b}
	Z	H1	75.62^{d}	42.90^{e}	23.47^{h}	0.7100^{b}	54.97^{h}
		H2	77.00^{c}	41.04^{f}	16.25^{i}	0.6000^{g}	50.77^{i}
		H3	74.06^{e}	43.85^{d}	41.00^{d}	0.6833^{d}	57.55^{g}
	K	H1	62.68^{g}	46.79^{h}	31.80^{g}	0.7267^{a}	78.94^{e}
		H2	63.65^{f}	45.33^{i}	46.66^{c}	0.6100^{f}	69.66^{f}
		H3	59.26^{h}	48.62^{g}	52.40^{b}	0.6700^{e}	90.65^{a}
S2	G	H1	85.94^{b}	48.19^{b}	77.34^{b}	0.6800^{c}	87.60^{b}
		H2	86.84^{a}	47.08^{c}	46.08^{f}	0.6433^{f}	77.78^{c}
		H3	84.01^{c}	49.88^{a}	79.88^{a}	0.6567^{e}	91.55^{a}
	Z	H1	84.42^{c}	38.87^{h}	56.46^{d}	0.6933^{b}	67.06^{f}
		H2	85.60^{b}	37.07^{i}	51.31^{e}	0.6367^{g}	63.61^{g}
		H3	82.99^{d}	39.84^{g}	60.25^{c}	0.6767^{d}	70.50^{e}
	K	H1	63.68^{f}	43.79^{e}	35.96^{h}	0.7067^{a}	67.11^{f}
		H2	64.43^{e}	42.14^{f}	31.30^{i}	0.6233^{h}	63.77^{g}
		H3	61.46^{g}	45.62^{d}	37.97^{g}	0.6833^{c}	73.33^{d}
S3	G	H1	87.42^{b}	50.91^{b}	55.45^{e}	0.7100^{a}	78.75^{b}
		H2	88.60^{a}	49.09^{c}	36.08^{i}	0.6500^{f}	67.67^{d}
		H3	85.26^{d}	51.77^{a}	70.01^{a}	0.6567^{e}	82.73^{a}
	Z	H1	86.10^{c}	37.58^{h}	53.79^{f}	0.6867^{c}	48.22^{h}
		H2	87.27^{b}	36.01^{i}	46.19^{h}	0.6100^{h}	42.83^{i}
		H3	83.99^{e}	39.15^{g}	64.96^{c}	0.6667^{d}	63.45^{e}
	K	H1	64.16^{f}	41.85^{e}	58.41^{d}	0.7000^{b}	34.97^{f}
		H2	65.54^{g}	40.05^{f}	48.17^{g}	0.6333^{g}	52.72^{g}
		H3	63.31^{h}	42.89^{d}	66.96^{b}	0.6667^{d}	73.22^{c}

Similar letters in each column are not significant at 1% and 5% probability level
S1 = Control, S2 = 3.5 dS/m salinity, S3 = 7 dS/m salinity
G = Gascogen cultivar, K = Kuhdasht cultivar, Z = Zagros cultivar, H1 = control, H2 = Abscisic acid, H3 = Gibberellic acid

Before hormone spraying, with increase in salinity, significant reduction in CC was observed and the highest reduction reached 25.06% in Z at 3.5 dS/m salinity (Figure 2). After hormone spraying, the highest CC was obtained under GA_3 treatment (Table 2). It seems that GA_3 has an important effect on Chl stability and synthesis, even under salinity condition.

Reduction in leaf CC under NaCl stress is attributed to the destruction of Chl pigments and the instability of the pigment protein complex (Levitt 1980). The Chl depletion may be a result of inhibition of Chl biosynthesis. This inhibition is due to an increase in ethylene production by the elevated NaCl content (Khan 2003). Reduction in Chl concentrations is probably because of the inhibitory effect of the accumulated ions of various salts on the biosynthesis of different Chl fractions. Also, decrease in CC may be based on the formation of proteolytic enzymes such as chlorophyllase, which is responsible for the Chl degradation (Levent Tuna *et al*. 2008). It has also been shown that GA_3 alleviates the effects of salt stress on pigments (Shah 2007). This may well be attributed to the GA_3-generated enhancement of ultra-structural morphogenesis of plastids coupled with retention of Chl and delay of senescence caused by the hormone treatment (Shah 2007). Decrease in CC under salinity stress can be for this reason which Chl degradation is more than Chl synthesis (Uzma & Asghari 2006). Sairam *et al*. (2002) reported that reduction of CC in a tolerant wheat variety was lower than in a sensitive one. Akbari Ghogdi *et al*. (2012) documented that salt treatment reduced the CC at tillering stage and decreased it at flowering stage in wheat cultivars.

In the present experiment, ABA caused the lowest CF in salinity levels. However, with scrutiny comparison of GA_3 and ABA, it can be understood that ABA in higher salinity levels caused much less decrement. The ratio F_v/F_m is proportional in order to show maximum amount of PSII. The ratio for a functional leaf varies between 0.75 and 0.85 and a decline in this ratio is an indicator for photoinhibitory damage (DeEll *et al*. 1999).

There was a significant increase in SC with spraying of GA_3 under saline condition in comparison to the $Ctrl_s$ condition. The lowest amount of SC was achieved in Z under ABA treatment and the $Ctrl_s$ (Table 2). Interaction between ABA and salinity probably decreases SC to the lower amount than that of control. In brief, in the three cultivars G, K and Z and salinity levels, ABA as compared

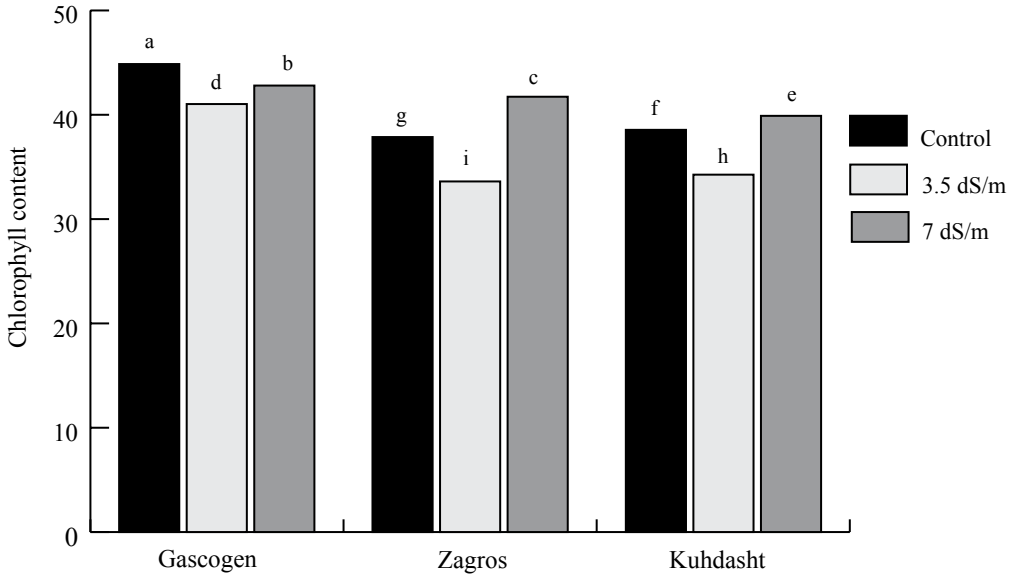

Figure 2. Chlorophyll content under salinity stress in the three wheat cultivars

to GA_3, decreased SC. Environmental factors such as salinity that affect water quality lead to changes in stomatal opening (Nelson *et al*. 1998). Salinity increases stomatal resistance, which could be explained by inhibition of plant growth due to water stress (Chatrath *et al*. 2000). To control the water status of stomatal pore, plants may use two hormone mediated strategies: 1) is to control stomatal pore width, and 2) is to control the hydraulic conductivity of the root (Ludewig *et al*. 1988). ABA in guard cells activates ionic channels and proton pump that are associated with stomatal closure (Goh *et al*. 2009). H_2O_2 acts as a local or systemic signal for leaf stomata closure (Chaves *et al*. 2009). Decrease in SC indicates that changes in the osmotic situation of root medium quickly affect shoot water relations (Rodriguez *et al*. 1997). Salinity causes ABA production in roots which is translocated to shoot and induces stomatal closure and limitation of cell growth (Lobna *et al*. 2009). Rahnama *et al*. (2010) reported that salinity reduced SC in different wheat genotypes and the largest reduction was observed in sensitive genotypes of wheat. Also, they suggested that root signals presumably cause a large decrease in SC of wheat genotypes under salinity.

ABA in $Ctrl_s$ reduced RWC. However, interaction between GA_3 and salinity levels increased the content of RWC (Table 2). RWC decreased by increase in salinity levels in wheat genotypes (Akbari Ghogdi *et al*. 2012). It seems that decrease in RWC decreases the turgor due to water limitation. Such an increase in the RWC of salinized plants over that of the control or hormone-treated salinized plants may be due to the accumulation of ABA to levels that cause stomatal closure, which reduces water loss, maintains turgor and improves the water use efficiency of plants and allows more growth with a given supply of water (Aldesuquy & Ibrahim 2001).

Generally, it is expected that GA_3 moderates the deleterious condition of saline stress in comparison to ABA in wheat. It is known that conduction of the present study in field is essential in order to assess effects of the factors in uncontrollable condition. However, in natural condition there are many factors that are out of control, thus the results of *in natura* studies may deviate from those of greenhouse condition. It is recommended to evaluate the factors of the present greenhouse study in field.

CONCLUSION

According to the present experiment, hormones and high saline levels have different effects on various parameters in wheat cultivars. High saline levels cause higher chlorophyll fluorescence, and relative water content. In contrast, lower membrane stability, chlorophyll content, and stomatal conductance have been caused under saline condition. Abscisic acid is more effective for decreasing adverse consequences of salinity on chlorophyll fluorescence, membrane stability and, relative water content. However, gibberellic acid has beneficial influence on chlorophyll content and stomatal conductance as compared by abscisic acid under saline stress. In sum, phytohormones play a significant role in moderating the effects of salinity on photosynthetic traits and membrane stability.

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