



Full Length Article

GR24 Triggered Variations in Morpho-Physiological Attributes of Sunflower (*Helianthus annuus*) under Salinity

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Abstract

Sunflower (*Helianthus annuus* L.) is a palatable oil crop worldwide and its production is threatened by salt stress. Phytohormones are helpful to alleviate the salt stress by regulating the plant metabolism. To evaluate the response of sunflower to salt stress and GR24, a synthetic strigolactone analogue was applied as foliar spray. Replicates of sunflower hybrids (FH-593 and FH-596) were grown in the pots under two levels of salinity (0, and 120 mM NaCl) and four levels of GR24 treatments (0, 3.35, 33.5 and 335 nM). The results showed that salinity inhibited the shoots and roots growth, whereas GR24 upgraded the growth under salinity. Leaf gas exchange attributes, photosynthetic pigments and water relation attributes were declined under salinity and GR24 application partially reversed adverse effects of salinity on gas exchange attributes. GR24 spray did not affect the photosynthetic pigments. Additionally, foliar application of GR24 decreased leaf water potential and turgor potential but raised osmotic potential and relative water contents in response to salt stress. The GR24 level 33.5 nM was most effective in alleviating the harmful impact of salinity. Both hybrids showed variable response to overcome salinity stress. © 2019 Friends Science Publishers

Keywords: Sunflower; Strigolactones; Salinity; Growth; Photosynthetic pigments

Introduction

Soil salinization has become the most imperative agricultural problem that is increasing progressively all over the world that declines the food production by restricting the use of cultivated area (Porcel *et al.*, 2012). Inhibitory impacts of salinity stress on water uptake (Munns and Tester, 2008) lead to reduced plant growth as well as yield (Chookhampaeng, 2011; Farooq *et al.*, 2015). Stomatal closure during salinity stress either directly or through hormones causes low transpiration rate (Jia *et al.*, 2002), which reduces stomatal conductance ultimately leading to reduction in carbon dioxide assimilation (Horie *et al.*, 2012). Salt stress disturbs the water relation attributes. Water uptake becomes restricted due to more negative solute potential, consequently more reduced water potential results due to salinity (Cha-um *et al.*, 2010; Hussain *et al.*, 2016), which declines plant growth (Eisa *et al.*, 2012). Best strategy of plants to survive under salt stress is osmotic adjustment (Gorai *et al.*, 2011).

Sunflower is a cash crop whose area and production is increasing from last decade in Pakistan (Shah *et al.*, 2013). Nonetheless, salinity stress negatively affects its production. Sunflower, being salt tolerant in nature, can be grown better in salinized soil (Mohamedin *et al.*, 2006). In fact, it is a pioneer plant used for reclamation of salt affected land (Zeng *et al.*, 2014). However, high concentration of salts in

soil adversely affects its growth and photosynthetic activities (Zeng *et al.*, 2014).

Plants are always subjected to various challenging environmental conditions. Plants are sessile in nature, yet they can adapt to varying environments by evolving complicated as well as precise mechanisms (Umehara *et al.*, 2008). The latest innovation in plant sciences is the discovery of phytohormones named strigolactones (Gomez-Roldan *et al.*, 2008). The strigolactones (SLs) function as signaling molecules both for fungal symbiosis and plant productivity through nutrient availability and plant architecture respectively (Akiyama *et al.*, 2005). These are chemically terpenoid lactones (Alder *et al.*, 2012) that are originally identified as seed germination stimulators of parasitic weeds like *Phelipanche* and *Striga* (Cook *et al.*, 1966). These phytohormones function as shoot branching suppressant and stimulator of seed germination and root nodulation (Brewer *et al.*, 2013). The SLs as multifunctional signaling molecules regulate the reproductive growth and architecture of plant (Kapulnik *et al.*, 2011). Moreover, the SLs mediated arbuscular mycorrhizal association under adverse conditions like nutrient deficiency, salinity and drought (Garcia-Garrido *et al.*, 2009) favour their positive response in stress alleviation (Lopez-Raez *et al.*, 2011).

The hypothesis of the current study was that whether the application of GR24 is effective in alleviating the adverse effects of salt stress on sunflower. The specific

objective of the current study was to assess the changes in acclimatizing the salinity stress through phytohormones like strigolactones as little work has been done to investigate the physiological roles of SLs under salt stress in sunflower.

Materials and Methods

To investigate the role of strigolactones in enhancing the salt tolerance in sunflower, an experiment was carried out in sand culture during the sunflower growing season of year 2016 and 2017. Achenes of two sunflower hybrids named FH-593 and FH-596, were obtained from the Ayub Agricultural Research Institute, Faisalabad, Pakistan. Achenes were sown in plastic pots (diameter = 25 cm; depth = 27.5 cm), each having 10 kg well washed dry sand. Completely randomized design (CRD) with four replicates was employed for experiment. Ten achenes of each sunflower hybrids (FH-593 and FH-596), were surface sterilization with 5% sodium hypochlorite solution and sown in pots having moist sand. After sowing, Hoagland's nutrient solution (2 L/pot) was added weekly. After an interval of ten days, thinning was done and four plants were maintained in each pot. Twenty four days old plants were treated with two salt levels (0 mM NaCl) and 120 mM NaCl in Hoagland's nutrient solution. To attain the 120 mM NaCl level, stepwise concentrations of NaCl in aliquots of 50 mM were raised after an acclimatization period of 4-week salinity. Plants were watered daily to replace the water loss. Foliar spray of each concentration of GR24 (0, 3.35, 33.5 and 335 nM) were applied to 36 days old plant. The 25 mL solution of each of GR24 levels was used to fully saturate the plants in each pot. Tween 20 @ 0.1% as surfactant was used to boost the absorbance of solution. After 2 weeks of GR24 spray, data for the following attributes were recorded.

Growth Attributes

Two plants per replicate were uprooted and cleaned. Shoot and root fresh weights and their lengths were recorded immediately. The dry weights of shoot and root in g plant⁻¹ were recorded after oven dried at 70°C until constant weight was attained.

Gas Exchange Attributes

Gas exchange parameters were recorded with the help of infrared gas analyzer, LCA-4 ACD (Hoddesdon, UK). subscript the 2 of net CO₂ assimilation rate (*A*), transpiration rate (*E*), water use efficiency (*A/E*), substomatal conductance (*C_s*), and stomatal conductance (*g_s*), were made from 10:30 a.m. to 12:30 p.m. on top third leaf of sunflower plant. The other information provided by the analyzer was; leaf chamber gas flow rate (*U*) 251 μmol s⁻¹, ambient pressure (*P*) 98.8 kPa; leaf surface area 6.25 cm²; ambient CO₂ concentration 352 μmol mol⁻¹; leaf chamber water vapor pressure 6.0 to 8.9 mbar; molar air flow/unit

leaf area (*U_s*) 22.06 mol m⁻² s⁻¹, leaf chamber temperature 28.4 to 32.4°C; *PAR* (*Q_{leaf}*) 942 μmol m⁻² s⁻¹ and relative humidity of chamber 41.2%.

Photosynthetic Pigments

The method devised by Arnon (1949) was used for the estimation of photosynthetic pigments. The extraction of the fresh leaf sample (0.5 g) in 80% acetone was carried out. After centrifugation at 12,000 × *g* for 15 min of extracted material, supernatants were run on UV-visible spectrophotometer (IRMECO U-2020). The absorbance of the supernatant at wavelengths of 480, 645 and 663 nm against a blank (80% acetone) was recorded afterward.

Leaf Water Relations

The top third petiolated leaf from each replicate was excised and its leaf water potential (ψ_w) was measured from 6.00 to 8.00 am with Scholander pressure chamber (Arimad-2-Japan) (Scholander *et al.*, 1964). The same leaf was frozen at -20°C for a week. After thawing cell sap was extracted from frozen leaf and leaf osmotic potential (ψ_s) was determined with vapor pressure osmometer (Wescor 5500). The equation $\psi_p = \psi_w - \psi_s$ was used to find the turgor potential of leaf.

Relative Water Contents (%)

The method of Jones and Turner (1978) was used to measure the relative water contents expressed in percentage. The samples of the fresh leaf were collected and weighed (FW), then, the samples were kept in distilled water for 24 h in dark. Turgid weights (TW) were taken. Lastly, dry weights (DW) were recorded by putting the samples in oven at 80°C for 48 h. The following formula is used to measure the relative water contents:

$$\text{LRWC \%} = \frac{\text{FW} - \text{DW}}{\text{TW} - \text{DW}} \times 100$$

Statistical Analysis

The experimental units were arranged in completely randomized design (CRD) with four replicates. The statistical analysis of all data was carried out in three-way analysis of variance (ANOVA) by computing the package of COSTAT computer software (Cohort software Berkeley, California). Data were compared by using least significant difference of means (Snedecor and Cochran, 1980).

Results

A three-way ANOVA depicted significant effects of salinity on growth attributes. Salt stress significantly reduced ($P \leq 0.001$) the fresh and dry masses of shoot and root, as well as their elongation (Table 1 and Fig. 1). The results showed that the fresh and dry weights of shoot

Table 1: Data of mean squares from analysis of variance for growth, photosynthetic pigments, gas exchange and water relation attributes of sunflower plants when treated to different levels of foliar-applied GR24 under control and saline conditions

Source of variance	df	Shoot fresh weight	Root fresh weight	Shoot dry weight	Root dry weight	Shoot length	Root length	A
Salinity (S)	1	10536.509***	26.742***	103.531***	0.410***	5200.213***	148.536***	1170.495***
GR24	3	872.605***	4.934***	23.568***	0.070***	1084.769***	10.161ns	22.031ns
Hybrids (HB)	1	29.485ns	14.260***	7.385***	0.086***	676.650***	5.347ns	13.727ns
S × GR24	3	216.331***	0.969ns	0.173ns	0.007ns	271.581**	5.202ns	28.362ns
S × HB	1	2779.926***	0.293ns	0.324ns	0.0001ns	409.556**	3.285ns	60.723*
GR24 × HB	3	298.482***	0.353ns	6.008***	0.010*	137.765*	11.452ns	4.671ns
S×GR24×HB	3	77.005*	1.245*	3.538***	0.0007	121.367ns	3.035ns	22.741ns
Error	48	18.585	0.396	0.366	0.003	44.821	4.189	11.281
Source of variance	df	E	g_s	C_i	C_i/C_a	A/E	Chl. a	Chl. b
Salinity (S)	1	29.160***	20664.063***	1555.316ns	0.011ns	70.760***	0.373*	0.268*
GR24	3	1.689***	1268.229ns	1856.591*	0.016*	4.943*	0.065ns	0.060ns
Hybrids (HB)	1	1.587**	189.062ns	140.126ns	0.0005 ns	23.495***	0.4078*	0.020ns
S × GR24	3	1.130**	301.562ns	342.668ns	0.003ns	3.525ns	0.0543ns	0.062ns
S × HB	1	0.201ns	264.062ns	35.850ns	0.0007ns	11.122*	0.076ns	0.060ns
GR24 × HB	3	0.260ns	126.562ns	175.329ns	0.002ns	5.952*	0.138ns	0.040ns
S×GR24×HB	3	0.479ns	768.229ns	670.974ns	0.005ns	2.042ns	0.111ns	0.035ns
Error	48	0.197	506.771	511.587	0.004	1.637	0.073	0.042
Source of variance	df	Carotenoids	Chl. a/b	Total chlorophyll	Water potential	Osmotic potential	Turgor potential	RWC%
Salinity (S)	1	0.005ns	6.854**	0.126ns	2.305***	1.444***	0.142**	1710.896***
GR24	3	0.009ns	0.907ns	0.0202ns	0.733***	0.054*	1.198***	87.795ns
Hybrids (HB)	1	0.138***	4.307*	0.054ns	0.864***	0.327***	0.174**	91.137ns
S × GR24	3	0.023ns	2.179*	0.225ns	0.220***	0.098***	0.331***	495.115***
S × HB	1	0.0007ns	0.319ns	0.615ns	0.129***	0.012ns	0.036ns	529.491***
GR24 × HB	3	0.078***	3.464**	0.548ns	0.131***	0.012ns	0.214***	29.222ns
S×GR24×HB	3	0.065***	2.660*	0.0509ns	0.011ns	0.025ns	0.003ns	119.043*
Error	48	0.007	0.740	0.132	0.007	0.015	0.018	39.595

*, **, *** Significant at 0.05, 0.01 and 0.001 levels respectively; ns = non-significant; A = net CO₂ assimilation rate; E = Transpiration rate; g_s = Stomatal conductance; C_i = Substomatal CO₂ concentration; C_i/C_a = Relative internal CO₂ concentration; Chl. a = Chlorophyll a; Chl. b = Chlorophyll b; Chl. a/b = Chlorophyll a/b ratio; WUE (A/E) = Water use efficiency

and root significantly increased ($P \leq 0.001$) when sunflower hybrids were treated with strigolactone (GR24). Plant treated with GR24 showed much higher ($P \leq 0.001$) shoot length as compared to control plants. The significant interaction between salinity and GR24 (S × GR24) showed that foliar application of GR24 particularly @ 33.5 nM prominently enhanced shoot length under saline and non-saline conditions. The GR24, at concentration of 33.52 nM had significant influence ($P \leq 0.001$) on growth attributes of the both sunflower hybrids, except for the root length. Foliar spray of GR24 had non-significant effect on root length in both sunflower hybrids under saline and non-saline regime (Table 1 and Fig. 1). A significant interaction between GR24 and hybrids showed that GR24 spray raised the shoot fresh and dry weights and root fresh weight in FH-596 and root dry weights and shoot lengths in FH-593 under saline and non-saline regimes (Table 1 and Fig. 1).

The data presented in Table 1 showed that the saline regimes significantly ($P \leq 0.001$) declined net CO₂ assimilation rate (A), transpiration rate (E), stomatal conductance (g_s), and water use efficiency (A/E) in both hybrids. The salt stress did not influence the sub-stomatal CO₂ concentration (C_i) and C_i/C_a ratio of plants of both sunflower hybrids (Table 1 and Fig. 2). Foliar spray of GR24 slightly enhanced ($P \leq 0.05$) the sub-stomatal CO₂ concentration, C_i/C_a ratio and water use efficiency under normal and hyperosmotic conditions in both hybrids (Table 1 and Fig. 2). Despite of GR24 foliar treatment, net CO₂

assimilation rate and stomatal conductance were found to be ineffective in both hybrids. A significant interaction between salinity and GR24 showed that GR24 significantly increased transpiration rate under salt stress (Table 1 and Fig. 2). Overall response of both hybrids remained uniform but FH-596 excelled FH-593 with respect to water use efficiency (Table 1 and Fig. 2).

The photosynthetic pigment of sunflower leaves showed slight variations under salt stress than in non-stressed plants (Table 1 and Fig. 3). Imposition of salinity through root growth medium profoundly ($P \leq 0.05$) decreased the chlorophyll a , chlorophyll b and chlorophyll a/b ratio but total chlorophyll and carotenoid contents remained unchanged in both hybrids. Photosynthetic pigments were not modulated by GR24 foliar spray. However, a highly significant ($P \leq 0.001$) interaction between GR24 and hybrids showed that GR24 raised the carotenoids contents and chlorophyll a/b ratio in sunflower hybrid FH-596 under saline and non-saline regimes (Table 1; Fig. 3).

A marked reduction ($P \leq 0.001$) in leaf water potential, osmotic potentials, turgor potential and relative water contents (RWC) of leaf of both sunflower hybrids was observed under salt regime. Foliar treatment of GR24 caused a considerable decrease ($P \leq 0.001$) in leaf water potential and turgor potential but substantial increase ($P \leq 0.05$) in osmotic potential and relative water contents of both sunflower hybrids under saline conditions. A highly

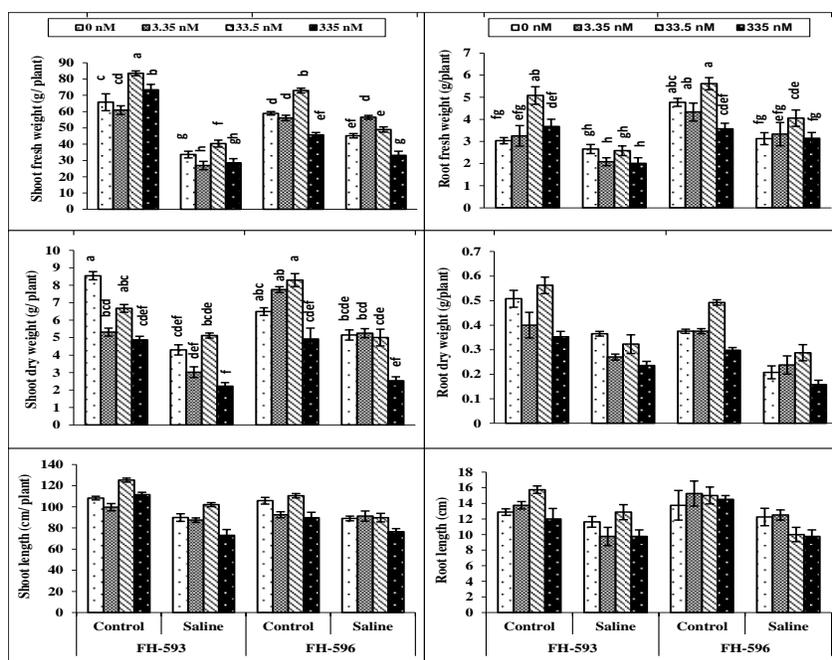


Fig. 1: Growth attributes of sunflower plants when 36 days old plants were treated to different levels of foliar-applied GR24 under control and saline condition
 LSD 5% (S×GR24×HB) = Shoot fresh weight = 6.13; Root fresh weight = 0.895; Shoot dry weight = 2.72; Root dry weight = ns; Shoot and Root lengths = ns

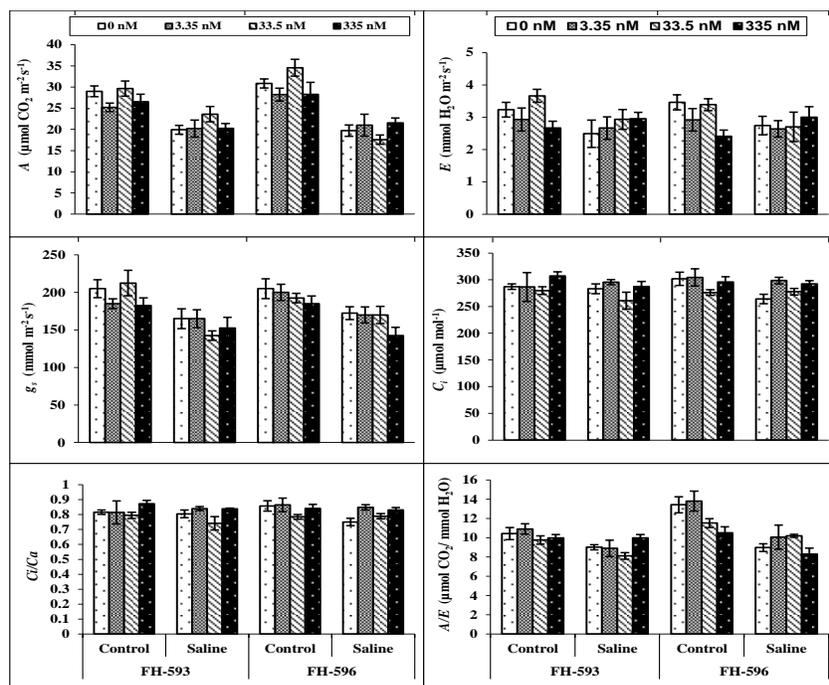


Fig. 2: Gas exchange attributes of sunflower plants when 36 days old plants were treated to different levels of foliar-applied GR24 under control and saline condition
 LSD 5% (S×GR24×HB) = non-significant for all gas exchange attributes

significant ($P \leq 0.001$) interaction between salinity and GR24 indicated that GR24 alleviated the adverse effect of saline stress by increasing the osmotic potential and water

use efficiency in both hybrids. The Hybrid FH-593 showed significant reduction ($P \leq 0.001$) in leaf water potential and turgor potential as compared to FH-596 (Table 1; Fig. 4).

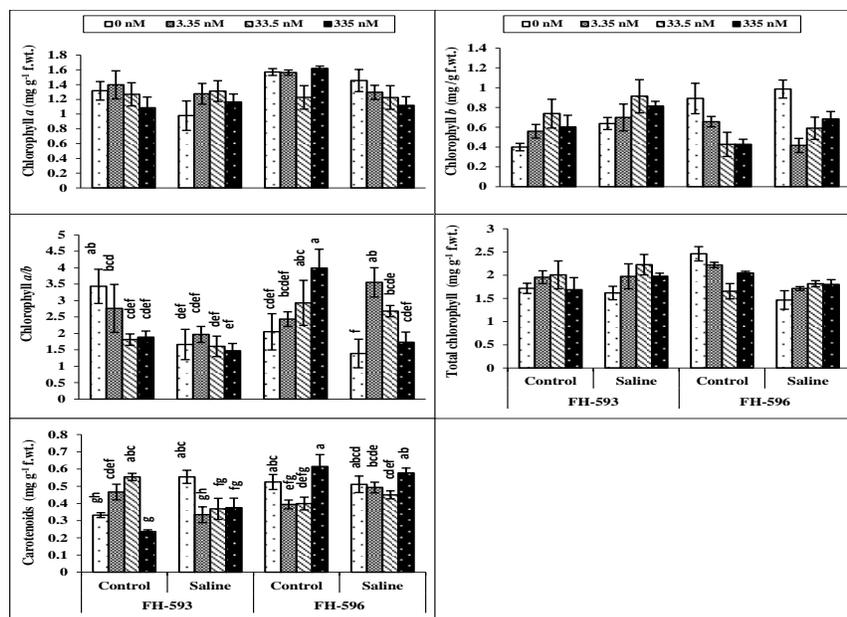


Fig. 3: Photosynthetic pigments of sunflower plants when 36 days old plants were treated to different levels of foliar-applied GR24 under control and saline condition
 LSD 5% (S×GR24×HB) = Chlorophyll a and b = ns; Chlorophyll a/b = 1.223; Total chlorophyll = ns;
 Carotenoids = 0.119

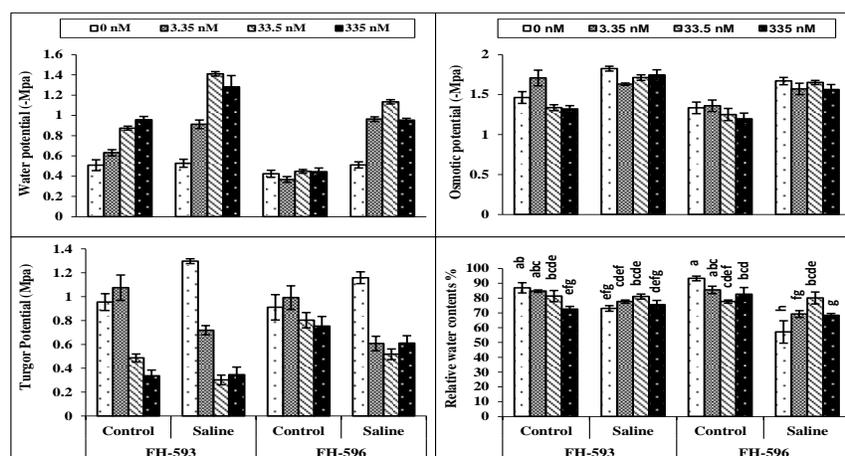


Fig. 4: Leaf water relation attributes of sunflower plants when 36 days old plants were treated to different levels of foliar-applied GR24 under control and saline conditions
 LSD 5% (S×GR24×HB) = Water, osmotic and turgor potentials = ns; Relative water contents = 8.95

Discussion

To evaluate the salinity tolerance in plants, growth is considered as an important criterion (Shahbaz and Ashraf, 2013). Under saline condition, reduction in plant growth was mainly due to complex intermingled physiological, biochemical and molecular processes (Shahbaz *et al.*, 2012). In view of current results, the exposure of salt stress caused drastic reduction in all growth attributes of sunflower hybrids like other plants *e.g.*, wheat and barley (Puniran-Hartley *et al.*, 2014), wheat (Kausar and Shahbaz, 2017) and sunflower

(Lalarukh and Shahbaz, 2018). In current study, growth attributes were improved by foliar application of GR24. In our experiment, GR24 treatment increased the shoot and root fresh and dry masses coincide with earlier findings of Kotze (2010) in *Nicotiana benthamiana* seedlings and Daws *et al.* (2008) in parasitic plants. In our present outcomes, foliar application of GR24 amplified shoot elongation is harmonizing to the discoveries of Agusti *et al.* (2011) and Germain *et al.* (2013) *via* promoting inter-fascicular growth of stem. However, the increase in shoot length in response to GR24 was also accompanied with increase in biomass

production. The GR24 mediated the plant growth via improved activity of meristem (Brewer *et al.*, 2009), repression of branch outgrowth (Dun *et al.*, 2012), accumulation of biomass (Daws *et al.*, 2008) and acceleration of arbuscular mycorrhizal fungi (AMF) symbiotic associations (Besserer *et al.*, 2006). In our consequences, GR24 showed no effect on root length which was contrary to results of Kapulnik *et al.* (2011) and Peret *et al.* (2011). The possible reason might be the suppression of root length but expansion of lateral root and root hair under stress condition (Sanchez-Calderon *et al.*, 2005) as our results showed increase in root fresh and dry weights.

This study showed dramatic decline in gas exchange properties under saline conditions which are equivalent to the findings of Neocleous and Vasilakakis (2007) in red raspberry and Abbasi *et al.* (2014) in maize. First mechanism of plant against salinity is to conserve the water by reducing stomatal conductance that consequently decrease the CO₂ assimilation (Abogadallah, 2010) and transpiration rates (Taiz and Zeiger, 2006). The GR24 indicated slightly positive affect on gas exchange attributes because of its role in regulation of light harvesting genes as reported earlier by Mashiguchi *et al.* (2009) in *Arabidopsis* and Mayzlish-Gati *et al.* (2010) in tomato. Antagonistic to our results, GR24 treatment also enhanced the stomatal conductance and photosynthetic activity in lettuce under saline stress (Aroca *et al.*, 2013). This deviation might be due to variation in environmental conditions on various species or the outcomes of some integrated genes involved in stress physiology.

The decline in photosynthetic pigments under salt stress is the outcome of today-study that correspond with the results of Azooz *et al.* (2011), Rasool *et al.* (2013) and Alqarawi *et al.* (2014) for *Vicia faba* (broad bean), *Cicer arietinum* (chickpea) and *Ephedra alata* (joint-pine) respectively. Our study showed non-significant effect of GR24 on photosynthetic pigments. Conversely to our results, the application of GR24 on tomato enhanced the genes expression related to photosynthetic pigments and light harvesting complexes (Mayzlish-Gati *et al.*, 2010).

It is quite clear from present research that the plant water relations were disturbed due to limited water uptake and very low solute potential, thereby more negative water potential (Cha-um *et al.*, 2010) reduces the plant growth (Eisa *et al.*, 2012). Osmotic adjustment is the best approach to cope with stress (Gorai *et al.*, 2011). Our results showed that water potential, turgor potential, and leaf relative water contents decreased under salinity coincided with the previous outcomes of Jabeen and Ahmad (2012) and Perveen *et al.* (2012) for wheat and sunflower respectively. Exogenous application of GR24 increased the osmotic potential and relative water contents of leaf that favor its positive role in stress tolerance. Variable behavior of GR24 toward water relations indicated a complex interaction between ABA and GR24 (Ma *et al.*, 2017) that is further needed to explore. Hence, we assume that the sound effects of GR24 are cross-talk with other phytohormones in response to salt stress.

Conclusion

Salinity adversely declined the biomass and growth of both sunflower hybrids. Photosynthetic pigments, gas exchange and water relation attributes reduced significantly under salt stress. Foliar application of GR24 ameliorated the inhibiting effects of salinity by improving plant biomass as well as shoot length. Photosynthetic pigments are not affected by foliar spray of GR24. The GR24 did not affect net CO₂ assimilation rate, stomatal conductance but enhanced the transpiration rate, sub-stomatal CO₂ concentration, C_i/C_a ratio and water use efficiency. The GR24 considerably increased the osmotic potential and relative water contents but declined the water potential and turgor potential of both sunflower hybrids under salinity.

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References

- Abbasi, G.H., J. Akhtar, M. Anwar-Ul-Haq, S. Ali, Z. Chen and W. Malik, 2014. Exogenous potassium differentially mitigates salt stress in tolerant and sensitive maize hybrids. *Pak. J. Bot.*, 46: 135–146
- Abogadallah, G.M., 2010. Antioxidative defense under salt stress. *Plant Signal. Behav.*, 5: 369–374
- Agusti, J., S. Herold, M. Schwarz, P. Sanchez, K. Ljung, E.A. Dun, P.B. Brewer, C.A. Beveridge, T. Sieberer and E.M. Sehr, 2011. Strigolactone signaling is required for auxin-dependent stimulation of secondary growth in plants. *Proc. Natl. Acad. Sci. USA*, 108: 20242–20247
- Akiyama, K., K. Matsuzaki and H. Hayashi, 2005. Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. *Nature*, 435: 824–827
- Alder, A., M. Jamil, M. Marzorati, M. Bruno, M. Vermathen, P. Bigler, S. Ghisla, H. Bouwmeester, P. Beyer and S. Al-Babili, 2012. The path from β -carotene to carlactone, a strigolactone-like plant hormone. *Science*, 335: 1348–1351
- Alqarawi, A.A., E.F. AbdAllah and A. Hashem, 2014. Alleviation of salt-induced adverse impact via mycorrhizal fungi in *Ephedra aphylla* Forsk. *J. Plant Interact.*, 9: 802–810
- Arnon, D.T., 1949. Copper enzyme in isolated chloroplasts polyphenoloxidase in *Beta vulgaris*. *Plant Physiol.*, 24: 1–15
- Aroca, R., J.M. Ruiz-Lozano, A.M. Zamarreno, J.A. Paz, J.M. Garcia-Mina and M.J. Pozo, 2013. Arbuscular mycorrhizal symbiosis influences strigolactone production under salinity and alleviates salt stress in lettuce plants. *J. Plant Physiol.*, 170: 47–55
- Azooz, M.M., A.M. Youssef and P. Ahmad, 2011. Evaluation of salicylic acid (SA) application on growth, osmotic solutes and antioxidant enzyme activities on broad bean seedlings grown under diluted seawater. *Intl. J. Plant Physiol. Biochem.*, 3: 253–264
- Besserer, A., V. Puech-Pages, P. Kiefer, V. Gomez-Roldan, A. Jauneau, S. Roy, J.C. Portais, C. Roux, G. Bécard and N. Sejalón-Delmas, 2006. Strigolactones stimulate arbuscular mycorrhizal fungi by activating mitochondria. *PLoS Biol.*, 4: 1239–1247
- Brewer, P.B., H. Koltai and C.A. Beveridge, 2013. Diverse roles of strigolactones in plant development. *Mol. Plants*, 6: 18–28
- Brewer, P.B., E.A. Dun, B.J. Ferguson, C. Rameau and C.A. Beveridge, 2009. Strigolactone acts downstream of auxin to regulate bud outgrowth in pea and *Arabidopsis*. *Plant Physiol.*, 150: 482–493

- Cha-um, S., M. Ashraf and C. Kirdmanee, 2010. Screening upland rice (*Oryza sativa* L. ssp. *indica*) genotypes for salt-tolerance using multivariate cluster analysis. *Afr. J. Biotechnol.*, 9: 4731–4740
- Chookhampaeng, S., 2011. The effect of salt stress on growth, chlorophyll content, proline content and antioxidative enzymes of pepper (*Capsicum annuum* L.) seedling. *Eur. J. Sci. Res.*, 49: 103–109
- Cook, C.E., L.P. Whichard, B. Turner, M.E. Wall and G.H. Egley, 1966. Germination of witchweed (*Striga lutea* Lour.): Isolation and Properties of a Potent Stimulant. *Science*, 154: 1189–1190
- Daws, H.W., J. Pritchard and V. Staden, 2008. Butenolide from plant-derived smoke functions as a strigolactone analogue: Evidence from parasitic weed achene germination. *S. Afr. J. Bot.*, 74: 116–120
- Dun, E.A., A.S. Germain, C. Rameau and C.A. Beveridge, 2012. Antagonistic action of strigolactone and cytokinin in bud outgrowth control. *Plant Physiol.*, 158: 487–498
- Eisa, S., S. Hussain, N. Geissler and H.W. Koyro, 2012. Effect of NaCl salinity on water relations, photosynthesis and chemical composition of quinoa (*Chenopodium quinoa* Willd.) as a potential cash crop halophyte. *Aust. J. Crop Sci.*, 6: 357–368
- Garcia-Garrido, J.M., V. Lenzemo, V. Castellanos-Morales, S. Steinkellner and H. Vierheilig, 2009. Strigolactones, signals for parasitic plants and arbuscular mycorrhizal fungi. *Mycorrhiza*, 19: 449–459
- Farooq, M., M. Hussain, A. Wakeel and K.H.M. Siddique, 2015. Salt stress in maize: effects, resistance mechanisms and management. A review. *Agron. Sustain. Dev.* 35: 461–481
- Germain, A.S., S. Bonhomme, F.D. Boyer and C. Rameau, 2013. Novel insights into strigolactone distribution and signaling. *Curr. Opin. Plant Biol.*, 16: 583–589
- Gomez-Roldan, V., S. Fernas, P.B. Brewer, V. Puech-Pages, E.A. Dun, J.P. Pillot, F. Letisse, R. Matusova, S. Danoun and J.C. Portais, 2008. Strigolactone inhibition of shoot branching. *Nature*, 455: 189–194
- Gorai, M., M. Ennajeh, H. Khemira and M. Neffati, 2011. Influence of NaCl-salinity on growth, photosynthesis, water relations and solute accumulation in *Phragmites australis*. *Acta Physiol. Plantarum*, 33: 963–971
- Horie, T., I. Kahara and M. Katsuhara, 2012. Salinity tolerance mechanisms in glycophytes: An overview with central focus on rice plants. *Rice*, 5: 1–11
- Hussain, M.I., D.A. Lyra, M. Farooq, N. Nikoloudakis and N. Khalid, 2016. Salt and drought stresses in safflower: a review. *Agron. Sustain. Dev.* 36: 4
- Jabeen, N. and R. Ahmad, 2012. Improvement in growth and leaf water relation parameters of sunflower and safflower plants with foliar application of nutrient solutions under salt stress. *Pak. J. Bot.*, 44: 1341–1345
- Jia, W., Y. Wang, S. Zheng and J. Zhang, 2002. Salt-stress induced ABA accumulation is more sensitive triggered in roots than in shoots. *J. Exp. Bot.*, 53: 2201–2206
- Jones, M.M. and N.C. Turner, 1978. Osmotic adjustment in leaves of sorghum in response to water deficits. *Plant Physiol.*, 61: 122–126
- Kapulnik, Y., P.M. Delaux, N. Resnick, E. Mayzlish-Gati, S. Winer, C. Bhattacharya, N. Séjalon-Delmas, J.P. Combier, G. Bécard and E. Belausov, 2011. Strigolactones affect lateral root formation and root-hair elongation in *Arabidopsis*. *Planta*, 233: 209–216
- Kausar, F. and M. Shahbaz, 2017. Influence of strigolactone (GR24) as a seed treatment on growth, gas exchange and chlorophyll fluorescence of wheat under saline conditions. *Intl. J. Agric. Biol.*, 19: 321–327
- Kotze, L.M., 2010. An investigation into the effects of smoke water and GR24 on the growth of *Nicotiana benthamiana* seedlings. *M.Sc. Thesis*. Stellenbosch University, Stellenbosch, South Africa
- Lalarukh, I. and M. Shahbaz, 2018. Alpha-tocopherol induced modulations in morpho-physiological attributes of sunflower (*Helianthus annuus*) grown under saline environment. *Intl. J. Agric. Biol.*, 20: 661–668
- Lopez-Raez, J.A., M.J. Pozo and J.M. Garcia-Garrido, 2011. Strigolactones: A cry for help in the rhizosphere. *Botany*, 89: 513–522
- Ma, N., C. Hu, L. Wan, Q. Hu, J. Xiong and C. Zhang, 2017. Strigolactones improve plant growth, photosynthesis, and alleviate oxidative stress under salinity in rapeseed (*Brassica napus* L.) by regulating gene expression. *Front. Plant Sci.*, 8: 1671
- Mayzlish-Gati, K., E. Sasaki, Y. Shimada, M. Nagae, K. Ueno, T. Nakano, K. Yoneyama, Y. Suzuki and T. Asami, 2009. Feedback-regulation of strigolactone biosynthetic genes and strigolactone-regulated genes in *Arabidopsis*. *Biosci. Biotechnol. Biochem.*, 73: 2460–2465
- Mayzlish-Gati, E., S.P. LekKala, N. Resnick, S. Winer, C. Bhattacharya, J.H. Lemcoff, Y. Kapulnik and H. Koltai, 2010. Strigolactones are positive regulators of light-harvesting genes in tomato. *J. Exp. Bot.*, 61: 3129–3136
- Mohamedin, A.A.M., A.A.A. El-Kader and N.M. Badran, 2006. Response of sunflower (*Helianthus annuus* L.) to plants salt stress under different water table depths. *J. Appl. Sci. Res.*, 2: 1175–1184
- Munns, R. and M. Tester, 2008. Mechanisms of salinity tolerance. *Annu. Rev. Plant Biol.*, 59: 651–681
- Neocleous, D. and M. Vasilakakis, 2007. Effects of NaCl on red raspberry (*Rubus idaeus* L. 'Autumn bliss'). *Sci. Hortic.*, 112: 282–289
- Peret, B., M. Clement, L. Nussaume and T. Desnos, 2011. Root developmental adaptation to phosphate starvation: Better safe than sorry. *Trends Plant Sci.*, 16: 442–450
- Perveen, S., M. Shahbaz and M. Ashraf, 2012. Changes in mineral composition, uptake and use efficiency of salt stressed wheat (*Triticum aestivum* L.) plants raised from seed treated with triacontanol. *Pak. J. Bot.*, 44: 27–35
- Porcel, R., R. Aroca and J.M. Ruiz-Lozano, 2012. Salinity stress alleviation using arbuscular mycorrhizal fungi. A review. *Agron. Sustain. Dev.*, 32: 181–200
- Puniran-Hartley, N., J. Hartley, L. Shabala and S. Shabala, 2014. Salinity-induced accumulation of organic osmolytes in barley and wheat leaves correlates with increased oxidative stress tolerance: in planta evidence for cross tolerance. *Plant Physiol. Biochem.*, 83: 32–39
- Rasool, S., A. Ahmad, T.O. Siddiqi and P. Ahmad, 2013. Changes in growth, lipid peroxidation and some key antioxidant enzymes in chickpea genotypes under salt stress. *Acta Physiol. Plantarum*, 35: 1039–1050
- Sanchez-Calderon, L., J. López-Bucio, A. Chacon-Lopez, A. Cruz-Ramirez, F. Nieto-Jacobo, J.G. Dubrovsky and L. Herrera-Estrella, 2005. Phosphate starvation induces a determinate developmental program in the roots of *Arabidopsis thaliana*. *Plant Cell Physiol.*, 46: 174–184
- Scholander, P.F., H.T. Hammel, E.A. Hemmingsen and E.D. Bradstreet, 1964. Hydrostatic pressure and osmotic potential in leaves of mangroves and some other plants. *Proc. Natl. Acad. Sci. USA*, 52: 119–125
- Shah, N.A., K.M. Aujla, M. Ishaq and A. Farooq, 2013. Trends in sunflower production and its potential in increasing domestic edible oil production in Punjab, Pakistan. *Sarhad J. Agric.*, 29: 7–13
- Shahbaz, M. and M. Ashraf, 2013. Improving salinity tolerance in cereals. *Crit. Rev. Plant Sci.*, 32: 237–249
- Shahbaz, M., M. Ashraf, F. Al-Qurainy and P.J.C. Harris, 2012. Salt tolerance in selected vegetable crops. *Crit. Rev. Plant Sci.*, 31: 303–320
- Snedecor, G.W. and G.W. Cochran, 1980. *Statistical Methods*, 7th edition. Iowa State University Press, Ames, Iowa, USA
- Taiz, L. and E. Zeiger, 2006. *Plant Physiology*, 4th edition, p. 764. Sinauer Associates, Inc., Publishers, Sunderland, USA
- Umehara, M., A. Hanada, S. Yoshida, K. Akiyama, T. Arite, N. Takeda-Kamiya, H. Magome, Y. Kamiya, K. Shirasu, K. Yoneyama, J. Kyoizuka and S. Yamaguchi, 2008. Inhibition of shoot branching by new terpenoid plant hormones. *Nature*, 455: 195–200
- Zeng, W.Z., C. Xu, J.W. Wu, J.S. Huang, Q. Zhao and M. S. Wu, 2014. Impacts of salinity and nitrogen on the photosynthetic rate and growth of sunflowers (*Helianthus annuus* L.). *Pedosphere*, 24: 635–644

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