



### **Full Length Article**

## **Influence of Strigolactone (GR24) as a Seed Treatment on Growth, Gas Exchange and Chlorophyll Fluorescence of Wheat under Saline Conditions**

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### **Abstract**

Strigolactones are generally considered as the signaling molecules. A pot experiment was conducted to explore the role of strigolactone (GR24) as seed treatment on wheat under saline conditions. Seeds of two wheat cultivars (S-24 and PARI-73) were sown in sand. Two salt treatments [control (non-saline) and 150 mM (NaCl)] nourished with full strength Hoagland's nutrient solution were applied as root growing medium while four strigolactone (GR24) levels (water (0), 0.001, 0.01 and 0.1 mg L<sup>-1</sup>) were applied as seed treatment for 16 h. Imposition of salt stress significantly reduced growth attributes while plants developed from seeds raised with GR24 showed variable response on growth under salt stress. Pre-sowing seed treatment with GR24 showed non-significant effect on shoot fresh and dry weight and root length. Net CO<sub>2</sub> assimilation rate of both wheat genotypes increased due to GR24 application. In chlorophyll fluorescence plants showed increasing response towards application of GR24 with respect to co-efficient of photochemical quenching (q<sub>N</sub>) and non-photochemical quenching (NPQ) under non-saline. Root-medium salinity significantly enhanced the concentrations of Na<sup>+</sup> ions and decreased K<sup>+</sup> ions in shoot and roots. Pre-seed treatment with GR24 did not modulate concentration of shoot and roots Na<sup>+</sup> and K<sup>+</sup> ions. Overall, the wheat cultivar S-24 showed better performance for growth parameters and non-significant behavior towards the photosynthetic rate. Both the cultivars showed uniform response in chlorophyll fluorescence. © 2017 Friends Science Publishers

**Keywords:** Strigolactone; Salinity; Wheat; Photosynthesis; Growth

### **Introduction**

Environmental factors may stimulate plant growth negatively or positively. Plants response to external factors (nutrient deficiency, light, crowding and insects) through biochemical communication system. A systematic response is found in plants in response to these external factors (Stes *et al.*, 2015). Hormones, development, as well as environmental factors regulate shoot branching through the complex interactions in which these factors interact with each other but there is currently no ideal model to explain this phenomenon (Crawford *et al.*, 2010). Shoot architecture is a highly plastic process suggesting that plants response to signals coming from either endogenous hormones or external environment and adjust their branching characteristics to these environmental changes (Leyser, 2009; Janssen *et al.*, 2014). Shoot branching network involves three steps: one is long distance systemic signaling, second is local gene activity and lastly perception of external signals (Wolters and Jurgens, 2009).

Strigolactones (SLs) are considered as a new class of hormones. Natural SLs isolated from root exudates and first

natural SL was named as strigol. But its structural details have published after 20 years of its discovery (Besserer *et al.*, 2006; Zwanenburg *et al.*, 2009). Till now, 15 stimulants have been isolated from root exudates. They occur in very minute amount and production per plant may be 25–30 pg and isolation is very difficult (Koltai and Kapulnik, 2011). SLs are produced both in monocots and dicots and are generally synthesized both in roots and stems and transported to the plant apex, thereby inhibiting shoot branching (Kebrom *et al.*, 2013; Al-Babili and Bouwmeester, 2015). Strigolactones are produced in two forms (as endogenous hormones and root secretions). Strigolactones are involved in various roles like promoting symbiotic interactions (arbuscular mycorrhizal fungi) (Evangelisti *et al.*, 2014); enhancing cell elongation within the root but inhibiting root hairs and asymmetric root growth (Ruyter-Spira *et al.*, 2011); affecting developmental processes (Yoneyama *et al.*, 2013), involving in light harvesting mechanism (Mayzlish-Gati *et al.*, 2010) and leaf senescence (Woo *et al.*, 2001); performing cross-talk with other major hormones like auxin, ABA and ethylene (Kohlen *et al.*, 2011); controlling leaf shape, lamina joint

inclination (Li *et al.*, 2014) and tiller angle (Sang, 2014); delaying leaf senescence and reducing secondary growth and controlling PCD (Programmed cell death), photomorphogenesis and modulating biotic/abiotic stress responses (Xiong *et al.*, 2014; Ha *et al.*, 2014; Ueda and Kusaba, 2015). Strigolactones are widely distributed and GR24 is its synthetic analogue (Gomez-Roldan *et al.*, 2008; Tsuchiya and McCourt, 2009). Most roles are reported by application of GR24 on *Arabidopsis*, petunia, pea and rice (Brewer *et al.*, 2013) and new roles are emerging continuously (Torres-Vera *et al.*, 2014). GR24 has been initially developed for its two most important characteristics; one is its high germination activity and second is its increased stability compared to natural SLs. Only few studies are reported in literature about the hormonal function of SLs (Fukui *et al.*, 2013).

Salinity causes adverse effects on crops (Shahbaz *et al.*, 2012; Perveen *et al.*, 2015). Abiotic stresses greatly reduce the crop productivity and salinity is also important among all abiotic stresses (Mehta *et al.*, 2010; Shahbaz *et al.*, 2013). Approximately salinity affects 1% agriculture land (Tuteja, 2007). Salt greatly suppresses the photosynthesis process in plants and this suppression depends on different factors. These factors are photosynthetic pigments, stomatal performance and generation of essential metabolites and antioxidants (Aziz *et al.*, 2013; Nusrat *et al.*, 2014). Salt stress not only suppresses photosynthetic activity but also photosynthetic machinery of plants is inhibited. Salt stress also affects the cell organelles like chloroplast and it is the site for most of photosynthetic processes (PSI and PSII) and generation of reactive oxygen species (ROS) (Nusrat *et al.*, 2014). Plants avoid salt stress by various means like shoot damage but better root growth has been reported (may be due to exclusion of sodium) (Perveen *et al.*, 2013). Under salt stress, stomatal aperture decreased and resulted in low CO<sub>2</sub> availability to plants (Kausar and Shahbaz, 2013). Plants develop multigenic responses/mechanisms for salt tolerance; these will then regulate many physiological/biochemical processes (Shabala *et al.*, 2010; Rafique *et al.*, 2015; Shabbir *et al.*, 2015). Salinity disturbs uptake/distribution of essential nutrients and balanced absorption (Srieng *et al.*, 2015). Excess Na<sup>+</sup> in root cells competes with K<sup>+</sup> for uptake causing ionic imbalance (Bavei *et al.*, 2011). Uptake of K<sup>+</sup> is reduced due to having similar physiochemical properties of Na<sup>+</sup> under high salinity (Hossain *et al.*, 2011). Salt stress induces disturbance in various metabolic processes such as photosynthesis, stomatal regulation and protein synthesis (Nusrat *et al.*, 2014).

Wheat is grown all over the world and covered larger cultivated land, nourishes most of the world's population. Same situation in Pakistan (largest food grain crop/large proportion of cultivated land). There is no information available about the influence of pre-sowing seed treatment of strigolactone (GR24) on wheat under saline conditions.

The present study performed to explore whether or not strigolactone (GR24) could enhance the antagonistic impacts of salt stress (NaCl) on wheat.

## Materials and Methods

A pot experiment was conducted to explore the effect of pre-seed treatment with strigolactone (GR24) on wheat under saline conditions. Seeds of two wheat cultivars [salt tolerant cultivar S-24 (Shahbaz *et al.*, 2008) and salt sensitive cultivar PARI-73 (Kamboh *et al.*, 2002)] were obtained from Ayub Agricultural Research Institute, Faisalabad, Pakistan. Seeds of both cultivars (S-24 & PARI-73) were surface sterilized in sodium hypochlorite and soaked for 16 h in four levels of GR24 solution (Distilled Water, 0.001, 0.01 and 0.1 mg L<sup>-1</sup>) at room temperature. After 16 h pre-sowing treatment, seeds were placed on blotting paper to remove additional moisture. Strigolactone (GR24) (M. wt. 298.2) was obtained from Department of Organic Chemistry, Radboud University Nijmegen Heyendaalseweg 135, HG 03-0186525 AJ NIJMEGEN, The Netherlands. Ten seeds per pot were shown in plastic pots containing thoroughly washed river sand. Thinning was performed to six plants per pot after thirty days of sowing. Salinity (150 mM NaCl) treatment was applied to fifty day-old plants. There were two salt (NaCl) levels [control (0 mM) and 150 mM (NaCl)]. Hoagland's nutrient solution (full strength) was applied @ 2 liters/pot every week. Salt treatment (in full strength Hoagland's nutrient medium) was applied in an aliquot of 50 mM solution/pot every day so that desired level was attained. Data for morphological and physiological attributes were recorded of 4 weeks of salinity treatment. Two plants were uprooted carefully, washed with distilled water and recorded shoot and root fresh weights and length. The plants were oven-dried to constant weight and dry weights were recorded. In addition, following physiological attributes were recorded.

## Gas Exchange Characteristics

Gas exchange characteristics were recorded using Infra-red gas analyzer LCA-4 ACD (Analytical Development, Hoddesdon, UK) at vegetative growth stage from flag leaf. Gas exchange attributes like net CO<sub>2</sub> assimilation rate (*A*), transpiration rate (*E*), sub-stomatal conductance (*C<sub>i</sub>*), stomatal conductance (*g<sub>s</sub>*), water use efficiency (*A/E*) and (*C<sub>i</sub>/C<sub>a</sub>*) from 11:00 am to 1:00 pm. States of convenient infrared gas analyzer amid information estimations were: encompassing weight (P) 98.8 kPa; gas stream rate (U) 251 μmol s<sup>-1</sup>; concentration of ambient carbon dioxide was 350 μmol mol<sup>-1</sup>.

## Chlorophyll Fluorescence

The polyphasic rise of fluorescence transients was measured by means of an OS5p Modulator Fluorometer (ADC

BioScientific Ltd, Great Amwell Herts, UK) (Strasser *et al.*, 1995). All leaf samples were kept in dark for 30 minutes before measurements of activity of photosystem-II.

### Mineral Nutrients (Na<sup>+</sup> and K<sup>+</sup>) Determination

Mineral ions (Na<sup>+</sup> and K<sup>+</sup>) in shoot and root were determined by following Allen *et al.* (1985). Hundred mg dried ground shoots and root material was digested in 2 ml of H<sub>2</sub>SO<sub>4</sub> in a digestion flask. After digestion, the mixture was diluted with distilled water up to 50 mL, filtered and filtrate was used for Na<sup>+</sup> and K<sup>+</sup> ions determination with the help of a flame photometer (Sherwood, 410).

### Statistical Analysis

The three-way analysis of variance (ANOVA) was applied by using the package of COSTAT computer (Cohort software Berkeley, California) to analyze the significance of data. The experiment was laid down in a completely randomized design (CRD) with four replications.

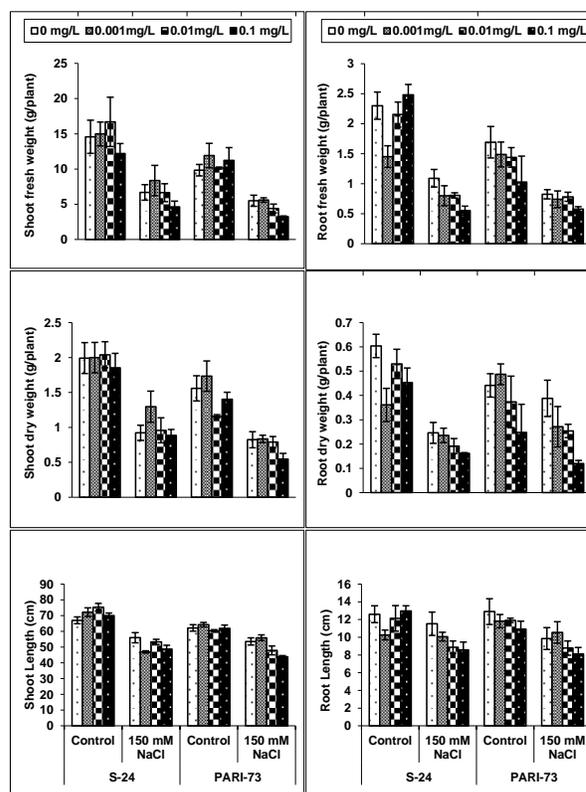
### Results

Imposition of saline conditions (150 mM NaCl) significantly reduced the shoot and root fresh and dry weights of both wheat cultivars i.e. S-24 and PARI-73. Seed treatment with various levels of GR24 significantly reduced the root fresh and dry weights, while it did not alter the shoot fresh and dry weights of both wheat cultivars. Cultivar S-24 showed higher growth as compared to PARI-73 (Table 1; Fig. 1).

Shoot and root lengths of both wheat cultivars significantly reduced under saline conditions. Application of GR24 as pre-seed treatment further reduced the root length in both the cultivars while behavior was variable with respect to shoot length under saline and non-saline conditions (Table 1; Fig. 1). Cultivar S-24 was superior as compared to those of PARI-73 for both shoot and root lengths under both saline and non-saline conditions.

Salt medium markedly reduced the total leaf area per plant of both the wheat cultivars i.e. S-24 and PARI-73. Pre-seed treatment with GR24 further reduced total leaf area per plant under saline condition while total leaf area per plant did not affect under non-saline conditions (Table 1; Fig. 2). Cultivar S-24 showed better performance as compared to PARI-73 with respect to total leaf area per plant under both saline regimes.

Chlorophyll fluorescence attributes like photochemical quenching (q<sub>p</sub>), electron transport ratio (ETR) and efficiency of photosystem-II (F<sub>v</sub>/F<sub>m</sub>) did not alter either by salt stress or pre-seed treatment with GR24 (Table 2; Fig. 2). Seed treatment with GR24 slightly enhanced the co-efficient of non-photochemical quenching (q<sub>N</sub>) and non-photochemical quenching (NPQ) in both wheat cultivars, while salt stress tremendously reduced both these attributes of both the wheat cultivars (Table 2; Fig. 2).



**Fig. 1:** Growth attributes of salt stressed and non-stressed wheat plants raised from seed treated with GR24

Net CO<sub>2</sub> assimilation rate (*A*) of both wheat cultivars (S-24 and PARI-73) reduced significantly under saline conditions. Applications of various GR24 levels showed an increase in *A* in both wheat cultivars under salt stress (Table 2; Fig. 3). Both cultivars showed uniform response. GR24 application did not alter transpiration rate (*E*), sub-stomatal conductance (*C<sub>i</sub>*), water use efficiency (*A/E*) and *C<sub>i</sub>/C<sub>a</sub>*. In S-24, seed treatment with GR24 slightly reduced stomatal conductance (*g<sub>s</sub>*). Transpiration rate (*E*) was not modulated by imposition of salinity. Seed treatment with GR24 slightly increased stomatal conductance (*g<sub>s</sub>*) only @ 0.1 mg/L level under saline and non-saline stress in both wheat cultivars. Among both wheat cultivars, *E* was high in PARI-73 as compared to S-24 while wheat cultivars did not differ significantly with respect other gas exchange attributes (Table 2; Fig. 3).

Saline stress (150 mM) through root growing medium significantly increased shoot and root Na<sup>+</sup> ion contents in two wheat cultivars i.e. S-24 and PARI-73 (Table 3; Fig. 4). Seed-priming treatment with GR24 did not alter shoot and root Na<sup>+</sup> ion in both wheat cultivars under various salt stress conditions. Imposition of salinity significantly decreased shoot and root K<sup>+</sup> contents in both wheat cultivars (S-24 and PARI-73). Pre-sowing seed treatment with GR24 did not modulate the shoot and root K<sup>+</sup> ions (Table 3; Fig. 4).

**Table 1:** Mean squares from analyses of variance of data for growth attribute and chlorophyll fluorescence of salt stressed and non-stressed wheat plants raised from seed treated with GR24

Source of Variance	df	Shoot fresh weight	Root fresh weight	Shoot dry weight	Root dry weight	Shoot length
GR24	3	15.9ns	0.415*	0.259ns	0.081**	49.46*
Salinity (S)	1	797.7***	15.46***	11.17***	0.665***	4018.7***
Cultivars (Cvs)	1	131.6***	2.350***	2.404***	0.009ns	391.1***
GR24 × S	3	3.272ns	0.169ns	0.031ns	0.002ns	71.62*
GR24 × Cvs	3	6.898ns	0.335ns	0.045ns	0.029ns	81.97**
S × Cvs	1	14.92ns	1.456**	0.230ns	0.089*	257.0***
GR24 × S × Cvs	3	5.523ns	0.443*	0.146ns	0.028ns	45.18 ns
Error	48	9.765ns	0.143	0.098	0.015	17.48
Source of Variance	df	Root length	Leaf area	Fv/Fm	ETR	q <sub>p</sub>
GR24	3	7.526ns	80225.2**	0.003ns	0.763ns	0.006ns
Salinity (S)	1	91.6***	1781735.1***	0.002ns	18.60ns	0.00008ns
Cultivars (Cvs)	1	1.175 ns	147540.9**	0.0009ns	4.358ns	0.014ns
GR24 × S	3	6.619 ns	42505.4*	0.003ns	7.625ns	0.006ns
GR24 × Cvs	3	3.719ns	17611.9ns	0.009*	5.585ns	0.005ns
S × Cvs	1	0.460ns	94744.0**	0.00009ns	14.17ns	0.003ns
GR24 × S × Cvs	3	2.379ns	17915.5ns	0.004ns	6.332ns	0.003ns
Error	48	3.634ns	13153.6	0.003	5.102	0.003

\*, \*\*, \*\*\* = significant at 0.05, 0.01 and 0.001 levels, respectively; ns = non-significant

**Table 2:** Mean squares from analyses of variance of data for chlorophyll fluorescence and gas exchange characteristics salt stressed and non-stressed wheat plants raised from seed treated with GR24

Source of Variance	df	NPQ	q <sub>N</sub>	A	E	g <sub>s</sub>
GR24	3	0.021**	0.007*	41.36*	0.248ns	31780.5**
Salinity (S)	1	0.322***	0.116***	1227.6***	0.265ns	142689.9***
Cultivars (Cvs)	1	0.012ns	0.0005ns	46.86ns	2.237**	232.1ns
GR24 × S	3	0.0002ns	0.002ns	26.32ns	0.044ns	31574.1**
GR24 × Cvs	3	0.002ns	0.0007ns	36.19*	0.850**	8751.3ns
S × Cvs	1	0.00005ns	0.00002ns	45.51ns	0.140ns	41005.8*
GR24 × S × Cvs	3	0.017*	0.006*	4.365ns	0.257ns	37197.8**
Error	48	0.004	0.002	11.82ns	0.187	6834.8
Source of Variance	df	C <sub>i</sub>	A/E	C <sub>v</sub> /C <sub>a</sub>		
GR24	3	817.7ns	2.421ns	0.007ns		
Salinity (S)	1	12302.9***	454.9***	0.099***		
Cultivars (Cvs)	1	1578.4ns	14.96ns	0.013ns		
GR24 × S	3	1306.9*	14.71ns	0.011*		
GR24 × Cvs	3	1559.3*	22.33ns	0.013*		
S × Cvs	1	20.46ns	27.89ns	0.0007ns		
GR24 × S × Cvs	3	1315.5*	14.86ns	0.011*		
Error	48	460.3	9.939ns	0.004		

\*, \*\*, \*\*\* = significant at 0.05, 0.01 and 0.001 levels, respectively; ns = non-significant

**Table 3:** Mean squares from analyses of variance of data for mineral nutrients (Na<sup>+</sup> and K<sup>+</sup> ions) of salt stressed and non-stressed wheat plants raised from seed treated with GR24

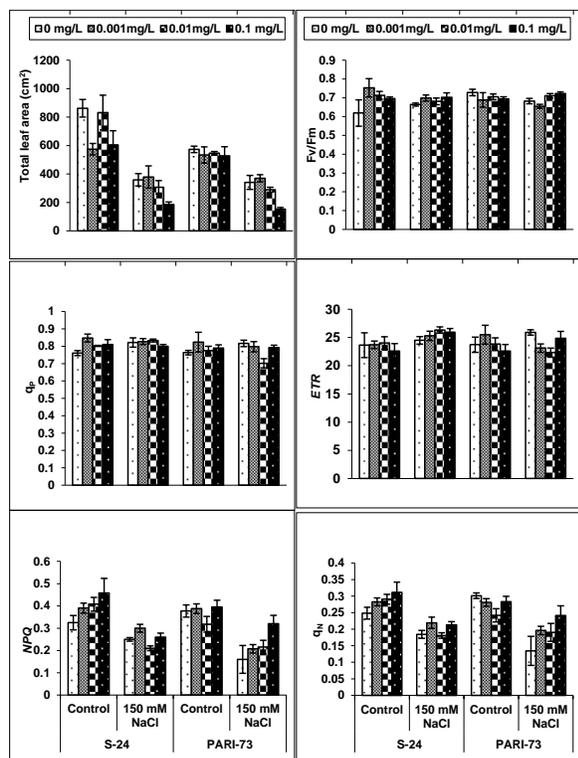
Source of Variance	df	Shoot Na <sup>+</sup>	Root Na <sup>+</sup>	Shoot K <sup>+</sup>	Root K <sup>+</sup>
GR24	3	1.882ns	0.309ns	6.313ns	5.266ns
Salinity (S)	1	1718.1***	9075***	492.0***	569.4***
Cultivars (Cvs)	1	66.83**	16ns	11.52ns	0.076ns
GR24 × S	3	6.244ns	0.815ns	58.29***	33.64***
GR24 × Cvs	3	8.180ns	3.424ns	5.819ns	38.91***
S × Cvs	1	12.78ns	5.641ns	104.8***	8.41ns
GR24 × S × Cvs	3	0.297ns	1.471ns	24.16*	35.42***
Error	48	6.160	4.477	5.876	3.522

\*, \*\*, \*\*\* = significant at 0.05, 0.01 and 0.001 levels, respectively; ns = non-significant

## Discussion

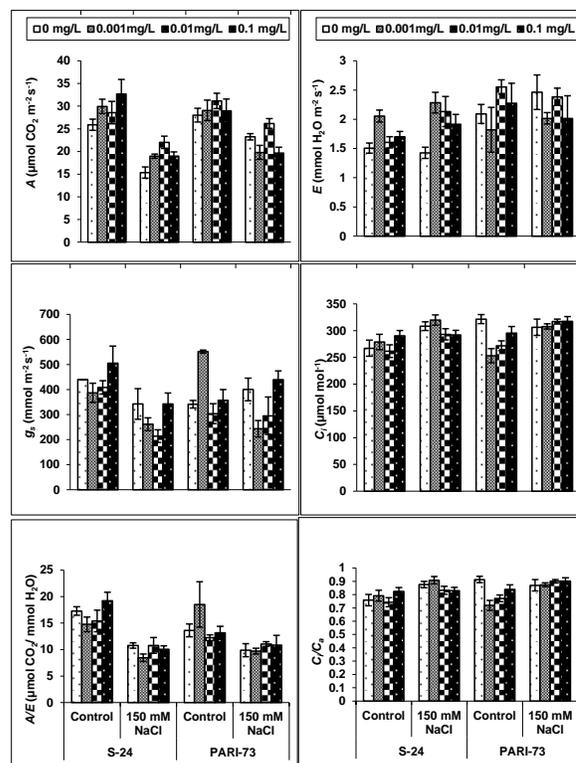
In current experiment, imposition of salt stress caused an adversarial impact on growth attributes. Under salinity stress, growth inhibition is a key morphological effect

(Shahbaz and Ashraf, 2013; Zulfiqar and Shahbaz, 2013; Nusrat *et al.*, 2014; Vu *et al.*, 2015; Masood and Shahbaz, 2016) and marker, which has been studied in various crops. In this experiment GR24 was used as Strigolactone analogue to study effect of GR24 and salt stress (150 mM)

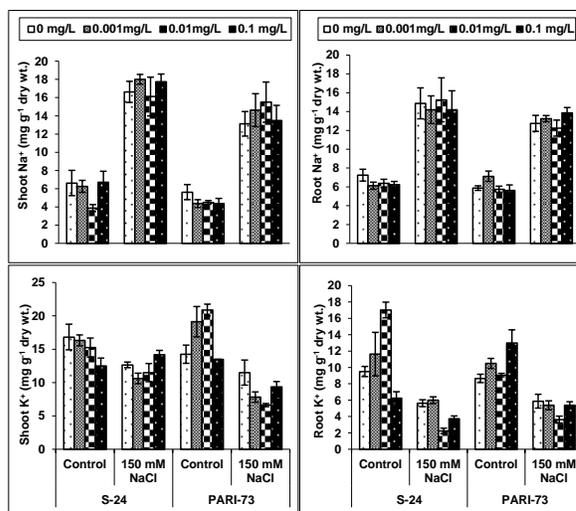


**Fig. 2:** Total leaf area and chlorophyll fluorescence of salt stressed and non-stressed wheat plants raised from seed treated with GR24

in two wheat cultivar S-24 & PARI-73. Seed treatment with GR24 slightly reduced growth attributes except shoot fresh and dry weight and root length. In the current study, reduction in shoot length might be related to suggestion that strigolactone not only involved in regulating shoot branching and root development but also to maintain shoot elongation (Ruyter-Spira *et al.*, 2011). Germain *et al.* (2013) suggested that dwarfism developed in plants not due to increased branching but might be due to low resources for main stem to develop. Strigolactone stimulated internode elongation (plant height) leading to better gain yield and biomass independently from gibberellin (Boyer *et al.*, 2014). But in contrast to our results it has also been reported that various concentrations of GR24 ( $10^{-6}$  to  $10^{-8}$  M) were supplied as exogenous application to *Nicotiana benthamiana* seedlings caused biomass accumulation. Similar findings also previously reported regarding increased germination and biomass accumulation (Daws *et al.*, 2008). Salt-induced decrease and increase in efficiency of PS II and non-photochemical quenching (NPQ), respectively in wheat (Akram *et al.*, 2012) and rice (Habib *et al.*, 2013). Electron transport membrane system and Photosystem II (PSII) activity impaired in plants by the salt stress (Ashraf and Ashraf, 2012; Kanwal *et al.*, 2013). Photosynthesis mechanism is a key physiological process disturbed by salinity and damaging effects extensively



**Fig. 3:** Gas exchange characteristics of salt stressed and non-stressed wheat plants raised from seed treated with GR24



**Fig. 4:** Mineral nutrients (Na<sup>+</sup> and K<sup>+</sup> ions) of salt stressed and non-stressed wheat plants raised from seed treated with GR24

studied on various crop such as wheat and rice (Cha-um *et al.*, 2010). The performance of photosynthetic process is affected by salinity like change in the metabolic processes or stomatal limitation to CO<sub>2</sub> diffusion (Chaves *et al.*, 2009; Abbasi *et al.*, 2014). Salt stress causing decrease in substomatal CO<sub>2</sub> concentration on one side but increased due to limitation in CO<sub>2</sub> consumption because of less

photosynthesis (Elfeel and Abohassan, 2015). In present study, net CO<sub>2</sub> assimilation rate and stomatal conductance were decreased in both wheat cultivars under saline conditions, nonetheless, the lessening in these properties are enhanced by seed treatment of GR24. Photosynthetic rate (A) and stomatal conductance (g<sub>s</sub>) expanded by seed treatment of GR24. Improvement in photosynthesis process is a comprehensive outcome of increased CO<sub>2</sub> fixation and assimilation and light use efficiency (Wang *et al.*, 2010). However, in our experiment seed treatment showed very slight effect on photosynthetic efficiency. Only NPQ and q<sub>N</sub> showed positive response towards application of GR24 as seed treatment. The difference might be due to different environmental conditions on plant species. Essential mineral nutrients uptake decreased due to imposition of salinity among various crops such as in rice (Shahbaz and Zia, 2011), wheat (Perveen *et al.*, 2012) and sunflower (Shahbaz *et al.*, 2011) etc. Sodium uptake increased during salinity due to high availability of Na<sup>+</sup> contents in root growing medium. For K<sup>+</sup> contents, various findings have been reported in various crops i.e. salinity may not alter K<sup>+</sup> uptake and may considerably decreased K<sup>+</sup> contents both in roots and shoots (Shahbaz *et al.*, 2011). Root growing medium significantly increased shoot and root sodium contents and decreased K<sup>+</sup> contents in two wheat cultivar under saline regimes (Perveen *et al.*, 2012), which are in agreement with our findings. Seed-priming treatment with GR24 did not increase/decrease shoot and root Na<sup>+</sup> and K<sup>+</sup> ion in two cultivars under two salt stress conditions.

## Conclusion

Salt stress adversely affected not only growth of both wheat cultivars, but also severely disturbed gas exchange characteristics and chlorophyll fluorescence. Seed treatment with GR24 slightly increased net CO<sub>2</sub> assimilation rate (A) and slightly reduced stomatal conductance (g<sub>s</sub>) and had non-significant effect on transpiration rate (E), sub-stomatal CO<sub>2</sub> concentration, water use efficiency and C<sub>i</sub>/C<sub>a</sub> ratio. Salinity significantly reduced the non-photochemical quenching (NPQ) and the co-efficient of non-photochemical quenching (q<sub>N</sub>) of two cultivars while GR24 application slightly enhanced NPQ and q<sub>N</sub>. Salinity significantly increased and decreased shoot and root Na<sup>+</sup> and K<sup>+</sup> ion contents, respectively in wheat cultivars. Seed-priming treatment with GR24 did not alter shoot and root Na<sup>+</sup> and K<sup>+</sup> ion contents in both wheat cultivars under various salt stress conditions.

## 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
- Akram, M., S. Farooq, M. Ashraf, M. Afzaal, R. Arshad and F. Azam, 2012. Detecting differences in some elite wheat lines for salt tolerance through multi-parameters evaluation i. morphological and yield parameters. *Pak. J. Bot.*, 43: 435–443
- Al-Babili, S. and H.J. Bouwmeester, 2015. Strigolactones, a novel carotenoid derived plant hormone. *Annu. Rev. Plant Biol.*, 66: 161–186
- Allen, S.K., A.K. Dobrenz, M.H. Schonhorst and J.E. Stoner, 1985. Heritability of NaCl tolerance in germinating alfalfa seeds. *Agron. J.*, 77: 90–96
- Aziz, R., M. Shahbaz and M. Ashraf, 2013. Influence of foliar application of triacontanol on growth attributes, gas exchange and chlorophyll fluorescence in sunflower (*Helianthus annuus* L.) under saline stress. *Pak. J. Bot.*, 45: 1913–1918
- Bavei, V., B. Shiran, M. Khodambashi and A. Ranjbar, 2011. Protein electrophoretic profiles and physicochemical indicators of salinity tolerance in *Sorghum bicolor* L. *Afr. J. Biotechnol.*, 10: 2683–2697
- Besserer, A., V. Puech-Pages, P. Kiefer, V. Gomez-Roldan, A. Jauneau, S. Roy, J. Portais, C. Roux, G. Bécard and N. Sejalón-Delmas, 2006. Strigolactones stimulate arbuscular mycorrhizal fungi by activating mitochondria. *PLoS Biol.*, 4: 1239–1247
- Boyer, F., D. de Saint, A. Germain, J.B. Pouvreau, G. Clave, J.P. Pillot and A. Roux, 2014. New strigolactone analogs as plant hormones with low activities in the rhizosphere. *Mol. Plant*, 7: 675–690
- Brewer, P.B., H. Koltai and C.A. Beveridge, 2013. Diverse roles of strigolactones in plant development. *Mol. Plant.*, 6: 18–28
- 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
- Chaves, M.M., J. Flexas and C. Pinheiro, 2009. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. *Ann. Bot.*, 103: 551–560
- Crawford, S., N. Shinohara, T. Sieberer, L. Williamson, G. George, J. Hepworth, D. Müller, M.A. Domagalska and O. Leyser, 2010. Strigolactones enhance competition between shoot branches by dampening auxin transport. *Development*, 137: 2905–2913
- Daws, H.W., J. Pritchard and V. Staden, 2008. Butenolide from plant-derived smoke functions as a strigolactone analogue: evidence from parasitic weed seed germination. *S. Afr. J. Bot.*, 74: 116–120
- Elfeel, A.A. and R.A. Abohassan, 2015. Response of *Balanites aegyptiaca* (L.) Del. *Var. Aegyptiaca* seedlings from three different sources to water and salinity stresses. *Pak. J. Bot.*, 47: 1199–1206
- Evangelisti, E., T. Rey and S. Schornack, 2014. Cross-interference of plant development and plant-microbe interactions. *Cur. Opin. Plant Biol.*, 20: 118–126
- Fukui, K., S. Ito and T. Asami, 2013. Selective mimics of strigolactone actions and their potential use for controlling damage caused by root parasitic weeds. *Mol. Plant*, 6: 88–99
- 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. Fermas, 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
- Ha, C.V., M.A. Leyva-Gonzalez, Y. Osakabe, U.T. Tran, R. Nishiyama, Y. Watanabe, M. Tanaka, M. Seki, S. Yamaguchi, N.V. Dong, K. Yamaguchi-Shinozaki, K. Shinozaki, L. Herrera-Estrella and L.S. Tran, 2014. Positive regulatory role of strigolactone in plant responses to drought and salt stress. *Proc. Natl. Acad. Sci. USA*, 111: 851–856
- Habib, N., M. Ashraf and M. Shahbaz, 2013. Effect of exogenously applied nitric oxide on some key physiological attributes of rice (*Oryza sativa* L.) plants under salt stress. *Pak. J. Bot.*, 45: 1563–1569
- Hossain, M.A., M. Hasanuzzaman and M. Fujita, 2011. Coordinate induction of antioxidant defense and glyoxalase system by exogenous proline and glycinebetaine is correlated with salt tolerance in mungbean. *Front. Agric. Chin.*, 5: 1–14
- Janssen, B.J., R.S. Drummond and K.C. Snowden, 2014. Regulation of axillary shoot development. *Curr. Opin. Plant Biol.*, 17: 28–35
- Kamboh, M.H., Y. Oki and T. Adachi, 2002. Effect of increasing salinity on growth and mineral composition of wheat varieties and role of sodium exclusion capacity in salt tolerance mechanisms. *J. Fac. Environ. Sci. Technol. Okayama Univ.*, 7: 99–106

- Kanwal, S., M. Ashraf, M. Shahbaz and M.Y. Iqbal, 2013. Influence of saline stress on growth, gas exchange, mineral nutrients and non-enzymatic antioxidants in mungbean [*Vigna radiata* (L.) wilczek]. *Pak. J. Bot.*, 45: 763–771
- Kausar, F. and M. Shahbaz, 2013. Interactive effect of foliar application of nitric oxide (NO) and salinity on wheat (*Triticum aestivum* L.). *Pak. J. Bot.*, 45: 67–73
- Kebrom, T.H., W. Spielmeier and E.J. Finnegan, 2013. Grasses provide new insights into regulation of shoot branching. *Trends Plant Sci.*, 18: 41–48
- Kohlen, W., T. Charnikova, Q. Liu, R. Bours, M.A. Domagalska, S. Beguerie, F. Verstappen, O. Leyser, H. Bouwmeester and C. Ruyter-Spira, 2011. Strigolactones are transported through the xylem and play a key role in shoot architectural response to phosphate deficiency in nonarbuscular mycorrhizal host *Arabidopsis*. *Plant Physiol.*, 155: 974–987
- Koltai, H. and Y. Kapulnik, 2011. Strigolactones as mediators of plant growth responses to environmental conditions. *Plant Signal. Behav.*, 5: 1–5
- Leyser, O., 2009. The control of shoot branching: an example of plant information processing. *Plant Cell Environ.*, 32: 694–703
- Li, X., S. Sun, C. Li, S. Qiao, T. Wang, L. Leng, H. Shen and X. Wang, 2014. The Strigolactone-related mutants have enhanced lamina joint inclination phenotype at the seedling stage. *J. Genet. Genom.*, 41: 605–608
- Masood, A. and M. Shahbaz, 2016. Morpho-physiological modulations in rice (*Oryza sativa*) by foliar application of phospholipase-C inhibitor neomycin under saline conditions. *Int. J. Agric. Biol.*, 18: 710–718
- Mayzlish-Gati, E., S.P. LekKala, N. Resnick, S. Wininger, 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
- Mehta, P., A. Jajoo, S. Mathur and S. Bharti, 2010. Chlorophyll a fluorescence study revealing effects of high salt stress on PS II in wheat leaves. *Plant Physiol. Biochem.*, 48: 16–20
- Nusrat, N., M. Shahbaz and S. Perveen, 2014. Modulation in growth, photosynthetic efficiency, activity of antioxidants and mineral ions by foliar application of glycinebetaine on pea (*Pisum sativum* L.) under salt stress. *Acta Physiol. Plant.*, 36: 2985–2998
- 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
- Perveen, S., M. Shahbaz and M. Ashraf, 2013. Influence of foliar-applied triacontanol on growth, gas exchange characteristics, photosynthetic pigments and chlorophyll fluorescence at different growth stages in wheat (*Triticum aestivum* L.) under saline conditions. *Photosynthetica*, 51: 541–551
- Perveen, S., R. Farooq and M. Shahbaz, 2015. Thiourea-induced metabolic changes in two mung bean [*Vigna radiata* (L.) Wilczek] (Fabaceae) varieties under salt stress. *Braz. J. Bot.*, 39: 41–54
- Rafique, H.M., H.N. Asghar, Z.A. Zahir and M. Shahbaz, 2015. Evaluation of plant growth promoting bacteria for inducing stress tolerance in plants against petroleum hydrocarbons. *Pak. J. Agric. Sci.*, 52: 905–914
- Ruyter-Spira, W. Kohlen, T. Charnikova, A.V. Zeijl, L.V. Bezouwen, N.D. Ruijter, C. Cardoso, J.A. Lopez-Raez, R. Matusova, R. Bours, F. Verstappen and H. Bouwmeester, 2011. Physiological Effects of the Synthetic Strigolactone Analog GR24 on Root System Architecture in *Arabidopsis*: Another Belowground Role for Strigolactones? *Plant Physiol.*, 155: 721–734
- Sang, D., 2014. Strigolactones regulate rice tiller angle by attenuating shoot gravitropism through inhibiting auxin biosynthesis. *Proc. Natl. Acad. Sci., USA*, 111: 11199–11204
- Shabala, S., L. Shabala, T.A. Cui, J. Pang, W. Percey, Z. Chen, S. Conn, C. Eing and L.H. Wegner, 2010. Xylem ionic relations and salinity tolerance in barley. *Plant J.*, 61: 839–853
- Shabbir, R.N., M.Y. Ashraf, E.A. Waraich, R. Ahmad and M. Shahbaz, 2015. Combined effects of drought stress and NPK foliar spray on growth, physiological processes and nutrient uptake in wheat. *Pak. J. Bot.*, 47: 1207–1216
- Shahbaz, M. and B. Zia, 2011. Does exogenous application of glycinebetaine through rooting medium alter rice (*Oryza sativa* L.) mineral nutrient status under saline conditions? *J. Appl. Bot. Food Qual.*, 84: 54–60
- Shahbaz, M. and M. Ashraf, 2013. Improving salinity tolerance in cereals. *Crit. Rev. Plant Sci.*, 32: 237–249
- Shahbaz, M., M. Ashraf and H.R. Athar, 2008. Does exogenous application of 24-epibrassinolide ameliorate salt induced growth inhibition in wheat (*Triticum aestivum* L.)? *Plant Growth Regul.*, 55: 51–64
- 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
- Shahbaz, M., M. Ashraf, N.A. Akram, A. Hanif, S. Hameed, S. Joham and R. Rehman, 2011. Salt-induced modulation in growth, photosynthetic capacity, proline content and ion accumulation in sunflower (*Helianthus annuus* L.). *Acta Physiol. Plant.*, 3: 1113–1122
- Shahbaz, M., N. Noreen and S. Perveen, 2013. Triacontanol modulates photosynthesis and osmoprotectants in canola (*Brassica napus* L.) under saline stress. *J. Plant Interact.*, 8: 250–259
- Srinieng, K., T. Saisavoey and A. Karnchanat, 2015. Effect of salinity stress on antioxidative enzyme activities in tomato cultured *in vitro*. *Pak. J. Bot.*, 47: 1–10
- Stes, E., S. Depuydt, K.A. De, C. Matthys, K. Audenaert, K. Yoneyama, S. Werbrouck, S. Goormachtig and D. Vereecke, 2015. Strigolactones as an auxiliary hormonal defence mechanism against leafy gall syndrome in *Arabidopsis thaliana*. *J. Exp. Bot.*, 66: 5123–5134
- Strasser, R., J. Srivastava and A. Govindjee, 1995. Polyphasic chlorophyll 'a' fluorescence transients in plants and cyanobacteria. *J. Photochem. Photobiol.*, 61: 32–42
- Torres-Vera, R., J.M. García, M.J. Pozo and J.A. Lopez-Raez, 2014. Do strigolactones contribute to plant defence? *Mol. Plant Pathol.*, 15: 211–216
- Tsuchiya, Y. and P. McCourt, 2009. Strigolactones: a new hormone with a past. *Curr. Opin. Plant Biol.*, 12: 556–561
- Tuteja, N., 2007. Mechanisms of high salinity tolerance in plants. *Methods Enzymol.*, 428: 419–438
- Ueda, H. and M. Kusaba, 2015. Strigolactone regulates leaf senescence in concert with ethylene in *Arabidopsis*. *Plant Physiol.*, 169: 138–147
- Vu, T.S., D. Zhang, W. Xiao, C. Chi, Y. Xing, D. Fu and Z. Yuan, 2015. Mechanisms of combined effects of salt and alkaline stresses on seed germination and seedlings of *melilotus officinalis* (fabaceae) in northeast of china. *Pak. J. Bot.*, 47: 1603–1611
- Wang, C., L. Zhang, M. Yuan, Y. Ge, Y. Liu, J. Fan, Y. Ruan, Z. Cui, S. Tong and S. Zhang, 2010. The microfilament cytoskeleton plays a vital role in salt and osmotic stress tolerance in *Arabidopsis*. *Plant Biol.*, 12: 70–78
- Wolters, H. and G. Jurgens, 2009. Survival of the flexible: hormonal growth control and adaptation in plant development. *Nat. Rev. Genet.*, 10: 305–317
- Woo, H.R., K.M. Chung, J.H. Park, S.A. Oh, T.S.H. AhnHong, S.K. Jang and H.G. Nam, 2001. ORE9, an F-box protein that regulates leaf senescence in *Arabidopsis*. *Plant Cell*, 13: 1779–1790
- Xiong, G., Y. Yamada, Y. Wang and J. Li, 2014. Action of strigolactones in plants. *Enzymes*, 35: 57–84
- Yoneyama, K., T. Kisugi, X. Xie and K. Yoneyama, 2013. Chemistry of strigolactones: why and how do plants produce so many strigolactones? In: *Molecular Microbial Ecology of the Rhizosphere: Two Volume Set*. F.J. Bruijn (ed.). John Wiley & Sons, Inc., Hoboken, N.J., USA
- Zulfiqar, S. and M. Shahbaz, 2013. Modulation of gas exchange parameters and photosystem-II activity of canola (*Brassica napus* L.) by foliar-applied triacontanol under salt stress. *Agrochimica*, 57: 193–200
- Zwanenburg, B., A.S. Mwakaboko, A. Reizelman, G. Anilkumar and D. Sethumadhavan, 2009. Structure and function of natural and synthetic signalling molecules in parasitic weed germination. *Pest Manage. Sci.*, 65: 478–491

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