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Original article

Strigolactones Affect Growth Parameters and Some Antioxidant Enzyme Activities in Wheat (*Triticum aestivum* L.) under Salt Stress

Ezgi Önay [a] & Sefer Demirbaş [b,*]

[a] Department of Agricultural Biotechnology, Institue of Natural and Applied Sciences, University of Tekirdağ Namik Kemal University, Tekirdağ, Türkiye
[b] Department of Agricultural Biotechnology, Faculty of Agriculture, University of Tekirdağ Namik Kemal University, Tekirdağ, Türkiye

Abstract

External applications of strigolactones affect plant growth positively owing to the potential of adapting plants to the tolerance system under stress conditions. In this study, the effect of synthetic analogue strigolactone (GR24) pre-treatment to the seeds of salt-tolerant and salt-sensitive bread wheat (*Triticum aestivum* L.) varieties on growth parameters, antioxidant enzymes, such as superoxide dismutase (SOD), ascorbate peroxidase (APX) and glutathione reductase (GR) activity under salt stress were investigated. Salt stress has inhibited shoot development. Root development of the tolerant one was better than sensitive one under salt stress conditions. Salt application to sensitive variety caused the inhibition of APX and GR activities, and pre-treatment increased these activities. In conclusion, GR24 pre-treatment has an encouraging role in the growth of wheat plants by stimulating these antioxidant enzymes against salinity.

Keywords: Antioxidant Defence System, GR-24, Salinity, Seed Priming, Tolerance.

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* **Corresponding author:**

Demirbaş Sefer is an Associate Professor in the Department of Agricultural Biotechnology at Tekirdağ Namık Kemal University in Tekirdağ, Turkey. His research interests include Plant Stress Physiology, Biotechnology, and Genetics. He has lived, worked, and studied in Tekirdağ, Türkiye.
Email: sdemirbas@nku.edu.tr

INTRODUCTION

Salinity stress affects the productivity of agricultural land (Munns & Tester, 2008). High salt concentrations produce ionic toxicity in plants, resulting in osmotic stress and cellular ion imbalance, leading to the generation of reactive oxygen species (ROS) (Saddig et al., 2021). These imbalances at the cellular level can inhibit photosynthesis, resulting in metabolic toxicity, drying of membranes, and disorders of nutrient intake. These disorders affect the cellular respiration balance and cause changes in net biomass gain (Courtney et al., 2016). Antioxidant defense systems cleanse or degrade ROS and reduce atmospheric oxygen forms produced in various cellular regions during processes such as photorespiration, photosynthesis and respiration (Hasanuzzaman et al., 2020). Non-compressible ROS increases disrupting the stable structure of the protein, carbohydrate, nucleic acids, and lipids causing oxidative damage. Superoxide dismutase (SOD) functions to keep the ROS level in balance, disrupts the two-molecule superoxide anion ($O_2^{\cdot -}$) and forms hydrogen peroxide (H_2O_2) which is converted into water with various ways (Luo et al., 2012). The ascorbate-glutathione (AsA-Glu) cycle is an effective defence system to decompose H_2O_2. It has several enzymes, including ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR) and glutathione reductase (GR) (Bartoli et al., 2017). Strigolactones (SLs) are new terpenoid plant growth regulators that affect the root fungus symbiosis, plant growth, germination of parasitic plants, and physiological effects under stress conditions (Aliche et al., 2020; Umehara et al., 2008; Visentin et al., 2016). Many techniques and chemicals such as SLs applied to seeds and plants prior to encountering stressors have been investigated over the years to improve plant tolerance (Jisha et al., 2013; Ma et al., 2017; Ling et al., 2020; Günay et al., 2022).

World wheat (*Triticum aestivum* L.) production in 2020 is 777 million tonnes. The production value for Türkiye is 20.5 million tonnes and it decreased by %13.7 in 2021 (Anonymous, 2022). Bread wheat production was 750 million tons from more than 220 million hectares of land each year (Molero et al., 2019). Since wheat is a valuable plant, its use as a grass is less. In Türkiye, grass-cutting is more common in cases such as weed infestation or late planting and maturation (Çeri & Acar, 2019). Moderate salinity in soil decreases wheat yield by 28% (Zörb et al. 2019). Considering the increasing salinity problem, the present study aimed to investigate the effect of the AsA-Glu cycle on the enzyme system pre-treatment of synthetic analogue strigolactone (GR24) on morphological development, and some antioxidant enzymes of salt-tolerant and sensitive wheat varieties.

MATERIALS and METHODS

Plant material, GR24 treatment and growth conditions

Triticum aestivum L. 'Sultan-95' (salt sensitive) and 'Tosunbey' (salt tolerant) varieties were used. GR24 (purchased from Prof. Dr. Zwanenburg, Nijmegen University, The Netherlands) was used in wheat seeds to increase plant tolerance against salt stress. GR24 was dissolved with 1 mL acetone and diluted with distilled water to the final volume (Demirbas & Acar, 2008). Three groups were set up dry sowing (DS), watered sowing (WS), and GR24 treated sowing (GRS). The seeds were sown without any application (DS) as a negative control. WS group was used to determine the effect of water application before sowing, and the GRS group was used to assess the impact of the GR24 application. The seeds waited in 0 (WS)-hydropriming and 20 μM GR24 (GRS)-hormopriming solutions for 60 min. After treatment, twenty seeds were sown in a plastic pot (1.5 L) containing perlite and watered with dH_2O. The plant cultivation was carried out in a growth room at 25±2°C/15±2°C (day/night) with a 16-h daylight period for 22 days.

Salt stress and plant harvesting

Salt stress application was carried out with Hoagland solution (100 ml/pot) containing 0 and 200 mM NaCl to fifteen-day-old seedlings. On the seventh day after salt application, the leaves of seedlings were harvested, frozen in liquid nitrogen, and stored at -30°C until biochemical analysis.

Plant growth parameters

Five randomly selected twenty-two-day-old seedlings (Zadoks 14) per replicate were divided into roots and shoots. Firstly, they were measured with a ruler for length (cm) (Root length: RL, shoot length: SL) and weighted for the fresh weight (Shoot fresh weight: SFW, root fresh weight: RFW) (mg). Then, they were dried in an oven for 48 hours at 65°C to determine dry weights (Shoot dry weight: SDW, root dry weight: RDW) (mg).

Plant analysis methods

Total protein and SOD, APX and GR activities

The frozen sample (200 mg) was homogenized in 50 mM sodium phosphate (Na-P) buffer (pH 7.8) containing 1 mM $EDTA.Na_2$ for total protein, SOD, APX, and GR analyses. The homogenates were centrifuged at 14000 rpm for 30 min at 4°C, and the supernatants were used for the determination of the parameters. According to the Bradford method, the total protein concentration of the enzyme extract was determined (Bradford, 1976). SOD (EC 1.15.1.1) activity was measured as the inhibition of photochemical reduction of nitro-blue tetrazolium at 560 nm (Beauchamp and Fridovich, 1971; Giannipolities and Ries, 1977). APX (EC 1.11.1.11) activity was measured according to Nakano and Asada (1981). One unit of APX was defined as 1 mmol mL^{-1} AsA oxidized in the reaction mixture containing 0.05 M Na-P buffer (pH 7), 0.5 mM AsA, 0.1 mM $EDTA.Na_2$, 1.2 mM H_2O_2, and the enzyme extract at 290 nm per min. GR (EC 1.6.4.2) activity was measured according to Foyer & Halliwell (1976). The reaction mixture contained Na-P buffer (pH 7.8), oxidized glutathione (GSSG), $NADPH.Na_4$, and the enzyme of extract. NADPH oxidation was determined at 340 nm, and one unit of

GR was defined as 1 mmol mL^{-1} GSSG reduced per min. The biochemical parameters were determined spectrophotometrically.

Statistical analysis

Each essay was repeated three times independently, and each data point was the mean of five replicates. The data were subject to one-way ANOVA using Statistical Package for the Social Sciences (SPSS) Program ver 18.0 (SPSS, Chicago, IL, USA), and the mean comparison was conducted using the Least Significant Difference (LSD) test at $p \leq 0.05$.

RESULTS and DISCUSSION

We found that there were differences between varieties of growth parameters in these study conditions. The best development in root and shoot was in the Tosunbey variety. The RL (30.62%), RFW (40.52%), RDW (25.23%) (Table 1), SFW (13.29%), and SDW (11.93%) values (Table 2) of salt-tolerant variety (Tosunbey) were significantly higher than salt-sensitive variety (Sultan-95) (p<0.01).

Table 1. Average values and significance groups for root parameters

RL		**Groups**						
Variety	**NaCl (mM)**	**DS**	**WS**	**GRS**	**Average of variety**		**Average of NaCl**	
Sultan-95	0	8.63h	12.98cde	12.23ef	Sultan-95	11.17b	0	12.75
	200	11.07fg	9.60gh	12.48def				
Tosunbey	0	16.08ab	12.48def	14.07cd	Tosunbey	14.59a	200	13.01
	200	16.67a	14.75bc	13.47cd				
Average of groups		13.11	12.45	13.06				
LSD	*Variety: 0.54***	*NaCl: - ns*		*Groups: - ns*	*VarietyxNaClxGroups:1.805 ***			
RFW		**Groups**						
Variety	**NaCl (mM)**	**DS**	**WS**	**GRS**	**Average of variety**		**Average of NaCl**	
Sultan-95	0	100.33de	112.33c	62.67h	Sultan-95	90.78b	0	107.33
	200	84.17g	87.50fg	97.67ef				
Tosunbey	0	109.33cd	129.33ab	130.00ab	Tosunbey	127.56a	200	111.00
	200	138.33a	123.67b	134.67ab				
Average of groups		108.04ab	113.21a	106.25b				
LSD	*Variety:6.75***	*NaCl:- ns*		*Groups:5.52***	*VarietyxNaClxGroups: 11.03***			
RDW		**Groups**						
Variety	**NaCl (mM)**	**DS**	**WS**	**GRS**	**Average of variety**		**Average of NaCl**	
Sultan-95	0	7.63	9.10	9.03	Sultan-95	8.80b	0	9.57b
	200	8.62	8.68	9.72				
Tosunbey	0	10.72	10.47	10.45	Tosunbey	11.02a	200	10.25a
	200	11.68	11.93	10.87				
Average of groups		9.66	10.05	10.02				
LSD	*Variety:0.56***	*NaCl: 0.50***		*Groups: - ns*	*VarietyxNaClxGroups: - ns*			

RL, root lengths (cm); RFW, root fresh weight (mg); RDW, root dry weight (mg); DS, dry sowing; WS, watered sowing; GRS, GR24 treated sowing. * p ≤ 0.05; ** p ≤ 0.01; ns: not significant.

Salt stress had an increasing effect on root development, and the increase in RDW (Table 1) value was statistically significant ($p<0.01$). It had a suppressive effect on shoot development, unlike root development, and the suppression in SL and SFW (Table 2) values was statistically significant ($p<0.01$).

When the comparison was made between the groups, there was a significant change in RFW (Table 1) in root development and in SFW (Table 2) in shoot development ($p<0.01$). Although there was a decrease in RFW and SFW values in the strigolactone application group (GRS) compared to the DS group, this decrease was not statistically significant ($p>0.05$).

This study investigated the responses of GR24 pre-treated salt-sensitive and -tolerant wheat varieties against salt stress based on the AsA-Glu cycle. The early response of plants to stress factors is critical in coping with stress (Zhu, 2016). The whole crop of wheat is used as straw or silage in livestock. Improving the salt tolerance level of wheat can increase grain yield and quality for humans, as well as increase the yield of silage, fresh grass, and straw in livestock. In this study, RL, SL, RFW, RDW, SDW, and RDW parameters were examined to observe growth. According to the results, the tolerant variety showed better development than the sensitive one. Especially, salt stress has inhibited shoot development. Generally, GR24 pre-treatment improved plant growth against salt stress conditions. This result is consistent with studies about GR24 pre-treatment in *Arabidopsis* by (Kapulnik et al., 2011), in wheat by Kausar & Shahbaz (2017), in rapeseed by Ma et al. (2017), and in rice by Ling et al. (2020).

Table 2. Average values and significance groups for shoot parameters

SL		**Groups**						
Variety	**NaCl (mM)**	**DS**	**WS**	**GRS**	**Average of variety**		**Average of NaCl**	
Sultan-95	0	28.53	24.72	27.63	Sultan-95	25.85	0	26.22a
	200	23.23	25.28	25.70				
Tosunbey	0	25.18	25.75	25.48	Tosunbey	24.44	200	24.08b
	200	23.10	23.45	23.70				
Average of groups		25.01	24.80	25.63				
LSD	*Variety:-* ^{ns}	*NaCl:1.08***		*Groups:-* ^{ns}	*VarietyxNaClxGroups: -* ^{ns}			
SFW		**Groups**						
Variety	**NaCl (mM)**	**DS**	**WS**	**GRS**	**Average of variety**		**Average of NaCl**	
Sultan-95	0	146.17	131.17	144.17	Sultan-95	133.92b	0	149.39a
	200	116.83	126.67	138.50				
Tosunbey	0	170.67	150.50	153.67	Tosunbey	151.72a	200	136.25b
	200	150.67	139.67	145.17				
Average of groups		146.08a	137.00ab	145.38a				
LSD	*Variety: 7.18***	*NaCl: 4.88***		*Groups:5.98***	*VarietyxNaClxGroups: -* ^{ns}			
SDW		**Groups**						
Variety	**NaCl (mM)**	**DS**	**WS**	**GRS**	**Average of variety**		**Average of NaCl**	
Sultan-95	0	17.50	19.80	18.75	Sultan-95	17.86b	0	19.43
	200	15.38	16.90	18.83				
Tosunbey	0	18.98	21.55	20.02	Tosunbey	19.99a	200	18.42
	200	20.60	19.53	19.25				
Average of groups		18.12	19.45	19.21				
LSD	*Variety:1.39**	*NaCl:-* ^{ns}		*Groups: -* ^{ns}	*VarietyxNaClxGroups: -* ^{ns}			

SL, shoot lengths (cm); SFW, shoot fresh weight (mg); SDW, shoot dry weight (mg); DS, dry sowing; WS, watered sowing; GRS, GR24 treated sowing. * $p \leq 0.05$; ** $p \leq 0.01$; ns: not significant.

We measured the SOD, APX, and GR activities. In the DS group, SOD activity significantly increased by 29.48% in the salt-sensitive variety and 24.50% in the salt-tolerant variety because of salt stress. In the WS group, salt stress caused increased activity by 23.53% in the salt-sensitive variety, and there is no significant change for the salt-tolerant variety. In the GRS group, SOD activity increased by 52.16% in the salt-tolerant variety because of GR24 pre-treatment, and it was not significantly affected under salt stress in the salt-sensitive variety (Figure 1).

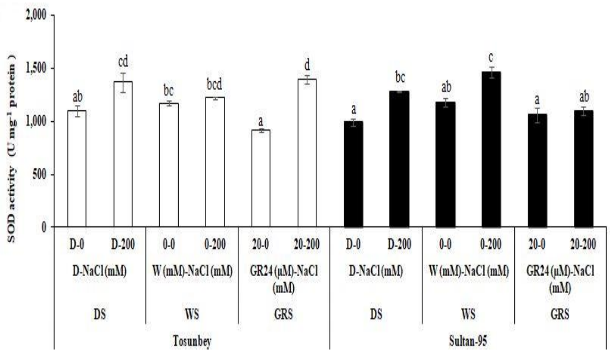

Figure 1. Changes in SOD activity in Sultan-95 and Tosunbey wheat varieties. Vertical bars indicate the mean ± SE of five replicates. Means followed by the same letter were not significantly different at $p \leq 0.05$ as determined by the LSD multiple range tests and the varieties were compared. D, dry; DS, dry sowing; W, water; WS, watered sowing; GRS, GR24 treated sowing.

In the DS group, salt stress decreased APX activity by 15.04% in the salt-sensitive variety. In contrast to this response, the activity increased by 93.37% in the salt-tolerant variety. In the WS group, salt stress caused an increase in APX activity by 117.24% in the salt-sensitive variety and by 17.98% in the salt-tolerant variety. In the GRS group, salt stress increased the activity by 85.63% in the salt-sensitive variety and 92.69% in the salt-tolerant variety (Figure 2).

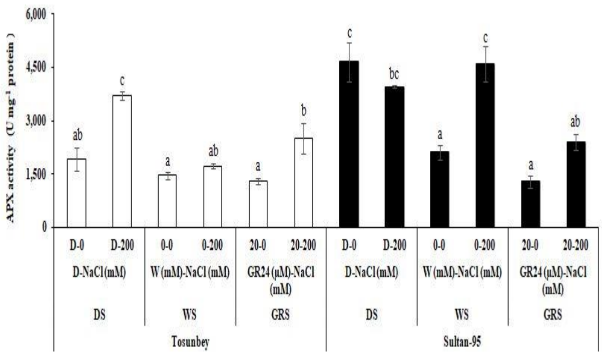

Figure 2. Changes in APX activity in Sultan-95 and Tosunbey wheat varieties. Vertical bars indicate mean ± SE of five replicates. Means followed by the same letter were not significantly different at $p \leq 0.05$ as determined by LSD multiple range test and the varieties were compared. D, dry; DS, dry sowing; W, water; WS, watered sowing; GRS, GR24 treated sowing.

In the DS group, salt stress decreased GR activity by 12.21% in the salt-sensitive variety, however, it increased the activity by 75.38% in the salt-tolerant variety. In the WS group, salt stress increased the activity by 157.42% in the salt-sensitive variety and 27.30% in the salt-tolerant variety. The GR activity increased by 94.20% in the GRS group in the salt-sensitive variety and 102.67% in the salt-tolerant variety (Figure 3).

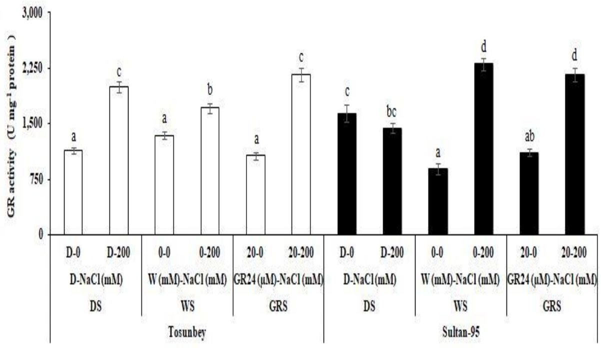

Figure 3. Changes in GR activity in Sultan-95 and Tosunbey wheat varieties. Vertical bars indicate mean ± SE of five replicates. Means followed by the same letter were not significantly different at $p \leq 0.05$ as determined by LSD multiple range test and the varieties were compared. D, dry; DS, dry sowing; W, water; WS, watered sowing; GRS, GR24 treated sowing.

The AsA-GSH cycle is an essential mechanism in plants to overcome the stress factors in different compartments such as chloroplast, mitochondria, and cytosol (Bartoli et al. 2017). Our biochemical results indicated that salt application to non-pre-treated sensitive variety caused the inhibition of APX and GR activity and the encouragement of SOD activity. These results are consistent with a study by Ling et al. (2020) determined that GR24 treatment has increased SOD activity in rice seedlings under salt stress. Ma et al. (2017) also showed a significant effect of strigolactone on SOD activity in rapeseed. Sedaghat et al. (2017) determined that GR24 alone and together with SA applications induced morphological (membrane stability, electrolyte leakage, stoma limitation, relative water content) and biochemical (SOD, APX, POX, CAT, MDA) performance in wheat under drought stress. In another study, Sedaghat et al. (2021) investigated the effect of GR24 application methods on photosynthesis, plant water status and antioxidant enzyme activities in winter wheat under drought stress. The researchers determined that GR24 applications increased photosynthesis rate and stomatal conductance removing stomal limitation and balancing plant water status. The GR24 applications increased especially root development and yield in winter wheat in their study. H_2O_2 content in winter wheat decreased and SOD, POX, CAT, and APX activities increased because of GR24 application under drought stress. Their results like our results indicated that GR24 application induced plant biochemical responses under drought stress. In our salt stress study, hydro- (WS) and hormopriming (GRS) treatments increased the APX and GR activity in this variety. SOD, APX, and GR activity of salt-tolerant variety increased under salt stress in both groups. In this study, pre-treatments in DS and WS groups against salt stress would increase SOD activity in a salt-sensitive variety. In contrast to the responses of SOD, APX activity was positively affected by all applications, but GR activity has increased in all applications in both varieties except for the salt-sensitive variety in DS. For APX activity, increase in DS more than other applications in the salt-tolerant variety. Although salt stress caused an increase in GR activity in the salt-tolerant varieties, it was determined that hydro- and hormopriming caused an increase in the activity in both varieties under salt stress.

Conclusion

As a result, it has been shown that 20 μM GR24 pre-treatment to salt-tolerant and sensitive wheat varieties' seeds before exposure to salt stress stimulates the AsA-Glu cycle enzyme system and has an encouraging role in salt tolerance in the wheat plant. Moreover, additional studies about other antioxidant enzymes, lipid peroxidation, and ROS level and its interaction with other phytohormones (abscisic acid, cytokinins, etc.) in root and shoot levels to understand the effect of strigolactone on growth and the yield in field conditions for yield of fresh grass, silage, and straw will be required.

Declaration of Interest Statement

The authors declare no conflict of interest.

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