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Research paper

Effect of salinity stress on the root proteome pattern of spring bread wheat

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Abstract
In this experiment, the effect of salt stress on the root proteome pattern of Arg (tolerant to salinity) and Moghan3 (sensitive to salinity) cultivars of wheat was investigated by two-dimensional polyacrylamide gel electrophoresis. Salinity was applied at two levels of 0 and 150 mM in the third-leaf stage for three weeks under greenhouse conditions. The proteome analysis of the roots revealed 120 reproducible protein spots, among which 15 spots showed significant changes in expression. In Moghan3, four protein spots with a significant reduction in expression were identified. In the tolerant cultivar of Arg, 11 protein spots showed significant changes in expression, among which five protein spots had an increased expression and six protein spots had a decreased expression. These proteins were classified based on their function into several groups such as the proteins involved in metabolism and energy, reactive oxygen species scavenging and detoxification, the proteins associated with cell walls, and the proteins involved in folding and degradation. Probably, the tolerance to salt stress in the Arg cultivar was related to the increased expression of pyruvate dehydrogenase, phosphoglycerate mutase, catalase, and malate dehydrogenase proteins. While in the sensitive variety of Moghan3, the decrease in the expression of enolase, peroxidase, and glutathione peroxidase proteins under salinity stress conditions probably caused oxidative stress in the plants due to increased production of reactive oxygen species. These findings can be useful for improving the salt tolerance in the breeding programs of wheat.

Keywords: proteome analysis; reactive oxygen species; salt stress; two-dimensional electrophoresis

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Introduction

Wheat is one of the most important crop plants and plays a vital role in the nutrition of the world population. Due to the limited area of arable land, increasing wheat production requires increased yield per hectare. Also, to ensure the sustainability of this crop, it is necessary to produce more tolerant cultivars under environmental stresses.

One of the important challenges of plant scientists is to develop tolerant genotypes under environmental stresses (Koyro *et al*. 2012). Salt stress is one of the most important abiotic stresses in the world. It is estimated that about 20 percent of the world's land and about half of the irrigated areas are affected by salinity (Kang *et al*. 2010). The increasing salinity of arable land has devastating results

and it is predicted that 50% of arable land will be lost by 2050 (Wang *et al*. 2003). Salinity adversely affects substances such as proteins, lipids, and nucleic acids (Apel and Hirt 2004), metabolic and physiological processes (Sadak *et al*. 2020), and consequently crop yield (Ahmad *et al*. 2019).

Breeding for agronomic traits has resulted in the yield increase, however, improvement of root traits may also increase yield and guarantee yield success under stress conditions. The root is the first plant organ to experience the effect of salinity stress. Therefore, the adaptation of this organ can play an important role in tolerance to salinity. Roots can regulate the entry of ions into the vascular system and, as the first obstacle, block the entry of ions into the plant (Krishnamurthy *et al*. 2011).

Although the study of changes in gene expression at the transcription level has led to the identification of genes that play a key role in stress tolerance, including tolerance to salinity stress, these studies alone are not enough for understanding the underlying mechanisms of salinity stress because some genes change during transcription, translation, and post-translation. Protein data analysis along with studying physiological characteristics provides valuable information to breeders for designing crop molecular breeding strategies to withstand abiotic stresses (Hosseini Salekdeh *et al*. 2009). Therefore, the proteomic approach is used as a useful tool for investigating the response of plants to various stresses (Abdalla and Rafudeen 2012). The present study aimed to investigate the effect of salt stress on the root protein pattern of two contrasting spring wheat cultivars and to identify proteins that respond to salt stress using two-dimensional gel electrophoresis.

Materials and Methods

Plant materials

In this study, two wheat cultivars of Moghan3 (salt-sensitive) and Arg (salt-tolerant) were used (Anonymous 2013). Seeds were sown in 1.5-liter pots containing perlite in the greenhouse of the University of Tabriz in 2017. After the two-leaf stage, the plants were irrigated with the Hoagland nutrient solution and continued until salinity stress was imposed at the third-leaf stage. Salinity was applied at two levels (Hoagland salt-free nutrient solution as the control and 150 mM salinity by adding sodium chloride to the nutrient solution). Salinity stress continued for three weeks until the symptoms of stress in plant shoots appeared and then roots were sampled. The root samples were immediately frozen in liquid nitrogen and stored at -80 °C until protein extraction.

Proteomic analysis

Protein extraction from the root tissues was

performed according to the method of Damerval *et al*. (1986) with slight modifications. The concentration of sample proteins was measured by the Bradford (1976) method. For making the first dimension gel (O'Farrell 1975), tubes with 11 cm length and 3 mm diameter were used. For the preparation of two tubular gels, 600 mg of urea was weighed per gel and poured into the beaker. Then, 710 µL of deionized ddH_2O water, 290 µL of 30% polyacrylamide, and 500 µL of NP-40 were added. After the urea was completely dissolved, ampholines with pH 3-10 and pH 5-8 were added equally to the solution. Then, 3.75 µL of APS 10% and 2.5 µL of TEMED were added and the beaker was shaken gently. The isoelectric focusing voltage settings were performed in three steps: 200 volts for half an hour, 400 volts for 16 hours, and 600 volts for one hour. The second dimension was performed by SDS-PAGE with the 15% polyacrylamide gel. Then, the proteins were stained with silver nitrate. The gels were scanned using a BioRad GS-800 scanner. Image analysis was performed by the PDQuest software. A t-test was used to identify spots with a significant change in expression. For each spot, expected proteins were searched based on the isoelectric point (*pI*) and molecular weight (MW) referring to the protein databases using the TagIdent program. The induction factor (IF) was also used to determine the type of change in the protein expression such that IF spots greater than 2 were considered as the increased expression and IF spots less than 0.5 were regarded as the decreased expression.

Results and Discussion

Analysis of the gel images resulted in the identification of 120 repeatable protein spots. Of the 120 spots, 55 spots showed a change in expression based on the IF index in the tolerant cultivar of Arg, from which only 11 had a significant change in expression (Figure 1). Of these 11 spots, five spots showed increased expression and six spots showed decreased expression (Figure 2). In the susceptible cultivar of Moghan3, 16 protein spots had changes in expression based on the IF index. Of these, only four spots showed significant changes, which decreased the expression (Figures 1 and 3). The list of 15 proteins with significant changes in response to salinity stress in the two tolerant and susceptible cultivars was provided in Table 1.

Salt stress-responsive proteins

The proteins that responded to salt stress were classified into four groups based on their function. Most of the proteomic changes due to salt stress were related to proteins involved in the metabolic reactions and pathways and energy production. In the second place, proteins involved in reactive oxygen species (ROS) scavenging and detoxification showed

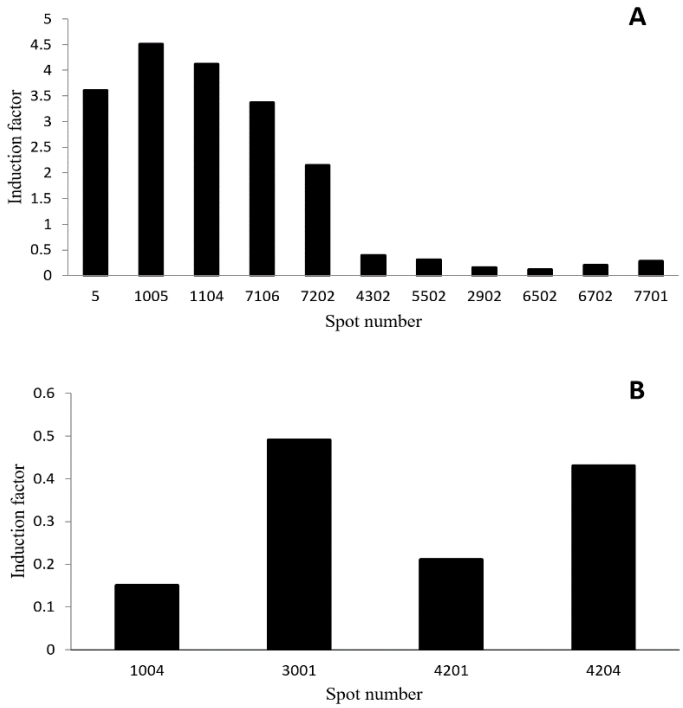

Figure 1. Changes in expression of wheat proteins under sodium chloride stress in A) tolerant cultivar of Arg and B) susceptible cultivar of Moghan3.

the highest change in expression in terms of the number of spots. Next, were the folding and degradation proteins and the proteins associated with the cell wall (Figure 4).

Proteins involved in metabolism and energy production

Salinity stress has a profound effect on plant energy metabolism. In many studies on the proteomics of different plant species, the effect of salinity stress on the change in the expression of this group of proteins has been reported (Gao *et al*. 2011; Guo *et al*. 2012; Kang *et al*. 2012; Podda *et al*. 2013). These include alpha and beta subunits of ATP synthase (Neupane *et al*. 2019), aconitate hydratase (Moeder *et al*. 2007), glyceraldehyde-3-phosphate dehydrogenase, malate dehydrogenase (MDH), pyruvate kinase, phosphoglycerate kinase (Dai *et al*. 2013), fructose bisphosphate aldolase, triosephosphate isomerase (Bandehagh *et al*. 2011), and enolase (Xu *et al*. 2010). Alpha and beta subunits of ATP synthase play an important role in energy production by converting ADP to ATP (Neupane *et al*. 2019). MDH and aconitate hydratase belong to the tricarboxylic acid cycle (TCA) cycle (Lushchak *et al.* 2014). Fructose bisphosphate aldolase (Ziveri *et al.* 2017), glyceraldehyde-3-phosphate dehydrogenase, pyruvate kinase, phosphoglycerate kinase, triosephosphate isomerase, and enolase are linked to the sugars' glycolysis pathway (Berg *et al.* 2002).

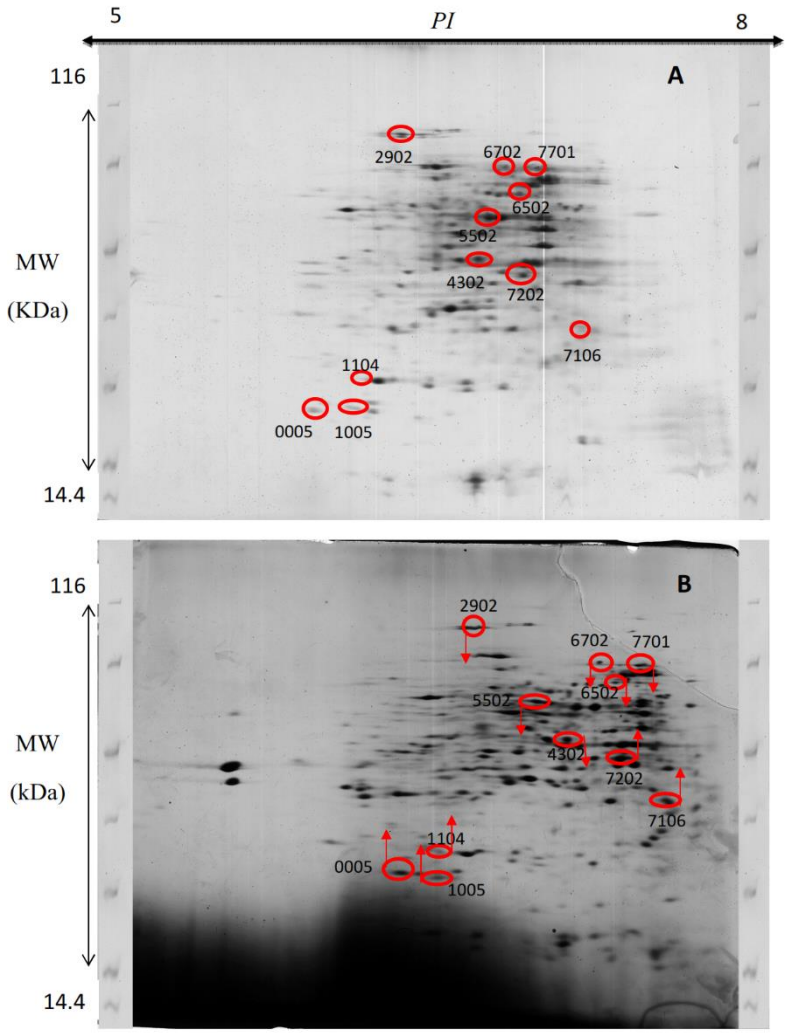

Figure 2. Root proteome pattern of the tolerant wheat cultivar of Arg under A) control (0 mM) and B) NaCl stress (150 mM) conditions.

Spot 1005, which showed a significant change in expression under salinity stress, was identified as phosphoglycerate mutase (PGM). This protein showed an increased expression in the tolerant cultivar of Arg. PGM is a glycolysis enzyme that catalyzes the reversible conversion of glycerate-3 phosphate to glycerate-2 phosphate (Johnsen and Schonheit 2007). Increased expression of this enzyme has been indicated in wheat seedlings under salt stress (Caruso *et al*. 2008) and in rice under cold stress conditions (Yan *et al*. 2006). Also, Bazargani *et al*. (2011) reported a decreased or increased expression of different isoforms of this enzyme in different wheat cultivars under water-deficit stress. An increment in the expression of this enzyme may help the tolerant cultivar by the production of more energy under salt stress.

Spot 1104 was identified as the MDH

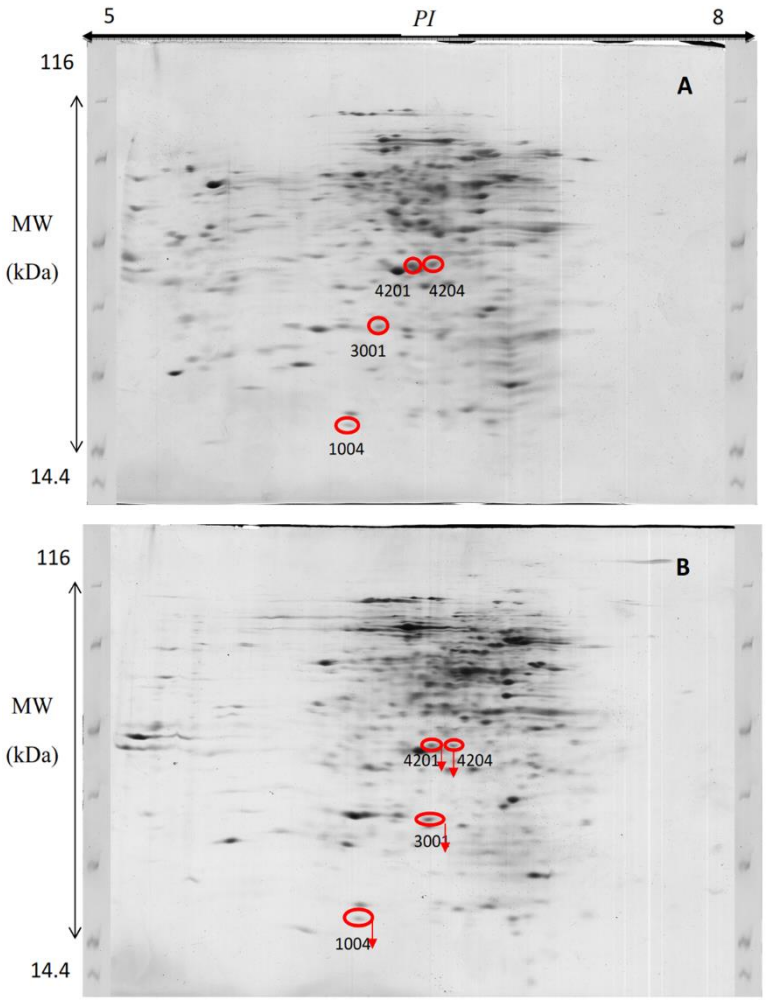

Figure 3. Root proteome pattern of the susceptible wheat cultivar of Moghan3 under A) control (0 mM) and B) NaCl stress (150 mM) conditions.

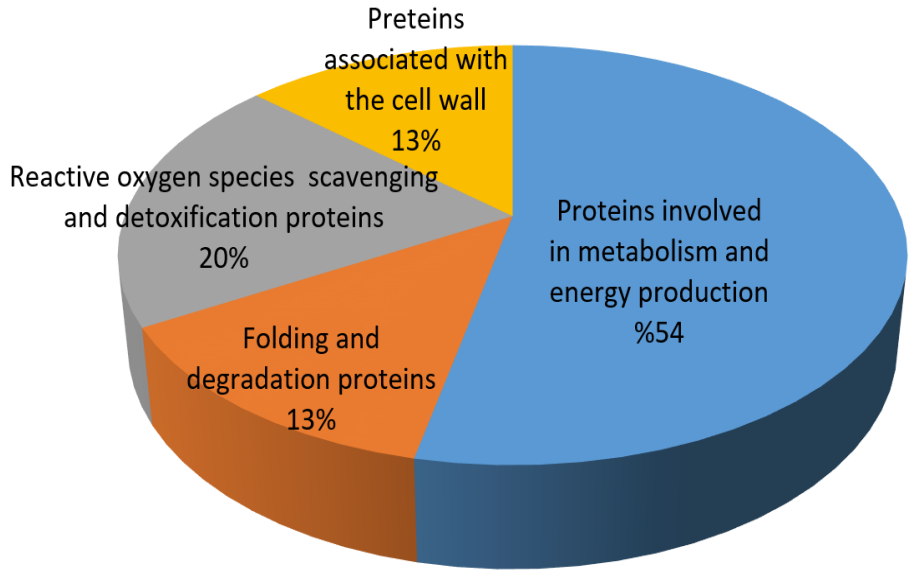

Figure 4. Functional grouping of proteins with a significant change of expression in the roots of Arg and Moghan3 wheat cultivars in response to salinity stress.

Table 1. Characteristics of protein spots with changes in expression in the Arg and Moghan3 cultivars of wheat under sodium chloride stress.

Cultivar	Spot No.	Protein	Accession No.	Change in expression	Theoretical		Experimental		Functional group
					MW[+]	*pI*[++]	MW	*pI*	
Arg	0005	Caffeoyl-CoA-methyltransferase	Q41720	Increase	28.60	5.30	29.87	5.64	Cell wall
	1005	Phosphoglycerate mutase	240082	Increase	30.00	5.43	31.09	5.86	Metabolism and energy
	1104	Malat dehydrogenase	Gi/3273828	Increase	35.80	5.70	34.74	6.08	Metabolism and energy
	7106	Pyruvate dehydrogenase	SGN-U315305	Increase	43.37	6.87	44.68	7.00	Metabolism and energy
	7202	CAT 1	C139229	Increase	56.58	6.68	56.29	6.86	ROS[+++] scavenging and detoxification
	4302	Glycosyl hydrolase family 1 protein	t3g09260	Decrease	60.30	6.95	60.75	6.61	Cell wall
	5502	HSP 70	76003	Decrease	67.10	5.76	73.63	6.67	Folding and degradation
	2902	Lipoxygenase 1	TC146955	Decrease	96.39	5.73	106.40	6.34	Metabolism and energy
	6502	Methionine Synthase	NP-001235794.1	Decrease	84.28	5.93	81.02	6.79	Metabolism and energy
	6702	Sucrose synthase 2	NP-199730.1	Decrease	92.06	5.07	91.72	6.74	Metabolism and energy
	7701	HSP90 protein	SGN-U316401	Decrease	90.67	5.19	90.41	6.88	Folding and degradation
Moghan3	1004	Glutathione peroxidase	SGN-U322657	Decrease	19.70	5.11	19.52	6.23	ROS scavenging and detoxification
	3001	Peroxidase	C140370	Decrease	36.55	5.91	33.13	6.53	ROS scavenging and detoxification
	4201	Enolase	SGN-U312378	Decrease	47.80	5.68	49.37	6.55	Metabolism and energy
	4204	Enolase	SGN-U31237	Decrease	47.80	5.68	49.17	6.65	Metabolism and energy

[+]Molecular weight; [++]Isoelectric point; [+++]Reactive oxygen species

enzyme which showed a significant increase in expression in the Arg cultivar under salinity stress. MDH is found in the cytosol, mitochondria, and peroxisomes (Gietl 1992). This NAD^+-dependent enzyme has a role in plant metabolism and oxidation or reduction of different substrates and participates in the TCA cycle (Kumar *et al*. 2000). Increased activity of this enzyme has been reported in Arabidopsis (Ndimba *et al*. 2005) and bread wheat (Wang *et al*. 2008) under water-deficit stress. The decrease in the MDH activity at the beginning of stress and its increase at the later stages of water-deficit stress was observed in the wild watermelon (Yoshimura *et al*. 2008). Increased expression of this enzyme has also been reported to offset the increased ATP demand for the rapid growth of young rice seedlings when imposed to salinity stress (Dadashi Dooki *et al.* 2006). However, the reduction of this enzyme in wheat (Guo *et al*., 2012) and rapeseed roots (Banaei-Asl *et al*. 2015) has been reported under salinity conditions. It seems that increased activity of MDH helps maintain a higher activity of the TCA cycle as well as synthesizing more amino

acids.

Spot 7106 showed a significant increase in the expression under salinity in the tolerant cultivar of Arg, which was related to pyruvate dehydrogenase (PDH). Dihydrolipoamide dehydrogenase and PDH participate in the PDH complex that converts pyruvate to acetyl-CoA and links cytosolic glycolytic metabolism to TCA (Manaa *et al*. 2011). Increased expression of this enzyme is effective in maintaining the higher activity of the TCA and probably provides part of the energy required for cell detoxification reactions.

Spots 4201 and 4204, which had a significant decrease in expression under salinity stress in the susceptible cultivar of Moghan3, were identified as the enolase enzyme. Enolase is a reversible dehydration catalyst for converting 2-phosphoglycerate to phosphoenolpyruvate (Voet *et al*. 2008). Phosphoenolpyruvate allows the transfer of the phosphoryl group to ADP to form ATP (Berg *et al*. 2002). Regulation of the enolase enzyme is essential in the energy pathway. It is one of the enzymes involved in the glycolysis process and the Krebs cycle (Riccardi *et al*. 1998). It responds to many environmental stresses including salinity (Umeda *et al*. 1994; Forsthoefel *et al*. 1995) and water deficit (Forsthoefel 1995; Riccardi *et al*. 1998; Merwitz *et al*. 2011) in a variety of plants. The decreased expression of this enzyme may have caused the susceptibility of Moghan3 to salinity stress.

Spot 2902, which was decreased in the salinity stress conditions in the Arg cultivar, was related to the lipoxygenase (LOX) enzyme. One of the important enzymatic systems related to the alteration of lipids of the cell membranes is the LOX enzyme system. LOXs play a crucial role in defense against biotic and abiotic stresses (Viswanath *et al*. 2020). Linoleic and linolenic acids are the most abundant unsaturated fatty acids in the structure of plant cells and the most common substrates for the LOX enzyme activity (Siedow 1991). Under sodium chloride stress, the rate of energy metabolism is reduced in plants to conserve energy (Bandehagh and Taylor 2020) and limit ROS (Asada, 1999). Jiang *et al.* (2007) in a study on the Arabidopsis roots, found that 11 proteins that were involved in the citrate cycle, electron transport, glycolysis, and pentose pathways decreased in abundance under the sodium chloride stress. On the other hand, Molina *et al.* (2002) reported that under in vitro conditions, sodium chloride increased the lipoxygenase activity and lipid peroxidation in tomatoes. Ben-Hayyim *et al.* (2001) also suggested that the sodium chloride stress increases the activity of this enzyme in the orange plant. However, they emphasized that this increase in the LOX activity was unique under sodium chloride stress conditions since

it was not observed under osmotic stress conditions after the application of polyethylene glycol.

Spot 6502, which significantly decreased in the expression under salt stress in the tolerant cultivar of Arg, was related to methionine synthase. Contrary to our results, Sanchez-Aguayo *et al.* (2004) reported that under salinity stress, methionine production, which requires increased expression of methionine synthase and s-adenosylmethionine synthase, was increased in tomatoes. Witzel *et al.* (2009) also indicated the higher expression of S-adenosylmethionine synthase 1 under salinity stress conditions in at least one genotype of barley.

Spot 6702 which significantly decreased in expression under salt stress in the Arg cultivar belonged to sucrose synthase. Sucrose synthase plays an essential role in sucrose breakdown and energy supply (Li *et al*. 2002). Activation of the energy metabolism is essential to provide energy for the biosynthesis of stress-responsive proteins and osmolytes as well as for the transfer of active ions under salinity stress conditions (Kosova *et al*. 2013). Also, stress conditions disrupt the photosynthetic rate (Sharma *et al*. 2020). This enzyme is affected by soil salinity (Peng *et al.* 2016). Elavumoottil *et al.* (2003) selected the cells of *Brassica oleracea* L. var. *Botrytis* from the cultures grown in the medium supplemented with different levels of NaCl. They showed that the sucrose synthase activity was higher in the salt-adapted cells than in the controls. Peng *et al.* (2016) reported sucrose accumulation in the cotton leaves in reaction to soil salinity. The increase in sucrose content under other abiotic stresses such as cold (Strand *et al*. 2003) and water-deficit stress (Yang *et al.* 2001; Adabavazeh and Razavizadeh 2015) has also been reported. The reduction in the expression of sucrose synthase in the salt-tolerant cultivar of Arg under salt stress is an unusual finding that can be attributed to the experimental error and/or conditions in which the experiment was conducted. For example, Dubey and Singh (1999) indicated that the increase in the sucrose phosphate synthase activity was higher in the sensitive cultivars of rice than in the tolerant genotypes.

ROS scavenging and detoxification proteins

Osmotic and ionic stresses caused by salinity, result in oxidative stress in plants because of the increased production of ROS during vital cell processes. ROS can damage the structure of proteins, lipids, and nucleic acids (Ahmad *et al*. 2009). Plants need to strengthen their tolerance mechanisms such as improving the cell defense system and the removal of reactive oxygen radicals to maintain homeostasis under stress conditions (Apel and Hirt 2004).

Spot 7202, which showed a significant increase in the expression under salinity stress

in the tolerant cultivar of Arg, was identified as the catalase (CAT) enzyme. CAT accumulates in peroxisomes and plays an important role in alleviating oxidative stresses (Apel and Hirt 2004). CAT removes H2O2 by converting it to water and oxygen (Sharma *et al*. 2012) and improves the efficiency of the energy system in plants (Mallick and Mohn 2000). Ford *et al*. (2011) reported that water stress in three wheat cultivars increased the ROS scavenging capacity through the increase in antioxidant enzymes such as superoxide dismutase (SOD) and CAT. Increased CAT activity was also observed with increasing water-deficit stress in the study of Hojati *et al.* (2011) on *Carthamus tinctorius.*

Spot 3001, which showed a significant decrease under salt stress in Moghan 3, was related to peroxidase (POX) enzymes. POXs catalyze several oxidative reactions by utilizing H_2O_2 (Kawano 2003). Antioxidant enzymes help plant cells to tolerate stress conditions by removing oxygen-free radicals. Heidari (2009) also reported a decrease in the POX activity in wheat when salinity was imposed. However, some reports have shown an increase in the POX activity in wheat (Barakat 2011), sorghum (Heidari 2009), rice (Higa *et al*. 2001), and Arabidopsis (Jiang *et al.* 2007) in the salinity stress conditions.

Spot 1004, which significantly decreased in the expression under salt stress in the sensitive cultivar of Moghan 3, belonged to glutathione peroxidase (GPX). Reports have shown that GPX responds to stresses such as salt, cold (Yoshimura *et al*. 2004), and drought (Miao *et al*. 2006). This enzyme acts as a redox transducer and scavenger under stress conditions (Miao *et al*. 2006). It is effective in removing hydroperoxides and lipid peroxides in plants (Kuhn and Borchert 2002)

Proteins involved in folding and degradation

Spots 5502 and 7701, which had a reduced expression under salt stress in the tolerant cultivar of Arg, were related to the heat-shock proteins (HSPs), HSP70, and HSP90, respectively. These proteins are classified into five major families: HSP70, HSP90, HSP100, chaperonins, and small HSPs (Wang *et al*. 2004). Stresses usually affect adversely the function of proteins. Folding and degrading proteins as molecular chaperones are responsible for protein assembly, folding, translocation, and degradation, and play a vital role in protecting plants against various stresses (Wang *et al*. 2004). Vitamas *et al.* (2012) showed the decreased expression of HSP90 protein under cold stress conditions. However, Yang *et al.* (2014) showed up-regulation of some *HSP*s genes under NaCl stress in both roots and leaves of *Tamarix hispida*. According to Kausar *et al.* (2013), the HSP70 protein expression declined in the susceptible barley genotype but increased in the tolerant genotype under drought-stress

conditions. Alvarez *et al.* (2014) also reported higher levels of HSP70 protein expression in the tolerant cultivars of wheat than in the susceptible cultivars during drought stress. On the other hand, Manaa *et al.* (2011) showed that salinity stress induced higher expression of HSP70 in the sensitive genotypes of soybean than in the tolerant genotypes. Yoshimura *et al*. (2008) also showed the increased expression of various types of heat shock proteins including HSP20.1, HSP70, HSP82, and HSP90 in the wild watermelon under water deficit stress. Increased expression of HSP70 has also been reported in wheat (Demirevska *et al.* 2008) in drought stress conditions. It looks like the expression of HSPs depends on the plant species, type and amount of stress, and other environmental conditions.

Proteins associated with the cell wall

Spot 0005, which showed a significant change in expression under salinity stress, is related to methyltransferase protein, which showed an increased expression in the tolerant cultivar of Arg. Plants have various defense mechanisms to deal with the effects of environmental stresses, which are associated with the synthesis of special proteins. Among these proteins are the proteins involved in the lignin synthesis such as caffeoyl-CoA 3-O-methyltransferase (Busam *et al*. 1997). Increased lignin content and thickened cell wall have been observed under salt stress conditions (Chun *et al*. 2019). Caffeoyl-CoA 3-O-methyltransferase has also been increased in the wild watermelon roots in the water deficit-stress conditions (Yoshimura *et al*. 2008).

Spot 4302, which significantly decreased in expression under salt stress in the tolerant cultivar of Arg, was related to the glycoside hydrolase family 1 (GH1) protein, which plays a role in cell wall expansion (Davies and Henrissat 1995). Sodium chloride stress reduces the amount of water available to the plant which results in the retarding plant growth because of reduction in cell turgor and inhibition of cell expansion (Kurth *et al*. 1986). Jiang *et al*. (2007) identified four proteins of the glycosyl hydrolase family, three of which belonged to the GH1 family and one to the GH17 family in the roots of Arabidopsis under salinity stress. Each of these four GH proteins exhibited a distinct expression pattern. According to Jiang *et al*. (2007), the diversity in the expression patterns indicated the existence of different physiological processes responding to salinity stress.

Conclusions

Proteomic analysis of the root tissue by two-dimensional electrophoresis and silver nitrate staining resulted in the detection of 120 repeatable protein spots. Fifteen spots had significant changes in expression based on the t-test. By applying salinity stress, the tolerant

cultivar showed a higher change in the expression of PGM, MDH, CAT, and PDH. Increased expression of these proteins has likely contributed to energy conservation and ROS scavenging and is associated with the increased salinity tolerance in the tolerant cultivar of Arg. However, the significant decrease in the expression of enolase and GPX under sodium chloride stress is probably caused by the oxidative stress in plant cells due to the increased production of ROS during the accomplishment of vital cell processes.

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Conflict of Interest

The authors declare that they have no conflict of interest with any people or organization concerning the subject matter discussed in the manuscript.

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تأثیر تنش شوری بر الگوی پروتئوم ریشه گندم نان بهاره

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چکیده

در این آزمایش اثر تنش شوری بر الگوی پروتئوم ریشه ارقام ارگ (متحمل به شوری) و مغان ۳ (حساس به شوری) گندم با الکتروفورز ژل پلی آکریل آمید دو بعدی بررسی شد. شوری در دو سطح صفر و ۱۵۰ میلی مولار در مرحله سه برگی به مدت سه هفته در شرایط گلخانه‌ای اعمال شد. پس از تجزیه پروتئوم ریشه، ۱۲۰ لکه پروتئینی تکرارپذیر آشکار شد که از میان آن‌ها ۱۵ لکه تغییر بیان معنی‌دار نشان دادند. در مغان ۳ چهار لکه پروتئینی دارای کاهش بیان معنی‌دار شناسایی شد. در رقم متحمل ارگ، ۱۱ لکه پروتئینی تغییر بیان معنی‌دار نشان دادند که در میان آن‌ها پنج لکه پروتئینی افزایش بیان و ۶ لکه پروتئینی کاهش بیان داشتند. این پروتئین‌ها بر اساس عملکرد به چند گروه مانند پروتئین‌های دخیل در متابولیسم و انرژی، مهار و سم زدایی گونه‌های اکسیژن فعال، پروتئین‌های مرتبط با دیواره سلولی و پروتئین‌های دخیل در تاخوردگی و تخریب طبقه بندی شدند. احتمالا تحمل به تنش شوری در رقم ارگ با افزایش بیان پروتئین‌های پیروات دهیدروژناز، فسفوگلیسرات موتاز، کاتالاز و مالات دهیدروژناز ارتباط داشت. درحالی که در رقم جساس مغان۳ کاهش بیان پروتئین‌های انولاز، پراکسیداز و گلوتاتیون پراکسیداز در شرایط تنش شوری احتمالا به علت افزایش تولید گونه‌های اکسیژن فعال سبب تنش اکسیداتیو در گیاه شده است. این یافته‌ها می‌تواند برای بهبود تحمل به شوری در برنامه‌های اصلاحی گندم مفید واقع شود.

واژه‌های کلیدی: الکتروفورز دوبعدی؛ تجزیه پروتئوم؛ تنش شوری؛ گونه‌های اکسیژن فعال