Assessment of Changes in Some Biochemical Traits and Proteomic Profile of UCB-1 Pistachio Rootstock Leaf under Salinity Stress

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Abstract

University of California at Berkeley I or UCB-1 pistachio rootstock is propagated from the cross between *Pistacia integerrima* male × *Pistacia atlantica* female. So far, no report has been presented on the proteomic profile of Pistacia genus. In this research, 7-month-old UCB-1 rootstocks that were produced by tissue culture method and grown in pots containing 1/3 perlite, 1/3 clay and 1/3 sand were exposed to the three different concentrations of NaCl including 0, 100 and 200 mM for 30 days in the controlled conditions in the greenhouse. In the first step, under these three different concentrations of NaCl, the content of malondialdehyde and activities of guaiacol peroxidase, superoxide dismutase, catalase and peroxidase were evaluated. Malondialdehyde content increased up to 100 mM NaCl and then decreased. Activities of guaiacol peroxidase, superoxide dismutase and catalase increased with increasing concentration of NaCl, while peroxidase activity reduced. In the second step, 0 and 100 mM NaCl were selected to evaluate changes in the proteomic profile of this rootstock using MALDI-TOF/TOF method. In this study, ribonucleoside-diphosphate reductase small chain, polcalcin Phl p 7-like and golgin subfamily A member 5 were identified for the first time in response to salinity stress and have not been previously reported to be involved in the response of plant under abiotic stresses. Moreover, in this study, five unknown proteins were identified in UCB-1 pistachio under salinity stress.

Keywords Salinity · UCB-1 pistachio rootstock · Proteomics · Two-dimensional electrophoresis · Lipid peroxidation · Antioxidant enzymes

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Introduction

One of the most important members of Anacardiaceae family is pistachio, which has at least 11 species; *P. integerrima* and *P. atlantica* are used as rootstocks for *P. vera* cultivation, while *P. vera* is solely an economic and cultivated species (Moazzzam Jazi et al. 2017). At the University of California at Berkeley, with a controlled pollination and cross between *P. integerrima* male × *P. atlantica* female, a hybrid pistachio rootstock was produced and was named UCB-1(Ahmad et al. 2005). UCB-1 is more resistant to cold (Epstein et al. 2004) and salt stresses (Ahmad et al. 2005; Ferguson et al. 2002; Akbari et al. 2018) and has a higher yield (Ferguson et al. 2002) and greater *Verticillium* tolerance (Morgan et al. 1992) than other pistachio rootstocks, and for these reasons, UCB-1 is the best rootstock for California climates and likely the other areas in the world. Also, as regards the important role of rootstock in resistance to abiotic stresses, such as salinity in grafted plants, UCB-1 can be the most favorable rootstock for *Pistacia* genus (Akbari

et al. 2018). The United States of America, Iran, and Turkey are the main pistachio breeders in the world, and Iran has a 3000–4000 year history of pistachio agriculture (Moazzzam Jazi et al. 2017). Also, leaf, flower, resin and seeds of pistachio have pharmacological attributes, such as antioxidant, antimicrobial and anti-inflammatory properties (Bozorgi et al. 2013; Tsokou et al. 2007).

Pistachio is classified as a salt-tolerant glycophyte type; however, under moderate and high salinity stresses, its yield is extremely decreased (Hajiboland et al. 2014; Moazzam Jazi et al. 2016). In the last decades, lack of precipitation, global warming and drought in Iran have extremely decreased the forest area of wild pistachio, and consequently increases in soil salt content, which is the most important reason for limitation in the growth and development of rainfed trees, such as pistachio, has happened (Ziya Motalebipour et al. 2016; Moazzam Jazi et al. 2016). Therefore, there is an urgent need for conservation management of this rootstock that warrants fertility, productivity and long growth in this valuable product (Ziya Motalebipour et al. 2016; Moazzam Jazi et al. 2016). Responsive proteins in reaction to salt stress in this study using proteomic analysis can be used in modern breeding programs to produce a more resistant pistachio rootstock under unfavorable conditions of stress.

Agronomical yield, agricultural productivity and plant growth are extremely limited when plants are exposed to soil salinity (Schwarz et al. 2010). Soil salinity severely affects fruit trees; for example, under low concentration of 25 mM NaCl, almond shoot growth is extremely repressed by salt in the soil solution (Zrig et al. 2011). Therefore, researchers and scientists, via selection and breeding of different cultivars, are able to present a stress-resistant cultivar to minimize the effects of abiotic stresses, such as salinity and drought (Cuartero et al. 2006). Also, genetic complexity of resistance to salinity and drought stresses has compelled researchers to use classic methods for improvement of plants tolerance, such as selection of resistant rootstocks in grafted plants (Ashraf and Foolad 2007). It is now more than 50 years that grafting has been used for decreasing destructive effects in plants under abiotic stresses to improve plants tolerance (Schwarz et al. 2010; Lee et al. 2010; Flores et al. 2010). In the recent decade, valuable rootstocks have been widely available and have been used to reclaim destructive effects of salinity stress in woody fruit crops (Massai et al. 2004; Colla et al. 2006). In 2016, a research demonstrated that resistant trees to soil salinity can be extremely recovered by grafting onto resistant rootstocks (Zrig et al. 2016). Resistance to salinity stress is different between different species and severely depends on their root system (Moya et al. 2002). Furthermore, functional relation between rootstock and scion in grafted plants is another ability of woody plants to become more resistant under salinity stress (Moya et al. 2002; Flores et al. 2010; Schwarz et al. 2010).

Resistance to salinity stress is a twisted process including biochemical, physiological and molecular reactions (Mostek et al. 2015). For a better understanding of the plants' mechanisms in reaction and response to different stresses such as cold, salinity and drought, plant proteomic analysis is quite necessary (Molassiotis et al. 2013). Plant proteomic analysis provides fundamental and important information about the expression of proteins and modifications of post-translation under different stresses (Barkla Bronwyn et al. 2013; Molassiotis et al. 2013).

Also, for identification of proteins that are involved in the plant resistance like VlWRKY3 in grape under different biotic and abiotic stresses (Guo et al. 2018), proline in barley under drought stress (Bandurska et al. 2017), NAM, ATAF, and CUC (NAC) transcription factor in rice under drought and salinity stresses (Hu et al. 2006) and AtHAP5A in Arabidopsis under freezing stress (Shi and Chan 2014), several new techniques are available (Ashoub et al. 2013; Capriotti et al. 2014). Five main essential and important groups of proteins in plants have been identified under salinity stress and are directly related to salt resistance: (I) late embryogenesis abundant proteins (LEA proteins); (II) heat shock proteins (HSPs); (III) proteins involved in carbon metabolism; (IV) enzyme scavengers of ROS; and (V) osmolyte biosynthetic enzymes (Passamani et al. 2017). Also, under salinity stress and in reaction to salt stress, proteins associated with protein synthesis/degradation, proteins associated with ion transportation and proteins associated with signal transduction are also involved in plants such as wheat (*Triticum durum* L.) (Capriotti et al. 2014), rice (*Oryza sativa*) (Yan et al. 2005) and sugar beet (*Beta vulgaris* L.) (Wakeel et al. 2011). Also, Capriotti in 2014 proved that proteins that are identified in these studies can be used as molecular markers for breeding plans in the future (Capriotti et al. 2014).

It is specified that plants can be strongly affected by salinity stress, and considerable information is available about the biochemical, cellular and molecular mechanisms of *Pistacia* genus under different stresses (Moriana et al. 2018; Akbari et al. 2018; Abbaspour et al. 2012; Chelli-Chaabouni et al. 2010). Analysis of proteome in this study is able to help us to comprehend and identify the reacting mechanisms of UCB-1 pistachio rootstock to salt stress. Also, information of this study about the responsive proteins of pistachio under salinity stress can be used in the modern and classical breeding programs (Agrawal et al. 2012). In the first step, this research was done to evaluate changes in the malondialdehyde (MOD) content and guaiacol peroxidase (GPX), superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) enzymes activities under three different NaCl concentrations in 7-month-old UCB-1 pistachio rootstock leaves after 30 days of exposure to treatment. In the second step, the proteomic profile of this rootstock under 100 mM NaCl was compared with 0 mM using MALDI TOF/TOF

method for better comprehension of mechanisms controlling reactions of UCB-1 rootstock to salinity stress.

Materials and Methods

Plant Materials, Growth Conditions and Induction of Salt Stress

Recently, one of the most important rootstocks for pistachio that has been extremely cultivated in the United States of America is UCB-1, which is severely tolerant to salinity stress (Akbari et al. 2018; Ferguson et al. 2002). UCB-1 was produced by the University of California and is a hybrid cross between *Pistacia integerrima* male × *Pistacia atlantica* female (Ferguson et al. 2002). In this research, 6-month-old UCB-1 uniform rootstocks that were produced by tissue culture method were prepared and transplanted into the pots containing 1/3 perlite, 1/3 clay and 1/3 sand. After 4 weeks preculturing UCB-1 rootstocks in pots and irrigating them every 4 days by 1 L of ½ Hoagland's nutrient solution, three different concentrations of NaCl including 0 as control, 100 and 200 mM were made using Hoagland's complete nutrient solution and were used to apply salinity stress. Irrigation was performed for 30 days with an every 4 days irrigation frequency (Akbari et al. 2018). To avoid the osmotic stress, different concentrations of salinity stress were gently applied, and 1 L of deionized water was used after every four irrigations to stop NaCl accumulation (Akbari et al. 2018). 28 °C during the day and 18 °C at night, 70% relative humidity, and 16/8 h light/dark (450–550 lmol m^{-2} s^{-1} flux density) were the green house conditions (Akbari et al. 2018). 8-month-old UCB-1 rootstock leaves were collected and immediately put in an aluminum paper and frozen in liquid nitrogen and stored at − 80 °C for all analyses.

MDA Content

Thiobarbituric acid or TBA reaction was used to determine lipid peroxidation in UCB-1 rootstock under salinity stress (Heath and Packer 1968). Frozen samples were homogenized with two volumes of ice-cold 0.1% (w/v) TCA and centrifuged for 20 min at 16,000×g. Assay admixture containing 1 ml of the supernatant and 2 ml of 0.6% (w/v) TBA in 20% (w/v) TCA was heated at 92 °C for 36 min and then quickly cooled in an ice bath. After centrifugation (12,000×g for 15 min at 3 °C), the absorbance of the supernatant was read at 532 nm, and the quantities corresponding to nonspecific sorption (600 nm) were reduced. Lipid peroxidation crops were calculated as the quantity of TBA-reactive materials. The content of malondialdehyde was measured according to the molar extinction coefficient of 155/(mM cm).

Enzymes Extraction

UCB-1 fresh leaf samples were submersed for 3 min in liquid nitrogen, then were kept at − 80 °C for further analyses. 5 ml of extraction buffer, containing 50 mM K-phosphate buffer, 0.1 mM Na2-EDTA with pH 7.6 was used to extract enzymes from 0.5 g of leaf tissue using a mortar and a pestle. The homogenate was centrifuged at 16,000×g for 20 min, and the supernatant was used to assay different enzymes. All stages in the provision of enzyme extracts were done at 3 °C.

GPX Activity

In this study, the total GPX activity was assessed in 2 ml of reaction mixture, including 0.1 μmol L^{-1} EDTA, 100 mmol L^{-1} phosphate buffer (pH 7.0), 15.0 mmol L^{-1} H$_2$O$_2$, 5.0 mmol L^{-1} guaiacol, and 50 μL enzyme extract. By appending enzyme extract, reaction began, and increase in absorbance was registered at 470 nm for 1 min. The activity of enzyme was quantified using the quantity of tetraguaiacol formed by its molar extinction coefficient (26.6 mmol L^{-1} cm^{-1}). The outcomes were shown as μmol H$_2$O$_2$ min^{-1} mg^{-1} protein, taking into account that 4 mol H$_2$O$_2$ is decreased to generate 1 mol tetraguaiacol (Plewa et al. 1991).

SOD Activity

By using xanthine, cytochrome C and xanthine oxidase, McCord and Fridovich method was used to evaluate the SOD activity (McCord and Fridovich 1969). One unit of SOD was determined as the quantity of enzyme that prevents the speed of Ferricytochrome C reduction by 50%.

CAT Activity

By calculating the reduction at 240 nm for 1 min, due to H$_2$O$_2$ consumption, Aebi method was used to determine the activity of CAT (Aebi 1984).

POD Activity

In this study using pyrogallol as a substrate, Kwak method was applied to assay POD activity (Kwak et al. 1995). One unit of POD activity was determined as the quantity of enzyme essential to take 1 mg of purpurogallin from pyrogallol in 20 s, at 420 nm.

Data Analysis for MDA, GPX, SOD, CAT and POD

Three replicates were considered for each treatment in completely random designs. One-way ANOVA by SPSS package program (version 13.0) was used for the purpose of data analysis. Significant diversities between treatments were

evaluated using Duncan's multiple range tests ($P < 0.05$). The results of this study were reported as mean values ± standard deviation (SD).

Protein Extraction and 2-Dimensional Gel Electrophoresis (2D) Analysis

Three biological replicates were considered for this study. After 30 days of NaCl treatment, trichloroacetic acid (TCA)-acetone method, modified from Hurkman and Tanaka (Hurkman and Tanaka 1986), was used to extract UCB-1 leaf proteins, and for this purpose 500 mg of fresh leaves in liquid nitrogen were homogenized by a mortar and a pestle. The powder was put in a 1.5-mL microtube, and 1 mL of cold extraction buffer that contains 1 mM ethylenebis (oxyethylenenitrilo) tetraacetic acid (EGTA), 20 mM Tris–HCl (pH 7.5), 1 mM phenylmethyl sulfonyl fluoride (PMSF) and 1 mM dithiothreitol (DTT) was added to the tube. For 90 min at 4 °C, the microtubes were incubated and then centrifuged at 20,000×g for 45 min. After centrifuging, the outcoming supernatant was carried over to a microtube, and with four volumes of cold acetone including 0.08% β-mercaptoethanol and 12% TCA at − 10 °C for 15 h was precipitated. The microtube again at 20,000×g for 45 min was centrifuged, and then the pellet was washed seven times using cold acetone including 0.08% β-mercaptoethanol at − 10 °C for 4 h. The protein was kept for 24 h to air-dry, and then by using a rehydration buffer containing 2 M thiourea, 7 M urea, 4% 3-[(3-cholanidopropyl) dimethylammonio]-1-propanesulfonic acid (w/v), 0.01% (w/v) bromophenol blue, 40 mM DTT and 0.5% (v/v) immobilized pH gradient (IPG) buffer 4–7 was rehydrated. Bradford method (Bradford 1976) was used to quantify the concentrations of protein, and for drawing the standard curve bovine serum albumin (BSA) was applied.

For the first-dimensional, 17 cm IPG strips (Bio-Rad, USA) were applied to perform isoelectric focusing with pH 4–7. Then, 400 μL of protein, containing 850 μg protein, was loaded to IPG strips for 14–18 h at 24 °C for identification of proteins, and then at 20 °C, IEF was done on an Ettan IPG-phor system (GE Healthcare, USA) using the following position: 100 V for 1 h, 200 V for 2 h, 4000 V for 3 h, 1000 V for 2 h, 4000 V for 1 h, and a gradient of 9000 V for 2 h (50 μA per strip) (Yuan et al. 2016).

2D balance buffer [2% sodium dodecyl sulfate (SDS), 6 M urea, 30% glycerol (v/v), 50 mM Tris–HCl, pH 8.8] including 1% DTT for 20 min and again identical 2D balance buffer including 2.5% iodoacetamide for 20 min were used to balance IEF strips. 13% polyacrylamide-SDS gels were prepared, and balance strips were put on them and sealed using 0.6% agarose dilution including bromophenol blue. Also, the EttanDaltSix electrophoresis system (GE Healthcare, USA) was used to perform second dimensional SDS–polyacrylamide gel electrophoresis (SDSPAGE), and Coomassie brilliant blue gel (CBB) R-250 (CBB; Sigma, USA) was used for visualization of spots.

Image and Data Analysis

Three replicates were considered for each treatment in completely random designs. The image scanner III (GE Healthcare, USA) was applied to visualize the image of gels and the gels were analyzed with version 7 Melani software. Also, the measurement of percentage volume (vol%) was used to evaluate plenty of each protein spot. The percentage volume of each protein spot in 0 and 100 mM NaCl conditions was considered to assess the significant difference of each protein by t test method using SPSS 13.0 software (Student's t test, $P < 0.05$). Protein spots were normalized as the proportion of the content of a single spot to the whole set of spots available in the gel. To measure the fold change of each protein spot, protein percentage volume data were transferred to an Excel file, and protein spots with considerable level (Duncan's test at significant $P < 0.05$) and 1.5-fold change were applied for mass spectrometry. The level of fold change for each protein was calculated based on increasing or decreasing the percentage volume of each protein spot in 100 mM NaCl compared to 0 mM. The results of the protein percentage volume were reported as mean values and percentage coefficients of variations (%CV) for each protein spot (in three replicates).

Protein Identification

Desirable protein spots were cut off from the gel, and wash solution including 50% acetonitrile/50 mM ammonium bicarbonate (NH_4CHO_3) was used to destain spots for 1 h at 28 °C. After alkylation of protein, solution was taken, and spots at room temperature were left to dry. After drying the spots, trypsin solution was applied to digest proteins at 37 °C for one night. After digestion of proteins, 50% acetonitrile and 0.1% TFA in water were used for washing the peptides and were then put onto the MALDI target plate to dry. In the final step, peptides were handled for MALDI-TOF/TOF at University of York (England) by MALDITOF/TOF analyzer (Applied Biosystems, USA). Version 2.2 MASCOT software (Matrix Science, London, UK) was applied for analysis of the mass spectrometry data using the NCBI (http://www.ncbi.nlm.nih.gov/) and NCBI protein databases (https://www.ncbi.nlm.nih.gov/refseq/about/nonredundantproteins/). Following criteria were considered in the databases for spectra search: trypsin as enzyme, carbamidomethylation of cysteine as fixed modification, MS/MS tolerance (0.8 Da), peptide tolerance (200 ppm) and variable modifications (oxidation (M)) (Fatehi et al. 2012).

Results

MDA Content

Lipid peroxidation in the leaves of UCB-1 pistachio rootstock was measured as MDA content and is shown in Fig. 1. Increasing salinity from 0 to 100 mM NaCl led to an increase in MDA content, but this amount of MDA decreased at 200 mM NaCl compared to the 100 mM (Fig. 1). Also, no significant difference was observed between 0 and 200 mM NaCl. 0.54, 0.84 and 0.58 μmol/g fr wt% were measured under 0, 100 and 200 mM NaCl, respectively (Fig. 1).

GPX Activity

In order to determine the response of GPX to salinity stress in UCB-1 pistachio rootstock, its activity was measured. With increasing NaCl concentrations, the activity of GPX increased. 0.012, 0.029 and 0.034 μmol H_2O_2 min^{-1} mg^{-1} protein were calculated for GPX activity in UCB-1 pistachio rootstock leaf under 0, 100 and 200 mM NaCl, respectively (Fig. 2).

SOD Activity

As shown in Fig. 3, 100 and 200 mM NaCl treatments increased the activity of SOD in UCB-1 pistachio rootstock leaf compared to control. SOD activity was calculated 2.87, 3.2 and 3.77 units/mg of protein under 0, 100 and 200 mM sodium chloride in UCB-1 rootstocks leaf, respectively (Fig. 3).
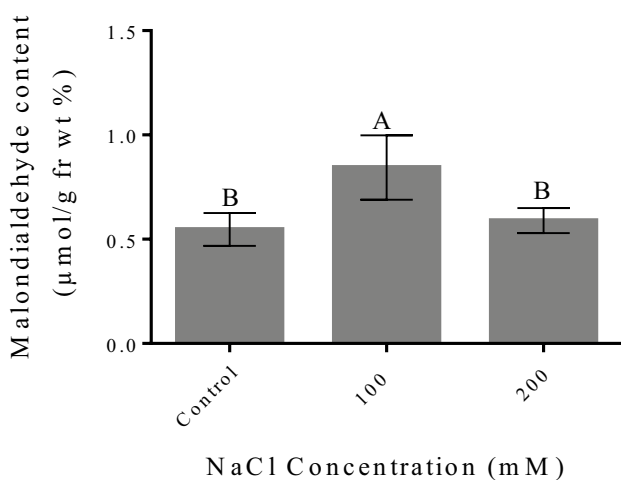

Fig. 2 The effect of different concentrations of NaCl on the GPX activity in UCB-1 pistachio rootstocks leaf. Bars with different letters are significantly different at $P < 0.01$, according to Duncan's multiple range tests

CAT Activity

CAT activity enhanced with increasing NaCl concentrations. Under 0, 100 and 200 mM sodium chloride, 0.015, 0.019 and 0.022 units/mg protein were calculated in leaf of UCB-1 pistachio rootstocks (Fig. 4).

Fig. 1 The effect of different concentrations of NaCl on the MDA content in UCB-1 pistachio rootstocks leaf. Bars with different letters are significantly different at $P < 0.01$, according to Duncan's multiple range tests
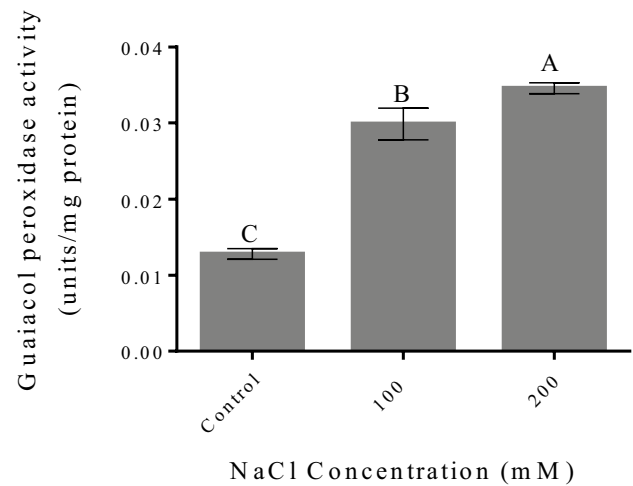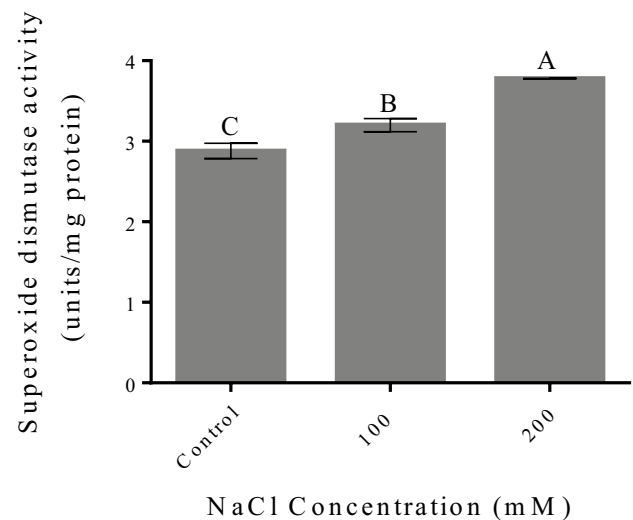

Fig. 3 The effect of different concentrations of NaCl on the SOD activity in UCB-1 pistachio rootstocks leaf. Bars with different letters are significantly different at $P < 0.01$, according to Duncan's multiple range tests

Fig. 4 The effect of different concentrations of NaCl on the CAT activity in UCB-1 pistachio rootstocks leaf. Bars with different letters are significantly different at $P < 0.01$, according to Duncan's multiple range tests

Fig. 5 The effect of different concentrations of NaCl on the POD activity in UCB-1 pistachio rootstocks leaf. Bars with different letters are significantly different at $P < 0.01$, according to Duncan's multiple range tests
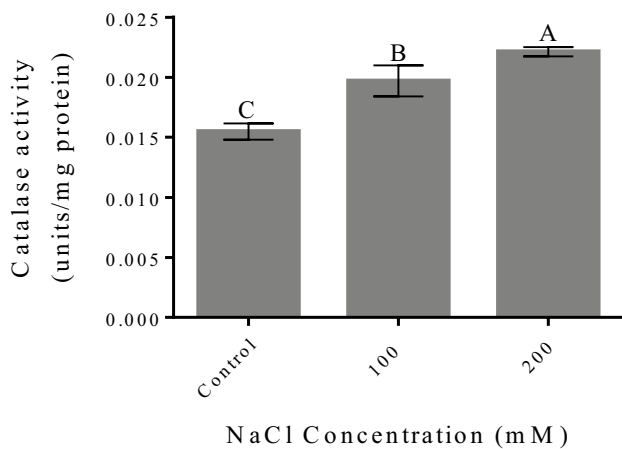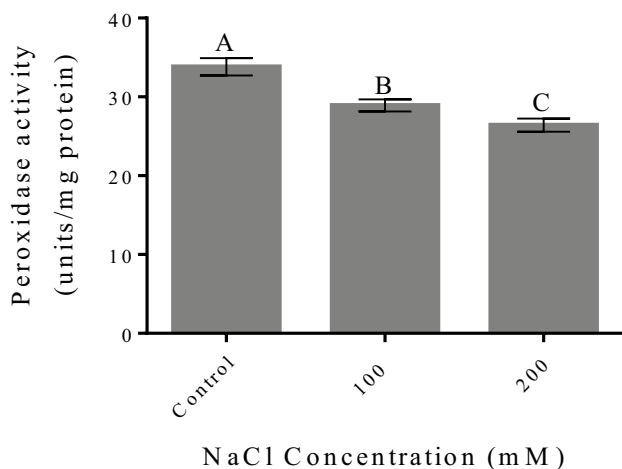
POD Activity

The POD activity significantly decreased in the UCB-1 rootstocks leaf at all stress concentrations. In UCB-1 rootstock leaf, the amounts of 33.81, 28.92 and 26.41 units/mg of protein were estimated for POD activity under 0, 100 and 200 mM NaCl, respectively (Fig. 5).

Analysis of Two-Dimensional Gel Electrophoresis

The proteome maps of UCB-1 pistachio leaf in different NaCl conditions were produced from two-dimensional gel electrophoresis (2-DE), as shown in Fig. 6. The protein spots were spread from pH 4–7, and their molecular masses ranged from 10 to 100 kDa. More than 406 protein spots were detected on gels. Of these spots, 25 protein spots had 1.5-fold variations between 100 and 0 mM NaCl environments and these spots were selected for MALDI TOF/TOF analysis (Table 1 and Supplementary Table 1). Of these 25 spots, 15 spots were up-regulated, and 10 spots were down-regulated by the salinity stress (Fig. 6, Table 1, Supplementary Table 1).

MALDI-TOF/TOF Identification and Classification of Responsive Proteins

Twenty-five salinity-responsive proteins which had 1.5-fold variations between 100 and 0 mM NaCl environments were selected for MALDI-TOF/TOF mass spectrometry identification. Mass data were analyzed by Mascot schedule and NCBI non-redundant protein database. All identified salinity responsive proteins by MALDI TOF–TOF are listed in Table 1 and supplementary data for these 25 responsive proteins are listed in Supplementary Table 1. Generally, these responsive spots represented 20 unique proteins, which were classified into nine functional categories: photosynthesis (20%), enzymatic antioxidant defense system (12%), replication and repair of DN (4%), energy pathway (12%), non-enzymatic antioxidant defense system (4%), transportation of material (16%), calcium-binding proteins (4%), transcription factor (4%) and chaperone (4%), as shown in Fig. 7 and Table 1. Also, 5 unknown function proteins (20%) were determined under salinity stress in UCB-1 pistachio (Fig. 7, Table 1). The photosynthetic related proteins consist of the 50S ribosomal protein L13 chloroplastic (spot 337), ribulose-1.5-bisphosphate carboxylase/oxygenase large subunit (spot 446), ribulose bisphosphate carboxylase small chain (spot 229), ribulose bisphosphate carboxylase/oxygenase activase 1 (spot 66) and PREDICTED: phosphoribulokinase chloroplastic (spot 161) (Table 1). The enzymatic antioxidant defense system-related proteins consist of superoxide dismutase [Cu–Zn] isoform X1 and X2 (spots 261 and 81) and Catalase 2 (spot 326) (Table 1). Ribonucleoside-diphosphate reductase small chain A was recognized as the only protein involved in the replication and repair of DNA (spot 76) (Table 1). As shown in Table 1, proteins involved in the energy pathway included ATP synthase CF1 epsilon subunit plastid (spot 64), external NADH-ubiquinone oxidoreductase 2 mitochondrial-like protein (spot 243) and ADP-glucose pyrophosphorylase (AGPase) small subunit (spot 198). Phytoene synthase 2 was detected as the only protein involved in the non-enzymatic antioxidant defense system (spot 243) (Table 1). As shown in Table 1, the transportation of material related proteins consisted of the Vesicle-associated membrane protein (VAMP) 722- and 724-like (spots 96 and 188), Golgin subfamily A member
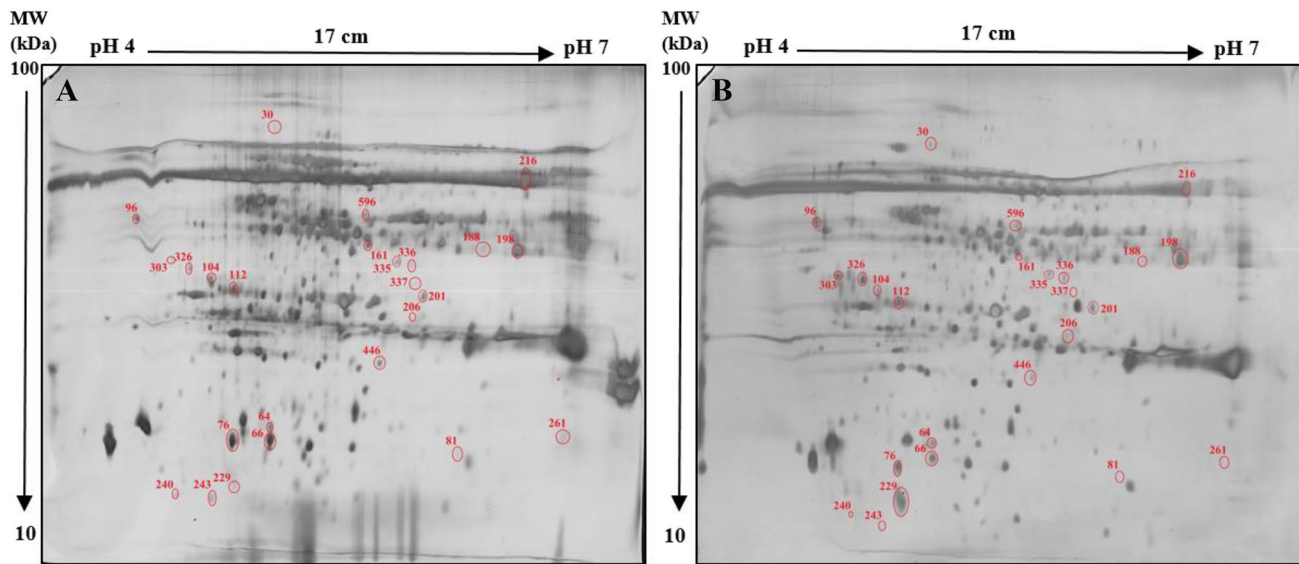
Fig. 6 Proteome maps of UCB-1 pistachio rootstock leaf. Responsive protein spots to NaCl stress are marked. **a** UCB-1 rootstock under the control condition; **b** UCB-1 rootstock under the NaCl condition. The pH range, molecular weight (MW), and IPG length are shown on the gels

5 (spot 303) and PREDICTED: ABC transporter C family member 12-like (spot 104). The protein involved in calcium-binding proteins was recognized as polcalcin Phl p 7-like (spot 336) (Table 1). One protein was determined as transcription factor entitled PREDICTED: nascent polypeptide-associated complex subunit alpha, muscle-specific form-like isoform X2 (spot 112) (Table 1). Stromal 70 kDa heat shock-related protein, chloroplastic (spot 30), was determined as chaperon (Table 1). 5 unknown function proteins were identified under salinity stress including uncharacterized protein LOC107620721, PREDICTED: uncharacterized protein LOC105974023, PREDICTED: uncharacterized protein LOC109219975 partial, PREDICTED: uncharacterized protein LOC109178037 and hypothetical protein CISIN_1g0462972 mg partial (spots 596, 201, 335, 216 and 206), respectively (Table 1).

Discussion

One of the most important abiotic stresses is soil salinity, which reduces water potential and causes nutrients to be unbalanced in plants, and they adversely affect plant development and growth (Mansour and Salama 2004; GENC et al. 2007). One of the actions that can be performed to decline the destructive effects of different stresses is usage of rootstock and grafting in plants. Selection of a tolerant rootstock is mandatory in most plants and hence, usage of grafting method to choose a salt resistant root system as rootstock may enhance salt resistance in plants (Zhang et al. 2018). In grafted plants, rootstock root system is responsible for

resistance in response to salinity stress. In this procedure, if the rootstock is effectively chosen, it will strengthen water and nutrient absorption (Kumar et al. 2018), enhance nitrogen and carbon metabolism (Shahid et al. 2018) and consequently enhance salt resistance in plants. Grafting technique not only enhances the tolerance of plants in different stress conditions, but also preserves good strains of seeds and stabilizes heterosis (Penella et al. 2014). For example, grafted tomato decreased transportation of Cl^- and Na^+ by roots to aerial sections under salinity stress (Estan et al. 2005) and precipitated absorption of K^+ by roots to adjust itself to unfavorable conditions of salinity stress (Fan et al. 2011). In this example, a grafted tomato enhanced photosynthetic ability and improved salt resistance by enhancement of the antioxidant enzymes activity (He et al. 2009). In leaves of grafted cucumber, the level of photoinhibition was significantly declined under salinity stress (Huang et al. 2011), and metabolism ability of nitrogen was elevated (Liu et al. 2013). Also, it is specified that grafted seedlings absorbed more phosphorous and nitrogen under salinity stress in watermelon (Uygur and Yetisir 2009). Accordingly, understanding the molecular basis of salt stress resistance mechanisms in rootstocks is necessary for genetic engineering and breeding programs of salt resistance in plants. In spite of intensive studies on plants' response to salt stress, there have not been any studies on the proteomic profile of *Pistacia* genus or Anacardiaceae family with proteomic method. In this study, the 8-month-old UCB-1 rootstocks that were exposed to 0, 100 and 200 mM NaCl for 30 days were used as experimental samples. All analyses were performed using the 8-month-old UCB-1 rootstock leaves. The MDA content and GPX,

Table 1 Identified salinity responsive proteins using MALDI TOF-TOF in UCB-1 pistachio rootstock

Identity	Spot ID	[a]gilNumber	[b]Expression change	[c]Coverage %	[d]MS score	[e]The pI/MW(kDa)	[f]Exp pI/MW(kDa)
Photosynthesis							
50S ribosomal protein L13, chloroplastic [*Auxenochlorella protothecoides*]	337	gil760449171	−11.24	28	70	10.12/25.571	6/57
Ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit, partial (chloroplast) [*Irvingia malayana*]	446	gil667480396	−2.75	30	85	5.01/16.604	5.92/34
Ribulose bisphosphate carboxylase small chain 1, chloroplastic [*Solanum lycopersicum*]	229	gil822092500	2.73	35	75	7.57/20.522	4.99/15
Ribulose bisphosphate carboxylase/oxygenase activase 1, chloroplastic [*Ananas comosus*]	66	gil1035955400	−1.6	24	91	5.45/56.863	5.15/20
PREDICTED: phosphoribulokinase, chloroplastic [*Ricinus communis*]	161	gil255555933	−2.75	31	95	5.83/45.221	5.66/66
Enzymatic antioxidant defense system							
PREDICTED: superoxide dismutase [Cu–Zn] isoform X1 [*Elaeis guineensis*]	261	gil743856149	−119.61	33	52	5.86/15.689	6.37/20
PREDICTED: superoxide dismutase [Cu–Zn] isoform X2 [*Elaeis guineensis*]	81	gil743856159	−78.45	38	56	5.52/13.608	6.19/20
Catalase-2 [*Arabidopsis lyrata* subsp. lyrata]	326	gil1190998802	2.283	27	85	6.63/57.206	4.60/58
Replication and repair of DNA							
Ribonucleoside-diphosphate reductase small chain A [*Ipomoea nil*]	76	gil1109197042	−166.12	26	66	4.99/39.924	5/20
Energy pathway							
ATP synthase CF1 epsilon subunit (plastid) [*Pistacia vera*]	64	gil1206251589	3.11	51	68	5.41/14.875	5.15/21
External NADH-ubiquinone oxidoreductase 2, mitochondrial-like protein [*Corchorus olitorius*]	243	gil1137217082	−142.84	41	64	9.30/6.845	4.41/19
ADP-glucose pyrophosphorylase small subunit (chloroplast) [*Hordeum vulgare* subsp. vulgare]	198	gil27464770	1.82	32	62	5.79/55.030	6.50/71
Non-enzymatic antioxidant defense system							
Phytoene synthase 2, partial [*Solanum nigrum*]	240	gil808787572	−90.96	19	67	5.03/17.382	4.43/18

Table 1 (continued)

Identity	Spot ID	[a]giINumber	[b]Expression change	[c]Coverage %	[d]MS score	[e]The pI/MW(kDa)	[f]Exp pI/MW(kDa)
Transportation of material							
PREDICTED: vesicle-associated membrane protein 722-like [*Populus euphratica*]	96	giI743944410	5.56	44	73	8.94/25.100	4.37/81
Vesicle-associated membrane protein 724-like [*Durio zibethinus*]	188	giI1269876990	−30.36	49	72	8.84/25.503	6.43/69
Golgin subfamily A member 5 [*Setaria italica*]	303	giI514767116	2.73	40	76	6.22/38.813	4.52/58
PREDICTED: ABC transporter C family member 12-like [*Gossypium arboreum*]	104	giI1050628876	2.18	17	74	8.48/176.086	4.69/55
Calcium-binding proteins							
Polcalcin Phl p 7-like [*Dendrobium catenatum*]	336	giI1179503649	2.87	43	63	6.56/11.085	6.45/12
Transcription factor							
PREDICTED: nascent polypeptide-associated complex subunit alpha, muscle-specific form-like isoform X2 [*Nelumbo nucifera*]	112	giI720021779	2	35	78	11.42/56.554	4.85/48
Chaperone							
Stromal 70 kDa heat shock-related protein, chloroplastic [*Ananas comosus*]	30	giI1147605449	2.53	31	214	5.40/75.595	4.86/100
Unknown function							
Uncharacterized protein LOC107620721 [*Arachis ipaensis*]	596	giI1021574340	1.85	28	50	8.72/26.348	5.66/76
PREDICTED: uncharacterized protein LOC105974023 [*Erythranthe guttata*]	201	giI848912603	2.95	9	57	9.01/59.381	6.05/51
PREDICTED: uncharacterized protein LOC109219975, partial [*Nicotiana attenuata*]	335	giI1111066705	2.29	19	53	6.51/32.860	5.83/62
PREDICTED: uncharacterized protein LOC109178037 [*Ipomoea nil*]	216	giI1109217218	1.85	54	61	6.51/11.470	6.51/100
Hypothetical protein CISIN_1g0462972 mg, partial [*Citrus sinensis*]	206	giI641832128	6.05	23	74	5.67/25.887	5.94/45

[a]Number in NCBI, SWISS Prot

[b]+ and − indicate protein spots whose abundance increase (+) or decrease (−)

[c]Percentage of predicated protein sequence covered by matched sequences

[d]Statistical probability of true positive identification of the predicted protein calculated by MASCOT

[e]TpI/TMW: isoelectric point of predicted protein/molecular mass of predicted protein

[f]EpI/EMW: isoelectric point of protein on gel/molecular mass of protein on gel
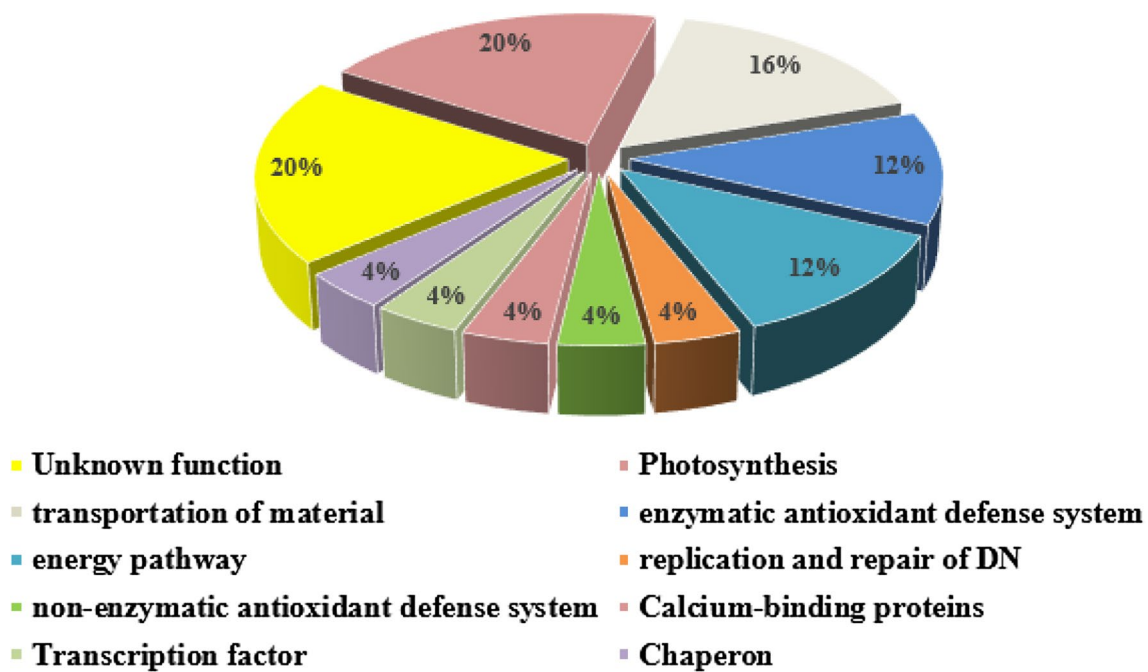
Fig. 7 Functional distribution of identified responsive proteins in UCB-1 pistachio under NaCl

CAT, SOD and POD activities were calculated under these three different stress. Also, under 100 mM NaCl, changes in the leaf proteomic profile of this rootstock were compared to 0. The results of this study showed that MDA increases under salinity stress in leaves of UCB-1 pistachio rootstock up to 100 mM NaCl, and then decreases. In citrus plants, MDA increased under salinity stress (Tanou et al. 2009). In a research in 2008, Yaser and coworkers showed that in green bean, MDA content increases under salinity stress, significantly (Yasar et al. 2008). Also, another study in cowpeas showed that under salinity stress plants' growth reduces, while MDA content increases (Cavalcanti et al. 2004). ROS generation under salinity stress is unavoidable (Abogadallah 2010), and ROS causes membrane lipid peroxidation and membrane fluidity reduction. Lipid peroxidation is measured as MDA, which is a product of lipid peroxidation (Dhindsa and Matowe 1981; Wise and Naylor 1987). The content of MDA is a significant pattern in evaluating the resistance of plants under stress situations. The results of a study showed that salt-tolerance genotypes have less lipid peroxidation (Taïbi et al. 2016), and this result is quite similar to our result under 200 mM NaCl. In this study, increasing MDA content under 100 mM NaCl compared to 0 mM is an oxidative damage of salinity on UCB-1 pistachio rootstock, while decease in the content of MDA under 200 mM NaCl compared to 100 mM may indicate the adaptive reaction of this rootstock under salinity stress. In this study, with increasing the concentrations of NaCl, GPX, CAT, and SOD activities increased in all samples. Several previous studies

showed that GPX enzyme activity in soybean under drought stress (Moloi et al. 2016) and in *pearl millet* under salinity application at reproductive and vegetative stages (Heidari and Jamshidi 2011), CAT activity in *pearl millet* at reproductive and vegetative stages under salinity stress (Heidari and Jamshidi 2011), and SOD activity in salt-sensitive and salt-tolerance genotypes of colza (*Brassica napus* L.) under sodium chloride stress (Jalali-e-Emam et al. 2011) increase, significantly. Also, Ahmad et al. in several studies showed that CAT and SOD enzymes activity along with the content of MDA increases under salinity stress in different plant species, significantly (Ahmad et al. 2016; Ahmad et al. 2017; Ahmad et al. 2018; Ahmad et al. 2019). It is proved that different abiotic stresses produce reactive nitrogen species (RNS) and reactive oxygen species (ROS), resulting in nitrosative and oxidative stress in plants (Molassiotis and Fotopoulos 2011), but on the other hand, Molassiotis et al. concluded that RNS and ROS are able to coordinately adjust plant stress responses to harmful environmental conditions (Molassiotis et al. 2016). The concentration of alkyl hydroperoxides or H_2O_2 and other reactive oxygen species or ROSs, such as hydroxyl radical (OH^-), superoxide radical ($O2^{\cdot-}$), and singlet oxygen ($^1O2$) can be enhanced either by their decreased activity of the defense system or enhanced production (Foyer et al. 1997; Bela et al. 2015). ROSs may hurt intracellular biomacromolecule, resulting in enzyme deactivation, membrane lipid peroxidation, and DNA damage (Abogadallah 2010). Also, stability and synthesis of protein can be affected by ROSs (Abogadallah 2010). Under

oxidative stress conditions, the activities of antioxidant enzymes such as catalase (CAT), superoxide dismutase (SOD), and guaiacol peroxidase (GPX) are commonly increased in plants. For example, SOD and POD enzymes activity increased in the leaves and stems of apple rootstock under NaCl stress (Molassiotis et al. 2006). Also, the activity of the aforementioned enzymes generally has a correlation with enhanced resistance (Foyer et al. 1997). The functions of GPX, SOD, and CAT are not completely understood. One of the most important peroxidase enzymes is guaiacol peroxidase located in the cytosol, apoplast, vacuole, and cell wall (Uarrota et al. 2016). It is proved that under salinity stress, guaiacol peroxidases enzyme is involved in the detoxification of induced ROS in plants (Uarrota et al. 2016). GPXs protect cells from stress induced by oxidative damage and are involved in plant development and growth. Detoxification of organic hydroperoxides and H_2O_2 is the main role of GPX isoenzymes in plants. Under salinity stress in UCB-1 rootstock pistachio, GPX may increase to protect cells from oxidative damage and enhance plant development and growth. Superoxide dismutases or SOD, which is an antioxidant enzyme, has the main role in preventing oxidative stress caused by extreme superoxide anion or O^{-2} (Smirnoff 1993). This enzyme catalyzes the dismutation of O^{-2} with excellent performance, resulting in the generation of O_2 and H_2O_2 (Smirnoff 1993). Increasing SOD under salinity stress in our study may enhance the ability of UCB-1 rootstock to scavenge ROS under this stress and lead to normal growth. CAT, which is an antioxidant enzyme in various plant tissues (Chawla et al. 2013), reacts with H_2O_2 straightly to form oxygen and water (Smirnoff 1993). Also, CAT is mostly related to an enhanced resistance to salinity stress (Mittova et al. 2004). Inthis study, CAT may increase to reduce the destructive effects of salinity, including ROSs, and to enhance the resistance of this rootstock under NaCl stress. In this research, POD activity decreased with increasing the concentration of NaCl in UCB-1 pistachio rootstock leaf. Previous studies reported the reduction of POD activity in carrot (Bano et al. 2014) and salt-tolerant variety Pokkali (*Oryza sativa* L.) (Dionisio-Sese and Tobita 1998) under salinity stress. The produced hydrogen peroxide is scavenged by a variety of peroxidases (Dionisio-Sese and Tobita 1998), and this enzyme catalyzes H_2O_2 by oxidation of co-substrates, such as antioxidants and/or phenolic compounds (Dionisio-Sese and Tobita 1998). Plants use multiple isoforms of antioxidant enzymes to scavenge the produced ROS by salinity stress (Kim et al. 2005b), and it is specified that NaCl stress can either inhibit or stimulate the expression of the isoforms of many antioxidant enzymes (Kim et al. 2005b). For example, in potato, new SOD and POD isoenzymes emerged in response to salinity stress (Rahnama and Ebrahimzadeh 2005). In a previous study, POD enzyme activity decreased in the *Broussonetia papyrifera* leaves

under 100 and 150 mM NaC1 treatment compared to the normal condition, while POD isoenzyme activity increased in the leaves of this plant (Zhang et al. 2013) and this matter can be the main reason of POD enzyme activity decreasing in the leaves of this rootstock. Also, since the metabolic responses to the salinity stress are a complex process, under salinity stress, many processes such as growth, energy metabolism, accumulation of compatible osmolytes, ion partitioning, and carbon metabolism are modified (Bohnert and Sheveleva 1998). At the cellular level, it is specified that salinity stress affects the cell wall by the increment in the polymerization of monolignols of the root (Cruz et al. 1992) and reduction in cell expansion (Iraki et al. 1989). Also in plants, peroxidases are involved in the biosynthesis of cell wall (Negrel and Lherminier 1987), including suberization and lignification (Polle et al. 1994; Espelie et al. 1986). In several plant systems, a reverse relationship was reported between POD enzyme activity and growth rate (Lee and Lin 1995; Gardiner and Cleland 1974; Carpita and Gibeaut 1993; Chen and Kao 1995), and in this study, decreasing POD enzyme activity can be reversely related to the growth rate of UCB-1 pistachio rootstock under salinity stress.

In recent decades, proteomics method has emerged as a valuable tool to identify potential biomarkers in plants in response to different environmental conditions (Molassiotis et al. 2013). For example, in a research and using proteomics method, Tanou et al. (Tanou et al. 2009) discovered 85 leaf proteins under salinity stress in Citrus aurantium, most of the researches in plants have been done on this family using proteomics method (Tanou et al. 2010). For the most part, changing environmental conditions causes rapid changes in the structure, level and composition of different protein and RNA molecules, and these changes lead to the stress acclimation or signal transduction events in plants (Beckers and Conrath 2007). For example, Molassiotis and colleagues showed that ROS (in the form of H_2O_2), which is the production of salinity stress in plants (Tanou et al. 2012) and acts as the key component of redox homeostasis (Lounifi et al. 2013), in the first step is able to change many genes expression levels and proteins abundance and consequently is able to alter photosynthesis pattern in plants (Molassiotis et al. 2016). For these reasons, in the present research, comparative proteomics was conducted to investigate changes in the proteomic profile of UCB-1 pistachio rootstock under NaCl stress to recognize the main proteins involved in response to salinity stress. According to the results of this study, 25 proteins and their families that are listed below were identified in response to salinity stress in this rootstock.

Proteins Involved in the Photosynthesis

In response to 100 mM NaCl stress, some fundamental proteins of the photosynthesis were detected in the UCB-1

pistachio rootstock compared to the normal condition, including 50S ribosomal protein L13, chloroplastic (spot 337), ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) large subunit (spots 446), ribulose bisphosphate carboxylase small chain (RBCS, spots 229), ribulose bis-phosphate carboxylase/oxygenase activase 1 (RCA 1, spot 66) and phosphoribulokinase, chloroplastic (spot 161). In two previous studies in whitetop (*Lepidium draba* L.) and *Aegilops tauschii* and in response to exogenous glucose and moisture stress, it was determined that 22 and 28.5% of changes in the proteomic profile of these two plants belonged to the photosynthesis-related proteins, respectively (Rezaee et al. 2018; Nazari et al. 2018). Tanou et al. proved that the largest category (44.7%) of the NaCl-responsive proteins was associated with photosynthesis (Tanou et al. 2009).

50S Ribosomal Protein L13, Chloroplastic

11.24-fold downregulation was observed for this protein under salinity stress in UCB-1 rootstock. Under short term of salinity in soybean, a research showed that 50S ribosomal protein L12-3 decreases significantly (Sobhanian et al. 2010), but another study reported that this protein increases under long-term salinity stress in barley (Fatehi et al. 2012). Ribosomal proteins (RPs), which have large and small subunits, have the main role in sustaining the durability of the ribosomal complex and in mediating synthesis of protein (Moin et al. 2016). In this study, decreasing 50S ribosomal protein L13 demonstrates the inhibitory effect of sodium chloride on UCB-1 protein biosynthesis and likely leads to a reduction in plant development.

Ribulose-1.5-bisphosphate Carboxylase/Oxygenase (RuBisCO) Large Subunit

Our results showed that RuBisCO large subunit was down-regulated 2.75-fold under 100 mM NaCl, while in *Sorghum* under 100 mM NaCl, RuBisCO large subunit increased 110%, which was reported by Ngara et al. (2012). Zhang and colleagues reported that in cotton diploid wild species, eight RuBisCO subunits down-regulated significantly (Zhang et al. 2016). One of the main enzymes that has an essential role in the assimilation of photosynthetic carbon is RuBisCO, and plants can produce better yield by increasing the assimilation of photosynthetic carbon (Raines 2011). RuBisCO plays the main role in photorespiratory and photosynthetic response paths, and RuBisCO affinity for CO_2 in different plants on the proportion of their carboxylase to oxygenase activities is accessible (Yeoh et al. 1980). Therefore, under abiotic stress such as salinity, plants can improve their tolerance along with better yield by higher amount of RuBisCO. Most likely, in this study, RuBisCO downregulation occurs because of the light response inactivation or CO_2

influx reduction. Also, it can be concluded that reduction in RuBisCO activity may be clarified by loss of RuBisCO protein when the rootstock was under salinity stress (Parry et al. 2002).

Ribulose Bisphosphate Carboxylase Small Chain

In this study, RuBisCO small chain was up-regulated 2.73-fold under salinity stress in UCB-1 rootstock. A previous study showed that this protein up-regulated 1.14-fold under late salinity stress in rice (Lakra et al. 2018). One of the main proteins in the stroma of chloroplasts is RuBisCO, which exists in plants as a complex of 8 small and 8 large subunits. Ribulose bisphosphate carboxylase is a small sub-unit of ribulose-1,5-bisphosphate carboxylase/oxygenase (Pichersky et al. 1986). It is specified that RuBisCO subunits are sensitive to fragmentation under moisture stress situations. This event leads to producing the isoforms of various isoelectric points and molecular weights, and enhancing in the number of rubisco subunit (Salekdeh et al. 2002; Guo et al. 2016; Budak et al. 2013).

Ribulose Bisphosphate Carboxylase/Oxygenase (RuBisCO) Activase 1

RuBisCO activase 1 was down-regulated 1.60-fold in response to 100 mM NaCl. Increasing 1.7- and 2.5-fold of RuBisCO activase was reported by Parker in rice under short- and long-term salinity, respectively (Parker et al. 2006), while the proteomic analysis of diploid and tetraploid black locust under salinity stress showed that in 4X plants, RuBisCO activase content decreased by 20% (Wang et al. 2013). One of the members of AAA^+ family is RuBisCO activase, which has various chaperone-like functions (Bhat et al. 2017). Preservation of the catalytic activity of RuBisCO is the principal role of the activase. Activase, through the removal of inhibitory sugars from the energetic position of carbamylated RuBisCO and uncarbamylated, preserves the catalytic activity of RuBisCO (Portis 2003). Direct decrease in stomatal conduction followed by low CO_2 concentrations may be induced under salinity stress, and subsequently increasing activase activity may happen (Parker et al. 2006). In this study, RuBisCO activase content downregulation may cause a reduction in Calvin-Benson cycle activity. This would hold a suitable assimilation valency of photosynthetic CO_2 by lightening energy consumption to intensify salinity resistance.

Predicted: Phosphoribulokinase, Chloroplastic

In this study, a significant 2.75-fold downregulation of phosphoribulokinase protein was observed under 100 mM NaCl in UCB-1 pistachio rootstock. Also, Srivastava and

colleagues observed that phosphoribulokinase decreases after 1 and 24 h of 150 mM NaCl treatment (Srivastava et al. 2008). Furthermore, under salinity stress in Arabidopsis, Seki et al. (2002) reported that phosphoribulokinase decreases significantly (Seki et al. 2002). A necessary photosynthetic enzyme that catalyzes the ATP-dependent phosphorylation of ribulose 5-phosphate into ribulose 1,5-bisphosphate is phosphoribulokinase, its principal function is regeneration of ribulose 1,5-bisphosphate, which is the primary substrate and CO_2-acceptor molecule of the Calvin Cycle (Miziorko 2000). Under NaCl stress, downregulation of phosphoribulokinase points toward inhibition of the Calvin cycle and pentose phosphate pathway, thereby explaining the decline in NADPH content (Srivastava et al. 2008).

Proteins Involved in the Enzymatic Antioxidant Defense System

Superoxide Dismutase [Cu–Zn] Isoform X1 and X2

[Cu–Zn] superoxide dismutase (SOD) isoforms X1 and X2 were illustrated to decrease after 30 days growing under 100 mM NaCl. Cu–Zn SOD isoforms X1 and X2 decreased 119.61- and 78.45-fold, respectively. Parker and coworkers in 2006 showed that chloroplast [Cu–Zn] SOD in rice increased 1.7-fold after 7 days of treatment by 50 mM NaCl (Parker et al. 2006). Also, Hernandez and coworkers illustrated that in NaCl-susceptible variety, Cu–Zn SOD activity reduced 35%, while in the NaCl-resistant plants, Cu–Zn SOD remained fixed (Hernández et al. 2001). In *Vigna unguiculata* L., and under 100 mM NaCL, mitochondrial and cytosolic Cu–Zn SOD I and protoplasts Cu–Zn SOD II decreased remarkably (HernÁNdez et al. 1994). Also, the transcripts of copper-zinc SOD in underground stems' organs of *Polygonum sibiricum* were significantly down-regulated after 3% NaHCO3 stress (Qu et al. 2010). Reactive oxygen species (ROSs) are produced as a result of abiotic stresses, such as salinity and drought. The first line of cell advocacy versus ROSs is SODs family. Copper-zinc SOD (Cu–Zn SOD), iron-SOD (Fe-SOD), and manganese-SOD (Mn-SOD) are three different kinds of SODs, which are placed in various plant sub-cellular organelles (Grene 2002; Hernandez and Almansa 2002). A section of an enzymatic detoxification system is engendered by SOD to scavenge ROSs (Asada 1999; Parker et al. 2006). When the concentration of CO_2 decreases in the stroma, SOD [Cu–Zn] activity increases to maintain electron flux in the thylakoids. In this study, downregulation of Cu–Zn SOD isoforms X1 and X2 may be related to the results of H_2O_2-products of Cu–Zn SOD.

Catalase 2

Catalase 2 was up-regulated 2.28-fold in response to 100 mM NaCl. Under salinity stress, and in bread wheat, catalase was up-regulated significantly, which was reported by Peng in 2009 (Peng et al. 2009). Also, Molassiotis et al. showed that enzymatic and non-enzymatic antioxidant activities as well as contents of H_2O_2 increased in leaves and stems of apple rootstock under different abiotic stresses (Molassiotis et al. 2006). In cells, H_2O_2 detoxification is done with glutathione peroxidase, ascorbate peroxidase, thioredoxin peroxidase, and catalase (Mehlhorn et al. 1996). Under stress situation, a remarkable enhancement in CAT activity in leaves can preserve chloroplasts and give a sustained electron flow (Foyer and Shigeoka 2011). When plants are exposed to water deficiency of salinity stress, increasing CAT activity of leaves allows the removal of photorespiratory H_2O_2, which is produced under violent abiotic stresses (Sofo et al. 2015).

Proteins Involved in the Replication and Repair of DNA

Ribonucleoside-Diphosphate Reductase Small Chain A

In this research, ribonucleoside-diphosphate (RDP) reductase decreased 166.12-fold under salinity stress. No report about the RDP reductase under abiotic stresses is available. RDP reductase, which brings the ribonucleotide diphosphate reduction to deoxy-ribonucleotide, is an enzyme containing Fe and is a major enzyme in DNA synthesis. RDP reductase or ribonucleotide reductase (RDR) is a main target of the DNA damage checkpoint pathways in mammals, higher plants, and yeasts (Huang et al. 1998). The reduction of all four ribonucleotide diphosphates (NDPs) into their corresponding deoxyribonucleosides (dNDPs) is done by RDP reductase (Kolberg et al. 2004). RDP reductase contains two large subunits (R1) and two small subunits (R2) (Wang and Liu 2006). The R1 subunit is the aim of feedback adjustment, which warrants that dNTPs are not overproduced in cells, and ensures that enough NDPs are left for synthesis of RNA (Wang and Liu 2006). The R2 subunit is necessary for the reduction of NDP to dNDP (Wang and Liu 2006). In mammal and yeast, it is indicated that damaged RDP reductase frequently leads to p53-dependent apoptosis, growth delay, and cell cycle arrest. Also, higher mutation rate happens when RDP reductase activity increases (Wang and Liu 2006). Forasmuch as increasing RDP reductase activity increases mutation rate, most likely in this study, RDP reductase small chain decreases for decreasing RDP reductase activity to reduce mutation rate in UCB-1 rootstock under salinity stress.

Proteins Involved in the Energy Pathway

ATP Synthase CF1 Epsilon Subunit (Plastid)

In this study, ATP synthase CF1 epsilon subunit (plastid) was up-regulated 3.11-fold under 100 mM sodium chloride. ATP synthase CF1 increased in cotton under drought stress (Deeba et al. 2012), in rice (Kim et al. 2005a), and in the roots and shoots of maize under salinity stress (Zuther et al. 2004), significantly. One of the main enzymes in energy transduction in mitochondria and chloroplasts is ATP synthase, which decreases the destructive effect of stress in plants. Water stresses such as salinity and drought reduce CO_2 assimilation by reduction of the net ATP value (Tezara et al. 1999). Also, ATP synthesis induction assists plants to enhance their resistance to abiotic stresses (Zhang et al. 2008). Furthermore, when ATP synthase was overexpressed in Arabidopsis, greater resistance was observed under drought stress (Zhang et al. 2008). In this study, similarly, this protein was up-regulated to enhance the resistance of UCB-1 pistachio rootstock under salinity stress by increasing energy transduction.

External NADH-Ubiquinone Oxidoreductase 2, Mitochondrial-Like Protein

Decreasing 142.84-fold was calculated for external NADH-ubiquinone oxidoreductase 2, mitochondrial-like protein in UCB-1 pistachio rootstock under salinity stress. Also, Witzel and coworkers showed that in barley and under salinity stress, (NADH)-ubiquinone oxidoreductase decreased significantly (Witzel et al. 2014). Complex I or NADH-ubiquinone oxidoreductase is the first enzyme in the electron transition chain (Walker 1992), and is associated with the inner membrane of mitochondria with their NADH reaction position facing either internal alternative NADH-ubiquinone oxidoreductases (the mitochondrial matrix) or external alternative NADH-ubiquinone oxidoreductases (the cytoplasm). Little information is available about the external NADH-ubiquinone oxidoreductases. The internal mitochondria membranes have three multi-subunit enzyme complexes that act to transmit electrons from NADH to oxygen (Walker 1992). Ripening-induced proteins and abscisic acid are involved in abiotic stress responses (Zhang et al. 2015), and these proteins increase under abiotic stresses such as drought and salinity (Zhang et al. 2015). Ripening-induced proteins are able to bind to a wide number of respiratory electron transport chain genes and affect decreasing NADH-ubiquinone oxidoreductase.

ADP-Glucose Pyrophosphorylase (AGPase) Small Subunit

The result of our research showed that under salinity stress, this protein was up-regulated 1.82-fold in UCB-1 pistachio rootstock. Yin and colleagues reported that AGPase increases during the early development stages under salinity concentration (160 mM NaCl) in tomato (Yin et al. 2010). One of the most important regulatory enzymes in starch biosynthesis is AGPase, which catalyzes the transformation of glucose-1-phosphate and ATP to ADP-glucose. AGPase, which is a heterotetramer, has two B and two S subunits (Li et al. 2002). It can be concluded that most likely, AGPase small subunit increases in order to increase AGPase for adjustment of starch synthesis under salinity stress.

Protein Involved in the Non-enzymatic Antioxidant Defense System

Phytoene Synthase 2

In our study, the expression of phytoene synthase (*PSY*) 2 decreased 90.96-fold under salinity stress. A previous study reported that *PSY2* is significantly induced under ABA and salinity stresses in *Daucus carota* (Simpson et al. 2018). Phytoene synthase is the first enzyme and one of the most important points of adjustment in carotenoid biosynthesis path (Simpson et al. 2018). Carotenoids synthesis can be adjusted by sequestration and reposition in various kinds of plastids (Deruere et al. 1994; Vishnevetsky et al. 1999) at the epigenetic surface and even at the post-translational area (Cazzonelli et al. 2009). Carotenoids, which in plants intercede abiotic stress resistance responses, are abscisic acid precursors (Simpson et al. 2018). The synthesis of abscisic acid precursors occurs through induction of *PSY* expression (Simpson et al. 2018). Previous studies showed that salt stress induces the *PSY* expression in the root of *A. thaliana* (Meier et al. 2011; Ruiz-Sola et al. 2014), and the expression of *PSY3* in the roots of maize and rice, whereas *PSY1* and *PSY2* are only induced in the leaves of maize and rice by light (Welsch et al. 2008; Li et al. 2009). Also, a previous study on carrot showed that *PSY1* is expressed in leaves, while *PSY2* expression is higher during root development (Fuentes et al. 2012). Another research showed that *Daucus carota PSY2* gene expression is induced by ABA in roots of carrot, which is associated with the attendance of ABREs in its promoter. ABA-responsive element binding proteins, which are induced by ABA and abiotic stresses such as salinity and drought, are the mediators of *PSY2* induction under salinity stress through ABA in *Daucus carota* (Simpson et al. 2018). The same research showed that three ABREs are necessary for the ABA response, and most likely, *Daucus carota* AREB3 is the mediator of *Daucus carota PSY2* induction under salt stress through ABA. Carotenoids function as

collectors of light energy for photosynthesis and also act as quenchers of triplet O_2 and chlorophyll (Demmig-Adams and Adams 2002). In addition, carotenoids dissipate additional energy through the xanthophyll cycle and can function as the strong chloroplast membrane stabilizers, which are divided between the lipid phase of thylakoid membranes and light-harvesting complexes, decreasing susceptibility to lipid peroxidation and membrane fluidity (Demmig-Adams and Adams 2002). Therefore, decrease in carotenoid content under salt stress shows that the conservation by carotenoid is not an important mechanism in plants (Taïbi et al. 2016).

Proteins Involved in the Transportation of Materials (Endocytosis and Exocytosis)

Vesicle-Associated Membrane Protein (VAMP) 722- and 724-Like (Exocytosis)

VAMPs 722- and 724-like were up- and down-regulated 5.56- and 30.36-fold under 100 mM NaCl, respectively. A previous study reported that VAMP 722 is down-regulated under abscisic acid application in Arabidopsis (Yi et al. 2013). Also, they observed more growth inhibition in Arabidopsis by abscisic acid, which is an abiotic stress hormone and the plant growth barrier (Yi et al. 2013). Another study reported that VAMP 722 is up-regulated at 4 and/or 24 h of salt treatment in cotton (Peng et al. 2014). Also, VAMP 722 may become activated in response to pathogen attack (Sup Yun et al. 2013). A strong upregulation was recognized under salinity stress for VAMP 724 in *Ginkgo biloba* by Mohanta et al. (2012). VAMP 721/722 are involved in plant development, immunity, and growth (Yi et al. 2013), and specifically have a main role in plant development and growth because the VAMP 721/722-silenced plants are dwarf and the vamp 721/722 plants are lethal (Zhang et al. 2011; Kwon et al. 2008). Because of the smaller cell size in VAMP 721/722-silenced plants (Kwon et al. 2008), it is proved that VAMP 721/722 vesicles are employed in the default secretory pathway (Yi et al. 2013), which transports essential materials required for cell development and acts as a plant advocacy response (Yi et al. 2013). It is proved that ABA increases under salinity stress (Jia et al. 2002), and ABA suppresses plant growth by reducing the VAMP 722 abundance (Yi et al. 2013). Most likely, UCB-1 pistachio rootstock increases VAMP 722 level to enhance plant development and growth under salinity stress via transportation of molecules related to the plant growth and development such as lipids (Ichikawa et al. 2015) in the plasma membrane and cell wall (Yi et al. 2013). VAMP 724 forms a complex that is known as soluble N-ethylmaleimide-sensitive-factor attachment protein receptor or SNARE, which plays a main role in vesicle trafficking to vacuoles and transfers molecules to their goals. The main role carried out by VAMP 724 is

to move ROS from endosomes to vacuoles. Suppression of vesicle VAMP 724 expression in Arabidopsis plant inhibits assimilation of H_2O_2 containing vesicles with vacuoles (Leshem et al. 2006; Mohanta et al. 2012). Downregulation of this protein could be justified by the inability of this rootstock to move produced ROSs under salinity stress from endosomes to vacuoles.

Golgin Subfamily A Member 5 (Endocytosis and Exocytosis)

This protein was up-regulated 2.73-fold under salinity stress. In this study, this protein is reported for the first time in response to abiotic stresses, such as salinity stress. In the secretory pathway, Golgi apparatus partakes in glycosylation and transportation of lipids and proteins (Gillingham et al. 2002). In plant cells, protein N-glycosylation in the endoplasmic reticulumin and in Golgi apparatus is a necessary process (Kang et al. 2008). Also, N-glycosylation pathway in the endoplasmic reticulumin regulates protein quality control, cellulose biosynthesis, and salt tolerance (Kang et al. 2008). Interplays between the microtubules and Golgi are significant for the reorganization of the Golgi during mitosis (Gillingham et al. 2002). Golgins, which are long coiled-coil proteins and are well conserved in evolution, are present on the Golgi (Munro 2011). Golgins have roles in Golgi structure and membrane traffic, but their accurate function is unknown in most instances (Munro 2011). Golgins are goals of modification during apoptosis and mitosis, which are two operations involved in Golgi fragmentation (Munro 2011). According to the aforementioned issues, it can be concluded that most likely, Golgin subfamily A member 5 increases in response to salinity stress to increase glycosylation and transportation of lipids and proteins.

PREDICTED: ABC Transporter C Family Member 12-Like (Endocytosis)

Our results showed enhancement of 2.18-fold for this protein under salinity stress. In transgenic tobacco under salt and osmotic stresses, ABC transporter C family is up-regulated (Singh et al. 2016), and under 200 mM NaCl in cotton roots, this protein increased, significantly (Li et al. 2015). Terpenoids, alkaloids, quinines, and polyphenols, which are stress-related secondary metabolites, are transported by ABC transporters (Theodoulou 2000). Lee and coworkers showed that ABC transporter affected Na^+/K^+ homeostasis in Arabidopsis and elicited a salt stress reaction (Lee et al. 2004). Upregulation of an ABC transporter C family member 12-like in UCB-1 pistachio rootstock suggests that it may have a main role in salt stress responses. Probably, expression of this protein under salinity stress surges to increase transportation of stress-related secondary metabolites.

Calcium-Binding Proteins

Polcalcin Phl p 7-Like

In this study, polcalcin Phl p 7-like protein was up-regulated 2.87-fold under salinity stress. No report is available from the response of this protein under abiotic stresses. Polcalcins, which have two ''EF-hand'' motifs and range from 77 to 84 residues in length, are small Ca^{2+}-binding proteins (Ledesma et al. 1998; Rozwadowski et al. 1999; Suphioglu et al. 1997). The characteristic structural base of the greatest type of intracellular Ca^{2+}-binding proteins is EF-hand (Grabarek 2006; Kretsinger and Wasserman 1980; Gifford et al. 2007). Calcium has a main role in tube growth and pollen germination (MalhÓ et al. 2000). Polcalcin may act as a calcium reservoir and is also thought to be involved in intracellular signaling (Grote et al. 2008). Many studies proved that Ca^{2+} is able to directly reduce Na^+ toxicity and also indirectly improve K-alleviation of Na^+ toxicity (Shabala and Cuin 2008; Cramer 2002; Demidchik and Tester 2002). Many mechanisms in plants are controlled by sodium-calcium interactions (changes in the balance of sodium-calcium ions), such as photosynthesis, growth, mineral nutrition, ionization, and watering (Cramer 2002). Under salinity stress in two different pistachio cultivars, Ca^{2+} decrement was recorded by Rahneshan et al. (2018). According to the discussions above and because of the decrease in amount of Ca^{2+} under NaCl stress, most likely, UCB-1 pistachio rootstock increases polcalcins to reduce the destructive effects of Na^+ in response to salinity stress.

Transcription Factors

Predicted: Nascent Polypeptide-Associated Complex (NAC) Subunit Alpha, Muscle-Specific Form-Like Isoform X2

Our results showed that this protein was up-regulated twofold under 100 mM NaCl. Yan and colleagues in 2005 reported that in response to salinity stress in rice root, α-NAC was down-regulated significantly (Yan et al. 2005), while other studies showed that in response to salinity, NAC subunit alpha-like 3 in barley (Fatehi et al. 2012) and NAC in tomato (Chen et al. 2009) up-regulated significantly. NAC or nascent polypeptide-associated complex, which is involved in protein translocation and sorting (Yan et al. 2005; Chen et al. 2009), attaches to eukaryotic ribosomes and is the first cytosolic protein to contact nascent polypeptide fetters appearing from ribosome (Rospert et al. 2002). It is specified that NAC prevents mistargeting of nascent polypeptide fetters to the endoplasmic reticulum (Rospert et al. 2002). NAC is a heterodimeric complex of β chain and α chain (Yan et al. 2005). α-NAC acts as a transcriptional coactivator (Moreau et al. 1998; Yotov et al. 1998). If

α-NAC protein rate decreases, it probably affects the NAC function; changes in NAC function affect the processes of protein translation and gene transcription and ultimately lead to an erratic metabolism (Yan et al. 2005; Chen et al. 2009). Therefore, plants probably enhance the α-NAC protein concentration to reduce their own metabolism disorder under salinity stress.

Chaperon

Stromal 70 kDa Heat Shock-Related Protein, Chloroplastic

Under salinity stress in UCB-1 rootstock leaf, this protein was up-regulated 2.53-fold. Many reports are available in response to this protein under different situations, such as exposure to cold, UV light, biotic stresses, wound healing or tissue remodeling (Boston et al. 1996; Lindquist and Craig 1988; Vierling 1991). Also, Wang in 2004 showed that this protein is a key protein in response to abiotic stresses (Wang et al. 2004). Furthermore, the role of heat shock proteins under abiotic stresses using proteomic method was proved by Timperio et al. (2008). HSPs or heat shock proteins are proteins found in animal and plant cells. Heat shock proteins respond to a broad diversity of stresses (Park and Seo 2015). In eukaryotic and prokaryotic cells, HSPs are essential parts contributing to cellular homeostasis under detrimental and optimal growth situations (Wang et al. 2004; Lindquist and Craig 1988). Also, HSPs have the main role in protein folding, translocation, assembly, and depression during normal cellular development and growth (Lindquist and Craig 1988; Wang et al. 2004). Furthermore, under stress conditions, HSPs play a role in proteins' stabilization and assist refolding of proteins (Hüttner and Strasser 2012; Sitia and Braakman 2003). In animals and plants, there are five main families of HSPs, such as small HSP (sHSP), HSP60, HSP70, HSP90, and HSP100 (Wang et al. 2004; Gupta et al. 2010; Kotak et al. 2007). 70 kDa heat shock proteins or Hsp70 s function as molecular chaperones involved in fundamental cellular processes, such as protein transportation and folding (Latijnhouwers et al. 2010). Also, Hsp70s play a role in the cell's reaction to a diverse range of stress situations (Latijnhouwers et al. 2010). In plants, the protein involved in chaperone is represented by Stromal 70 kDa heat shock-related protein (Latijnhouwers et al. 2010), and one mechanism to obtain stress resistance is to synthesize Hsp70 as a response to a stressor factor (Lyytinen et al. 2012; Yocum 2001).

Unknown Function Proteins

Unknown (Hypothetical) Proteins

5 proteins in UCB-1 pistachio rootstock were found without any function by our results. Uncharacterized

protein LOC107620721, PREDICTED: uncharacterized protein LOC105974023, PREDICTED: uncharacterized protein LOC109219975 partial, PREDICTED: uncharacterized protein LOC109178037, and hypothetical protein CISIN_1g0462972 mg were up-regulated 1.85-, 2.95-, 2.29-, 1.85-, and 6.05-fold, respectively.

Conclusion

According to our results, MDA content increased at 100 mM NaCl compared to normal condition, while it decreased at 200 mM in comparison with the 100 mM. Decreasing content of MOD at 200 mM NaCl compared to the 100 mM in UCB-1 pistachio rootstock can indicate its adaptation ability in response to salinity stress. Based on our results, GPX, SOD, and CAT enzymes activity increased with increasing concentrations of salinity stress in all samples. Likely, increasing activity of GPX, SOD, and CAT enzymes occurred to scavenge produced ROS under salinity stress, and most likely, these enzymes have a fundamental role in protecting the UCB-1 pistachio rootstock under unfavorable conditions of salinity stress. Proteins play a main role in the response of plant stress which leads to stress-adapted reactions. Differential expression of 25 salt stress responsive proteins in this study reveals the considerable effect of salt stress on the leaf proteome of tolerant UCB-1 pistachio rootstock. In the tolerant UCB-1 pistachio rootstock, proteins involved in photosynthesis including 50S ribosomal protein L13, ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) large subunit, ribulose bisphosphate carboxylase small chain, ribulose bisphosphate carboxylase/oxygenase activase 1 and phosphoribulokinase assigned themselves the highest amount of protein expression variations in response to 100 mM NaCl. These results show that proteins involved in the photosynthesis can be considered as biomarkers in the breeding programs to increase the tolerance of other pistachio rootstocks to salinity stress. Also, these proteins are probably of particular significance in the adaptation of UCB-1 pistachio rootstock to salinity stress conditions. In addition to these results, the changes in proteomic profile observed in UCB-1 pistachio rootstock induced by 100 mM NaCl suggest the presence of a sophisticated antioxidant defense system that fine-tunes and regulates the activities of different enzymes to retain ROS homeostasis. Ribonucleoside-diphosphate reductase small chain, polcalcin Phl p 7-like and Golgin subfamily A member 5 are three proteins that were detected for the first time in response to abiotic stresses, and most likely, they are the key proteins in response of this rootstock to salinity and likely participate in plant resistance to NaCl stress. Based on our results, 5 unknown (hypothetical) proteins were found in the UCB-1 pistachio rootstock, which would be very valuable proteins

in response to salinity stress. These proteins should be further studied and other different bioinformatics surveys are needed to specify the function of these unknown proteins. The proteins identified in this research provide new information regarding the tolerance of UCB-1 pistachio rootstock to salinity stress.

Compliance with Ethical Standards

Conflict of interest The authors declare no conflict of interest.

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