Investigation on salt-response mechanisms in *Arabidopsis thaliana* from UniProt protein knowledgebase

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**ABSTRACT** Salt stress negatively affects plant growth and crop productivity. As an ideal model pathway of salt tolerance in glycophyte, 466 of 15,768 *Arabidopsis thaliana* proteins with the GO term of biological with known genetic background, Arabidopsis thaliana has been widely applied to disclose the process ‘response to salt stress’ were retrieved from UniPort and analyzed by bioinformatics tools of PANTHER, DAVID, KEGG, Cytoscape and STRING. Our results not only indicated the involvement of salt-responsive proteins in various pathways and interaction networks, but also demonstrated the more complicated cross-tolerances to both abiotic stresses (osmosis, water deprivation, abscisic acid, cold, heat, light and wounding) and biotic stresses (bacterium and fungus) and multiple subcellular locations of these salt-responsive proteins. Furthermore, protein activities of superoxide dismutase (SOD) and peroxidase (POD) in *Arabidopsis thaliana* were determined under salt, cold and osmotic stresses, which validated the hypothesis of cross-tolerance to multiple stresses. Our work will greatly improve the current knowledge of salt tolerance mechanism in glycophytes and provide potential salt-responsive candidates for promoting plant growth and increasing crop output.

**Introduction**

In the world, more than 20% irrigated lands are negatively affected by soil salinity, which seriously limits the plant growth and decreases the grain output (Zhao et al. 2013). Usually, osmosis tolerance, sodium ion exclusion and sodium ion accumulation tolerance are the main ways for plant to response to salt stress (Munns and Tester 2008). During this process, plant undergoes many changes including developmental, physiological, biochemical, and morphological (Abu et al. 2010).

Many plants have been used as research materials. Among them, arabidopsis is an ideal model plant, and great understandings of salt stress tolerance and adaptation have been obtained from arabidopsis (Ngara and Ndimba 2014). To discover novel phosphatidic acid-binding proteins associated with salt stress, an approach was launched in a previous research using lipid-affinity purification for the isolation of peripheral membrane proteins combined with mass spectrometry identification (McLoughlin et al. 2013). As a result, 42 phosphatidic acid-binding proteins had been identified including clathrin-assembly protein, glyceraldehyde 3-phosphate dehydrogenase and a phosphatidylinositol 4 kinase. Furthermore, a quantitative proteome research using two-dimensional difference gel electrophoresis (2D-DIGE) combined with mass spectrometry had been performed to display the differentially expressed microsomal proteins under salt stress between *Arabidopsis thaliana* and *Thellungiella salsuginea*, and identified 36 significantly altered proteins. Gene ontology classification showed these proteins were involved in transport and carbohydrate metabolism (Vera-Estrella et al. 2014). In our previous works, 2D-DIGE has been carried out to investigate the differential proteins between wild-type *Arabidopsis* and its salt-tolerant mutant. A total of 19 altered proteins were identified by MALDI-TOF mass spectrometry, which is mainly associated with redox homeostasis, signal transduction, and carbohydrate metabolism (Guo et al. 2014b). Furthermore, phosphoproteome of *Arabidopsis* roots has been studied with Pro-Q Diamond staining, and the results showed nonsynchronous differences between total salt-responsive proteins and phosphorylated proteins. The differential proteins majored in signal transduction, and reactive oxygen species (ROS) scavenging (Guo et al. 2014a). Proteomic technology has greatly improved our knowledge of *Arabidopsis* salt-response mechanisms. But there are still limitations in our understanding of the salt tolerance process. Each research only provides limited information, and some proteomic data of studies are still not available. In order to better demonstrate the details of salt-responsive proteins in *Arabidopsis*, a more data-rich and accessible resource should be explored.

Therefore, in the present work, a more comprehensive dataset associated with salt tolerance was retrieved from the UniProt public database (release 2018_08, [https://www.uniprot.org/](https://www.uniprot.org/)). The UniProt knowledgebase provides the most abundant resources including more than 60 million protein sequences, of which over 500,000 sequences have been manually curated by scientists. UniProt database is an ideal hub for the acquisition of protein information (Pundir et al. 2017; The UniProt Consortium 2017; Boutet et al. 2016; UniProt Consortium 2015). In 15,768 reviewed A.
proteins, 466 salt-responsive proteins were selected, which significantly exceeds the number of salt-responsive proteins provided by any single previous research. Based on integrated bioinformatic analysis (PANTHER, DAVID, KEGG, Cytoscape, and STRING), the complicated crosstalk, interactions and pathways would extend our knowledge of salt response and adaption in Arabidopsis. Further experimental validation has been performed to confirm the prediction of bioinformatic analysis. Those salt-responsive proteins might be the potential targets for increasing crop output in the future research.

Materials and methods

Selection criteria of salt-responsive proteins from UniProt database

Based on the GO annotation in the UniProt database (release 2018_08), 466 proteins involved in the biological process term of ‘response to salt stress’ were recruited from 157,68 reviewed A. thaliana proteins. Further, to investigate the coss-talk of salt-responsive proteins with the proteins involved in other stresses, 142, 283, 242, 323, 340, 137, 162, 451, and 129 reviewed proteins associated with the biological process term of ‘response to osmotic stress,’ ‘response to cold,’ ‘response to water deprivation,’ ‘defense response to bacterium,’ ‘response to abscisic acid,’ ‘response to heat,’ ‘response to wounding,’ ‘defense response to fungus,’ and ‘response to light stimulus’ were also selected respectively from the above A. thaliana UniProt knowledgebase (Supplementary Table 1).

Gene ontology classification

A web-accessible bioinformatic tool of DAVID (Database for annotation, visualization and integrated discovery, Version 6.8) (https://david.ncifcrf.gov/) and another online program PANTHER (Protein ANAlysis THRough Evolutionary Relationships) classification system (Version 13.1 released 2018-02-03) (http://pantherdb.org/) were applied for gene ontology enrichment analysis of the recruited proteins. Each protein was classified into one category. The Venn diagram was prepared by an online tool of ‘Calculate and draw custom Venn diagrams’ (http://bioinformatics.psb.ugent.be/webtools/Venn/).

Pathway analysis

The pathways of salt-responsive A. thaliana proteins were assessed through the online program of KEGG (Kyoto Encyclopedia of Genes and Genomes, Version 88.0, released 1 October 2018) (http://www.kegg.jp).

Protein–protein interaction

The protein–protein interaction network of the recruited proteins was analyzed by the software of STRING (search tool for recurring instances of neighbouring genes) database (Version 10.5, released 14 May 2017) (http://string-db.org/), and an open-source software of Cytoscape (an open source platform for complex network analysis and visualization) (Version 3.6.1).

Arabidopsis thaliana material, growth conditions and harvest

According to the previous method (Guo et al. 2014a; Guo et al. 2014b), the seeds of A. thaliana (ecotype Col-0) were germinated in the normal MS medium-containing plate under the conditions of 8/16 h light/dark cycle, 22/20°C day/night, 60 mmol m$^{-2}$ s$^{-1}$ light intensity. After 8 days, the resultant A. thaliana seedlings were divided into four groups. The first group was transferred to the cold-stress condition (8°C, day and night), the second group was transferred into drought-stress condition (MS medium supplemented with 200 mmol L$^{-1}$ mannitol), the third group was transferred into salt-stress condition (MS medium supplemented with 150 mmol L$^{-1}$ NaCl), and the fourth group was transferred into the normal MS medium-containing plate under normal conditions. The A. thaliana seedlings of the above four groups continued to grow for 4 days. Then, A. thaliana roots and rosette leaves were harvested, and stored at $-80^\circ$C for further analysis. Three replicates were performed for the above experimental design.

Enzyme activity assay

According to the determination protocol of superoxide dismutase (SOD) and peroxidase (POD) activities (Nanjing Jiancheng Bioengineering Institute) (Li et al. 2013), the above enzyme activities of A. thaliana roots and rosette leaves were assayed using the corresponding kit. The activity of SOD was defined as the inhibition of O2$^-$ production by the xanthine morpholine with xanthine oxidase. One unit of SOD activity was the SOD enzyme required to catalyze 1 µg substrate at 37°C. The graphs were drawn using the software of Graphpad Prism 6 for windows (Version 6.01).

Results

Bioinformatic enrichment of A. thaliana salt-responsive proteins

A total of 466 critically reviewed salt-responsive A. thaliana proteins were selected for the further enrichment analysis. According to their molecular function, the majority of proteins were related to binding activity (153, 32.8%), whereas other protein functions were mainly catalytic activity (117, 25.1%), transporter activity (42, 9.0%), signal transducer activity (36, 7.7%), general metabolism (35, 7.5%), transcription (32, 6.9%), protein synthesis and degradation (21, 4.5%), antioxidant activity (18, 3.8%), and structural molecule activity (12, 3.6%). As for subcellular localization, the majority of the salt-responsive proteins located in the cytoplasm (139, 29.8%). Other main localizations were nucleus (93, 20.0%), membrane (54, 11.6%), plastid (53, 11.4%), extracellular region (42, 9.0%), mitochondrion (25, 5.4%), endoplasmic reticulum (25, 5.4%), cell wall (21, 4.5%), and Golgi apparatus (12, 2.6%). Based on biological process, the majority of proteins was related to metabolic process (129, 27.7%), and response to stimulus (118, 25.3%). The others were cell communication (100, 21.5%), transcription (71, 15.2%), external encapsulating structure organization (12,
2.6%), and autophagy (3, 0.6%) (Figure 1). Domain analysis was performed through Interpro database of DAVID. The result showed 22 significant domains, including the Myb domain, Homeodomain-like domain, and Protein kinase domain (Table 1). KEGG analysis indicated 14 statistically significant pathways, such as glycolysis/gluconeogenesis, citrate cycle, arginine and proline metabolism, and glutathione metabolism (Table 1 and Figure 2).

Protein–protein interaction network of A. thaliana salt-responsive proteins

A protein–protein interaction network was constructed by the online software of STRING. Totally, 416 of 466 salt-responsive proteins were connected with each other through 2,063 edges. PPI enrichment was statistically significant ($p$-value < 1.0e–16) (Figure 3).

Cross-tolerance visualization of A. thaliana salt-responsive proteins involved in the response to other stresses

Among 466 salt-responsive proteins, 260 proteins also responded to other stresses (eg. osmotic stress, cold, water deprivation, bacterium defense, abscisic acid, heat, wounding, fungus defense, and light stimulus). Figure 4 showed that 116

![Figure 1: Pie diagrams of salt-responsive proteins in A. thaliana categorized by GO classifications based on their (A) molecular function, (B) subcellular localization, and (C) biological process.]

![Table 1: Enriched domains and pathways of salt-responsive proteins in A. thaliana.]

| Item             | Category                      | Count | Percentage (%) | $p$-Value |
|------------------|-------------------------------|-------|----------------|-----------|
| INTERPRO         | Myb domain                    | 38    | 8.2            | 5.80E–23  |
| INTERPRO         | SANT/Myb domain               | 39    | 8.4            | 9.90E–21  |
| INTERPRO         | Homeodomain-like              | 41    | 8.9            | 4.40E–16  |
| INTERPRO         | Glycoside hydrolase, family 1| 14    | 3              | 5.80E–12  |
| INTERPRO         | Annexin                       | 8     | 1.7            | 1.00E–11  |
| INTERPRO         | Annexin repeat                | 8     | 1.7            | 1.00E–11  |
| INTERPRO         | Annexin repeat, conserved site| 7     | 1.5            | 4.50E–10  |
| INTERPRO         | Glycoside hydrolase, catalytic domain | 17  | 3.7          | 6.10E–07  |
| INTERPRO         | Annexin, plant                | 5     | 1.1            | 8.00E–07  |
| INTERPRO         | Glycoside hydrolase, superfamily | 17 | 3.7          | 6.10E–06  |
| INTERPRO         | Myb domain, plants            | 11    | 2.4            | 8.20E–06  |
| INTERPRO         | BTB/POZ-like                  | 10    | 2.2            | 2.00E–05  |
| INTERPRO         | BTB/POZ fold                  | 10    | 2.2            | 1.90E–04  |
| INTERPRO         | Aldehyde dehydrogenase domain | 5     | 1.1            | 2.50E–04  |
| INTERPRO         | Aldehyde dehydrogenase, C-terminal | 5  | 1.1          | 2.50E–04  |
| INTERPRO         | Aldehyde dehydrogenase, N-terminal | 5  | 1.1          | 2.50E–04  |
| INTERPRO         | Nascent polypeptide-associated complex NAC domain | 4  | 0.9          | 2.70E–04  |
| INTERPRO         | Aconitase/3-isopropylmalate dehydratase, swivel | 4  | 0.9          | 2.70E–04  |
| INTERPRO         | Aldehyde/histidinol dehydrogenase | 5  | 1.1          | 3.20E–04  |
| INTERPRO         | Glycoside hydrolase, family 1, active site | 4  | 0.9          | 4.20E–04  |
| INTERPRO         | Cation/H+ exchanger, CPA1 family | 4  | 0.9          | 4.20E–04  |
| INTERPRO         | Protein kinase, ATP binding site | 28 | 6            | 5.70E–04  |
| KEGG_PATHWAY     | Arginine and proline metabolism | 9  | 1.9          | 1.00E–03  |
| KEGG_PATHWAY     | Tryptophan metabolism         | 8     | 1.7            | 2.00E–03  |
| KEGG_PATHWAY     | Biosynthesis of amino acids   | 21    | 4.5            | 2.50E–03  |
| KEGG_PATHWAY     | Carbon metabolism             | 21    | 4.5            | 3.40E–03  |
| KEGG_PATHWAY     | Cysamino acid metabolism      | 8     | 1.7            | 9.10E–03  |
| KEGG_PATHWAY     | Starch and sucrose metabolism | 12    | 2.6            | 1.00E–02  |
| KEGG_PATHWAY     | Glutathione metabolism        | 10    | 2.2            | 1.10E–02  |
| KEGG_PATHWAY     | Citrate cycle (TCA cycle)     | 8     | 1.7            | 1.20E–02  |
| KEGG_PATHWAY     | Glycolysis / Gluconeogenesis  | 11    | 2.4            | 1.40E–02  |
| KEGG_PATHWAY     | Pyruvate metabolism           | 9     | 1.9            | 1.80E–02  |
| KEGG_PATHWAY     | Amino sugar and nucleotide sugar metabolism | 12 | 2.6          | 1.80E–02  |
| KEGG_PATHWAY     | Carbon fixation in photosynthetic organisms | 8  | 1.7          | 1.90E–02  |
| KEGG_PATHWAY     | Peroxisome                    | 9     | 1.9            | 2.10E–02  |
| KEGG_PATHWAY     | Fructose and mannose metabolism | 7  | 1.5          | 3.50E–02  |
were involved in response to abscisic acid; 91 responded to water deprivation; 83 were also osmotic stress-related proteins; 82 were associated with response to cold; 36 salt-responsive proteins participated in defense response to bacterium; 29 were related to response to heat; 23 participated in response to wounding; 14 were related to defense response to fungus; and 14 were associated with response to light. The complicated cross-talk response of *A. thaliana* salt-responsive proteins with other stresses was presented in Figure 5.

**Multiple subcellular localizations of A. thaliana salt-responsive proteins**

Among the above 260 proteins involved in multiple stresses, 103 proteins had more than one subcellular localization (Figure 6). For example, protein BTB/POZ and TAZ domain-containing protein 3 (BT3) could localize in the cytoplasm, nucleus, cell wall, endoplasmic reticulum, membrane, mitochondrion, plastid, symplast, thylakoid and vacuole;
protein bifunctional enolase 2/transcriptional activator (ENO2) could be found in the cytoplasm, endoplasmic reticulum, membrane, mitochondrion, nucleus, plastid and symplast; and protein glyceraldehyde-3-phosphate dehydrogenase (GAPC1) could be mapped into the cytoplasm, endoplasmic reticulum, membrane, mitochondrion, nucleus, plastid, and vacuole (Figure 7). Those proteins were defined as double cross-talk proteins characterized by multi-location and multi-response to different stresses.

**Functional enrichment of double cross-talk proteins characterized by multi-location and multi-response to different stresses**

The molecular functions of the 103 multi-location proteins were further classified by UniProt database annotation and literatures. The results indicated that these proteins were mainly related to binding (63, 30.4%), transcription (37, 17.9%), catalytic activity (36, 17.4%), structural molecule activity (26, 12.6%), general metabolism (21, 10.1%), antioxidant activity (10, 4.8%), transporter activity (9, 4.3%), and protein synthesis and degradation (5, 2.4%) (Figure 8).

**Antioxidative activity determination of A. thaliana under salt, cold, and osmotic stress**

Under salt stress or other stresses, antioxidative activity is an important molecular function of these stress-responsive proteins. Our results showed POD and SOD were both salt-responsive proteins. Therefore, enzyme activities of POD and SOD in root and leaf were determined under three stresses (salt, cold, and osmotic stress). In comparison with the control, activities of POD and SOD were generally increased under salt, cold, and osmotic stresses at different check points.
(12, 24, 36, 48, 60, 72, 84, 96 h). However, control treatments did not change the SOD and POD activities as shown in Figure 9.

Discussion

Salt stress is a nonnegligible issue that significantly limits plant growth on the earth. Many scientists have paid great attention to investigate the mechanisms of plant salt-tolerance and salt-adaption using genomic and proteomic
technologies (Shah et al. 2018; Wu et al. 2016). *Arabidopsis thaliana* is an ideal material to investigate the salt-responsive molecules (Guan et al. 2018; Zhang et al. 2018; Huang et al. 2018). But previous research only provided limited information. Therefore, more detailed data would extend our knowledge of plant salt-response pathways. Here, we screened 466 reviewed salt-responsive proteins from UniProt database, which contained the most comprehensive information of plant salt tolerance and adaption. Integrated bioinformatic analysis demonstrated the complicated pathways, protein interactions and cross-talks under different stresses in *A. thaliana*.

Arginine and proline metabolism was a significantly enriched pathway. Among 466 salt-responsive proteins, 9 proteins, P-loop containing nucleoside triphosphate hydrolases superfamily protein (NOA1), aldehyde dehydrogenase 12A1 (ALDH12A1), aldehyde dehydrogenase 3H1 (ALDH3H1), aldehyde dehydrogenase 7B4 (ALDH7B4), arginine decarboxylase 1 (ADC1), arginine decarboxylase 2 (ADC2), delta1-pyrroline-5-carboxylate synthase 1 (P5CS1), ornithine-delta-aminotransferase (DELTA-OAT) and pyrroline-5-carboxylate (P5C) reductase (P5CR), were nodes of arginine and proline metabolism. The polyamines were catalyzed by ADC1 and ADC2, which were positively charged and involved in the binding with phospholipids, nucleic acids and membrane (Groppa and Benavides 2008). Previous studies have proved that polyamines are free radical scavenger and possess the molecular function of antioxidant activity. Therefore, proline metabolism might be an important way to protect *A. thaliana* from attaching free radicals under salt stress (Verbruggen and Hermans 2008).

Under salt stress, electron transport chain will be excessively attenuated, and the level of ROS dramatically increases,
such as the hydroxyl radicals, superoxide radicals, and hydrogen peroxide (Miller et al. 2010; Mittler et al. 2004). In order to maintain redox homeostasis in plant cell, ROS scavenging-related enzymes are activated to decrease the oxidative perturbation, including superoxide dismutases (Sarker and Oba 2018), ascorbate peroxidase (Ribeiro et al. 2017), glutathione S-transferase (Chan and Lam 2014), and glutathione peroxidase (Islam et al. 2015). In our present work, many enzymes with ROS-scavenging activities (glutathione S-transferase family protein, ascorbate peroxidase 1, glutathione S-transferase 6, glutathione S-transferase 7, glutathione S-transferase PHI 2, glutathione S-transferase phi 8, and glutathione peroxidase 6) participated in the tolerance of salt stress in A. thaliana. To validate the outcome of bioinformatic analysis, the enzyme activities of POD and SOD were detected under salt stress, and the results indicated that these two proteins were indeed salt-responsive proteins, and might play an important role in the process of scavenging ROS.

Based on bioinformatic analysis of 466 salt-responsive A. thaliana proteins, some proteins were characterized by multiple subcellular locations. For example, BT3 and ENO2 each had 10 and 7 subcellular locations. The former might play roles in the process of gametophyte development (Robert et al. 2009), and the latter could influence metabolite synthesis under salt stress (Chen et al. 2018). The multiple subcellular localizations of these proteins might indicate their versatile functions under salt stress. Further studies are necessary to disclose the functions of these salt-responsive proteins under the stress.

Many genes and proteins have been found to participate in response to more than one stress, which is called cross-tolerance to multiple stresses. Cross-tolerance is a vital strategy for plants to survive under different stresses, and many proteins are involved in this process (Tuteja 2007). A previous study has demonstrated that approximately 75% of 195 salt-inducible genes are associated with drought or cold stresses (Seki et al. 2002). Our present work displayed that cross-tolerance is more universal and complicated. The salt-responsive proteins were not only involved in abiotic responses (osmosis, water deprivation, abscisic acid, cold, heat, light and wounding) but also associated with biotic responses (bacterium and fungus), which greatly extended the knowledge of salt tolerance mechanism in A. thaliana. The salt-responsive protein POD has been confirmed to be involved in the tolerance to the temperature stress (Neilson et al. 2010), and SOD was also related to other stresses (Zhao et al. 2013). In order to verify the above universality of cross-tolerance to multiple stresses, the enzyme activities of POD and SOD in root and leaf of A. thaliana were measured under salt, cold and osmotic stresses, and the results were in agreement with our hypothesis and validated the prediction of bioinformatics.

Conclusion
This work provided new understanding on the salt-response mechanisms of A. thaliana proteins and on the pathways associated with salt stress response. Those potential biomarkers identified were characterized by multiple subcellular locations and multiple stresses responses, which we named as the ‘space-stress’ double cross-tolerance effects. These results provided a clue that A. thaliana has developed an economical way to respond to various stresses. Further researches are therefore necessary to further elaborate the functions of these targets in the process of stress tolerance and adaption, which will be helpful to promote plant growth and to increase crop output.

Disclosure statement
No potential conflict of interest was reported by the authors.

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References

Abu-Hena MK, Kim KH, Shin KH, Choi JS, Baik BK, Tsujimoto H, Heo HY, Park CS, Woo SH. 2010. Abiotic stress responsive proteins of wheat grain determined using proteomics technique. Aust J Crop Sci. 4(3):196–208.

Boutet E, Lieberherr D, Tognolli M, Schneider M, Bansal P, Bridge AJ, Pouss S, Bouguerel L, Xenarios I. 2016. UniProtKB/Swiss-Prot, the manually annotated section of the UniProt knowledgebase: how to use the entry view. Methods Mol Biol. 1374:23–54.

Chan C, Lam HM. 2014. A putative lambda class glutathione S-transferase enhances plant survival under salinity stress. Plant Cell Physiol. 55(3):570–89.

Chen C, Zhang Y, Ye P, Ma X, Zheng C, Zhang G. 2018. ENO2 knock-out mutants in Arabidopsis modify the regulation of the gene expression response to NaCl stress. Mol Biol Rep. 45(5):1331–1338.

Groppa MD, Benavides MP. 2008. Polyamines and abiotic stress, recent advances. Amino Acids. 34:35–45.

Guo ML, Gao WX, Li L, Li H, Xu YL, Zhou CX. 2014a. Proteomic and phosphoproteomic analyses of NaCl stress-responsive proteins in Arabidopsis roots. J Plant Interact. 9(1):396–401.

Guo ML, Li H, Li L, Cheng XM, Gao WX, Xu YL, Zhou CX, Liu FJ, Liu X. 2014b. Comparative proteomic analysis of Arabidopsis thaliana roots between wild type and its salt-tolerant mutant. J Plant Interact. 9(1):330–337.

Huang L, Yin X, Sun X, Yang J, Rahman MZ, Chen Z, Wang X. 2018. Expression of a grape VgTS3636-increased resistance to powdery mildew and osmotic stress in Arabidopsis but enhanced susceptibility to Botrytis cinerea in rice. Int J Mol Sci. 19(10). pii: E2985.

Islam T, Manna M, Reddy MK. 2015. Glutathione peroxidase of Penicillium glaucum (PgGPx) is a functional Cd2+ dependent peroxiredoxin that enhances tolerance against salinity and drought stress. PLoS One. 10(11). e0143344.

Li LX, Xiao Y, Cao LL, Yan X, Li C, Shi HY, Wang JW, Ye YH. 2013. Cerebroside C increases tolerance to chilling injury and alters lipid composition in wheat roots. PLoS One. 8(9). e73380.

McLoughlin F, Arisz SA, Dekker HL, Kramer G, de Koster CG, Haring MA, Munnik T, Testerink C. 2013. Identification of novel candidate phosphatidic acid-binding proteins involved in the salt-stress response of Arabidopsis thaliana roots. Biochem J. 450(3):573–581.

Miller G, Suzuki N, Ciftci-Yilmaz S, Mittler R. 2010. Reactive oxygen species homeostasis and signalling during drought and salinity stresses. Plant Cell Environ. 33(4):453–467.

Mittler R, Vanderwera S, Gollery M, Van Breusegem F. 2004. Reactive oxygen gene network of plants. Trends Plant Sci. 9(10):490–498.

Munns R, Tester M. 2008. Mechanisms of salinity tolerance. Annu Rev Plant Biol. 59:651–681.

Neilson KA, Gammullia CG, Mirzaei M, Imin N, Haynes PA. 2010. Proteomic analysis of temperature stress in plants. Proteomics. 10(4):828–845.

Ngara R, Ndomba BK. 2014. Model plant systems in salinity and drought stress proteomics studies: a perspective on Arabidopsis and Sorghum. Plant Biol (Stuttgart. 16(6):1029–1032.

Pundir S, Martin MJ, O’Donovan C. 2017. Uniprot protein knowledgebase. Methods Mol Biol. 1588:41–55.

Ribeiro CW, Kordes AP, Garighan JA, Jardim-Messeder D, Carvalho FEL, Sousa BHV, Caverzan A, Teixeira FK, Silveira JAG, Margis-Pinheiro M. 2017. Rice peroxisomal ascorbate peroxidase knockdown affects ROS signaling and triggers early leaf senescence. Plant Sci. 263:55–65.

Robert HS, Quint A, Brand D, Vivian-Smith A, Offringa R. 2009. BTB and TAZ domain scaffold proteins perform a crucial function in Arabidopsis development. Plant J. 58(1):109–121.

Sarker U, Oba S. 2018. Catalase, superoxide dismutase and ascorbate-glutathione cycle enzymes confer drought tolerance of Amaranthus tricolor. Sci Rep. 8(1):16496.

Seki M, Narusaka M, Ishida J, Nanjo T, Fujita M, Oono Y, Kamiya A, Nakajima M, Enju A, Sakurai T, et al. 2002. Monitoring the expression profiles of 7000 Arabidopsis genes under drought, cold and high-salinity stresses using a full-length cDNA microarray. Plant J. 31(3):279–292.

Shah T, Xu J, Zou X, Cheng Y, Nasir M, Zhang X. 2018. Omics approaches for engineering wheat production under abiotic stresses. Int J Mol Sci. 19(2390). 1–16.

Tuteja N. 2007. Mechanisms of high salinity tolerance in plants. Methods Enzymol. 428:419–438.

UniProt Consortium. 2015. Uniprot: a hub for protein information. Nucleic Acids Res. 43(Database issue):D204–D212.

The UniProt Consortium. 2017. Uniprot: the universal protein knowledgebase. Nucleic Acids Res. 45(D1):D158–D169.

Vera-Estrella R, Barkla BJ, Pantoja O. 2014. Comparative 2D-DIGE analysis of salinity responsive microsomal proteins from leaves of salt-sensitive Arabidopsis thaliana and salt-tolerant Thellungiella saluginosa. J Proteomics. 111:113–127.

Verbruggen N, Hermans C. 2008. Proline accumulation in plants: a review. Amino Acids. 35:753–759.

Wu X, Gong F, Cao D, Hu X, Wang W. 2016. Advances in crop proteomics: PTMs of proteins under abiotic stress. Proteomics. 16(5):847–865.

Zhang S, Yang R, Huo Y, Liu S, Yang G, Huang J, Zheng C, Wu C. 2018. Expression of cotton PLATZ1 in transgenic Arabidopsis reduces sensitivity to osmotic and salt stress for germination and seedling establishment associated with modification of the abscisic acid, gibberellin, and ethylene signalling pathways. BMC Plant Biol. 18(1):218.

Zhao Q, Zhang H, Wang T, Chen S, Dai S. 2013. Proteomics-based investigation of salt-responsive mechanisms in plant roots. J Proteomics. 82:230–253.