In-depth investigation on abiotic stress-responsive differentially expressed genes in *Arabidopsis* roots through GEO database

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**ABSTRACT**

Abiotic stresses limit the plant growth and productivity. Plants have developed various responsive mechanisms to survive these adverse environmental conditions. To better understand plants how to adapt environmental stress, we retrieved the *Arabidopsis* root responsive genes related to eight abiotic stresses (salt, cold, drought, osmotic, UV, wounding, heat, and heavy metal stresses) from the Gene Expression Omnibus (GEO) database. After quantile normalization of microarray data, a robust rank aggregation (RRA) algorithm was applied to determine the differentially expressed genes (DEGs). The resultant 213 DEGs, including 139 up-regulated and 74 down-regulated genes out of more than 20,000 genes, were further analyzed by the integrated bioinformatics approaches of PUBMED, PANTHER, DAVID, and STRING. The results indicated that the up-regulated DEGs were more positively involved in response to oxidative stress, regulation of transcription, and structure organization than the down-regulated DEGs. The former also had more complicated PPI interactions than the latter. Furthermore, qRT-PCR and enzyme activity have been done to validate the outcome of integrated bioinformatics analysis. Our work will facilitate to demonstrate the common molecular mechanisms responsive to differential abiotic stresses and these DEGs might be potential biomarkers for future abiotic stress-resistance studies.

**Introduction**

Agricultural production has been severely disrupted by various abiotic stresses such as salinity, drought, climate changes, and heavy metal around the world, which threatens the food security required for the growing global population. To improve plant resistance on these abiotic stresses and increase crop yield, many researches have been done to explore the adaption mechanisms plant evolved under variable field conditions for the past decades (Gong et al. 2020).

Microarray technology has been used to measure the abundance of thousands of mRNAs. But microarray is still cost-prohibitive experiment for each lab. It’s difficult for an individual lab to determine the *Arabidopsis* expression profilings in development stages, and growth responses under different stages. Therefore, the public repositories such as Gene Expression Omnibus provide an important platform to disclose the plant physiological mechanism using the available thousands of expression profiles unloaded by different labs. In order to effectively compare these microarray data and obtain the plant insights, integrated bioinformatic method has been applied to predict the molecular functions and biological pathways involved in *Arabidopsis* genes, or visualize the coexpressed genes based on this public data. In the previous research, more than 6000 microarray data have been selected from GEO to reveal the expression patterns of different tissues in *Arabidopsis*. Based on the analysis of integrated bioinformatics, the expression profiles of the same tissue are more similar to each other than these from other tissues in *Arabidopsis* (He et al. 2016). Another bioinformatic analysis of salt-responsive expression profilings have been done using the data from GEO. A rank aggregation method (RRA) was applied to screen 452 upregulated and 377 down-regulated DEGs under salt stress in *Arabidopsis*. Gene ontology enrichment analysis showed these DEGs were involved in signaling, transcription, and development (Zhang et al. 2017). Furthermore, integrated bioinformatics analysis was also used to reveal the DEGs under heavy metal through *Arabidopsis* GEO datasets. The results demonstrated that 168 DEGs were associated with the response under As, Cd, Pb and Cu. GO and KEGG pathway enrichments found these DEGs were related to responses to stress, responses to chemical, and responses to abiotic stimuli (Niu et al. 2019).

*Arabidopsis* is an ideal plant model for stress response research. The DEGs under salt, UV light, wounding, heat and cold stresses have been explored using microarray technique to disclose the interaction networks in *A. thaliana* root (Kilian et al. 2007). The drought-responsive DEGs in *A. thaliana* root have been studied, which were indicated to be related to DNA methylation, osmotic balance and apoptosis (Pandey et al. 2013). A novel DEG (IAR3) under high osmotic stress also have been documented by microarray analysis in *A. thaliana* root (Kinoshita et al. 2012). The DEGs responsive to heavy metal (Cd) were found to be associated with antioxidant capacity in *A. thaliana* root (López-Martin et al. 2008). In our previous work, we focused...
on the salt-responsive molecules using *A. thaliana* as the model plant. The results indicated the differential molecules were involved in cell wall metabolisms and reactive oxygen species (ROS) scavenging (Guo et al. 2014a). More importantly, the complicated cross-tolerances to different stresses such as osmosis, water deprivation, heat, UV-light and wounding has been shown in *A. thaliana* (Guo et al. 2019).

In the present work, to demonstrate the details of eight abiotic stresses (salt, cold, drought, osmotic, UV, wounding, heat, and heavy metal stresses) in *Arabidopsis* root, the DEGs were retrieved from the gene expression omnibus database (GEO). From more than 20,000 *Arabidopsis* genes, 213 DEGs were obtained using a rank aggregation method. Then, the molecular function was analyzed by the integrated bioinformatics tools, followed by experimental validation. These altered genes will facilitate better understanding on the stress-response mechanisms, and might be useful targets for promoting crop output and plant growth.

**Materials and methods**

*Retrieval of salt-responsive genes in Arabidopsis roots from GEO database*

The responsive gene expression profiling of the microarray data (GSM131257, GSM131258, GSM131469, GSM131470, GSM131281, GSM131282, GSM984523, GSM984525, GSM984528, GSM984529, GSM901072, GSM901073, GSM901074, GSM901078, GSM901079, GSM901080, GSM131409, GSM131410, GSM131437, GSM131438, GSM131469, GSM131470, GSM476827, GSM476828, GSM476829, GSM476839, GSM476840, GSM476841) related to eight stresses (salt, cold, drought, osmotic, UV, wounding, heat, and heavy metal (Cd) stresses) in *Arabidopsis* roots were downloaded from the GEO database (https://www.ncbi.nlm.nih.gov/geo/). Briefly the raw data were qualified by quantile normalization, and then the DEGs were screened by the limma package. Genes with *P*-value < 0.05 and |log2 fold change (FC)| > 1 were defined as DEGs. The resultant DEGs were further integrated by a robust rank aggregation (RRA) algorithm. The hypothesis of RRA method was that each gene is randomly ordered in experiment. If a gene has a high rank among all experiments, then its *P*-value is small (Niu et al. 2019; Zhang et al. 2017).

**Gene ontology classification and PPI network**

The online bioinformatic tools of PANTHER (Protein Analysis Through Evolutionary Relationships) classification system (Version 15.0 released 2019_04) (http://pantherdb.org/) and DAVID (Database for annotation, visualization and integrated discovery, Version 6.8) (https://david.ncifcrf.gov/) were applied for gene ontology enrichment analysis of the DEGs. Each gene was classified into one category. The analysis of PPI interaction networks was performed by the online STRING (search tool for recurring instances of neighboring genes) database (Version 11.0, released January 19, 2019) (http://string-db.org/).

**Table 1.** Summary of the datasets of stress-responsive experiments in *Arabidopsis* root from the GEO database.

| Stress                  | GEO datasets                                                                 | No. of Up-regulated DEGs | No. of Down-regulated DEGs | Figures |
|-------------------------|------------------------------------------------------------------------------|---------------------------|----------------------------|---------|
| Salt stress             | GSM131257, GSM131258, GSM131469, GSM131470                                   | 2,113                     | 2,456                      | Figure 1(A), Figure 2(A) |
| Cold stress             | GSM131257, GSM131258, GSM131281, GSM131282                                   | 2,216                     | 2,456                      | Figure 1(B), Figure 2(B) |
| Drought stress          | GSM984521, GSM984522, GSM984523, GSM984527, GSM984528, GSM984529             | 3,236                     | 3,239                      | Figure 1(C), Figure 2(C) |
| Osmotic stress          | GSM901072, GSM901073, GSM901074, GSM901078, GSM901079, GSM901080             | 717                        | 954                       | Figure 1(D), Figure 2(D) |
| UV stress               | GSM131257, GSM131258, GSM131407, GSM131410                                   | 761                        | 960                       | Figure 1(E), Figure 2(E) |
| Wounding stress         | GSM131257, GSM131258, GSM131437, GSM131438                                   | 586                        | 730                       | Figure 1(F), Figure 2(F) |
| Heat stress             | GSM131257, GSM131258, GSM131469, GSM131470                                   | 832                        | 578                       | Figure 1(G), Figure 2(G) |
| Heavy metal (Cd) stress | GSM476827, GSM476828, GSM476839, GSM476840, GSM476841                      | 278                        | 274                       | Figure 1(H), Figure 2(H) |

**Table 2.** Differential DEGs in *Arabidopsis* root under eight abiotic stresses.

| DEGs                  | Gene names                                                                 |
|-----------------------|-----------------------------------------------------------------------------|
| Up-regulated          | HSFA68 ; COR27 ; ATGSTU4 ; AT1G49230 ; ATG09850 ; AT3G5450 ; ADH1 ; AT2G43140 ; ATG29670 ; BXL1 ; ATG29580 ; AT2G37780 ; HSF1C ; ATG249010 ; ATG35490 ; ATG14800 | BXL2 ; ATG14800 ; AT2G27220 ; APP2-A6 ; ATG14540 ; ATG18840 ; ATG47780 ; ATG42780 |
| Down-regulated        | ATSG49880 ; FLA13 ; AT1G49230 ; ATG09850 ; AT3G5450 ; ADH1 ; AT2G43140 ; ATG29670 ; BXL1 ; ATG29580 ; AT2G37780 ; HSF1C ; ATG249010 ; ATG35490 ; ATG14800 | BXL2 ; ATG14800 ; AT2G27220 ; APP2-A6 ; ATG14540 ; ATG18840 ; ATG47780 ; ATG42780 |
Growth conditions and harvest of Arabidopsis root

According to previous publications (Guo et al. 2014a; Kilian et al. 2007), the ecotype Col-0 Arabidopsis seeds were germinated on the normal medium plate with 22/20°C day/night, 8/16 h light/dark cycle, 60 μmol·m−2·s−1 light intensity. After 7 days, the A. thaliana seedlings separately underwent the following stresses: the cold-stress condition (8°C), the osmotic stress condition (200 mmol·L−1 mannitol), the salt stress condition (150 mmol·L−1 NaCl), the wounding stress condition by punctuation of the leaves with needles, the drought stress condition by removing the lid of dish and exposing to a stream of air for 15 min, the UV stress condition by removing the lid of dish and irradiated with UV light for 15 min, the heat stress condition by removing the lid of dish and incubating at 40°C for 15 min, and the heavy metal stress condition (Cd).
Figure 2. Differential expression genes of Arabidopsis roots responding to abiotic stress. A. salt stress (GSM131257, GSM131258, GSM131469, GSM131470); B. cold stress (GSM131257, GSM131258, GSM131281, GSM131282); C. drought stress (GSM984521, GSM984522, GSM984523, GSM984527, GSM984528, GSM984529); D. osmotic stress (GSM901072, GSM901073, GSM901074, GSM901078, GSM901079, GSM901080); E. UV stress (GSM131257, GSM131258, GSM131407, GSM131410); F. wounding stress (GSM131257, GSM131258, GSM131437, GSM131438); G. heat stress (GSM131257, GSM131258, GSM131437, GSM131438); H. heavy metal Cd stress (GSM76827, GSM76828, GSM76839, GSM76840, GSM76841). The red points represent up-regulated genes (fold change > 2.0, P-value < 0.05). The green points represent down-regulated genes (fold change < 0.5, P-value < 0.05). The black points represent unchanged genes difference.
condition by exposing to a temperature of 35°C for 3 h, and the heavy metal condition (100 μmol·L⁻¹ CdCl₂), followed by another 3 days growth. Then the Arabidopsis roots were harvested and stored at –80°C.

**qRT-PCR analysis**

According to the previous method of RNA isolation and qRT-PCR analysis (Li et al. 2015; Li et al. 2019), the relative expression levels of Arabidopsis gene ascorbate peroxidase 2 (AT3G09640) was determined and Arabidopsis gene actin 2 (AT3G18780) was used as endogenous reference in Arabidopsis root. All experiments were performed in triplicate.

**Enzyme activity assay**

Peroxidase (POD) activity in Arabidopsis root was assayed using a commercial kit (Nanjing Jiancheng Bioengineering Institute) according to the previous publication (Guo et al. 2019). Briefly, the POD activity was determined by the catalyzing H₂O₂ of absorbance change at 420 nm. The plots were done by Graphpad Prism for windows (Version 8.0). All experiments were performed in triplicate.

**Results**

**Identification of stress-responsive DEGs in Arabidopsis root**

Dataset from eight stress-responsive experiments in Arabidopsis root were retrieved from the GEO database (Table 1). After the microarray data were qualified by quantile normalization (Figure 1), DEGs in Arabidopsis roots under eight abiotic stress were shown in Figure 2. Then, the RRA method was used to integrate the above DEGs. As a result, 139 up-regulated and 74 down-regulated genes were screened as the stress-responsive DEGs of Arabidopsis root (Table 2).

**Bioinformatics enrichment of stress-responsive DEGs**

Bioinformatics tools were used to analyze the 213 DEGs. For biological process, the main processes that the up-regulated DEGs are involved in are metabolic process, regulation of biological process, and response to oxidative stress. For subcellular location, the major locations of these DEGs are the chloroplast and the cell wall. For molecular function, the main functions are antioxidant activity and binding activity.

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**Figure 3.** GO classification of differential stress-responding genes in Arabidopsis root. (A) biological process classification of DEGs, (B) subcellular location classification of DEGs, (C) molecular functional classification of DEGs.
Figure 4. PPI networks of the DEGs under abiotic stresses in Arabidopsis root. (A) up-regulated DEGs, (B) down-regulated DEGs.
regulated DEGs related to were regulation of biological process (34.5%), metabolic process (22.3%), regulation of transcription (16.5%), and response to oxidative stress (14.3%) (Figure 3(A)). For molecular function, the major molecular functions involved were binding activity (43.2%), catalytic activity (22.3%), and antioxidant activity (13.7%) (Figure 3(C)). Whereas, the percentage of antioxidant activity involvement for down-regulated DEGs was 2.7% (Figure 3(C)).

**PPI network of salt-responsive DEGs**

Totally, 139 up-regulated stress-responsive DEGs were connected with 226 edges (PPI enrichment p-value: < 1.0e−16), and 74 down-regulated stress-responsive DEGs were connected with 27 edges (PPI enrichment p-value: < 5.22e−15) by STRING (Figure 4(B)).

**qRT-PCR analysis**

Our results showed *Arabidopsis* gene ascorbate peroxidase 2 (AT3G09640) was up-regulated among salt stress, cold stress, drought stress, osmotic stress, UV stress, wounding stress, heat stress, and heavy metal stress. Therefore, the relative expression of *Arabidopsis* gene ascorbate peroxidase 2 (AT3G09640) in *Arabidopsis* roots were assayed under the above stresses to validate the confidence of the bioinformatics outcome. The results indicated that the relative expression level of *Arabidopsis* gene ascorbate peroxidase 2 (AT3G09640) in *Arabidopsis* roots were significantly increased under different stresses (Figure 5).

**Enzyme activity determination stress conditions**

Our results showed peroxidase was up-regulated among salt stress, cold stress, drought stress, osmotic stress, UV stress, wounding stress, heat stress, and heavy metal stress. Therefore, POD activities of *Arabidopsis* roots were assayed under the above stresses to validate the confidence of the bioinformatics outcome. The results indicated that POD activities were all increased under different stresses (Figure 6).

**Discussion**

Abiotic stress negatively affects crop output and plant growth. To disclose the salt-tolerance mechanism in plant, many researches has used *A. thaliana* as a model plant (Zhang et al. 2018). In the past decades, some molecular targets and stress-responsive mechanisms have been demonstrated (Carrera et al. 2018), and cross-talking genes responsive to different stress have been reported. Our previous work indicated that there were complicated pathways, protein interactions and cross-talks under different stresses in *A. thaliana* (Guo et al. 2019). Many genes or proteins participated in response to more than one stress, which is called cross-tolerance to multiple stresses. Cross-tolerance is an important strategy for plants to survive under different stresses (Tuteja 2007). But it is still not well understood how plants respond to different stresses. Therefore, more details are needed to provide more information during the plant responses under multiple stresses.

In the present work, we retrieved DEGs under eight different stresses (salt stress, cold stress, drought stress, osmotic stress, UV stress, wounding stress, heat stress, and heavy metal stress), and integrated the DEGs using RRA method. The resultant 213 DEGs, including 139 up-regulated and 74 down-regulated genes out of more than 20,000 genes, were further analyzed by the integrated bioinformatics approaches. Among the up-regulated DEGs, the blue light-regulated *COR27* gene was associated with cold stress (Wang et al. 2017). Under heat stress, HSP70 was involved in thermotolerance by interacting with HsfA1 and inhibiting its nuclear localization (Hahn et al. 2011). HsfA9 also modulates the heat stress-related genes as a specific transcription repressor (Baniwal et al. 2007). Under cold stress, MYB15, a member of MYB family, were found to bind to the CBF genes promoters as another transcriptional repressor (Agarwal et al. 2006), and late elongated hypocotyl (LHY) also participated in the regulation of CBF expression as a transcriptional factor (Dong et al. 2011).

Based on the integrated bioinformatics analysis, response to oxidative stress was the main biological process. In the present work, POD, glutathione S-transferase U5 (GSTU5), L-ascorbate peroxidase 2 (APX2) were all up-regulated under eight stresses. Usually, the electron transport chain will be attenuated under salt stress and excessive ROS, such as hydrogen peroxide, hydroxyl radicals, and superoxide radicals produced (Miller et al. 2010). As the result, ROS scavenging enzymes such as the glutathione S-transferase family (Chan and Lam 2014) and POD (Islam et al. 2015) are activated to balance the redox homeostasis in plant cell. To validate the DEG cross-talk among different stresses, the enzyme activity of POD in *Arabidopsis* root was analyzed under all eight stress conditions. The results showed the stress cross-talk prediction agreed with the outcome of integrated bioinformatics analysis.

![Figure 5. qRT-PCR analysis of Arabidopsis gene ascorbate peroxidase 2 (AT3G09640) responses to different stresses (actin 2 (AT3G18780) was used as endogenous reference).](image-url)
Figure 6. Antioxidative enzyme POD activity in *Arabidopsis thaliana* root under different stresses. A. salt stress; B. cold stress; C. drought stress; D. osmotic stress; E. UV stress; F. wounding stress; G. heat stress; H. heavy metal Cd stress.
Conclusion

This work provided new light on the understanding of stress-tolerance DEGs under multiple stresses in Arabidopsis root, which improved our information on stress-response mechanisms in plant, and might become useful targets for promoting crop output and plant growth in the future.

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MG conceived the study, and designed the experiments. MG, XL, YJ, XY, and TM performed the experiments. MG, XL, JW, LL, YJ, XY and TM analyzed the raw data, and drafted the manuscript. All the authors participated in the revision of the manuscript.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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