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Arabidopsis SIMILAR TO RCD-ONE genes are ubiquitous and respond to multiple abiotic stresses through diverse signaling pathways

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The SIMILAR TO RCD-ONE (SROs) have been characterized as a group of plant-specific proteins which play important functions in stress responses and development. Here, we analyze the expression profiles of six *SRO* genes under different stress treatments in *Arabidopsis*. Our results revealed that RCD1 play an essential role in plant responses to various environmental stresses. SRO1 has partially overlapping functions with RCD1 in plant response to $HgCl_2$ and H_2O_2 stress. Analysis of the transcriptional expression of SROs indicated that both of the *RCD1* and *SRO1* transcripts were up-regulated by $HgCl_2$ and light, not by other stresses, and that of *SRO5* was induced by salt. Expression of *SRO3* and *SRO4* were not influenced by stresses. The different effects of these stresses on the expression of the *SRO* genes indicate that the SRO family is regulated by multiple signaling pathways. Sequence analyses of the SRO proteins implicate a highly preserved protein structure and are specific to plants, which might have implications for functional conservation. The ubiquitous expression and nuclear localization of SRO family suggested that their function might be related to transcription factor regulation and complex formation. Taken together, SRO family is critical for proper plant development and multiple stress responses.

Keywords. Arabidopsis; gene expression; SRO family; stress response

1. Introduction

Abiotic stress and biotic stress are major factors limiting plant growth and productivity. Accordingly, plants have evolved a complex mechanism to cope with the harmful conditions. Plant responses to changes in environmental conditions are mediated by a network of signaling events leading to downstream responses, including changes in gene expression and transcriptional regulation. Understanding the biochemical mechanism of plant response to exogenous stimulus not only helps to reveal its basic biological properties, but also is of critical importance for agriculture because these stresses limit crop production.

As a specific gene family in plants, SRO (SIMILAR TO RCD ONE) has been reported to be involved in development and abiotic stress responses (Belles-Boix *et al.* 2000; Katiyar-Agarwal *et al.* 2006; Jaspers *et al.* 2009), and the most of the SRO proteins contain two conserved domains: poly (ADP-ribose) polymerase catalytic (PARP) and C-terminal RCD1-SRO-TAF4 (RST) domains (Jaspers *et al.* 2010). The members of SRO family in *Arabidopsis* include RCD1, AtSRO1, AtSRO2, AtSRO3, AtSRO4 and AtSRO5 (Teotia and Lamb 2011). Several reports showed that SROs participate in plant normal growth and development, and play important roles in plant response to stresses (Ahlfors *et al.* 2004; Borsani *et al.* 2005; Teotia and Lamb 2009). RCD1 (radical-induced cell death 1) was the first identified SRO protein in *Arabidopsis*, which belongs to the WWE protein-protein interaction-domain protein family and interacts with several transcription factors and protect plants against the oxidative damage and the other stresses (Vainonen *et al.* 2012; Brosche *et al.* 2014). Together with its closest homolog, SIMILAR TO RCD-ONE1 (SRO1) has part of the function of RCD1. Recent studies reported that SRO1 play important roles in abiotic stress responses. The *sro1* mutants showed resistance to apoplastic ROS and salt stress, but hypersensitive to heavy metal mercury stress, which also demonstrate unequal genetic redundancy between RCD1 and SRO1 in plant (Jaspers *et al.* 2009; Teotia and Lamb 2009; You *et al.* 2014). These suggest that the two homologous genes have both redundant and independent functions under different stress conditions. Another member of the

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Arabidopsis SRO family, SRO5, is required for the response to oxidative and salt stress by pairing with its neighbouring gene P5CDH (Borsani *et al.* 2005). Meanwhile, it was found that a SRO5 ortholog from tomato can functionally complement the *Arabidopsis sro5* mutant under salt stress (Babajani et al. 2009). SRO2, SRO3 and SRO5 showed changes in transcript levels in response to light stress, salt treatment and exposure to O_3 in *Arabidopsis* (Jaspers *et al.* 2010).

The previous study suggests that the wheat SRO genes could improve plant seedling growth and abiotic stress tolerance by modulating redox homeostasis (Liu *et al.* 2014). In rice, the members of SRO family, OsSRO1c and OsSRO1a, were also reported to play an important role in multiple abiotic stress tolerance of rice by promoting H_2O_2 accumulation through interaction with various stress-related proteins (You *et al.* 2013; You *et al.* 2014; Sharma *et al.* 2016). These studies revealed a function for the SRO protein family in environmental stress responses. However, the relationships, functions and gene expression patterns of *Arabidopsis* SRO genes have been still further characterized.

In the present study, we describe the SRO gene family in *Arabidopsis* and analyzed their gene structure and multiple protein sequence alignment. The expression analysis showed different profiles between members of the SRO family in responses to a variety of abiotic stresses and in tissue and subcellular distribution. To rationally improve the plant's response to environmental challenges, the study will give to provide a preliminary understanding of the natural mechanisms required to cope with adverse condition.

2. Material and methods

2.1 *Plant materials and phenotypic analysis*

The *Arabidopsis* ecotype Columbia (Col-0) was used in this study. The T-DNA insertion lines for RDC1 (AT1G32230) SALK_116432 and SRO1 (At2g35510) Salk_126383 were ordered from the *Arabidopsis* Biological Resource Center (ABRC) (*http://www.arabidopsis.org/abrc/*). The homozygous mutant plants were screened by PCR amplification according to the method provided by the Salk Institute Genomic Analysis Laboratory (*http://signal.salk.edu*).

Surface-sterilized seeds were planted on MS medium and kept for 3 days at 4°C in the dark to break dormancy. The plates were then transferred to a culture room at 22°C with a 16 h light/8 h dark photoperiod. For seedling growth, 7-day-old seedlings were transferred from the germination medium to 1.2% agar that was supplemented with stress treatments and placed vertically. The phenotypes of WT, *rcd1* and *sro1* were then analyzed, such as the elongation of root, number and length of lateral roots and the number of true leaves.

2.2 *Real-time PCR analysis*

Total RNA was extracted from *Arabidopsis* 14-day-old Col-0 seedlings grown on MS medium using TRIzol reagent (Invitrogen). The RNA was treated with RNase-free DNase I (TaKaRa) to remove genomic DNA 5 μg of total RNA and M-MLV reverse transcriptase (Promega) was used for reverse transcription according to the manufacturer's instructions. The resulting cDNA was diluted 10-fold and used as a template for the qRT-PCR amplification, which was performed with the primers listed in supplementary table 1. The qRT-PCR was carried out on the Stratagene Mx3005 qPCR system using SYBR Green to monitor double-stranded DNA products for 40 cycles, which was programmed for 40 cycles consisting of 95°C for 15 s; 55°C for 15 s; and 72°C for 30 s. The relative expression level was calculated by $2^{-\Delta\Delta Ct}$ and all the experiments were repeated three times. UBQ10 (AT4G05320) was the internal control. The relative expression levels were then normalized to that of the untreated control plant.

2.3 *Histochemical detection of b-glucuronidase (GUS) activity*

The promoter fragments of RCD1 and SRO1 were then cloned into pCABIA1381 and then transformed by floral infiltration into WT Arabidopsis through *Agrobacterium tumefaciens* strain GV3101. Using the method of Jefferson *et al.* (1987), the transgenic plants containing the *RCD1* and *SRO1* promoter-GUS constructs were tested for GUS activity by incubating the excised tissues in GUS staining buffer (1 mg/mL X-Gluc, 1 mmol/L EDTA, 0.1% Triton X-100, 2 mmol/L Ferri cyanide, 2 mmol/L Ferro cyanide, and 50 mmol/L Na-Phosphate buffer, pH 7.0) at 37°C for 5 h. Staining was terminated by replacing the staining solution with 70% ethanol solution. The stained samples were stored at 4°C until microscopic observations.

2.4 *Confocal imaging for subcellular localization*

For GFP analysis, five lines of transgenic plants were screened for the subcellular localization of RCD1 and SRO1, with the EGFP transgenic plants as a control. The fluorescence of the GFP::RCD1 and GFP::SRO1 fusion protein in guard cell of the transgenic plants stained with DAPI (4′,6-diamidino-2-phenylindole) was excited at 488 nm and fluorescence was detected at 500-530 nm for GFP with an FV1000 confocal laser scanning microscope (Olympus).

2.5 *Sequence alignments and phylogenetic analysis*

Protein sequences for six SROs in *Arabidopsis* were obtained from the Arabidopsis Biological Resource Center (ABRC)

(*http://www.arabidopsis.org/abrc/*) and were aligned with the DNAMAN program (version 4.0; Lynnon Corporation, Quebec, Canada) to identify conserved points. Phylogenetic analyses of six AtSROs were performed using the neighbor-joining method of CLUSTALW with the neighbor-joining method based on the conserved PARP domains of SRO proteins.

3. Results

3.1 *The SIMILAR TO RCD-ONE gene family in Arabidopsis*

The *Arabidopsis* genome encodes six SRO isoforms, which consists of RCD1 and SRO1 to SRO5. Accession numbers and location in each chromosome are shown in supplementary table 2. The six *Arabidopsis SRO* genes are unevenly distributed on four chromosomes. Three genes (*RCD1*, *SRO2-SRO3*) are dispersed through chromosome 1, *SRO1* is the only gene in chromosome 2, *SRO4* is located in chromosome 3 and *SRO5* is present in chromosome 5. Based on full length protein sequences, a detailed amino acid sequence comparison and phylogenetic tree analysis of all proteins are shown in figure 1. The multiple sequence alignment indicates that several characteristic domains are well conserved along the amino acid sequence, such as PARP and RST domain, which are highly conserved in SRO protein family and is specific to plants. In addition to that, two *Arabidopsis* SRO family members RCD1 and SRO1 contain an N-terminal WWE domain, which was involved in protein-protein interactions and predicted to have a globular structure. However, several studies were found that RST domain was critical for SRO proteins interacting with the plant specific transcription factors, not WWE domain (Katiyar-Agarwal *et al.* 2006; Jaspers *et al.* 2009).

Phylogenetic analysis revealed three pairs of proteins showing stronger similarity to each other than to the rest of the SRO family. RCD1 and SRO1 are 65.2% identical to each other, SRO2 and SRO3 are 64.6%, and SRO4 and SRO5 showed a 55.4% identity. Figure 2 shows the genomic structure of the *SRO* gene. Although the number of the exons is similar, the exon-intron structure is very different. In contrast, the number and structure of the gene *RCD1* and *SRO1* were similar, excepting for that *RCD1* has an exon more than *SRO1*. In the rest of the *SRO* gene, *SRO2/3/4/5*, not only their exon–intron number is very similar, but the structure is also conserved. These results suggested a high degree of conservation among the SRO family proteins in the exon-intron organization.

3.2 *Spatio-temporal expression profiles of SRO family genes in Arabidopsis*

To identify spatio-temporal expression patterns of SRO family, we carried out quantitative real-time RT-PCR to detect 24 h rhythms of *SROs* gene expression levels in *Arabidopsis*, with each subject contributing a single data point to a time series spanning 4 h. As shown in figure 3, SRO family has a dramatic difference in the temporal gene expression patterns. The transcript levels of the *RCD1*, *SRO1* and *SRO5* were lower when compared to other *SROs* at 14:00, and gradually up-regulated and reached the peak at 22:00. In contrast, temporal patterns of the *SRO2-SRO4* expression were similar, which have been indicated to rapid increase at 8:00 and highest transcription activity always appears at 10:00, and then start to oscillate with a little amplitude. These results suggested that SROs have functional redundancy and play different roles in physiological processes.

3.3 *SROs are involved in multiple abiotic stresses responses*

Considering that several SROs were reported to be involved in responses to various environmental stresses (Belles-Boix *et al.* 2000; Ahlfors *et al.* 2004; Katiyar-Agarwal *et al.* 2006; Jaspers *et al.* 2009; Zhao *et al.* 2018), we investigated the expression profiles of *SRO* gene in *Arabidopsis* exposed to multiple stress treatments at the transcriptional level using quantitative real-time RT-PCR. Under stress conditions, the mRNA abundance of SROs was indicated in figure 4. The transcript levels of *RCD1* are slightly enhanced by ABA, H_2O_2, NaCl and mannitol treatment. However, the highest transcription activity of *RCD1* was induced after treatments with $HgCl_2$ and high light. Together with its closest homolog, *SRO1* have a similar transcriptional pattern under stress condition. The rest of the members, such as *SRO3* and *SRO4*, transcript levels were only significantly increased by mannitol treatment. The above results reveal that the SRO family exhibit different stress regulated expression patterns in *Arabidopsis*.

To further examine whether SROs are involved in multiple abiotic stress responses, we tested the growth of 7-day-old seedlings of *rcd1* and *sro1* under several stress conditions. Seeds were germinated on MS agar medium for 7 days, and the seedlings were transferred to MS medium containing 200 μmol/L $HgCl_2$, 5 mmol/L H_2O_2, 10 μmol/L ABA, 150 mmol/L NaCl or 200 mmol/L mannitol, and photographs were taken after 15 days (figure 5). As expected, the *rcd1*mutant seedlings showed hypersensitivity to multiple stresses, including $HgCl_2$, H_2O_2, ABA and high light, most of seedlings died. The *sro1* mutant plants, although not as sensitive as the *rcd1* mutant plants, also displayed slightly sensitive than WT seedlings under $HgCl_2$ and H_2O_2 treatment, but not under ABA and high light treatment. The above results showed that *rcd1* and *sro1* mutants exhibited similar responses to $HgCl_2$ and H_2O_2 stress, which may suggest that RCD1 and SRO1 have partially overlapping functions in plant response to $HgCl_2$ and H_2O_2 stress.

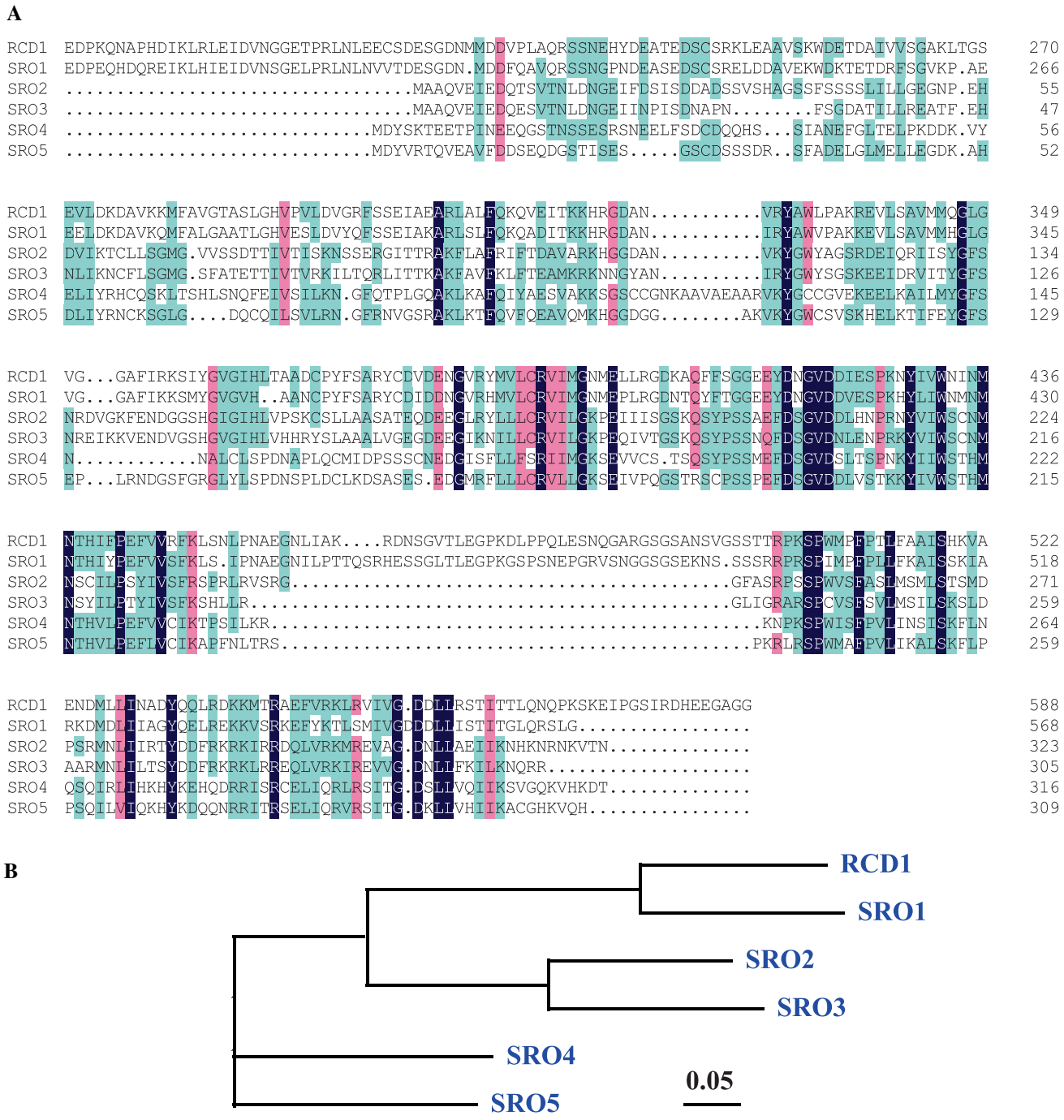

Figure 1. Amino acid sequence analysis of the AtSRO family. (**A**) Alignment of the amino acid sequence of the AtSRO family. Homologous sequences were obtained through the *Arabidopsis* Information Resource, and the multiple sequence alignment was performed using DNAMAN software. (**B**) Phylogenetic tree of the AtSRO family. The amino sequences of the six AtSRO proteins were organized in to a phylogenetic tree with the DNAMAN. The length of the branch line indicates the extent of divergence according to the scale at the bottom.

3.4 *Expression patterns of SRO family genes in different tissues and subcellular distribution*

To examine the tissue-specific expression pattern of SRO family genes, we transformed *Arabidopsis* with an *RCD1* and *SRO1* promoter-GUS construct respectively. Histochemical staining of transgenic *Arabidopsis* seedlings showed that RCD1 and SRO1 are ubiquitously expressed and was particularly highest in rapidly developing tissues, such as young leaves and vascular tissues (figure 6A), which suggested that they play important roles in resistance to stress in the respiratory electron transport process. Our

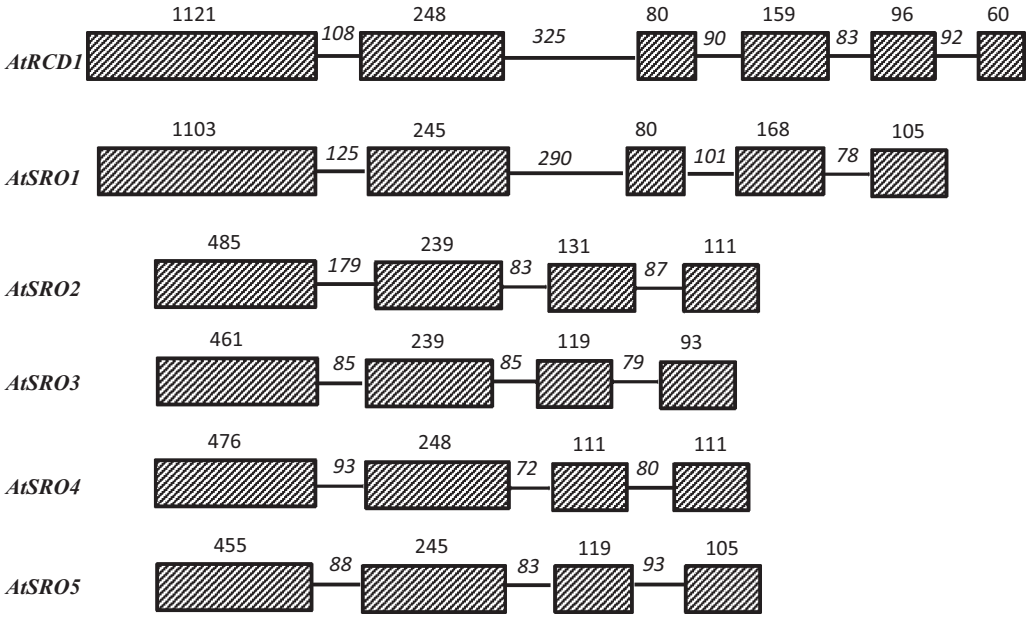

Figure 2. Genomic organization of the AtSRO family. The structure of the AtSRO genes is shown with exons indicated by slashed boxes and introns shown as black lines. The numbers represent the length of the corresponding exon or intron.

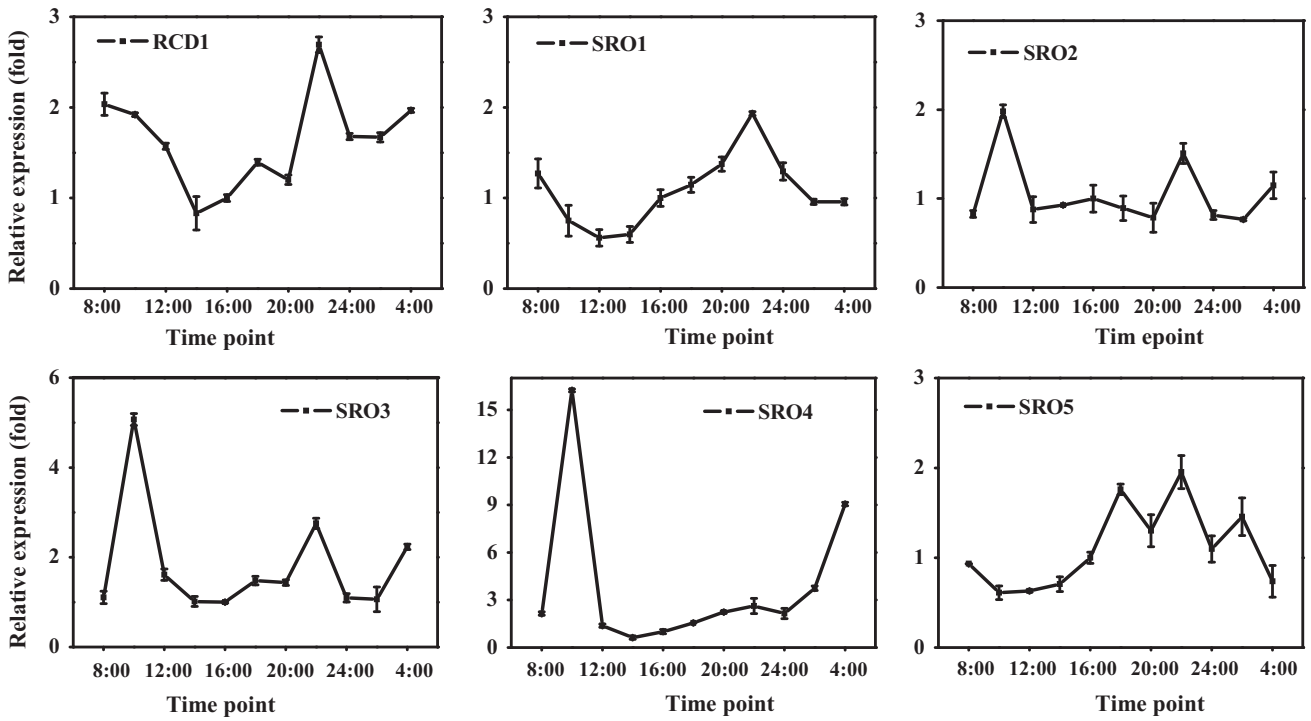

Figure 3. Temporal expression patterns of AtSRO genes in *Arabidopsis*. Transcript levels of AtSRO at different time point.The mean value of three replicates was normalized using UBQ10 as the internal control. See the section 'Material and methods' for details.

results indicate a similar expression pattern for the RCD1 and SRO1, in agreement with several previous studies (Jaspers *et al.* 2009, 2010; Teotia and Lamb 2011). The data from the *Arabidopsis* Information Resource (TAIR) showed that SRO5 was also ubiquitously expressed. And there are no reports on other SROs, such as SRO2, SRO3 and SRO4. The expression patters of the SRO family genes imply that they may function during the entire growth stage and stress response.

Previous research has suggested that the RCD1, SRO1 and SRO5 amino acid sequence of the SRO family have nuclear localization signal (NLS), and all their proteins are

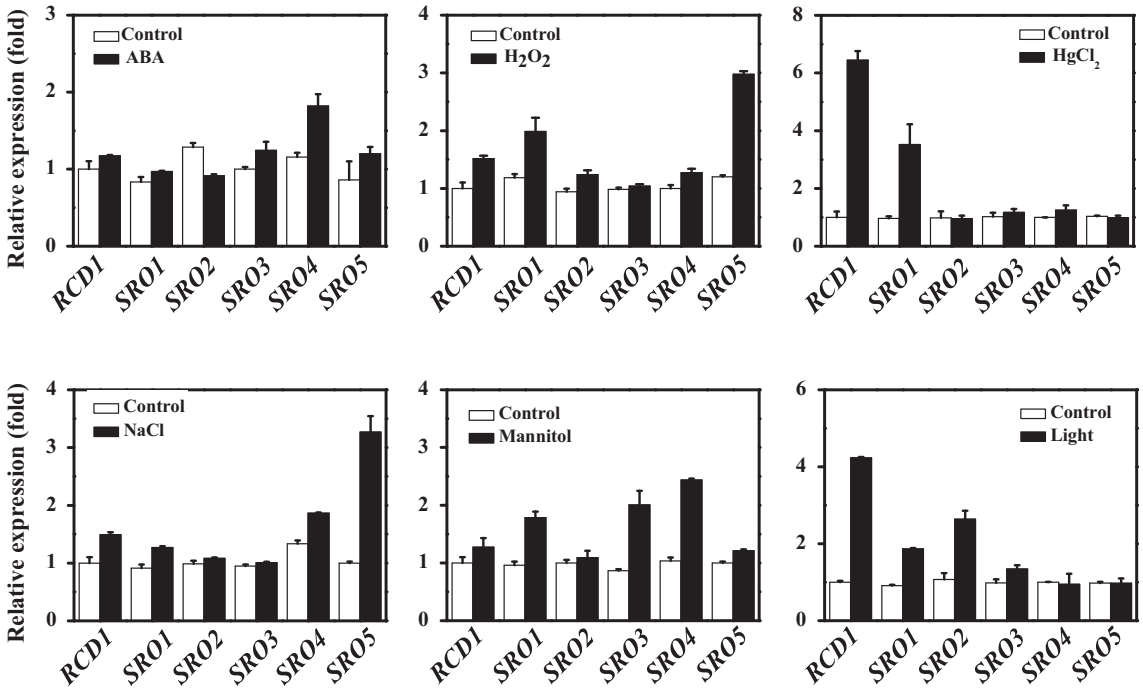

Figure 4. *SRO* family gene expression responses to stresses in *Arabidopsis.* Steady state transcript levels of *Arabidopsis* SRO family genes were investigated by qPCR. Total RNA was extracted from control and stress-treated 2-week-old WT seedlings. Expression of *RCD1* and *SRO1-SRO5* was assayed by qRT-PCR with gene specific primers. UBQ10 was used as the internal control. Relative expression levels were calculated by $2^{-\Delta\Delta Ct}$ and normalized to the WT without $HgCl_2$ treatment. Three independent qRT-PCR assays were performed and Error bars indicate SD.

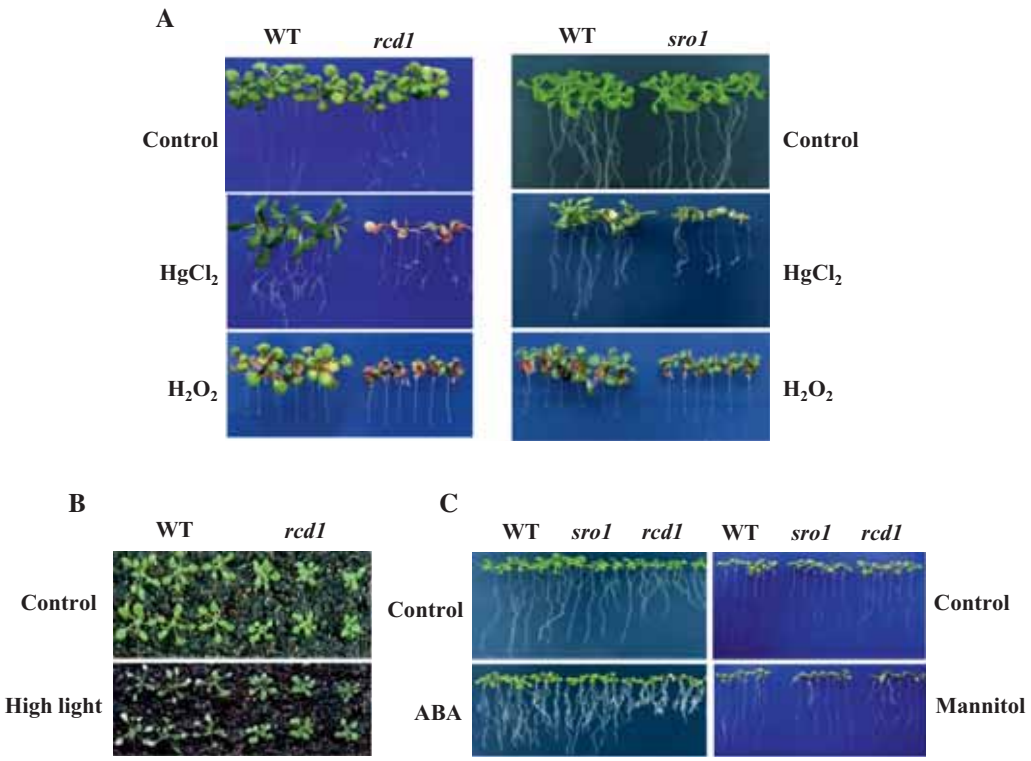

Figure 5. The abiotic stresses responses of the SROs. (**A**) Phenotype of the *rcd1* and *sro1* seedlings grown for 15 days under 200 μmol/L $HgCl_2$ and 5 mmol/L H_2O_2 treatment. (**B**) Phenotype of 2-week-old *rcd1* seedlings treated by high-light (800 ± 50 μm s^{-1} m^{-2} at 21°C) for 3 days. (**C**) Phenotype of the *rcd1* and *sro1* seedlings for 15 days under 10 μmol/L ABA and 200 mmol/L mannitol treatment.

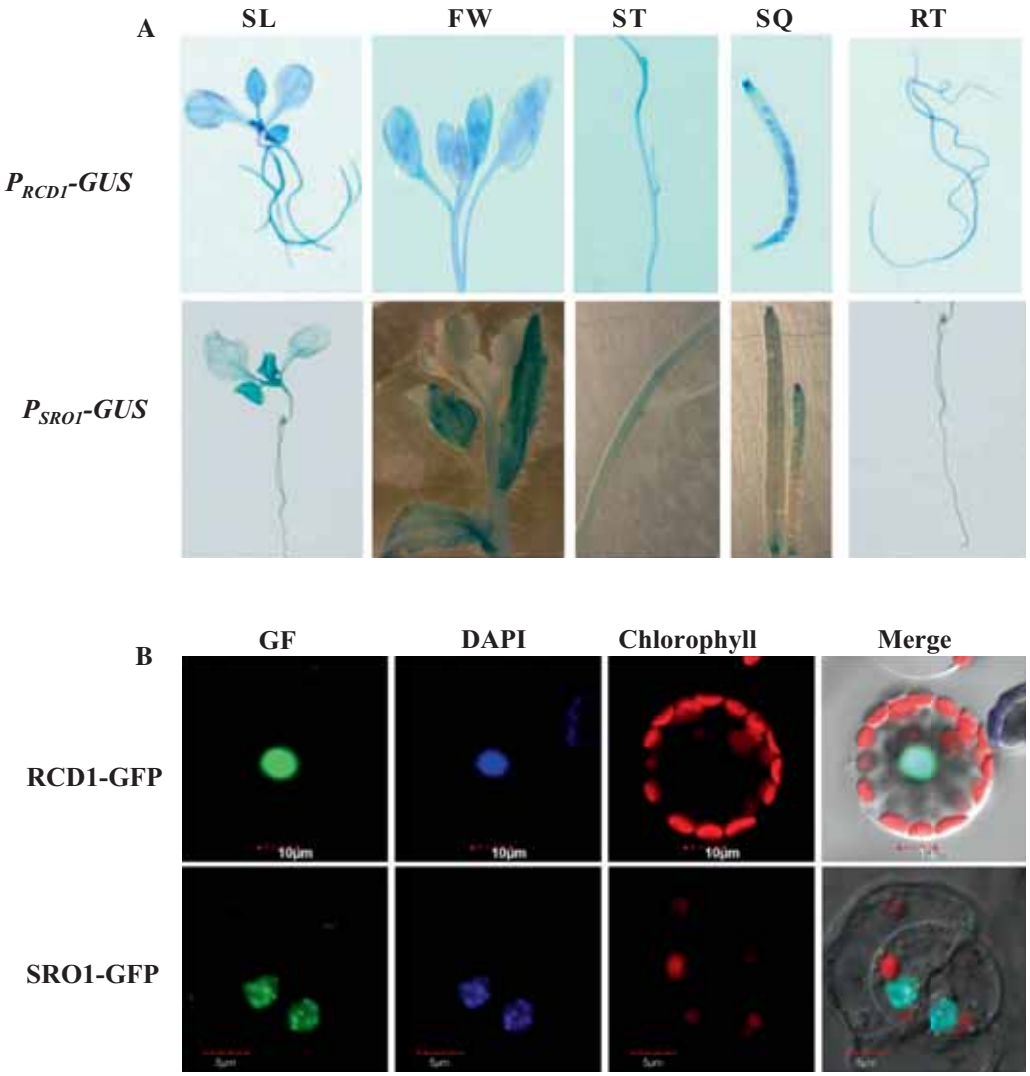

Figure 6. Tissue expression and subcellular localization of SROs in *Arabidopis*. (**A**) Histochemical localization of GUS activity directed by SROs family member RCD1 (top) and SRO1 (bottom) promoter::GUS fusions in transgenic *Arabidopsis* plants. SL: 2-week-old seedlings; FW: flower; ST: stem; SQ: silique; RT: root. (**B**) Subcellular localization of the RCD1-GFP (top) and SRO1-GFP (bottom) fusion protein. Bars = 10 μm, 5 μm respectively.

localized in the nucleus (Borsani *et al.* 2005; Katiyar-Agarwal *et al.* 2006; Zhao *et al.* 2018). We also investigated the cellular localization of RCD1 and SRO1 by examining transgenic plants harbored a transgene that encoded a translational fusion between green fluorescent protein (GFP) and RCD1 or SRO1. The green fluorescence signal showed that both of the RCD1 and SRO1 are present predominantly in the nucleus under control conditions. To further examine this finding, DAPI (4′,6-diamidino-2-phenylindole) staining was used in a co-localization imaging analysis. Both of the green fluorescence of the RCD1::GFP and SRO1::GFP fusion protein co-localized tightly with the blue fluorescence produced by the binding of DAPI to double-stranded DNA in the cells. These results implied that SRO family may play an important role as a class of transcriptional regulator in the nucleus of *Arabidopsis* cells.

4. Discussion

The SROs are a plant-specific protein family with a unique domain architecture which is conserved in all land plants. However, only a few of them including RCD1, SRO1, and SRO5 from *Arabidopsis* have been characterized. Here, we performed a comprehensive functional analysis of the SRO family in *Arabidopsis,* including genomic organization, subcellular localization, tissue expression pattern and gene expression profile in response to multiple stresses. Based on their genomic and protein sequences, three pairs of proteins show stronger similarity to each other than to the rest of the family, respectively RCD1 and SRO1, SRO2 and SRO3, SRO4 and SRO5. RCD1 and SRO1 have an identical protein domain structure and were divided into group I, while the others form group II (Jaspers *et al.* 2009; Jaspers *et al.* 2010;

Teotia and Lamb 2011).These data suggest that SROs presumably originated from more recent sequence duplication events. Nuclear localization of SRO family implied that SROs may play an important role in regulation of stress-responsive gene transcription as a regulator of transcription factors. Histochemical analysis indicated that SROs are present throughout the plant, especially high in young leaves and vascular tissues, which are consistent with ROS generation under normal growing conditions. Together, these data with previous studies suggested that SROs contribute to plant response to oxidative stress caused by normal metabolism and stress.

Several SROs have been previously characterized in *Arabidopsis* (Belles-Boix *et al.* 2000; Ahlfors *et al.* 2004; Borsani *et al.* 2005; Katiyar-Agarwal *et al.* 2006; Jaspers *et al.* 2009; Jaspers *et al.* 2010; Teotia and Lamb 2011; Zhao *et al.* 2018). RCD1 is an important regulator of stress and hormonal and to as well as developmental responses. RCD1 and its closest homolog SRO1 have partly redundant roles in stress and developmental responses. And SRO5 is required for the proper response to oxidative and salt stress. In our study, gene expression analysis indicates that members of the SRO family respond differentially to multiple abiotic stresses. And the response of the members of the SRO family to these stresses varies to some extent. For example, RCD1 was found to be induced by most of the stresses, while other SROs responded to less stresses. Such differential stress-related responsiveness may also imply the specific involvement of the members of the SRO family in different abiotic stress responses.

Previous studies showed that the expression of AtRCD1 and AtSRO1 were only slightly stress responsive and developmentally regulated, whereas AtSRO5 has been indicated as a common stress response factor (Belles-Boix *et al.* 2000; Borsani *et al.* 2005; Katiyar-Agarwal *et al.* 2006; Jaspers *et al.* 2009; Jaspers *et al.* 2010; Teotia and Lamb 2011). In this paper, AtRCD1 and AtSRO1 showed the strongest response to $HgCl_2$ stress and was the only gene significantly up-regulated by $HgCl_2$, whereas transcript levels for other genes remained unaltered. These may reflect the key role of RCD1 and SRO1 in heavy metal stress. All *SROs* gene expressions responded to the mannitol treatment, although different degrees were observed. High light treatments specifically up-regulate *RCD1*, *SRO1* and *SRO2* transcription, respectively. It is possible that RCD1, SRO1 and SRO2 participate in the response of *Arabidopsis* to the high light stress together. When *Arabidopsis* seedlings of *rcd1* and *sro1* were treated with $HgCl_2$, H_2O_2, ABA and mannitol stress, the obvious phenotypic difference was observed (Figure 5). The fact that not all stress conditions affect the expression of the *AtSRO* family in the same way suggests that specific signals, and not just general stress, are needed for the responses observed.

In conclusion, our study shows that SROs genes are responsive to multiple stresses, although the individual gene may function in different way. The diverse effects of these stresses on the expression of the family also suggest that different members of the SRO gene family may be coordinately, but differentially regulated under specific environmental stress conditions, and supported the important roles of SROs in these stress responses in *Arabidopsis*.

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