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Abiotic Stress Responses in Plants: A Focus on the SRO Family

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1. Introduction

Plants are sessile organisms and as such must have mechanisms to deal with both abiotic and biotic stresses to ensure survival. The term “abiotic stress” includes many stresses caused by environmental conditions such as drought, salinity, UV and extreme temperatures. Due to global climate change it is predicted that abiotic stresses will increase in the near future and have substantial impacts on crop yields (Intergovernmental Panel of Climate Change; <http://www.ipcc.ch>). Therefore, understanding abiotic stress responses and the connection between such responses and agronomically important traits is one of the most important topics in plant science. Often plants will experience more than one abiotic stress at a time, making it difficult to determine the effect of a single stress under field conditions. Therefore, much of the progress in understanding plant defence signaling and response has come from laboratory studies, especially those using the model plant species *Arabidopsis thaliana*, which belongs to the family Brassicaceae.

1.1 Responses to different abiotic stresses share common components

An understanding of abiotic stress responses depends on an understanding of the molecular processes underlying those responses. Plant defences against different abiotic stresses have both common and unique elements. Common elements include increases in reactive oxygen species (ROS) and cytosolic Ca^{2+} as well as activation of kinase cascades. In addition, stresses can lead to increased concentrations of hormones such as salicylic acid (SA), jasmonic acid (JA), abscisic acid (ABA) and ethylene, all of which have been implicated in response to environmental conditions (reviewed in (Hirayama & Shinozaki, 2010)).

The increase in ROS is an especially important common connection between different stresses. ROS are continuously produced in the plant through cellular metabolism and plants have many antioxidants and scavenging enzymes to maintain homeostasis. However, under stress conditions ROS accumulates. Although these molecules can damage cells (Moller et al., 2007), they are also known to have signalling functions (Foyer & Noctor, 2009). In fact, while excess ROS is toxic, a certain level of ROS production is necessary for a successful response to stress, including salt (Kaye et al., 2011). In addition, ROS accumulation has been shown to have a role in priming plants for enhanced stress resistance (reviewed in (Conrath, 2011)). However, excess ROS can lead to cell death (Kangasjarvi et al., 2005; Overmyer et al., 2005) and perturb development (Tognetti et al., 2011).

1.2 Abiotic stress causes largescale changes in gene expression

Plant defences are characterized by large reprogramming of gene expression, much of it through regulation of transcription. Research over the last two decades has led to the identification of many stress-inducible genes, especially since the publication of the *Arabidopsis* genome (*Arabidopsis* Genome Initiative, 2000), which allowed global gene expression experiments. Since 2000, several other plant species have had their genomes sequenced, allowing expansion of this type of analysis. Functional analysis has confirmed the importance of many of these genes in stress tolerance. More recently, genes whose expression is downregulated under stress conditions have received attention (Bustos et al., 2010). It is now understood that transcriptional repression responses are an integral part of adaptive responses to stress.

To mount an effective defence, ultimately a transcription factor needs to bind and activate or repress its target genes. Since there are both common and unique effects from different stresses, comparison of the transcriptional profiles of such stresses has revealed both common and unique gene activation and repression patterns and led to the development of models of transcriptional regulation of abiotic stress responses. The transcriptional control of stress can be divided into several temporal phases, most likely due to varying dependency on different signaling molecules or protein synthesis (Yamaguchi-Shinozaki & Shinozaki, 2006). Changes can begin within 15-30 minutes of exposure and last for several days (Kilian et al., 2007). The common stress transcriptome represents a shared response and is likely responsible for the widely observed cross-protection where exposure to a given stress increases the resistance of the plant to a second.

Many transcription factors involved in stress responses have been identified. Often the expression of genes encoding these transcription factors responds rapidly to abiotic stress treatments (Gadjev et al., 2006; Kilian et al., 2007). During domestication of crops, selection for stress tolerance has acted on such transcription factors (Lata et al., 2011), underlining their importance. These proteins have also been targets for development of abiotic stress tolerant transgenic plants (Hussain et al., 2011). Transcription factors that regulate stress responses belong to many different families. However, there are certain families that include a relatively large number of members that have been implicated in environmental response. These include the DREB1/CBF family of AP2 transcription factors (Lata & Prasad, 2011) as well as other AP2-type factors (Dietz et al., 2010), Class I homeodomain-leucine zipper proteins (Elhiti & Stasolla, 2009) and the WRKY family (Rushton et al., 2011). Interestingly, the families mentioned here are all plant-specific (Riechmann et al., 2000), suggesting that they may have evolved to help plants deal with the stress of life on land. However, members of transcription factor families that are found outside of plants have also been implicated in control of stress-inducible gene expression.

The activity of these transcription factors is also controlled at posttranscriptional levels. Of particular note, they can be regulated through protein-protein interactions and/or posttranslational modifications. For example, AtMEKK1 can phosphorylate WRKY53 and regulate its activity during senescence (Miao et al., 2007). DREB2A, which when constitutively active confers salt and high temperature tolerance (Sakuma et al., 2006b), interacts with the Med25 subunit of the Mediator complex to regulate gene expression (Elfving et al., 2011), while heterodimers of bZIP1 and bZIP53 act together to activate

transcription during low energy stress (Dietrich et al., 2011). Thus, the protein complexes in which transcription factors are found and the modifications they have are essential to determine their activity.

1.3 Epigenetic control of abiotic stress response

As discussed above, upon stress plants reprogram their transcriptome. Although transcription factors are important for this reprogramming, it is thought that alteration of chromatin structure is also critical (Arnholdt-Schmitt, 2004). Genomic DNA is packaged around nucleosomes into chromatin, the confirmation of which can restrict access of proteins to the DNA. Therefore, transcription is heavily influenced by dynamic changes in chromatin structure (Kwon & Wagner, 2007). Chromatin structure is regulated by several mechanisms, including histone and DNA modifications, chromatin remodelling, which uses ATP hydrolysis to alter histone-DNA contacts, and histone variants (JM. Kim et al., 2010; Pfluger & Wagner, 2007). Alterations in chromatin structure are known to impact stress tolerance (JM. Kim et al., 2010).

Posttranslational modifications of histones are one of the best-studied aspects of chromatin regulation. Over 25 sites of histone modification have been identified in *Arabidopsis* (Zhang et al., 2007) and the pattern of modification is known to alter upon stress (JM. Kim et al., 2008). For example, a decrease in trimethylation of histone H3 Lys27 (H3K27me₃), which is a marker of less transcriptionally active genes, is seen at cold-responsive loci upon exposure to cold (Kwon et al., 2009). Some of the proteins responsible for histone modifications have been implicated in abiotic stress response as well. The histone deacetylase HDA6 is involved in ABA signalling and salt stress response and required for jasmonate-induced gene expression in addition to a role in flowering time control (LT. Chen et al., 2010; K. Wu et al., 2008; Yu et al., 2011). It is also necessary for freezing tolerance (To et al., 2011a). Mutations in *HOS15*, which encodes a WD-repeat protein, cause hypersensitivity to freezing and *HOS15* increases deacetylation of histone H4 (Chinnusamy et al., 2008; J. Zhu et al., 2008). The histone acetylase *AtGCN5* has roles in gene expression in response to cold and light (Benhamed et al., 2006; Stockinger et al., 2001). Many more such connections are being discovered.

Another important level at which gene expression is epigenetically controlled is degree of nucleosome coverage of a gene. Generally, nucleosome density is decreased and chromatin structure relaxed when transcription is activated (Lieb & Clarke, 2005). Chromatin remodelling factors are necessary for the rearrangement of nucleosomes on DNA and several of these have been implicated in stress response. For example, the SWI/SNF family member *AtCHR12* has been shown to mediate the transient growth arrest seen under adverse environmental conditions (Mlynarova et al., 2007). Another member of this family, *SPLAYED* (*SYD*), also regulates stress pathways (Walley et al., 2008). DEAD-box helicases, which unwind duplex DNA or RNA, can also affect chromatin structure and several have been implicated in various stress responses (Vashisht & Tuteja, 2006). Interestingly, in *Arabidopsis* nucleosomal DNA is more highly methylated than flanking DNA and nucleosomes are enriched on exons (Chodavarapu et al., 2010). Genes whose coding regions are methylated tend to be longer and more functionally important and include many stress-regulated genes (Takuno & Gaut, 2011). In plants DNA methylation status is dynamic, regulated by DNA methylation and demethylation reactions and influenced by histone

modifications (reviewed in (He et al., 2011)). High DNA methylation is associated with silenced transposable elements. However, this modification also functions in gene regulation and transcribed genes will also contain methylated bases. Although the involvement of DNA methylation in abiotic stress response has not been extensively examined, it is involved in defence against gemini viruses (Raja et al., 2008, 2010) and important in the vernalization response (DH. Kim et al., 2009). In addition, the histone deacetylase HDA6, discussed above, has been shown to regulate silencing in cooperation with the DNA methyltransferase MET1 (To et al., 2011b), providing a link from DNA methylation to ABA and jasmonate signalling.

1.4 Costs of defense responses

Plants have developed many sophisticated defence pathways to allow them to thrive even in the presence of suboptimal environmental conditions. Phenotypes involved in tolerance or defence against environmental stress can be inducible or constitutive. The evolution of induced responses is thought to be the result of the high cost of maintaining the response in the absence of stress. This is because of the reallocation of energy and resources to defence from growth and reproduction (Walters & Heil, 2007). Research has begun to measure the benefits and costs of adaptation to stressful conditions, for example during cold acclimation (Zhen et al., 2011) and tolerance (Jackson et al., 2004). In addition, analysis of mutant and transgenic plants with derepressed stress responses to both biotic and abiotic stresses often have developmental abnormalities and reduced seed set. For example, *CONSTITUTIVE EXPRESSION OF PR GENES5 (CPR5)* was originally identified in a mutant screen for constitutive expression of systemic acquired resistance; the *cpr5* mutant has chlorotic lesions, reduced trichome development and stunted growth (Bowling et al., 1997). *CPR5* encodes a transmembrane protein that represses leaf senescence and pathogen-defence responses in *Arabidopsis* (Kirik et al., 2001; Yoshida et al., 2002). An altered cellular redox state is present in *cpr5* mutants, which underlies the chlorotic lesions and maybe the other developmental defects as well (Jing et al., 2008) and *CPR5* has been hypothesized to act as a repressor of ROS accumulation (Jing & Dijkwel, 2008).

The cost of stress response is reflected in a phenotype observed in plants exposed to chronic, sublethal abiotic stress, the so-called stress-induced morphogenetic response (SIMR; (Potters et al., 2007; Tognetti et al., 2011)). SIMR is characterized by reduced cell elongation, blockage of cell division in primary meristems and activation of secondary meristems (Potters et al., 2009). Plants displaying SIMR often show accumulation of antioxidants and other compounds that act as modulators of stress responses. It is thought that these changes allow the redistribution of resources to stress response pathways, permitting plants to acclimate to their environment. Another aspect of the SIMR response is accelerated flowering, a response that has been associated with many abiotic stresses, including nutrient deficiency (Wada et al., 2010; Wada & Takeno, 2010) and salinity (Ryu et al., 2011) and is thought to guarantee reproduction before any potential lethality caused by stress. SIMR has been hypothesized to be mediated by accumulation of ROS caused by the stressful conditions and subsequent alterations in auxin accumulation and signaling (Potters et al., 2007; Tognetti et al., 2011). In *Arabidopsis*, SIMR has been shown to be induced under several different abiotic stress conditions (Potters et al., 2007; 2009), including salt stress (Zolla et al., 2009) and exposure to the nonprotein amino acid amino-butyric acid (CC. Wu et al., 2010).

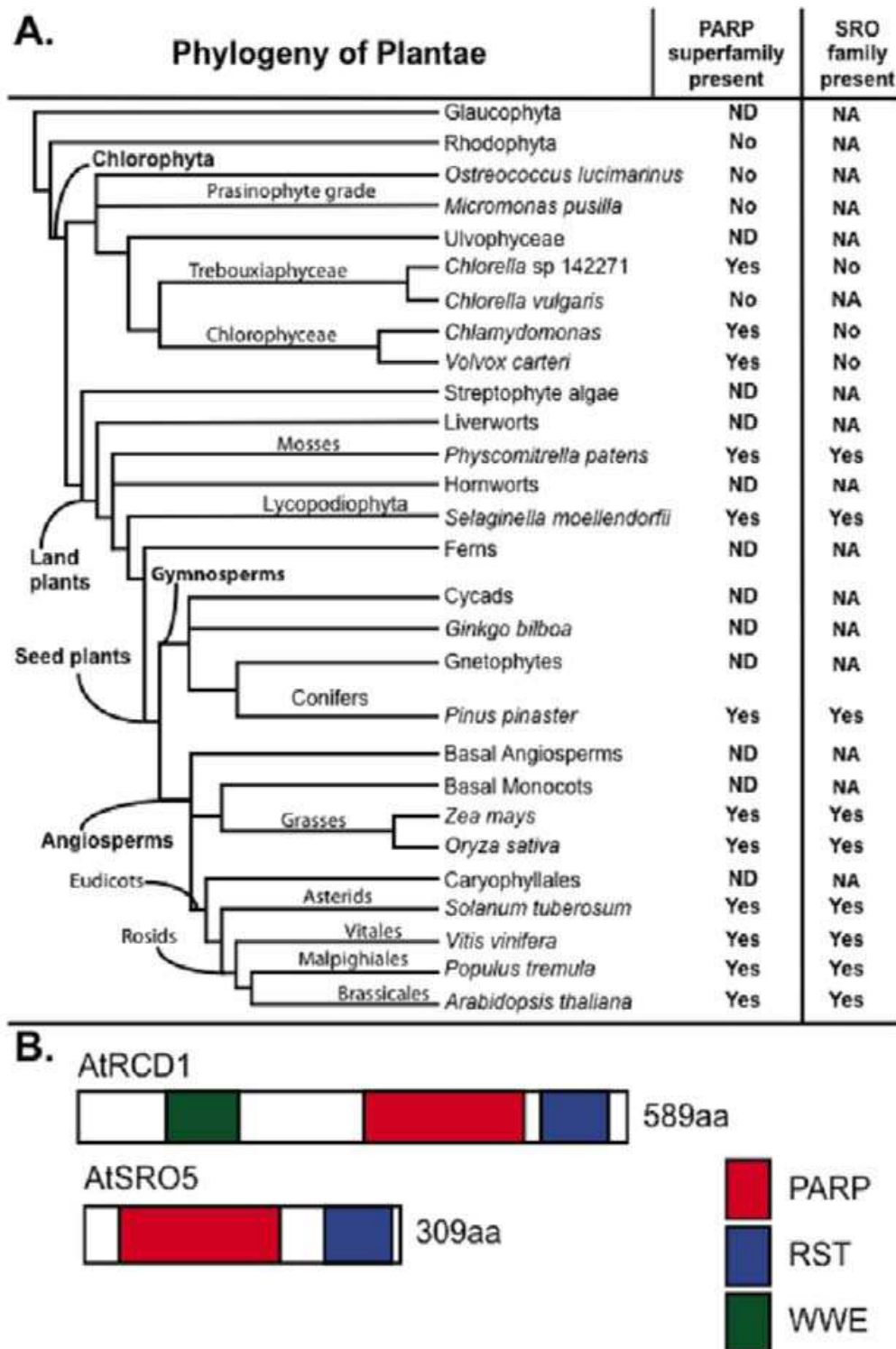


Fig. 1. The SRO family of PARP-like proteins is plant specific. A. Simplified phylogeny of Plantae. Branch lengths do not reflect genetic distance. Presence or absence of PARP superfamily members and SRO subfamily members are indicated, based on ((Citarelli et al., 2010) and searches of EuroPineDB (for *Pinus pinaster*; (Fernandez-Pozo et al., 2011)) and the potato genome (Potato Genome Sequencing Consortium, 2011)). B. Schematic representation of domains found in two representative *Arabidopsis* SRO family members. Protein domains are illustrated by colored boxes and defined according to Pfam 25.0 (Finn. et al., 2010).

2. The SRO family: A novel group of poly(ADP-ribose) polymerase-like proteins found only in land plants

The poly(ADP-ribose) polymerase (PARP) superfamily is distributed across the breadth of the eukaryotes (Citarelli et al., 2010) and was first identified as enzymes that catalyze the posttranslational modification of proteins by multiple ADP-ribose moieties (poly(ADP-ribosyl)ation; (Chambon et al., 1963)). It is now recognized that there are many types of PARPs and PARP-like proteins; they are characterized by a shared PARP catalytic domain but differ outside of this domain. The functions of these proteins have also expanded and some members of this family do not act in poly(ADP-ribosyl)ation. *Bona fide* PARPs attach ADP-ribose subunits from nicotinamide adenine dinucleotide (NAD⁺) to target proteins (MY. Kim, 2005). However, other members of the PARP superfamily have been shown to have either mono(ADP-ribose) transferase (mART) activity (Kleine et al., 2008) or to be enzymatically inactive (Aguiar et al., 2005; Jaspers et al., 2010b; Kleine et al., 2008; Till et al., 2008). Biologically, PARP superfamily members are involved in a broad range of functions, including DNA damage repair, cell death pathways, transcription and chromatin modification/remodeling (reviewed in (Hassa & Hottiger, 2008)).

Although non-enzymatically active PARP superfamily members have not been as well studied as those with known poly(ADP-ribosyl)ation activity, some information is available. Human PARP9 (HsPARP9), which does not have enzymatic activity, is inducible by interferon and is able to increase the expression of interferon-stimulated genes (Juszczynski et al., 2006), suggesting a role in host defense against viruses. Another enzymatically inactive PARP, HsPARP13, interacts with viral RNA from select viruses and recruits factors to degrade that RNA (G. Chen et al., 2009; Gao et al., 2002; Y. Zhu & Gao, 2008). HsPARP13 is also able to induce type I interferon genes by associating with the RIG-I viral RNA receptor in a ligand dependent manner, promoting oligomerization of this protein. This stimulates ATPase activity of RIG-I and enhancement of NF- κ B signaling (Hayakawa et al., 2011). Even those PARPs for which poly(ADP-ribosyl)ation activity has been demonstrated have functions that do not depend on such activity. For example, HsPARP1 was originally isolated based on its catalytic activity. However, it has been shown to function in gene expression non-enzymatically, both as a transcription factor/coregulator and at the chromatin level. For example, HsPARP1 functions as a coactivator of NF- κ B but enzymatic activity is not required for this function (Hassa et al., 2003; Oliver et al., 1999). HsPARP1 can bind directly to regulatory sequences, impacting transcriptional activity, as has been shown for the *CXCL1* promoter (Nirodi et al., 2001) or bind to other proteins that mediate the DNA binding, as has been shown for the *COX-2* promoter region (Lin et al., 2011). In addition, it can bind to nucleosomes and promote compaction of chromatin by bringing together neighboring nucleosomes in the absence of NAD⁺ or enzymatic activity (MY. Kim et al., 2004; Wacker et al., 2007). Clearly, the functions of PARP proteins extends beyond poly(ADP-ribosyl)ation.

2.1 The SRO family

Compared to mammals, in which the PARP superfamily has been greatly amplified, both in numbers and types (Hassa & Hottiger, 2008), plants have relatively few such proteins (Citarelli et al., 2010). The red and green algae do not encode members of this family or encode only one or two representatives (Fig. 1A; (Citarelli et al., 2010)). Land plants,

however, have several types of PARPs and PARP-like proteins, including a novel group of PARP proteins, the SRO family (Fig. 1A, B; (Citarelli et al., 2010; Jaspers et al., 2010b)). Although first identified in *Arabidopsis thaliana* (Belles-Boix et al., 2000), these proteins are found throughout land plants and consist of two subgroups (Citarelli et al., 2010; Jaspers et al., 2010b). The first is found in all examined groups of land plants and consists of relatively long proteins with a WWE protein-protein interaction domain (Aravind, 2001) in the N-terminus and a C-terminal extension past the PARP catalytic domain (Fig. 1B). This extension contains an RST domain (Jaspers et al., 2010a). The second subgroup is confined to the eudicot group of flowering plants. These proteins appear to be truncated relative to the other subgroup and likely arose from a partial gene duplication. They have lost the N-terminal region, including the WWE domain, and retain only the catalytic domain and the RST domain (Fig. 1B). The SRO family is characterized by changes in their putative PARP catalytic domains that suggest that they may not act enzymatically. *Arabidopsis thaliana* RADICAL-INDUCED CELL DEATH1 (RCD1), the first member of the SRO family identified, has been shown to be inactive and not even bind NAD⁺ (Jaspers et al., 2010b). However, the catalytic domains within this group show variability and this observation may not be applicable to all SRO family members (Citarelli et al., 2010).

<i>Arabidopsis thaliana</i> gene	Locus ID	Selected plant orthologs ^a	Expression pattern ^b	Enzyme activity	Associated with stress?
<i>AtRCD1</i>	<i>At1g32230</i>	<i>OsQ0DLN4</i> <i>OsQ336N3</i> <i>OsQ0J949</i> <i>OsQ654Q5</i> <i>VvA7PC35</i> <i>VvA5BDE5</i> <i>PtB9MU68</i> <i>PtB9GZJ6</i>	Expressed in all organs	No (Jaspers et al., 2010b)	Yes
<i>AtSRO1</i>	<i>At2g35510</i>	See <i>AtRCD1</i> ^c	Expressed in all organs	ND	Yes
<i>AtSRO2</i>	<i>At1g23550</i>	<i>PtB9INI8</i> <i>PtB9HDP9</i> <i>PtB9HDP8</i> <i>PtB9HDP5</i>	Expressed in all organs	ND	Yes
<i>AtSRO3</i>	<i>At1g70440</i>	See <i>AtSRO2</i> ^c	ND	ND	Yes
<i>AtSRO4</i>	<i>At3g47720</i>	<i>VvA5BFU2</i> <i>PtB9I3A2</i> <i>PtB9IES0</i>	ND	ND	ND
<i>AtSRO5</i>	<i>At5g62520</i>	See <i>AtSRO4</i> ^c	Expressed in all organs		Yes

Table 1. SRO family members found in *Arabidopsis thaliana*. ^aOrthologs as found in (Citarelli et al. 2010). ^bGenevestigator (Zimmermann et al., 2005). Those genes with no data are not represented on ATH1 GeneChip (Affymetrix). ^cRepresent paralogs in *Arabidopsis thaliana*. NA, not applicable; ND, no data; *Mt*, *Medicago truncatula*; *Os*, *Oryza sativa*; *Pp*, *Physcomitrella patens*; *Pt*, *Populus trichocarpa*; *Sm*, *Selaginella moellendorffi*; *Vv*, *Vitis vinifera*; *Zm*, *Zea mays*.

3. The SRO family and abiotic stress response

Although the SRO family is found in all examined land plants, almost all of the work on this family has been carried out using *Arabidopsis*. In this plant there are nine genes encoding members of the SRO family (Table 1; (Belles-Boix et al., 2000; Ahlfors et al., 2004)). Two paralogous genes, *RCD1* and *SIMILAR TO RCDONE1 (SRO1)*, encode members of the ubiquitous SRO subfamily, which contains the long N-terminal region containing a WWE protein-protein interaction domain (Fig. 1B). Consistent with their paralogous natures, *RCD1* and *SRO1* are partially redundant (Jaspers et al., 2009; Teotia & Lamb, 2009). The other four genes, *SRO2-5*, encode members of the eudicot-specific subfamily encoding truncated proteins.

3.1 Loss of *RCD1* and/or *SRO1* alters abiotic stress response

The SRO family was originally discovered based on the ability of one member, *Arabidopsis RCD1/CEO1*, to rescue oxidative stress response defects in mutant yeast (Belles-Boix et al., 2000). Mutants in this gene were discovered based on their hypersensitivity to ozone (Overmyer et al., 2000) and resistance to methyl viologen (Fujibe et al., 2004). *rcd1* mutants are also hypersensitive to other sources of apoplastic ROS, such as H_2O_2 (Overmyer et al., 2005; Teotia & Lamb, 2009) as well as salt (Katiyar-Agarwal et al., 2006; Teotia & Lamb, 2009). Conversely, *rcd* mutants are resistant to UV-B and the herbicide paraquat, which generate reactive oxygen species in the plastid (Ahlfors et al., 2004; Fujibe et al., 2004; Teotia & Lamb, 2009). In contrast, *sro1-1* plants are not resistant to the chloroplastic ROS induced by paraquat but are resistant to apoplastic ROS and high salt levels (Teotia & Lamb, 2009). Loss of either *RCD1* or *SRO1* confers resistance to osmotic stress (Teotia & Lamb, 2009). These results suggest that the relationship between *RCD1* and *SRO1* and their contribution to abiotic stress is complex and that the two genes may have some independent functions. In addition, loss of *RCD1* or *SRO1* alters responses to a number of different abiotic stresses, suggesting that these genes have broad functions. The stress responses of *rcd1; sro1* double mutant plants are technically difficult to access. Most *rcd1-3; sro1-1* plants die as embryos (Teotia & Lamb, 2009) and of those that germinate (approximately 40%), only 10-15% will produce more than 2-3 true leaves (Jaspers et al., 2009; Teotia & Lamb, 2009). However, these double mutant seedlings do display some photobleaching under normal light conditions, suggesting they are under photooxidative stress (Fig. 2A; (Teotia & Lamb, 2009)).

Consistent with the response changes upon exposure to multiple abiotic stresses, *rcd1* single mutants have been shown to accumulate ROS (Overmyer et al., 2000) and nitric oxide (Ahlfors et al., 2009) under non-stress conditions. In addition, expression of a number of stress-regulated genes is altered in this background (Ahlfors et al., 2004; Jaspers et al., 2009). For example, expression of *AOX1A*, encoding a mitochondrial alternative oxidase, is increased in *rcd1-1*. Cold and ABA regulated genes have reduced basal expression when *RCD1* is reduced. However, for the majority of genes whose expression was examined, loss of *SRO1* does not change expression levels (Jaspers et al., 2009), presumably due to the greater role *RCD1* plays in stress response (Jaspers et al., 2009; Teotia & Lamb, 2009). An exception is *tAPX*, encoding a plastid localized ascorbate peroxidase thought to be involved in defense against H_2O_2 (Kangasjarvi et al., 2008), whose expression is lower in *sro1-1* plants. *rcd1-3; sro1-1* double mutant plants exhibit

increased expression of stress response genes and accumulation of SUMOylated proteins (known to accumulate during stress; (Kurepa et al., 2003)) under nonstress conditions (Teotia et al., 2010). Taken together, these data suggest that RCD1 and SRO1 may function as inhibitors of some stress responses, perhaps through regulation of ROS accumulation, consistent with their function in responses to a broad range of abiotic stresses.

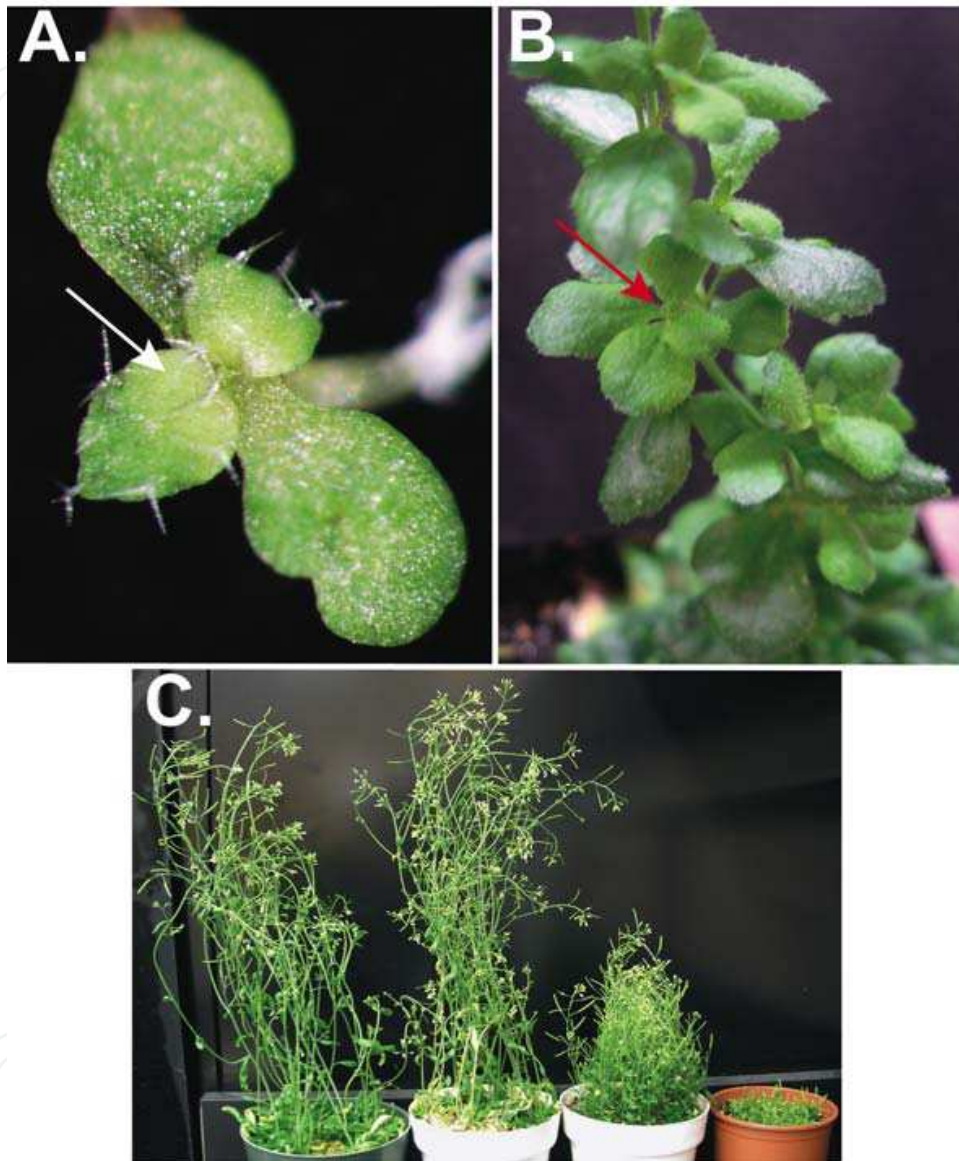


Fig. 2. Loss of *RCD1* or *RCD1* and *SRO1* leads to developmental defects. (a) *rcd1-3; sro1-1* seedling. White arrow points to potential photobleaching. (b) *rcd1-3* plant grown under short day conditions (8 hours light/16 hours dark). Red arrow points to an aerial rosette. (c) Adult Arabidopsis plants. From left to right: wild type, *sro1-1*, *rcd1-3*, *rcd1-3; sro1-1*.

3.2 Other SRO family members in Arabidopsis also contribute to stress responses

In contrast to the work on *RCD1* and *SRO1*, relatively little work has been done on *SRO2-5*. No functional data exists on *SRO3* or *SRO4* and they are not represented on the Affymetrix ATH1 genechip and, therefore, not in publically available expression databases (Table 1).

However, *SRO3* expression is significantly reduced under light stress and induced by salt stress and ozone (Jaspers et al., 2010b). *SRO2* has been shown to be upregulated in response to high light in chloroplastic ascorbate peroxidase mutants (Kangasjarvi et al., 2008). *SRO5* expression is relatively low under normal conditions but its expression has been shown to be induced by salt treatment (Borsani et al., 2005) and repressed by high light (Khandelwal et al., 2008). *sro5* plants were more sensitive to H₂O₂-mediated oxidative stress and to salt stress (Borsani et al., 2005). *SRO5* has also been implicated in regulation of proline metabolism under salt stress both at the small RNA level and by counteracting ROS accumulation caused by proline accumulation (Borsani et al., 2005). Inhibiting ROS accumulation may be a core function of the SRO family.

3.3 Loss of *RCD1* and *SRO1* leads to a SIMR-like phenotype

As discussed above, chronic exposure to abiotic stress can lead to a developmental syndrome termed SIMR (Potters et al., 2007; Tognetti et al., 2011). Single *rcd1* mutants display some phenotypes that resemble those of SIMR, including reduced height (Fig. 2C; Ahlfors et al., 2004; Teotia & Lamb, 2009) and shorter primary roots accompanied by a greater number of lateral roots (Teotia & Lamb, 2009). In addition, loss of *RCD1* leads to accelerated flowering under long day conditions (Teotia & Lamb, 2009). This correlates with accumulation of ROS and NO (Ahlfors et al., 2009; Overmyer et al., 2000), as well as changes in expression of stress-induced genes (Ahlfors et al., 2004; Jaspers et al., 2009). *sro1* plants display some subtle developmental defects, consistent with it playing a minor role compared to *RCD1* (Teotia & Lamb, 2009).

The *rcd1-3; sro1-1* double mutants are severely defective. The majority of *rcd1-3; sro1-1* individuals die during embryogenesis (Teotia & Lamb, 2009). *rcd1-3; sro1-1* plants are very small and pale green as seedlings (Fig. 2A); at least some of this decrease in size is caused by a decrease in cell elongation (Teotia & Lamb, 2009). However, double mutant plants also make fewer cells (Teotia & Lamb, 2011). In the roots of *rcd1-3; sro1-1* plants, the meristems are smaller with fewer mitotic cells and cell differentiation is disrupted. The specialized cell walls of several cell types such as lateral root cap cells and the conducting cells of the xylem, are often defective (Teotia & Lamb, 2011). These phenotypes resemble extreme SIMR phenotypes and are accompanied by molecular signs of chronic stress (Teotia et al., 2010). A reasonable hypothesis based on the available data is that *RCD1* and *SRO1* function to inhibit stress responses, particularly accumulation of ROS, and that in their absence, there is a derepression of these pathways, leading both to altered stress responses and developmental defects (Fig. 3A).

4. Molecular functions of the SRO family

Although the SRO family is a subgroup of the PARP superfamily, it does not appear likely that they act in poly(ADP-ribosyl)ation (Jaspers et al., 2010b). Therefore, the molecular function of these proteins remains to be elucidated. *RCD1* and *SRO1* accumulate in the nucleus in *Arabidopsis* (Jaspers et al., 2009), although there is one report that *RCD1* may also be found at the plasma membrane (Katiyar-Agarwal et al., 2006). *SRO5* has been reported in the mitochondria (Borsani et al., 2005) but also in other subcellular locations (Jaspers et al., 2010b). *RCD1*, *SRO1* and *SRO5* have all been shown to interact with

transcription factors in yeast two-hybrid assays (Belles-Boix et al., 2000; Jaspers et al., 2009, 2010b). These interactions are mediated by the RST domain characteristic of the SRO family (Fig. 3B), which is also found in the transcription initiation complex component TAF4 (Jaspers et al., 2010a). Based on localization and binding to transcription factors, members of the SRO family may act in gene expression regulation.

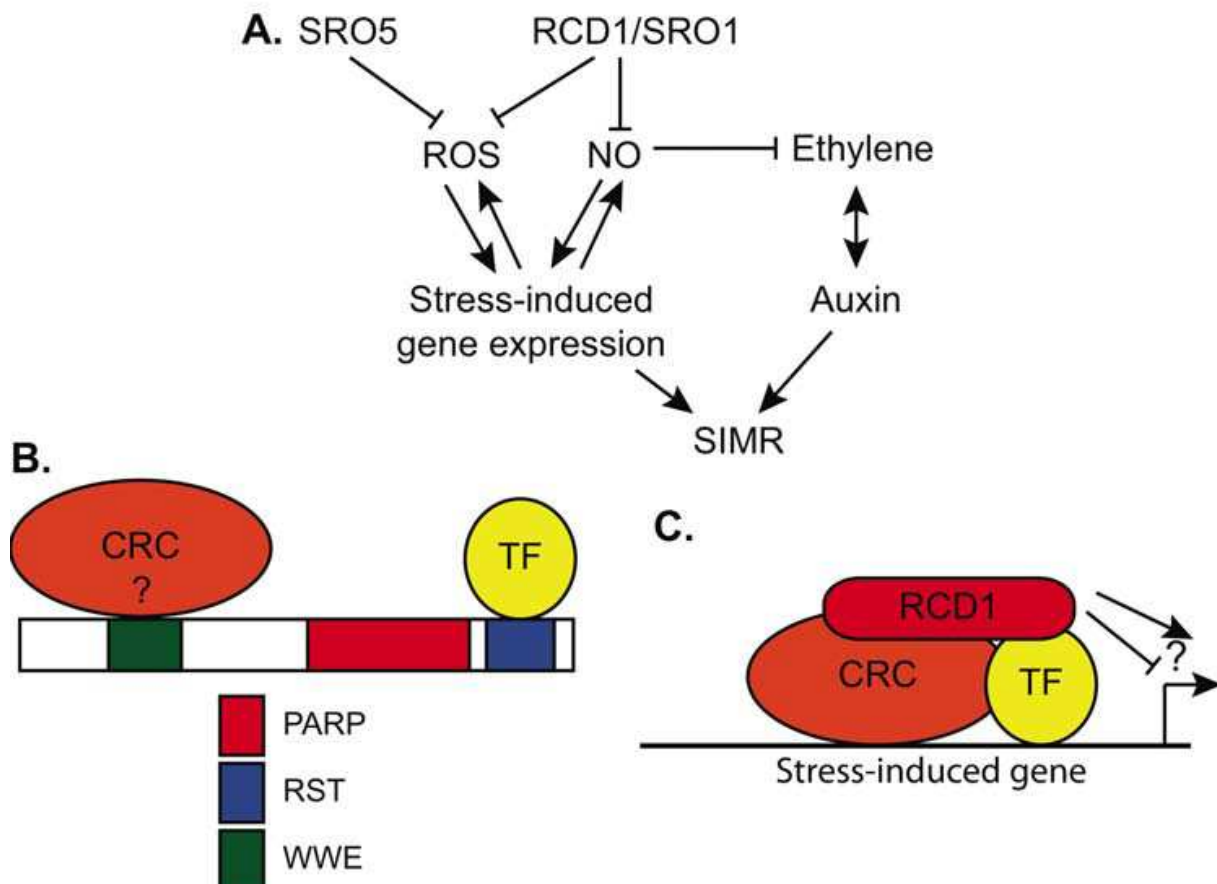


Fig. 3. Model of how SRO family members regulate abiotic stress. A. SRO family members inhibit accumulation of reactive oxygen species, which contributes both to altered abiotic stress responses and stress-induced morphogenetic response phenotypes. B. SRO family members act as scaffolds bringing together transcription factors bound to their RST domains with other proteins. Members that contain WWE domains may recruit chromatin remodeling complexes through their WWE domains. Domains shown as in Fig. 1B. C. SRO family containing complexes function to regulate gene expression.

The type of transcription factors bound by the SRO family members are diverse, including members of the bZIP, WRKY, bHLH, HSF and AP2/ERF families. A number of the identified transcription factors have been shown to be involved in abiotic stress responses. For example, SRO5 binds to a heat shock factor, HSFA1E (Jaspers et al., 2010b), which is necessary to induce expression of *HsfA2*, encoding a key regulator of the HSF network under salt and high light stress (Nishizawa-Yokoi et al., 2011). RCD1, SRO1 and SRO5 all bind to DREB2A (Jaspers et al., 2010b), an AP2/ERF transcription factor involved in cold acclimation (Sakuma et al., 2006a). Therefore, it is reasonable to hypothesize that the changes in stress-inducible gene expression seen in mutants of SRO

family members arise from changes in activity of the transcription factors they bind, although this has not been demonstrated.

It is not yet clear how the binding of SRO family members to transcription factors affects the function of these proteins. Other types of PARP superfamily proteins have roles in transcriptional regulation and epigenetic control of gene expression; these roles are not always dependent on poly(ADP-ribosyl)ation activity as discussed above. HsPARP13 is not enzymatically active and has been shown to be part of multicomponent complexes in which it appears to act as a scaffold, bringing different molecules together (G. Chen et al., 2009; Gao et al., 2002; Hayakawa et al., 2011; Y. Zhu & Gao, 2008). Therefore, we hypothesize that members of the SRO family act to regulate gene expression within complexes that they anchor (Fig. 3C). Since SRO family members do not appear to have any DNA binding domains, they must be recruited to chromosomes via other proteins. These SRO-containing complexes may act directly to induce or repress transcription or act via epigenetic modification of chromatin structure to influence gene expression. The RST domain binds to transcription factors and could recruit these proteins (Fig. 3B, C). In full length SRO family members that contain WWE domains, such as *RCD1*, this region could be available to recruit additional factors to the complex, such as chromatin remodeling factors (Fig. 3B, C).

Although we have been discussing the role of SRO family members in abiotic stress response, it is likely that they may also function to control gene expression in other pathways. For example, *RCD1* may have a role in control of phase change in Arabidopsis. In short days, *rcd1-3* plants cannot maintain reproductive fate; rather they bolt and then revert to vegetative fate, making aerial rosettes (Fig. 2B; (Teotia & Lamb, 2009)). The formation of the aerial rosettes is accompanied by ectopic expression of the floral repressor *FLOWERING LOCUS C (FLC)* in the bolt, where it should not be expressed. The expression of *FLC* is controlled at several levels, including epigenetic marking of histones (reviewed in (Y. He, 2009)) and by transcriptional activators (Yun et al., 2011). Therefore, the SRO family may help control gene expression beyond that involved in abiotic stress response.

5. Conclusions

The SRO family is a plant specific subfamily of PARP-like proteins that have roles in response to a number of abiotic stresses. It is interesting to note that the emergence of this family at the base of the land plants coincides with the need for protection from new stresses such as drought and increased light. Although the SRO proteins do not appear to have enzymatic activity, a possible mechanism by which they function is as part of multiprotein complexes that regulate gene expression. We hypothesize that the SRO family functions to prevent inappropriate gene expression in the absence of stress and, in their absence, ROS and other defence molecules accumulate at the expense of proper growth and development. Much work remains to test these hypotheses and clarify the contributions of individual SRO family members to stress responses as well as to move research of this important family into plants other than Arabidopsis, particularly crop plants.

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7. References

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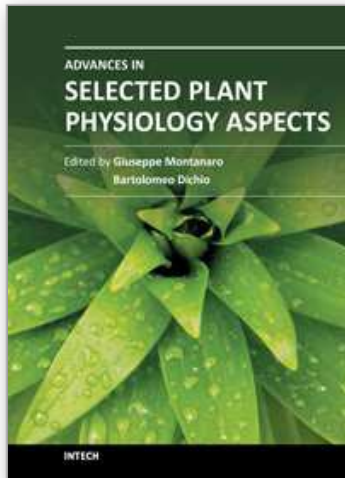
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The book provides general principles and new insights of some plant physiology aspects covering abiotic stress, plant water relations, mineral nutrition and reproduction. Plant response to reduced water availability and other abiotic stress (e.g. metals) have been analysed through changes in water absorption and transport mechanisms, as well as by molecular and genetic approach. A relatively new aspects of fruit nutrition are presented in order to provide the basis for the improvement of some fruit quality traits. The involvement of hormones, nutritional and proteomic plant profiles together with some structure/function of sexual components have also been addressed. Written by leading scientists from around the world it may serve as source of methods, theories, ideas and tools for students, researchers and experts in that areas of plant physiology.

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