ROS as Key Players of Abiotic Stress Responses in Plants

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Contents

Abstract Despite their toxic potential, reactive oxygen species (ROS) play an integral role as signaling molecules in the regulation of a broad range of biological processes such as growth, development, and responses to biotic and/or abiotic stimuli in plants. To some extent, various functions of ROS signaling are attributed to differences in the regulatory mechanisms of respiratory burst oxidase homologs (RBOHs) that are involved in a multitude of different signal transduction pathways activated in assorted tissue and cell types under fluctuating environmental conditions. To acclimate or survive under abiotic stress conditions, plants possess powerful strategies involving systemic signaling, retrograde signaling, and programmed cell death (PCD), in which ROS signals are integrated with other pathways to generate highly coordinated signaling networks. In this chapter, beneficial roles of ROS as signaling molecules in the regulation of abiotic stress responses in plants will be addressed.

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Abbreviations

ABA	Abscisic acid
ABI4	ABA-insensitive 4
ACC	1-Aminocyclopropane-1-carboxylic acid
ANAC017	A membrane-bound NAC 017
AOX	Alternative oxidase
APX	Ascorbate peroxidase
BCL2	B-cell lymphoma 2
BR	Brassinosteroid
CDPKs	Calcium-dependent protein kinases
CTR1	Constitutive triple response 1
DPI	Diphenyleneiodonium
EDS1	Enhanced disease susceptibility 1
EIN2	Ethylene-insensitive 2
EEE	Excess excitation energy
GUN1	Genomes uncoupled 1
IAA	Indole-3-acetic acid
JA	Jasmonic acid
LSD1	Lesion simulating disease 1
MAPK	Mitogen-activated protein kinase
NPQ	Non-photochemical quenching
MeJA	Methyl jasmonate
OST1	Open stomata 1
PA	Phosphatidic acid
PCD	Programmed cell death
PAD4	Phytoalexin-deficient 4
PRL1	Pleiotropic response locus 1
PQ	Plastoquinone
RBOH	Respiratory burst oxidase homolog
ROS	Reactive oxygen species
SA	Salicylic acid
SAA	Systemic acquired acclimation
SAR	Systemic acquired resistance
SID2	Salicylic acid induction deficient 2
TPC1	Two-pore channel 1
VPE	Vacuolar processing enzymes

1 Introduction

The reactive oxygen species (ROS) signaling network is highly conserved among aerobic organisms and controls a broad range of biological processes such as growth, development, and responses to biotic and/or abiotic stimuli (Mittler et al. 2011). Although early researches related to ROS metabolism focused on their potential toxicity and the different mechanisms to scavenge them, more recent studies have focused on the roles of ROS as signaling molecules. Why did plants acquire the ability to utilize ROS as signaling molecules during the evolutionary process? The existence of different types of ROS might be an advantage for the fine-tuning of complex signaling networks in cells, because coordinated production of ROS with different properties could at least partially contribute to generation of various signals. Indeed, specificity of ROS signaling was previously indicated by the finding that different sets of genes were upregulated in response to different types of ROS (Gadjev et al. 2006; Suzuki et al. 2011). In addition, almost any changes in cellular homeostasis could lead to alteration of redox state in particular organelles, followed by changes in cellular level of ROS. ROS can be therefore integrated with the activities of many other signaling components such as hormones, Ca^{2+}, and kinases and involved in a number of pathways underlying different biological outcomes (Petrov and Van Breusegem 2012). Mobility of ROS, especially H_2O_2, is also an advantage to act as a signaling molecule. H_2O_2, a relatively long-lived and small ROS, readily penetrates cell membranes and is freely diffusible between cells (Bienert et al. 2006). Diffusion of H_2O_2 that is facilitated by plasma membrane aquaporins could also influence the efficiency and direction of H_2O_2 signaling between cells (Bienert et al. 2007; Dynowski et al. 2008).

To utilize ROS as signaling molecules, nontoxic levels of ROS must be maintained in a delicate balance between production involving enzymatic reactions and the unavoidable production during basic cellular processes and the metabolic counter-process involving ROS scavenging pathways (Mittler et al. 2004). Another possible advantage for using ROS as signaling molecules is the specific localization of their production/scavenging mechanisms in different organelles, cell types, and tissues (Mittler et al. 2004; Miller et al. 2009b; Suzuki et al. 2011). Local increase in ROS production can be limited to particular locations in the cell or plant. Therefore, level of ROS throughout the cell or plant as well as spatial coordination of ROS signals can be tightly regulated. In plants, many antioxidant mechanisms that function in different organelles modulate cellular redox state by detoxifying excess ROS produced during basic biological processes such as photosynthesis and respiration (Miller et al. 2009b). In addition, NADPH oxidases, respiratory burst oxidase homologs (RBOHs), deliberately produce ROS in different cell types, tissues, or stages (Suzuki et al. 2011). The tight regulation of RBOH protein activity makes these enzymes good candidates for the fine-tuning of ROS production in terms of amplitude, duration, and localization in plants (Marino et al. 2012; Gilroy et al. 2014) (Fig. 1).

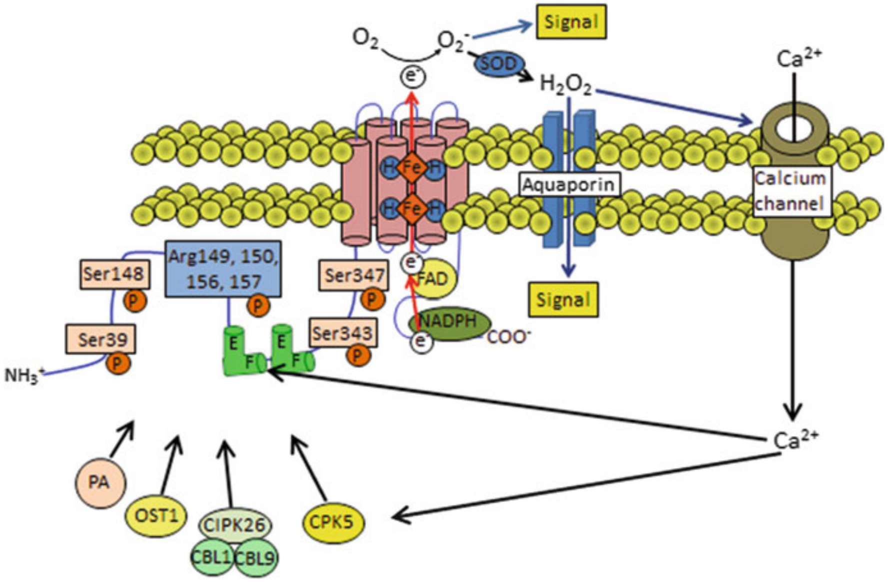

Fig. 1 Regulatory mechanisms of RBOH proteins in *Arabidopsis*. ROS can activate or suppress calcium channels to control the release of Ca^{2+} into cytosol. Ca^{2+} can directly or indirectly regulate the production of ROS by respiratory burst homolog (RBOH) proteins resulting in the generation of superoxide radicals that are dismutated to H_2O_2 spontaneously or via superoxide dismutase (SOD). H_2O_2 diffused into cytosol through aquaporin then functions as a signaling molecule. RBOHs have cytosolic FAD and NADPH-binding domains in the C-terminal region and six conserved transmembrane-spanning domains (*pink cylinders*). The N-terminal domain contains two EF-hand motifs and phosphorylation target sites that are important for activity of RBOHs. Binding of Ca^{2+} to EF-hand motifs is required for activation of RBOHs (Ogasawara et al. 2008; Drerup et al. 2013). Several kinases including OST1 (Sirichandra et al. 2009), CPK5 (Dubiella et al. 2013), and CBL1/9–CIPK26 complexes (Drerup et al. 2013) activate RBOH proteins by phosphorylation of the target sites (Ser or Arg residues). In addition, phosphatidic acid (PA) produced via function of phospholipase Dα1 (PLDα1) was also shown to activate RBOHD (Zhang et al. 2009b). *Abbreviations*: *CBL1* calcineurin B-like protein 1, *CBL9* calcineurin B-like protein 9, *CIPK26* calcineurin B-like interacting protein 26, *CPK5* calmodulin domain protein kinase 5, *OST1* open stomata 1, *FAD* flavin adenine dinucleotide, *NAD* nicotinamide adenine dinucleotide, *PA* phosphatidic acid

Being sessile organisms, plants evolved sophisticated strategies to acclimate to or survive under fluctuating environmental conditions. These strategies involve systemic signaling, retrograde signaling, and programmed cell death (PCD), in which ROS play beneficial roles as signaling molecules (Woodson and Chory 2008; Baxter et al. 2014; Szechynska-Hebda and Karpinski 2013; Petrov et al. 2015). Systemic signaling mechanisms evolutionally improved the ability of plants to alert all remote and unstressed tissues of the plant to the existence of a biotic or abiotic threat and to trigger the activation of resistance or acclimation pathways in these tissues (Suzuki et al. 2013; Szechynska-Hebda et al. 2010). Recent studies have highlighted the importance of rapid systemic responses for acclimation of plants to abiotic stimuli, focusing on temporal–spatial coordination between several players of complex network of cell-to-cell communication, active propagation of ROS wave and calcium wave, hormones, and electric signals (Miller et al. 2009b; Mittler et al. 2011; Baxter et al. 2014; Gilroy et al. 2014). Signaling networks between the organelles employ ROS as second messenger. Alterations in redox state and ROS metabolism in the chloroplast and mitochondria are sources for retrograde signals to regulate nuclear gene expression, which play an important role in the acclimation of plants to environmental stimuli (Rhoads and Subbaiah 2007; Pogson et al. 2008; Woodson and Chory 2008; Shapiguzov et al. 2012; Szechynska-Hebda and Karpinski 2013). In addition, chloroplastic ROS production and photosynthetic functions were recently shown to be regulated by cues perceived by cell wall or apoplastic spaces (Padmanabhan and Dinesh-Kumar 2010), suggesting that chloroplastic retrograde signaling might be a part of a large signaling network involving various cues generated from different organelles, and ROS might be an important mediator that integrates these different signals. PCD is one of the essential strategies for survival of plants that are subjected to severe biotic or abiotic stresses, because only cells that are destined to die can be eliminated to prevent the spreading of damage to the neighboring cells and maintain appropriate metabolic status in the rest of cells and tissues (Petrov et al. 2015). It is an active and genetically controlled process in which cells are selectively eliminated in multistep fashion through the involvement of high concentrations of ROS and specific proteases and nuclease (Petrov et al. 2015).

In this chapter, beneficial roles of ROS as signaling molecules in the regulation of abiotic stress responses of plants will be addressed, especially in the context of ROS-producing mechanisms, integration of ROS signals with other pathways, and plant-specific mechanisms that underlie response of plants to abiotic stimuli.

2 ROS-Generating Pathways and Their Regulatory Mechanisms in Plants

In plants, NADPH oxidases, respiratory burst oxidase homologs (RBOHs), are responsible for the production of ROS that act as important signaling molecules (Torres and Dangl 2005; Suzuki et al. 2011). In *Arabidopsis*, RBOHs constitute a multigenic family comprised of ten genes (i.e., AtRBOHA–AtRBOHJ). Very specific function of each RBOH isoform was implicated by the finding that expression of genes encoding each RBOH protein, except for RBOHD, is restricted to one or two organs (Suzuki et al. 2011; Marino et al. 2012). Indeed, several studies have revealed that different plant RBOHs are involved in a multitude of different signaling pathways underlying growth, development, and response to biotic and abiotic stress (Torres et al. 2005; McInnis et al. 2006; Monshausen et al. 2007; Jammes et al. 2009; Nishimura and Dangl 2010; Miller et al. 2009b; Suzuki et al. 2011). In addition, a previous study revealed distinctive expression profiles of nine RBOHs in rice in response to various abiotic stimuli, which demonstrated their linked but diverse functions (Wang et al. 2013).

Plant RBOHs consist of C-terminal region containing cytosolic FAD and NADPH-binding domains, six conserved transmembrane-spanning domains, and N-terminal extension containing two Ca^{2+}-binding EF-hand motifs and phosphorylation target sites that are important for their activity (Kobayashi et al. 2007; Oda et al. 2010; Kimura et al. 2012; Drerup et al. 2013). Previous studies in *Arabidopsis* have revealed several regulatory mechanisms of RBOH proteins, which involve protein phosphorylation, Ca^{2+}, calcium-dependent protein kinases (CDPKs), and phospholipase Dα1 (PLDα1) (Lin et al. 2009; Monshausen et al. 2009; Zhang et al. 2009b; Jakubowicz et al. 2010; Dubiella et al. 2013; Drerup et al. 2013). Mechanical stimulation of plant tissue can induce an increase in cytosolic Ca^{2+} via an influx from the apoplast across the plasma membrane (Monshausen et al. 2009). The increased Ca^{2+} then enhances RBOHC-dependent ROS production followed by the activation of positive feedback loop between Ca^{2+} and RBOHC to regulate root hair development (Monshausen et al. 2007, 2009; Takeda et al. 2008). Ca^{2+} binding and phosphorylation synergistically activate RBOHD and RBOHF in *Arabidopsis* (Ogasawara et al. 2008; Kimura et al. 2012). A Ca^{2+} increase in the cytosol and conformational changes in EF-hand motifs by Ca^{2+} binding were found to be necessary for the activation of RBOHD (Ogasawara et al. 2008). PLDα1 and its lipid product phosphatidic acid (PA) play an essential role in abscisic acid (ABA)-induced production of ROS in guard cells via the function of RBOHD and RBOHF (Zhang et al. 2009b). ABA-dependent stomatal movement involves binding of PA to Arg residues 149, 150, 156, and 157 in RBOHD and phosphorylation of Ser13 and Ser174 in RBOHF by OPEN STOMATA 1 (OST1) kinase (Sirichandra et al. 2009). These findings indicate integration between RBOHD and RBOHF in the regulation of ABA-dependent stomatal closure. The coordination between PA and OST1 however, still needs to be addressed in future studies. In a recent study, systemic acquired resistance to pathogen was shown to involve phosphorylation of RBOHD by calcium-dependent protein kinase 5 (CPK5) and H_2O_2 production (Dubiella et al. 2013), supporting the hypothesis that Ca^{2+}-dependent ROS production is required for the propagation of the ROS wave over long distances (Miller et al. 2009b). In addition, a recent finding demonstrated that the activity of RBOHF is regulated by direct Ca^{2+} binding to its EF-hands and Ca^{2+}-dependent phosphorylation by CBL1/9–CIPK26 complexes (Drerup et al. 2013). Taken together, these findings indicate that the diverse functions of RBOH proteins in plants might be, at least partially, attributed to differences in regulatory mechanisms.

RBOH proteins are not the only source of ROS in plant cells. Numerous pathways for ROS production exist in plants and include photosynthesis, respiration, glycolate oxidase, oxalate oxidase, xanthine oxidase, amine oxidase, excited chlorophyll, fatty acid oxidation, and peroxidases (Mittler 2002). These pathways were also found to play important roles in the response of plants to abiotic stresses. For example, oxalate oxidase was shown to be involved in ROS production in root cells during drought stress (Voothuluru and Sharp 2013). In addition, recent studies uncovered a role for peroxidase-dependent ROS in the regulation of root growth and response to potassium deficiency (Kim et al. 2010; Jia 2011; Kwasniewski et al. 2013). Interestingly, ROS production by peroxidases might not be functionally equivalent to ROS generated by RBOH proteins (Daudi et al. 2012; Wrzaczek et al. 2013). This hypothesis can be supported by the finding that stomatal closure and ROS burst induced by a yeast elicitor were not inhibited in *rbohD* and *rbohF* mutants in *Arabidopsis* (Khokon et al. 2010). Functional differences between RBOH proteins and peroxidases may be at least partially attributed to differences in the types of ROS generated via functions of these enzymes. Superoxide ($O_2^{\bullet -}$), generated by RBOH proteins, can activate specific signaling pathways distinct from those activated by H_2O_2 (Suzuki et al. 2011). Another possibility is that diverse functions between these different types of enzymes might be due to differences in their respective reductants. RBOH proteins utilize NADPH as a reductant for the generation of $O_2^{\bullet -}$. In contrast, different chemicals or compounds including phenols, organic acids, and auxin have been suggested as candidate reductants employed in the peroxidase-dependent generation of H_2O_2 (O'Brien et al. 2012). Pathways involving these different reductants could be integrated with ROS signals activated via the different functions of these enzymes.

3 Involvement of ROS in the Regulation of Systemic Acquired Acclimation to Abiotic Stress

Recent findings highlight the significance of cell-to-cell communication mediating long-distance systemic signaling in plants. Plants evolved sophisticated acclimation and defense mechanisms that can be activated in the tissue(s) locally exposed to biotic or abiotic stimuli, as well as in distal portions not directly exposed to these stimuli. These mechanisms play an important role in preventing further damage to the entire plant when part of tissues is exposed to biotic or abiotic stimuli. The activation of defense or acclimation mechanisms in systemic or non-challenged tissues is termed systemic acquired resistance (SAR) or systemic acquired acclimation (SAA), respectively (Karpinski et al. 1999; Rossel et al. 2007; Carr et al. 2010; Szechynska-Hebda et al. 2010; Dempsey and Klessig 2012; Spoel and Dong 2012; Shah and Zeier 2013; Baxter et al. 2014). A recent study revealed the existence of an H_2O_2-dependent long-distance signal induced by various abiotic stimuli (Miller et al. 2009b). RBOHD was shown to be required for the initiation and self-propagation of a rapid cell-to-cell signal transduction that is dependent upon H_2O_2 accumulation in the apoplast to generate a "ROS wave" (yellow arrows in Fig. 2) (Mittler et al. 2011). In addition, more recent study demonstrated the significance of the ROS wave in the SAA of plants to heat or high-light stresses

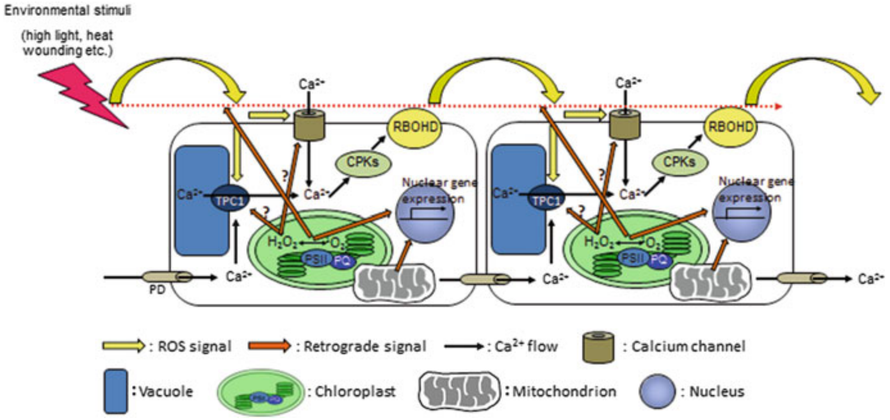

Fig. 2 Cellular pathways that regulate ROS-dependent systemic signaling and retrograde signaling. H_2O_2 generated via function of RBOHD is required for rapid signal propagation from cell to cell in response to different environmental stimuli, such as high light, heat, or wounding (Miller et al. 2009). The ROS and Ca^{2+} waves in cells are integrated via the function of respiratory burst homolog (RBOH) proteins, Ca^{2+}-dependent protein kinases, and calcium channels such as two-pore channel (TPC) 1. Changes in the redox state of PSII and the PQ pools in the chloroplast might activate electric signaling (red dotted arrow) at the plasma membrane involved in systemic responses (Szechynska-Hebda et al. 2010). The electric signal that is dependent upon the chloroplast redox state is also accompanied by ROS generation, implicating a cross talk between the RBOHD-dependent signal, electric signals on the plasma membrane, and ROS/redox signaling from chloroplast. Mitochondrial retrograde signaling (Rhoads and Subbaiah 2007; Pogson et al. 2008; Woodson and Chory 2008) could also play a key role in these responses as part of a cross talk network that senses different metabolic/environmental states and activates rapid systemic signaling. In addition, ROS produced via function of RBOH proteins or basic biological processes in different cellular components might induce different PCD pathways depending on abiotic stimuli. *Abbreviations*: *PD* plasmodesmata, *CPK* Ca^{2+}-dependent protein kinase

(Suzuki et al. 2013). The SAA of plants to abiotic stress is mediated by temporal–spatial interactions of the ROS wave, which function as a general priming signal, with stress-specific hormone or amino acid signals activated in systemic tissues. Calcium wave was recently shown to function as pivotal element of the systemic communication machinery (black arrows in Fig. 2) (Choi et al. 2014; Gilroy et al. 2014). In response to local stimulation with salt stress in the root tip, a wave of increased cytosolic Ca^{2+} level moves systemically through the plant paralleling with the ROS wave. The Ca^{2+} wave that travels at ~400 μm/s can spread through the root system and be transmitted to the aerial part of the plant. Application of the Ca^{2+} channel blocker lanthanum (La^{3+}) inhibited systemic induction of marker gene expression associated with ROS as well as Ca^{2+} wave, implying the link between ROS and Ca^{2+} wave. In addition, plant deficient in two-pore channel 1 (TPC1), a vacuolar ion channel, exhibited disruption of the propagation of the systemic Ca^{2+} wave.

4 Temporal Coordination Between ROS and Other Signals in the Regulation of Systemic Signaling in Plants

In response to changes in environmental conditions, early signaling events including increased Ca^{2+} levels in the cytosol, activation of MAPKs, accumulation of hormones, and production of ROS can all occur within seconds or minutes following application of abiotic stimuli (Benschop et al. 2007; Finka et al. 2012; Miller et al. 2009b). Early systemic responses of plants to abiotic stimuli have been previously described (Karpinski et al. 1999; Rossel et al. 2007; Muhlenbock et al. 2008; Szechynska-Hebda et al. 2010; Gordon et al. 2012). Studies employing transgenic plants expressing a luciferase reporter gene under the control of an APX1, APX2, or ZAT10 promoter demonstrated the activation of acclamatory responses within 5–20 min following application of high light both in leaves locally exposed to the stimuli and in distal tissues that were not directly exposed to the stimuli (Karpinski et al. 1999; Rossel et al. 2007; Szechynska-Hebda et al. 2010). Systemic responses to high light were shown to be associated with redox changes in the plastoquinone (PQ) pool, increased production of ROS and ethylene, reduction of maximal photochemical efficiency and non-photochemical quenching (NPQ), and changes in extracellular electric potential (Karpinski et al. 1999; Rossel et al. 2007; Szechynska-Hebda et al. 2010). In addition, amino acids involved in photorespiratory machinery, such as glycine, serine, and glycerate, rapidly accumulate in leaves directly exposed to high light within 60 s as well as in systemic tissues of plants at 15 and 45 min (Suzuki et al. 2013). Rapid local responses of these metabolites to high light were altered in the mutant lacking cytosolic APX1, demonstrating the involvement of H_2O_2 scavenging in this process.

In *Arabidopsis*, elevated levels of jasmonic acid (JA) accumulate in damaged tissues as well as undamaged systemic leaves within 30 s to 5 min in response to mechanical wounding (Glauser et al. 2009; Koo et al. 2009). The velocity of this long-distance signal leading to synthesis of JA in systemic tissues was 3.4–4.5 cm/min (Koo et al. 2009; Glauser et al. 2009). RBOHD-dependent long-distance signal is also a rapid auto-propagating systemic signal that travels at the rate of approximately 8.4 cm/min and is induced by various abiotic stimuli including mechanical wounding (Miller et al. 2009b). In addition, the potential involvement of electric signals that propagate with similar rates was also implicated in RBOHD-triggered rapid systemic signaling during wounding (Zimmermann et al. 2009; Mittler et al. 2011; Suzuki and Mittler 2012). These findings implicate the integration of JA and mobile signals such as ROS and electric signals. Peroxisomes that are responsible for the production of both H_2O_2 and JA might be a candidate of a key player to integrate JA and mobile ROS signals (Leon 2013). H_2O_2 is produced during the oxidation of glycolate to glyoxylic acid in photorespiratory processes (Mittler et al. 2004). JA is synthesized through the octadecanoid pathway involving the translocation of lipid intermediates from the chloroplast to the cytosol and later on into peroxisomes (Leon 2013). JA synthesized in the peroxisomes is transported to the cytosol, and JA-isoleucine conjugate, the bioactive form of the hormone, is then produced. Long-term responses to fluctuating environmental conditions regulate phenotypic changes such as growth, development, and survival of cells. Exposure of mature leaves to changes in light conditions and atmospheric CO_2 induces alterations in photosynthetic rate and tolerance to high light in new developing leaves not directly exposed to these environmental changes (Coupe et al. 2006; Araya et al. 2008; Jiang et al. 2012). Although alterations in photosynthetic rate and response to high light implicate ROS and redox signaling in the systemic regulation of long-term responses in new developing leaves (Muhlenbock et al. 2008; Li et al. 2009; Mittler et al. 2011), links between ROS signaling and these responses are still not uncovered.

Previous studies demonstrated that the biphasic production of ROS consists of a primary phase that occurs within minutes and a secondary phase that occurs within hours/days (Nishimura and Dangl 2010; Soares et al. 2009; Kunihiro et al. 2011; Mittler et al. 2011). For example, mechanical wounding induced an initial burst of $O_2^{\bullet -}$ within 3 min followed by later production of $O_2^{\bullet -}$ and H_2O_2 after 6 h (Soares et al. 2009). Inhibition of early phase of ROS production by an NADPH oxidase inhibitor suppresses later production of $O_2^{\bullet -}$ and accumulation of wound response proteins, indicating that an initial burst of ROS is required for the later phase of ROS production which regulates downstream acclamatory responses of plants to stress stimuli. In addition, a recent study suggests that these two phases of the ROS burst are linked via the ROS wave that communicates the initial ROS burst in the local tissue to the systemic tissue via a cell-to-cell relay mechanism (Miller et al. 2009b; Suzuki et al. 2013).

5 Spatial Coordination Between ROS and Other Signals in the Regulation of Systemic Signaling in Plants

To some extent, signals generated in plants during SAA are similar in local and systemic tissues. Rossel et al. (2007) compared the transcriptomes of local leaves, directly exposed to high light, and systemic leaves, not directly challenged by the stimulus. More than 70 % of the transcripts upregulated in local leaves in response to high light were also altered in their expression in systemic leaves, suggesting that similar signals exist between local and systemic tissues during SAA to high light. Similarities between local and systemic responses to high light is also supported by findings that alterations in ROS and redox signals and accumulation of amino acids associated with the photorespiratory pathway occurred both in local and systemic tissues (Muhlenbock et al. 2008; Szechynska-Hebda et al. 2010; Miller et al. 2009b). In addition, local application of heat or cold stimuli also can induce similar stress response proteins or transcripts in both local and systemic tissues (Gorsuch et al. 2010; Suzuki et al. 2013). In particular, induction of heat-responsive proteins in systemic tissue was shown to be RBOHD dependent (Suzuki et al. 2013).

Although signals generated in local and systemic tissues showed considerable overlap, previous studies have also demonstrated differences in alterations of transcripts or metabolites between these types of tissues. For example, ethylene accumulated both in local and systemic tissue in response to local application of high light; nevertheless, the signal regulated by EIN2 was shown to be required for induction of APX2 only in systemic tissues that are not directly subjected to high light (Muhlenbock et al. 2008). In addition, SID2 delays induction of APX2 only in leaves directly exposed to high light. These findings suggest that specific patterns of APX2 expression in local and systemic tissue might be regulated by the coordination between ethylene and salicylic acid (SA) signaling during SAA to high light. Moreover, spatial diversity in high-light responses between different leaves during SAA was also demonstrated by the findings that local high-light treatment resulted in the different expression levels of transcripts associated with regulation of ROS and redox signals depending on leaf position (Gordon et al. 2012).

How are signals generated in local and systemic tissues linked? The ROS wave may play a key role in propagating signals from local tissues to systemic tissues. The initial burst of ROS in a local group of plant cells triggers a cascade of cell-to-cell communication events that carries a systemic signal over long distances throughout different tissues of the plant (Miller et al. 2009b). Szechynska-Hebda et al. (2010) uncovered the pattern of systemic changes in NPQ, H_2O_2 concentration, and APX1 expression during SAA response of plants to high light. Wavelike patterns of APX1 expression in systemic tissue of plants correlate positively with H_2O_2 accumulation but negatively with NPQ (Szechynska-Hebda et al. 2010; Karpinski et al. 2013). The activation of systemic signals by local application of high light was recently shown to be accompanied by plasma membrane electrical signals in a light wavelength-specific manner (Szechynska-Hebda et al. 2010). In addition, the RBOHD-dependent ROS wave is associated with the generation and/or propagation of systemic potential variations (Suzuki et al. 2013). These finding suggest a link between electric signals in plants and ROS production.

6 Integration of ROS Signals with Other Signals

ROS signaling is integrated with various other signals including Ca^{2+} signaling, protein kinases, redox responses, and hormone signals. One good example of signaling networks associated with ROS signaling is MAPK cascade (Mittler et al. 2011; Petrov and Van Breusegem 2012). MPK3, MPK4, and MPK6 can all be activated by ROS and abiotic stresses, but different MKKs might transmit the signal depending on different stimuli (Jaspers and Kangasjarvi 2010). *Arabidopsis* overexpressing MKK2 exhibited constitutive MPK4 and MPK6 activity and resulted in increased tolerance of transgenic plans to salt and cold stress (Teige et al. 2004; Taj et al. 2010; Ismail et al. 2014). In contrast, overexpression of MKK9 that activates MPK3/MPK6 resulted in enhanced sensitivity of the transgenic plants to salt stress (Xu et al. 2008). In addition, activation of MPK6 by MKK3 was shown to be not required for salt stress response in plants (Takahashi et al. 2007). MEKK1 was suggested to be specifically required for the activation of MPK4 by H_2O_2 (Nakagami et al. 2006), and the signal between MEKK1 and MPK4 is mediated by MKK1 and MKK2 (Qiu et al. 2008). The MEKK1–MKK1/2–MPK4 pathway might play integral roles to regulate transcription factors that are highly responsive to ROS-generating conditions (Pitzschke et al. 2009). MPK8 could be a negative regulator of ROS wave (Marino et al. 2012). MPK8 which is activated by phosphorylation and direct binding of CaM in a Ca^{2+}-dependent manner has been shown to negatively regulate ROS production via control of RBOHD (Takahashi et al. 2011). Various forms of abiotic stress result in increased production of ROS which can be liked to signals caused by changes in the regulation of plant hormones (Fujita et al. 2006). Ethylene biosynthesis was found to be modulated by positive regulation via RBOH proteins and negative regulation via CTR1 (constitutive triple response 1) (Jakubowicz et al. 2010). In *Arabidopsis*, CTR1 can be inhibited by phosphatidic acid (PA) that positively enhances activation of RBOHD and RBOHF (Jakubowicz et al. 2010). Previous studies revealed the involvement of ethylene in the regulation of SAA to high light induced by local high-light application (Muhlenbock et al. 2008; Karpinski et al. 2013). In response to high light, alterations in the redox state of the PQ pool can initiate a signal that induces production of 1-aminocyclopropane-1-carboxylate (ACC, the immediate precursor of ethylene), ROS, and the expression of ethylene-regulated genes (Muhlenbock et al. 2008). Increased ROS production results in bleaching of leaves and programmed cell death that relies on regulation of ethylene-insensitive 2 (EIN2) by lesion stimulating disease 1 (LSD1) (Muhlenbock et al. 2008; Karpinski et al. 2013).

Involvement of brassinosteroid (BR) signaling in ROS-dependent stress responses was also supported by previous findings. For example, exogenous BR treatments resulted in enhanced tolerance to oxidative stress accompanied by induction of H_2O_2 production in apoplast and expression of RBOH, MPK1, and MPK3 (Xia et al. 2009). More recent studies demonstrated the involvement of BR in SAA to high light in cucumber (Xia et al. 2009, 2011; Li et al. 2013a). Although BRs are not directly involved in long-distance signaling, they affect other signals such as auxins and polyamines (Li et al. 2013a). A recent study indicated the involvement of auxin in SAA response of plants to high light. Large portions of the transcripts that are altered in their expression in the distal leaves overlap with auxin-responsive transcripts (Gordon et al. 2012), indicating a connection between SAA and developmental processes mediated by auxin. Integration between ethylene and BRs during SAA response to HL needs to be elucidated in future studies.

ROS can affect auxin biosynthesis, transport, metabolism, and signaling underlying regulation of stress responses in plants (Krishnamurthy and Rathinasabapathi 2013b). The integration of RBOH functions with auxin has been evidenced by the analyses of the various RBOH expressions following the exogenous auxin (IAA: indole-3-acetic acid) treatment in *Arabidopsis*. It was observed that RBOHD was highly activated in response to auxin (Peer et al. 2013). Auxin transport mutant *aux1* exhibited higher sensitivity to arsenite compared to WT plants, and H_2O_2

production was inhibited in *aux1* under this stress condition (Krishnamurthy and Rathinasababapathi 2013a). These results indicate that auxin transport plays positive role in induction of ROS production and protection of plants against arsenite. In addition, the auxin signaling mutant *tir afb2* showed reduced production of H_2O_2 and $O_2^{\bullet-}$ and increased activity of catalase and ascorbate peroxidase accompanied by enhanced tolerance to salt stress (Iglesias et al. 2010).

ABA is involved in a broad range of biological functions, and its integration with ROS has been evidenced in many reports (Ma et al. 2012; Sagi et al. 2004; Drerup et al. 2013; Kwak et al. 2003). For example, RBOHD and RBOHF function together to regulate stomatal closure, seed germination, root elongation, and Na^+/K^+ homeostasis under salt stress (Ma et al. 2012; Kwak et al. 2003). Overexpression of 9-*cis*-epoxycarotenoid in tobacco, an enzyme of ABA synthesis, enhanced tolerance of transgenic plants to drought and salt stress accompanied by increased ABA-induced production of ROS via the function of RBOHs (Zhang et al. 2009a). In addition, mild salt stress triggers biphasic changes in ROS production in *Arabidopsis* and maize, and RBOHD in *Arabidopsis* is required for ROS production following mild salt stress (Lin et al. 2009; Xie et al. 2011). Moreover, SAA of plants to heat stress was shown to be correlated with activation of the ROS wave and transient accumulation of ABA in systemic tissues, and these responses were suppressed in a mutant lacking RBOHD (Suzuki et al. 2013). The SAA response to heat stress was also attenuated in mutants deficient in ABA signaling. These results indicate that temporal–spatial interactions between RBOHD-dependent ROS and ABA mediate SAA to heat stress (Suzuki et al. 2013). Moreover, ABA and SA treatment have been shown to result in transient increases in H_2O_2 production which induces tolerance to heat, salt, high-light, and oxidative stress (Xia et al. 2009).

Integration of SA or JA signaling with ABA underlying stomatal closure has been addressed in a recent review (Song et al. 2014). ABA-deficient mutant *aba2-1* failed to close stomata in response to exogenous SA treatment, whereas guard cells of SA-deficient mutants *sid2* and *NahG* responded to ABA (Zeng and He 2010; Montillet and Hirt 2013; Song et al. 2014), indicating that SA signaling functions upstream of ABA signaling. SA-induced stomatal closure was inhibited by DPI, an NADPH oxidase inhibitor, and plants deficient in RBOHD exhibited defect in stomatal response to exogenous SA treatment (Kalachova et al. 2013). In contrast, several lines of other evidences suggested that SA mediates ROS production, not via NADPH oxidases, but rather via a peroxidase-catalyzed reaction (Mori et al. 2001; Song et al. 2014). The reduced stomatal apertures in SA-accumulating *siz1* mutant were rescued by the application of peroxidase inhibitors, but not by DPI (Miura et al. 2013). In addition, SA induces stomatal closure accompanied by extracellular ROS production mediated by peroxidase (Khokon et al. 2011). Mechanisms that regulate integration of SA signals to ROS-generating pathways need to be elucidated in future works. It was suggested that there is an overlap in the signals associated with stomatal closure between JA and ABA and that many common components including ROS production and Ca^{2+} oscillation are shared between these hormone signalings (Santino et al. 2013). *Arabidopsis* RBOHD and RBOHF were shown to be involved in the expression of methyl jasmonate (MeJA) response genes regulated by MYC2 transcription factor (Maruta et al. 2012).

7 Involvement of ROS in the Regulation of Retrograde Signaling

Under stress conditions, changes in the redox state of the chloroplast and mitochondria, ROS-producing organelles are the source of retrograde signaling that play crucial roles in stress acclimation of plants (Orange arrows in Fig. 2) (Suzuki et al. 2012; Choudhury et al. 2013). Three different processes in *Arabidopsis* were shown to induce chloroplast to nucleus signaling that alter the expression of nuclear genes, depending on the presence of GUN1 in the chloroplast and ABI4 in the nucleus: (1) accumulation of the chlorophyll biosynthesis intermediate Mg-protoporphyrin IX (Mg-Proto IX) and its methylester (Mg-Proto IX-ME), (2) inhibition of plastid gene expression (PGE) at the protein translation stage, and (3) changes in the redox state of the photosynthetic electron transfer (PET) chain (Koussevitzky et al. 2007; Woodson and Chory 2008).

Signals from the chloroplast to nuclei, modulated by changes in cellular redox state depending on the light intensity, might be an important process to respond to fluctuating light conditions (Szechynska-Hebda and Karpinski 2013). Under low light intensity, the transfer of signal from chloroplast to nucleus followed by changes in nuclear gene expression contributes to the adjustment of morphology of the leaves and cells, and number and structure of chloroplasts (Oelze et al. 2012). Light use efficiency is optimized at least partially by modulating stoichiometry of photosystems, light-harvesting antenna size, composition of the stromal enzymes, and activity of antioxidant systems (Muhlenbock et al. 2008; Pfannschmidt 2010; Foyer and Noctor 2011; Ruckle et al. 2012; Szechynska-Hebda and Karpinski 2013). Low light intensity can promote oxidation of PQ and reduction of thioredoxin, whereas high light intensity oppositely affects redox state in PQ pool and thioredoxin (Muhlenbock et al. 2008). Under high light intensity, PQ redox state and non-photochemical quenching (NPQ), the process to dissipate excess energy by heat, were shown to be potential regulators of retrograde signals that are required for at least regulation of APX1 and APX2 expression (Szechynska-Hebda et al. 2010). Imbalance between ATP and NADPH synthesis might be also an initiator of retrograde signaling (Szechynska-Hebda and Karpinski 2013). High proportion of NAD(P)H/NAD(P), ATP/ADP, and ATP/NADPH ratio could lead to inactivation of the photosynthetic electron transport chain components, resulting in production of $^1O_2$ and $O_2^{\bullet-}$ followed by deregulation of chloroplast metabolism and altered expression of stress response genes (Szechynska-Hebda and Karpinski 2013). In addition, excess excitation energy (EEE) also induces the changes in cellular ROS homeostasis and affects the expression of nuclear genes that control SAR and SAA (Rossel et al. 2007; Szechynska-Hebda et al. 2010). Progression of excess energy-induced PCD initiated by redox changes in PQ pool is regulated by the coordination between LSD1, EDS1, PAD4, and EIN2 that are associated with ethylene signaling and ROS production.

Upon illumination, chloroplast precursor, protochlorophyllide (PChlide), Mg-Proto IX, and Mg-Proto IX-ME produce $^1O_2$ that can act as a signaling molecule from chloroplast to nuclei (Tripathy and Oelmuller 2012). The $^1O_2$-dependent retrograde signaling has been extensively studied using the *Arabidopsis flu* mutant that massively accumulates PChlide and $^1O_2$ and exhibits growth retardation and cell death under constant dark/light cycle (op den Camp et al. 2003; Apel and Hirt 2004; Wagner et al. 2004; Laloi et al. 2007; Lee et al. 2007). Transcriptome analysis revealed a set of genes that can be specifically activated by $^1O_2$, not by H_2O_2 or $O_2^{\bullet -}$ (op den Camp et al. 2003; Gadjev et al. 2006; Suzuki et al. 2011), suggesting that chloroplast to nucleus retrograde signaling is at least partially regulated by $^1O_2$-specific signaling. Two plastid-localized proteins EXECUTER1 and EXECUTER2 are required for $^1O_2$-dependent gene regulation and cell death (Lee et al. 2007). Moderate light exposure induces acclimation mechanisms that protect plants against more severe high-light stress, and $^1O_2$ production and EXECUTER-dependent signal can be activated during this acclamatory process (Zhang et al. 2014), indicating the significance of $^1O_2$-dependent retrograde signaling in the regulation of light acclimation of plants. In addition, nuclear topoisomerase VI and oxygenation derivatives of linoleic acid, the prominent polyunsaturated fatty acid of chloroplast membrane lipid, might also play an important role to integrate $^1O_2$-dependent signal with regulation of nuclear gene expression (op den Camp et al. 2003; Tripathy and Oelmuller 2012). The oxidation of linoleic acid was shown to be not directly caused by $^1O_2$, but enzymatic reactions regulated by $^1O_2$ signals (op den Camp et al. 2003; Tripathy and Oelmuller 2012). Furthermore, $^1O_2$-linked cell death activator (soldat8) that encodes SIGMA6 factor of the plastid RNA polymerase was identified as specific suppressor of $^1O_2$-dependent stress responses in *flu* mutant (Coll et al. 2009). The other protein pleiotropic response locus 1 (PRL1) also affects the expression of $^1O_2$ response genes in *Arabidopsis* (Baruah et al. 2009).

In a recent study, integration between ABI4 and redox metabolism was investigated using the ascorbic acid-deficient mutants, *vtc1* and *vtc2* (Kerchev et al. 2011). The transcriptome signatures of *abi4*, *vtc1*, and *vtc2* mutants extensively overlap with large number of transcription factors and other regulatory genes (Kerchev et al. 2011). In addition, ABA and JA signaling synergistically function to regulate the growth of plants through ABI4 in ascorbic acid-dependent manner (Kerchev et al. 2011). Although it is still not clearly understood, H_2O_2 produced in chloroplasts was also implicated in retrograde signaling (Shapiguzov et al. 2012). H_2O_2-dependent retrograde signaling might be a combination of passive diffusion of H_2O_2 with indirect pathways involving ABA signaling (Mullineaux and Karpinski 2002; Galvez-Valdivieso and Mullineaux 2010). H_2O_2 might not be, however, the signaling molecule that directly affects nuclear gene expression; rather, redox-sensitive components such as oxidized proteins or peptides might mediate the signal transfer from the chloroplast to nucleus (Moller and Sweetlove 2010; Sierla et al. 2013).

Although mitochondrial retrograde signaling is poorly understood compared with the chloroplast to nucleus retrograde signaling, key regulators of mitochondrial retrograde signaling have been identified in recent studies. A membrane-bound NAC transcription factor, ANAC017, was found to be a regulator of

AOX1a, a marker gene of mitochondrial retrograde signaling (Ng et al. 2013). ANAC017 mediates H_2O_2-induced alterations in transcript abundance. The *abi4* mutants are insensitive to transcriptional derepression of AOX1a by the mitochondrial complex I inhibitor rotenone, indicating a role for ABI4 in redox regulation and mitochondria to nucleus retrograde signaling (Giraud et al. 2009). This work demonstrated the integral role of ABI4 to mediate mitochondrial and chloroplast retrograde signaling pathways, and perhaps it is the convergence point for mitochondria–plastid–nucleus coordination.

8 Programmed Cell Death Regulated by ROS Under Abiotic Stress

A low dose of ROS acts as signaling molecules that mediate at least part of stress responses, but they induce programmed cell death (PCD) at higher concentrations. PCD is a genetically controlled process in which only cells that are destined to die are selectively destroyed in a multistep fashion via the functions of specific proteases and nuclease (Petrov et al. 2015). Thus, no damage to the neighboring cells is inflicted. In addition, metabolism in the rest of cells and tissues can be appropriately adjusted to acclimate to or survive under stressed conditions by this process. Here, stress-specific pathways that positively regulate PCD will be mainly discussed. More detail of PCD under abiotic stress has been addressed in more extensive review (Petrov et al. 2015).

Severe drought enhances ROS production mainly due to decreased CO_2 fixation accompanied by increased leakage of electron to $O_{2,}$ which may result in induction of PCD (Gechev et al. 2012). ROS production is inhibited by suppression of chlorophyll synthesis and photosynthetic activity, and modification of sucrose metabolisms under drought (Petrov et al. 2015; Liu et al. 2013). Although plants possess mechanisms to prevent unnecessary PCD, leaf senescence executed by ROS-triggered PCD acts as an important adaptation process of plants to drought (Petrov et al. 2015). ROS-triggered PCD under drought was shown to be regulated by coordination between ABA and cytokinin (Munn-Bosch and Alegre 2004). PCD characterized by degradation of organelles, increased size of the vacuole, and plasmalemma collapse can be induced in root tip meristems under drought (Duan et al. 2010). This adaptive mechanism in the root might be a strategy of plants to enhance lateral root growth. Reorientation of polyamine metabolism, as well as stomatal closure, is a drought response mechanism in which ABA plays pivotal roles. In grapevine, ABA induces accumulation of polyamine that is metabolized by amine oxidases, and H_2O_2 can be produced as a by-product of this reaction (Toumi et al. 2010). H_2O_2 produced in this reaction might be a regulator of further stress response or induction of PCD. PCD acts as an important process to protect plants against flooding stress. Under this stress condition, aerenchyma is formed by PCD in selected cells to produce air channels in roots (Gunawardena et al. 2001). Significance of ROS in the formation of aerenchyma has been indicated by the finding that exogenous application of H_2O_2 stimulated formation of aerenchyma in rice (Steffens et al. 2011). In addition, expression of RBOHD was highly enhanced during water logging conditions in maize, suggesting that RBOHD-dependent production of H_2O_2 play a key role in the formation of aerenchyma (Rajhi et al. 2011). Furthermore, mitochondrial dysfunction and accumulation of metal ion was also shown to increase ROS production under flooding stress (Shabala et al. 2014).

Although involvement of $O_2^{\bullet -}$ produced via the function of NADPH oxidase is implicated in PCD pathway under salt and osmotic stress, signals activated by ionic salt and nonionic osmotic stress inducer (i.e., sorbitol) did not show extensive overlap (Monetti et al. 2014; Petrov et al. 2015), indicating the specificity of the mechanism regulating PCD under these stresses. Specific feature of salt-induced PCD is characterized by ion disequilibrium that may be due to invasion of Na^+ into the cytosol accompanied by a decrease in K^+ (Kim et al. 2014). Hydroxyl radicals in cells might affect K^+/Na^+ ratio and regulate enzymes involved in PCD (Demidchik et al. 2010). In addition, an anti-apoptotic protein BCL2 can regulate vacuolar processing enzymes (VPE) by modulating ion fluxes in rice (Kim et al. 2014). Overexpression of BCL2 exhibited enhanced PCD symptoms accompanied by significantly reduced K^+ efflux and represses the expression of VPEs. These findings suggest that maintenance of proper Na^+/K^+ ratios could be a key process to enhance salt stress tolerance in plants (Huh et al. 2002; Teakle and Tyerman 2010).

Mitochondria are responsible for the regulation of PCD induced during heat stress (Vacca et al. 2004). Functionally active cytochrome c can be released from the mitochondria in a ROS-dependent manner, and caspase-like protease that induces PCD is then activated (Vacca et al. 2004). Proline that was implicated in mitochondrial ROS metabolism (Miller et al. 2009a) might be a specific component to cause cell death during heat stress. Although it acts as an osmolyte and ROS detoxifier under salt and osmotic stresses, it can negatively impact on cells under heat stress (Lv et al. 2011). In addition, exogenous application of ascorbate or glutathione (i.e., unspecific antioxidants) induced PCD in *Arabidopsis* cells under heat stress. On the other hand, catalase that specifically detoxifies H_2O_2 suppressed PCD. These finding suggest that H_2O_2 functions as PCD-inducing signal, but other types of ROS might act as negative regulator of PCD during heat stress (Doyle and McCabe 2010). Furthermore, MPK6 was found to be a component of PCD under heat stress. Enhanced accumulation of ROS and cytosolic Ca^{2+} can activate NPK6 that functions upstream to hydrolases and proteases associated with PCD (Li et al. 2012).

Low temperature is also able to induce PCD in plants when combined with elevated light intensity. LSD1, a negative regulator of PCD, interacts with catalase, and its deficiency can enhance low-temperature-induced PCD in plants (Huang et al. 2010; Li et al. 2013b). LSD1 and EDS1 proteins antagonistically regulate the acclimation of plants to UV-C stress. Plants deficient in LSD1 exhibited enhanced PCD following UV-C treatment. On the other hand, knocking out of EDS1 repressed UV-C-induced PCD (Wituszynska et al. 2015). The UV-C response associated with LSD1 and EDS1 is regulated by the modulation of ROS homeostasis. In response to high dose of UV-B, a defense program involving SA, JA, ethylene, and senescence-associated processes is activated to prevent oxidative damage in plants (Bandurska et al. 2013). These findings indicate the cross talks in the pathways associated with PCD between low-temperature, high-light, UV-B and UV-C, and pathogen responses.

9 Conclusions

ROS play an integral role in the regulation of numerous responses to abiotic stresses in plants. The complexity in ROS responses to various environmental stimuli might be, at least partially, attributed to different regulatory mechanisms of ROS production via basic biological processes and NADPH oxidases (RBOHs) that function in an array of organelles, tissue types, and developmental stages under various environmental conditions. A key mechanism in coordinating the complex spatial and temporal responses in plants is the cascade of cell-to-cell communication events that result in the formation of a wave of ROS production and increase in cytosolic Ca^{2+} that rapidly propagates throughout the different tissues of the plant. Networks of ROS/redox signaling in the chloroplast and mitochondria contribute to a delicate balance of homeostasis within each organelle, as well as to cross talk between different cellular components by regulating important biological pathways such as nuclear gene expression and energy metabolism under stress conditions. Functions of chloroplasts and mitochondria might be the key mediators for signal transductions in the cell because they are involved in the regulation of important pathways including systemic signaling, retrograde signaling, and PCD under stress conditions. In addition, there is a great overlap in the regulatory mechanisms between RBOHD-dependent systemic response, chloroplast/mitochondrial retrograde signaling and PCD, suggesting a cross talk between these pathways. Detailed mechanisms to coordinate or integrate these different ROS-dependent pathways need to be elucidated in future works. In addition, we also need to address how different pathways switched depending on the different environmental stimuli. This question could be answered by studying integration between ROS signaling and sensors of different stimuli.

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