MINI-REVIEW

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Oxidative stress tolerance in plants

Novel interplay between auxin and reactive oxygen species signaling

Aparna Krishnamurthy and Bala Rathinasabapathi*

Horticultural Sciences Department; University of Florida; Gainesville, FL USA

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Biotic and abiotic stress conditions produce reactive oxygen species (ROS) in plants causing oxidative stress damage. At the same time, ROS have additional signaling roles in plant adaptation to the stress. It is not known how the two seemingly contrasting functional roles of ROS between oxidative damage to the cell and signaling for stress protection are balanced. Research suggests that the plant growth regulator auxin may be the connecting link regulating the level of ROS and directing its role in oxidative damage or signaling in plants under stress. The objective of this review is to highlight some of the recent research on how auxin's role is intertwined to that of ROS, more specifically H_2O_2, in plant adaptation to oxidative stress conditions.

Auxin and ROS

The plant growth regulator auxin has been well known for regulating many growth and developmental processes such as meristem development, cell division, cell elongation and maintenance of polarity.[1,2] More recently, auxin's function has also been connected to plant defense against stress. Oxidative stress is a component of many abiotic stress conditions such as drought,[3] high temperature stress,[4] salinity[5] and heavy metal stress[6] and biotic stress conditions such as herbivory[7] and plant pathogen interactions.[8] During these stress conditions, levels of reactive oxygen species (ROS) increase, potentially resulting in oxidations of DNA, proteins and lipids. During plant adaptation, however, cellular repair machineries reduce at least some of these oxidized macromolecules. At the same time, ROS have additional signaling roles in plant adaptation to the stress (**Fig. 1**).

Auxin and ROS are rapidly altered by environmental stress factors. ROS can have effects on auxin biosynthesis, transport, metabolism and signaling.[9] Major ROS molecules in cells include superoxide anion (O_2^-), hydroxyl radical (·OH), singlet oxygen ($^1O_2$) and hydrogen peroxide (H_2O_2). They are produced in various cell compartments mainly chloroplasts, mitochondria, peroxisomes, endoplasmic reticulum, plasma membrane, cell wall and apoplast and this aspect has been extensively reviewed.[10,11] Hydrogen peroxide is one of the major ROS compounds produced in and outside the cells during abiotic and biotic stress conditions.[12] Studies show that exogenous auxin application induces H_2O_2 in plants[13,14] and that may be the mode of action for auxin type herbicides.[15] On the contrary, exogenous auxin reduced the H_2O_2 accumulation in the roots of tomato through altered expression and activity of H_2O_2 scavenging enzymes catalases, Cu-Zn-superoxide dismutase (SOD) and peroxidases.[16] Reactive oxygen species production was shown to be essential for auxin-regulated gravitropism in maize roots.[17] Scavenging of ROS by the addition of antioxidants inhibited root gravitropism.[17] It was shown that phosphatidylinositol 3-kinase activation was required for auxin-induced H_2O_2 production and root gravitropism.[18] Pre-treatment with inhibitors of phosphatidylinositol 3-kinase stopped ROS production in root tissue and root protoplasts of maize, while the addition of exogenous auxin induced phosphatidylinositol 3-kinase activity.[18] A study on barley root tip indicated that the application of auxin signaling inhibitor reduced cadmium-induced H_2O_2 production and growth response.[19] Auxin-induced plant cell elongation is mediated by the production of ·OH, H_2O_2 and $O_2^{\cdot -}$.[20] The production of ·OH from O_2^- and H_2O_2 from peroxidase reactions act as cell wall loosening agents[20] and help in extensibility by breaking the backbones of cell wall polysaccharides.[21]

Arsenite (AsIII) is a toxic metalloid known to induce oxidative damage in cells. We used this as a tool to identify the role of auxin in oxidative stress tolerance in *Arabidopsis*.[22] The auxin transporter mutant *aux1* was more sensitive to AsIII than the wild-type. During AsIII stress, compared with *aux1*, wild-type *Arabidopsis* plants produced increased H_2O_2 which helped them tolerate the stress better than the mutant. This indicated that AUX1 had a positive role in induction of H_2O_2 production during stress.[22] Our results are corroborated by a study conducted on auxin signaling mutant.[23] The auxin signaling mutant, *tir1afb2* (double mutant for auxin receptors TIR1-Transport Inhibitor Response1 and AFB2-auxin signaling F-box 2)[24] showed reduced accumulation of H_2O_2 and superoxide anion, and had enhanced activities of antioxidant enzymes catalase and ascorbate peroxidase.[23] These results indicate that auxin homeostasis in specific

*Correspondence to: Bala Rathinasabapathi; Email: brath@ufl.edu

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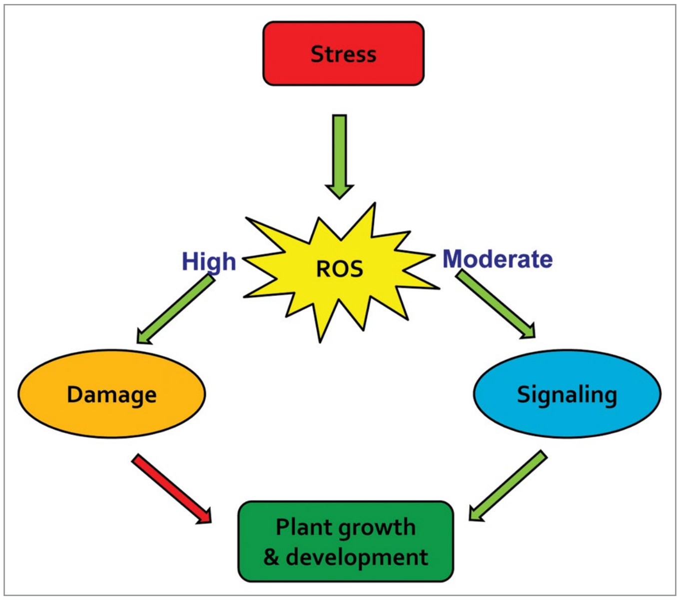

Figure 1. Dual role of reactive oxygen species (ROS) during stress. Green arrows indicate positive effects and red negative effects.

tissues is important to regulate the production of H_2O_2 through altered expression of antioxidant enzymes.

Auxin and ROS Signaling

Production of superoxide by NADPH oxidase is the first step in the formation of H_2O_2.[25,26] Auxin-induced NADPH oxidase activity has been recorded in isolated vesicles and elongating hypocotyls of soybean.[27] This activity was inhibited by the addition of thiol reagents like dithiothreitol, and reduced glutathione.[27] In *Arabidopsis* root, it is shown that transient increase in extracellular ATP(eATP) is perceived by the plasma membrane leading to the production of reactive oxygen species mainly through the action of NADPH oxidase (AtRBOHC) followed by the activation of Ca^{2+} channels.[28] *AtrbohC* mutants were impaired for eATP buildup, ROS production, increase in Ca^{2+} and transcription of mitogen-activated protein kinase 3 (MAPKinase3).[28] Mitogen-activated protein kinase was found to be induced by H_2O_2 treatment which in turn was able to activate antioxidant enzymes.[29] During salt stress tolerance, the H_2O_2 and Ca^{2+} signaling was triggered by H^+ coupled ion transporters like H^+-ATPase in *Populus euphratica*.[30] Exogenous supply of auxin induced H^+-ATPase activity in petunia pollen by hyper polarization of plasma membrane and transient increase in cytosolic Ca^{2+}.[31] Inhibitors of NADPH oxidase of plasma membrane blocked this process. Hydrogen peroxide application mimicked the exogenous IAA application in the male gametophyte indicating the process is mediated by production of ROS.[31]

Mitochondrial electron transport chain is a site of ROS production. A study on *Arabidopsis* mutant *abo6* coding a mitochondrial DEXH box RNA helicase indicated that these mutants accumulated more ROS than the wild-type and were impaired for auxin signaling, suggesting ABA's role in its enhancement of auxin signaling.[32]

There are lines of evidence in *Arabidopsis* for localized accumulation of auxin increasing H_2O_2 production.[14] Exogenous auxin application was found to produce H_2O_2 and induced an accumulation of irreversible inactive form of auxin, 2-oxindole-3-acetic acid (oxIAA).[14] This form of auxin was not transported from cell to cell and was found at high levels in auxin transporter (ABCB) mutants. The oxIAA was not able to activate auxin signaling suggesting the importance of auxin metabolism in manipulating auxin signaling.[14]

Thiol Reduction Systems in Auxin Regulation

Thiol reduction systems, NADPH-dependent thioredoxin reductases and glutathione (GSH) affect the developmental processes in *Arabidopsis* by interfering with auxin signaling.[33] In this study, Trx reductase (*ntra ntrb*-mutant with inactivated cytosolic and mitochondrial thioredoxin reductases) and glutathione biosynthesis mutations (*cad2-Cd hypersensitive*) negatively altered auxin transport and metabolism and the triple mutant *ntra ntrb cad2* had defects in the auxin-regulated phenotypes.[33] Low glutathione availability correlated with the reduction in expression of PIN auxin transporters PIN1, PIN2, PIN3, PIN4 and AUX1 and auxin response marker gene IAA1.[33] Triple mutant *ntra ntrb cad2* had flowerless phenotype similar to the pin mutants which was rescued by the addition of GSH. Also, the mutant calli lacked the ability to regenerate shoots in the absence of exogenous auxin. In the same way, mutants of ROXY1 and ROXY2, CC-type glutaredoxins show abnormalities in petal and anther development in flowers of *Arabidopsis*,[34-36] suggesting auxin-related phenotypes.

Parallel to these observations, *atgrxs17 Arabidopsis* mutant for a GSH-dependent thiol transferase (glutaredoxin) were sensitive to high temperature stress and accumulated higher amounts of ROS and displayed altered auxin response phenotype.[37] *Arabidopsis* mutants for AtGrxS17 displayed post embryonic growth phenotypes similar to that of auxin perception mutants.[37] These mutants had altered auxin sensitivity and polar auxin transport[37] compared with wild-type plants. Exogenous GSH application rescued hyponastic leaf curling caused by altered auxin levels in catalase2 (*cat2*) mutant which accumulates high levels of H_2O_2.[38] These results together indicate that thiol reduction pathways are involved in the regulation of auxin homeostasis and resulting phenotypes.

Role of H_2O_2 and Auxin in Abiotic Stress Tolerance

Reactive oxygen species in plants are known to be produced during biotic and abiotic stress conditions having dual roles (**Fig. 1**) of causing damage and signaling to induce defense responses.[39,40] Several studies suggest a link between auxin homeostasis and H_2O_2 in plant stress tolerance but the mechanistic details are not well understood. Auxin transport mutant *aux1* was more sensitive to arsenite stress than wild-type seedlings in *Arabidopsis*.[22] Wild-type plants recorded increased H_2O_2 on arsenite stress treatment but not in *aux1* mutant indicating a positive role of

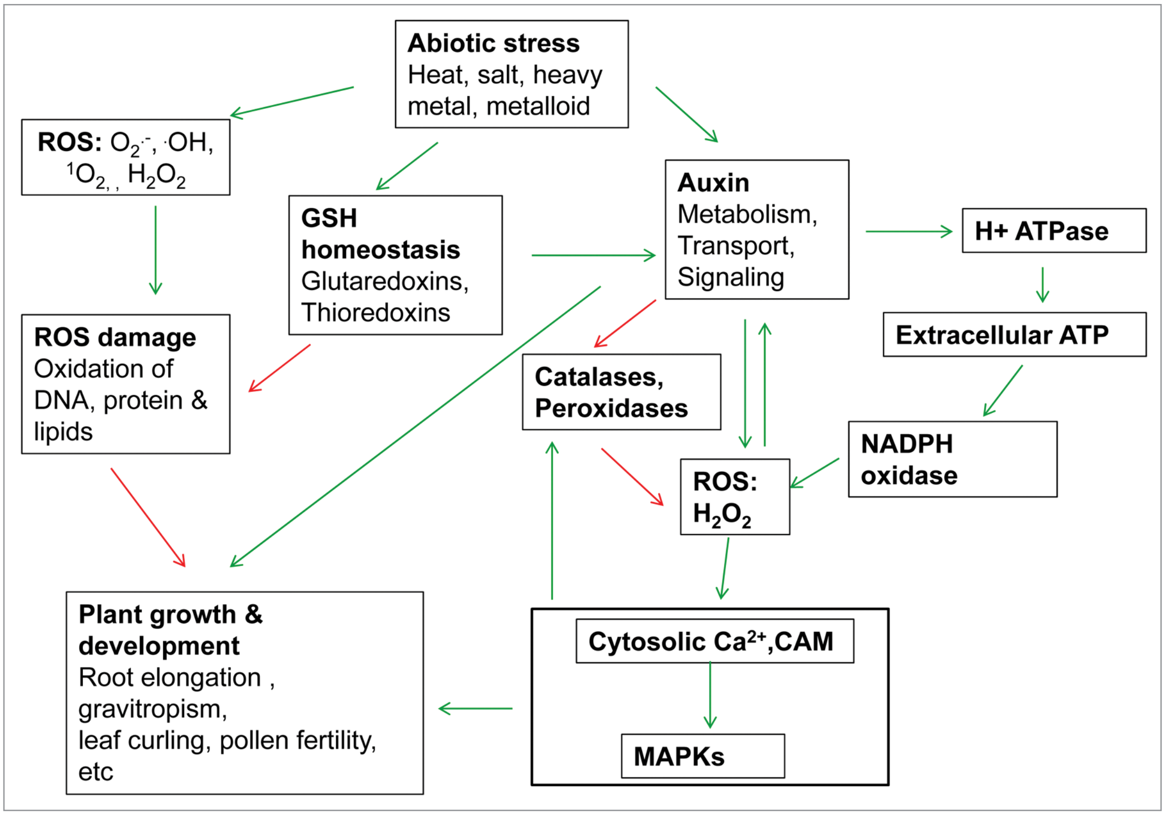

Figure 2. The metabolic interplay between auxin and hydrogen peroxide to control plant growth, development and stress tolerance. Green arrows indicate positive effects and red negative effects.

auxin transporter in production of ROS. Auxin transport mutant *aux1* was also found to be hypersensitive to high temperature and salt stress indicating a common functional role of auxin transport in stress tolerance to heat, salt and arsenite.[22] Increase in H_2O_2 was also correlated with reduced transcription of the catalase-3 in the wildtype.[22] This can be attributed to the reduced auxin transport and accumulation in the roots of *aux1* mutant and its inability to induce H_2O_2 signaling.

Several other phenotypes of the ROS signaling mutants were reversible by the addition of exogenous auxin signifying the cross-link between auxin and ROS. Defects in shoot regeneration from the calli and secondary root production in Trx reductase mutant *ntra ntrb cad2* were rescued by exogenous supply of auxin suggesting that the mutants were less sensitive to auxin or auxin was limiting in these mutants.[33] High temperature causes tissue specific reduction in auxin which leads to pollen sterility. Application of auxin completely reversed male sterility in barley and *Arabidopsis*.[41] This is consistent with the report in *Arabidopsis* that auxin transporter PIN8, expressed in the male gametophyte is critical for auxin homeostasis and normal development of the male gametophyte.[42] In the presence of cytosolic Ca, calmadulin (CaM) a calcium binding protein was able to bind to and activate catalase extracted from tobacco leaves.[43] Activation of catalase by Ca^{2+}CAM was found to be unique to plants and no such activation was found in bovine, human or fungal catalases, thus suggesting unique regulation of H_2O_2 concentration and signaling to environmental signals.[43] Because auxin could increase cytosolic calcium, the control on H_2O_2 levels by auxin could be due to CaM's effects on catalase activity. A recent study demonstrated that a catalase-deficient mutant (*cat2*) had reduced catalase activity, increased H_2O_2 accumulation and reduced auxin levels in the *Arabidopsis* leaves, leading to an "up curling phenotype" under photorespiratory conditions.[38] This implies that auxin levels in the leaves were modulated by H_2O_2 levels. Exogenous application of auxin was also able to rescue the mutant phenotype.[38] The same results of rescued phenotype could be achieved by the application of GSH which was found to induce the transcription of auxin biosynthetic genes.[38]

Accumulating evidence from studies in different plant species indicate that auxin's function in plants growth, development and more recently in stress response could be mediated via ROS signaling. Key events relating to auxin and ROS regulating plant growth, development and stress tolerance are summarized in **Figure 2**. The regulated processes include root gravitropism, extension growth, pollen tube growth, arsenite tolerance and high temperature stress tolerance. Further studies are required to examine the link between auxin and ROS homeostasis and the signaling cascades. These studies also open new possibilities to alter crop tolerance to stress by engineering auxin synthesis and metabolism, auxin signaling, ROS signaling and thiol-mediated regulatory pathways.[44] New uses for exogenous auxin to optimize crop performance under stress could be explored.[41]

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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