



ROS-hormone interaction in regulating integrative defense signaling of plant cell

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Abstract: The elaborate redox network of the cell, comprising of events like turnover of reactive oxygen species (ROS), redox sensing, signaling, expression of redox-sensitive genes, etc., often orchestrates with other bonafide hormonal signaling pathways through their synergistic or antagonistic action in the plant cell. The redox cue generated in plant cells under fluctuating environmental conditions can significantly influence other hormonal biosynthetic or signaling mechanisms, thereby modulating physiology towards stress acclimation and defense. There is also strong evidence of the recruitment of ROS as a 'second messenger' in different hormonal signaling pathways under stress. Moreover, the retrograde signaling initiated by ROS also found to strongly influence hormonal homeostasis and signaling. The present review, in this aspect, is an effort towards understanding the regulatory roles of ROS in integrating and orchestrating other hormonal signaling pathways or *vice versa* so as to unfold the relationship between these two signaling episodes of plant cells under environmental odds. We also accentuate the significance of understanding the utterly complex interactions, which occur both at metabolic and genetic levels between ROS and phytohormones during stress combinations. Furthermore, the significant and decisive role of ROS turnover, particularly the contribution of RBOH (respiratory burst oxidase homologs) in the synergism of redox and hormone signaling during systemic acquired acclimation under stress is also discussed.

Introduction

Being sessile and poikilothermic, plants are often exposed to several environmental stresses, individually or in combination. These environmental inputs, mostly non-conductive, need to be processed systematically for appropriate adaptive response in plant cells for their survival. Plant growth regulators or hormones could be the prime agents in orchestrating and processing the odd environmental cues necessary for conferring stress acclimation (Suzuki *et al.*, 2016; Souri *et al.*, 2020; Skalak *et al.*, 2021). Therefore, specific regulation of synthesis and functional control of growth regulators are prerequisites that determine plant performance under stresses. Hormones, particularly abscisic acid (ABA), salicylic acid (SA), ethylene (C₂H₄), jasmonic acid (JA), gibberellic acid (GA), indole-acetic acid (IAA), are known to regulate plant perception of unfavorable environmental cues and transduce to an adaptive

response. The roles of these hormones in integrating environmental stress with adaptive response and morphogenesis have been known for a long time (Verma *et al.*, 2016; Souri *et al.*, 2020; Skalak *et al.*, 2021). The last three decades also witnessed several works that strongly convey the significance of redox biology in regulating the stress tolerance of plants (Anjum *et al.*, 2016; Mittler, 2017; Bhattacharjee, 2019; Sies, 2021). In fact, in plants, apart from stress sensing, reactive oxygen species (ROS) control different environmental cues and regulate the initiation of different stress-response networks, thus significantly contributing to the defense mechanisms toward climate resilience (Bhattacharjee, 2019; Kollist *et al.*, 2019; Mittler *et al.*, 2022; Martin *et al.*, 2022). Works in the domain of plant redox biology strongly advocated the position of ROS as signaling molecule with several selective advantages, like their ability to have dynamic changes in their endogenous titer, their control over sub-cellular localization, the ability of long-distance transfer of cell propagating signals and above all, their linkage with cellular metabolism (Fichman and Mittler, 2020; Mittler *et al.*, 2011; Mittler, 2017; Bhattacharjee, 2019). The literature survey also proposes a strong relationship between ROS with

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other hormonal signaling for integrating responses under different environmental inputs. In fact, many works suggest the role of redox signaling in regulating the functioning of other hormones for processing information of unfavorable environmental cues necessary for appropriate response (Mittler *et al.*, 2011, 2022; Bhattacharjee, 2012; Bartoli *et al.*, 2013; Foyer and Noctor, 2013). Several works in this aspect proposed the feed-forward and backward interaction between hormonal and ROS signaling, necessary for the perception of unfavorable environmental cues, stress acclimation, and developmental processes (Table 1, Fig. 1). The stress acclimation performances, like regulation of stomatal conductance, hydraulic conductivity, secondary root formation, etc., which were previously thought to be regulated by hormonal signaling, now proved to be largely influenced and regulated by ROS-hormone interaction (Sakamoto *et al.*, 2008; Miller *et al.*, 2010; Bhattacharjee, 2019).

There is also evidence of both upstream and downstream redox regulation of hormonal pathways, where ROS not only act as a secondary messenger in downstream pathways of hormone signaling but can also influence hormone signaling by interfering with their biosynthesis and signaling episodes (Chen *et al.*, 1993; Mittler, 2017). For example, hydrogen peroxide (H₂O₂) has been found to be recruited as a

secondary messenger during ABA signaling and is also found to be involved in the up-regulation of the synthesis of ABA, C₂H₄ and SA (León *et al.*, 1995). Further, plant growth regulators or phytohormones like auxin, GAs, cytokinin (CKs), ABA, ethylene, SA, JA, brassinosteroids (BR), and strigolactones (SLs) may initiate important signaling cascades for stress adaptation. These signaling cascades do not act in isolation; rather, these pathways are interfered with and regulated by ROS, which can subsequently change the course of the signaling pathway in response to environmental stimuli (Peleg and Blumwald, 2011). With evolution, plants have developed several redox-sensitive proteins, some of which are the components of hormone signaling, that can modulate metabolism in response to stress. Those redox-sensitive molecules are mostly transcription factors (TFs) or protein molecules that act on several other TFs directly or indirectly, which can subsequently change an array of gene expression (Bhattacharjee, 2012; Sharma *et al.*, 2012; Mittler *et al.*, 2022). Most stress hormones (ABA, ethylene, SA, etc.) are linked to the redox status of a cell or directly to the endogenous titer of ROS for their functioning and controlling stress response mechanisms. According to

TABLE 1

Reactive oxygen species (ROS)-hormone interaction dependent molecular events and physiological response under different abiotic stress

ROS-hormone interaction	Stress condition	Molecular response	Physiological effect	References
SA-ROS	Drought	SA promotes ROS function via NADPH oxidase-dependent and independent pathway	Stomatal regulation under drought	Prodhan <i>et al.</i> (2018), Miura <i>et al.</i> (2013)
IAA-ROS	Drought	Oxidative degradation of IAA via POX	Altered auxin signaling under drought	Xia <i>et al.</i> (2015), Choudhury <i>et al.</i> (2017)
GA-ROS	Drought	Regulation of ROS level by low titer GA induced DELLA protein	Regulation of AOX defense under drought	Achard <i>et al.</i> (2009)
C ₂ H ₄ -ROS	Drought	C ₂ H ₄ induced promotion of H ₂ O ₂ synthesis via activation of RBOH	Stomatal closure under drought	Desikan <i>et al.</i> (2006)
C ₂ H ₄ -ROS	Cold stress	Ethylene-responsive TF-mediated activation of ROS hormone static genes	Cold tolerance through redox regulation	Klay <i>et al.</i> (2018)
ABA-ROS	Salinity stress	ABA-induced ROS generation and regulation of Na ⁺ /K ⁺ homeostasis	Regulation of ion homeostasis and salinity tolerance	Ma <i>et al.</i> (2012)
C ₂ H ₄ -ROS	Salinity stress	Ethylene-induced activation of RBOH F and genesis of ROS for redox signaling and activation of ion homeostatic genes	Ion homeostasis	Jiang <i>et al.</i> (2013)
ABA/C ₂ H ₄ /MJ-ROS	Drought	ABA and ET inhibit MJ-mediated stomatal closure by modulating ROS formation	Stomatal regulation under drought withdrawal condition	Medeiros <i>et al.</i> (2020)
ABA-ROS	Heat stress	ABA-dependent ROS formation towards redox signaling and AOX defense	AOX defense under heat stress	Yoshida <i>et al.</i> (2019)
ROS-ABA	Heat stress	ROS-induced ABA formation in systemic tissue	ABA and RBOH D-dependent ROS generation for long-distance signaling	Suzuki and Katano (2018)
ROS-ABA	Cold Stress	ABA-induced activation of RBOH for the generation of ROS	Cold acclimatization	Fang <i>et al.</i> (2019)

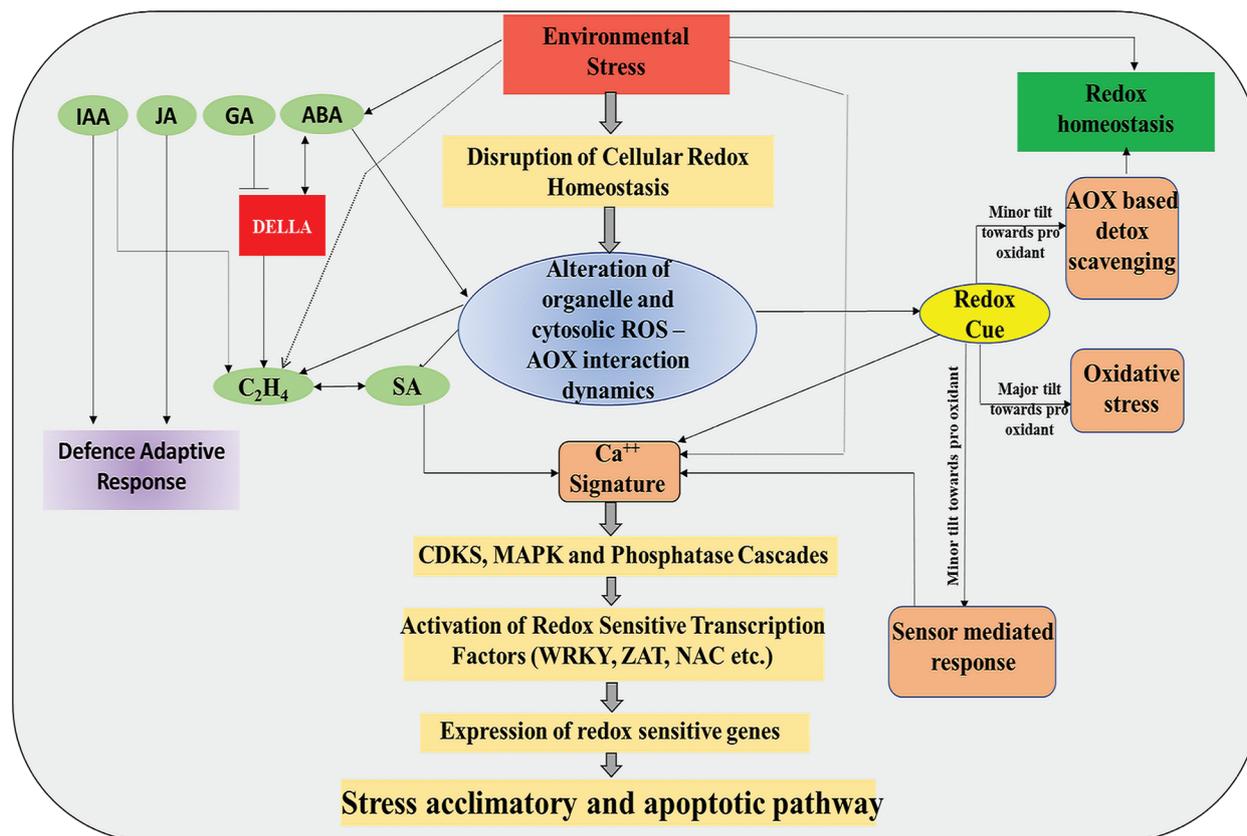


FIGURE 1. Diagram showing impact of environmental stress on hormonal and cellular redox homeostasis that leads to stress acclimatory and apoptotic pathways.

Mohanta *et al.* (2018), divalent calcium (Ca^{2+}) and ROS are the most versatile signaling molecules involved in the early events of abiotic stress signaling. Ca^{2+} ion outburst due to a stress response activates downstream calcium and ROS signaling through activation of several signaling intermediates and molecules, including Ca^{2+} -dependent protein kinases (CPK), calmodulin (CaM), calmodulin-like-proteins (CML), calcineurin B-like (CBL), and NADPH-oxidase, which further leads to regulation of the mitogen-activated protein kinases (MAPK) pathway and hormonal signaling cascades. Further, these signaling cascades activate downstream ABA, GA, BR, and nitric oxide (NO) systems and maintain cellular homeostasis. Activated cytosolic CPK, CaM, CML, and CBL further regulates NADPH-oxidase and mediates ROS production in a regulatory feedback mechanism, suggesting that early signaling events in plant abiotic stress responses are regulated through feedback mechanisms. Accordingly, a strong linkage showing feed forward and backward interaction between redox and hormone signaling towards the perception of environmental cues regulating plant performance under stress (Fig. 1) is quite evident from previous studies. Since the perception of unfavorable environmental cues and subsequent signal transduction to appropriate mechanisms towards acclimatory stress tolerance is one of the most important avenues in plant stress biology, understanding the intricate association between the *bona fide* hormonal signaling pathway with redox signaling deserves special attention. The present review is, therefore, an endeavor toward understanding the cellular language associated with integrative hormonal and redox signaling that regulates systemic responses of plants under

environmental stresses. Furthermore, the origin of biological signals in the form of redox cues under environmental stresses and their combinations with hormonal signals is also a matter of great interest in view of the maintenance of the health of the plant under stress and hence also, the subject of discussion (Mittler *et al.*, 2022; Martin *et al.*, 2022).

Integrative redox and hormone signaling under stress combination in plant cell

Though most of the studies related to plant responses to environmental stress centered around the solitary stress effect, in the field condition, plants are often encountered multiple stresses (Mittler, 2006, 2017). Under *in vivo* system, to acclimatize stress combinations, different stress-responsive signaling mechanisms need to be integrated where the signaling intermediates cross-talk (Mittler, 2006; Choudhury *et al.*, 2017). Further, climate change has introduced unpredictable imposition of stress combinations, which attracted the attention of stress biologists in recent times (Zandalinas *et al.*, 2018, 2020a; Devireddy *et al.*, 2021). Instead of having an additive effect, stress combinations imposed by climate change have been found to have unique responses, which have been substantiated in some recent works (Choudhury *et al.*, 2017; Zandalinas *et al.*, 2018, 2020a; Devireddy *et al.*, 2021). Since most of the system-level responses of plants under environmental stresses are regulated by signaling episodes of plant growth regulators (PGRs) or hormones, their interactions under stress combinations are inevitable to settle the mutual interest of plants. The hormones ABA and ethylene, as well

as their combination, have been proposed as key regulators of stress responses (Suzuki *et al.*, 2016; Devireddy *et al.*, 2021). There are many examples of ABA-induced transcriptional reprogramming of stress-responsive genes under multiple stresses like salinity, drought, and hyperthermia (Suzuki *et al.*, 2016). Similarly, drought, and hyperthermia stress combinations subjected to some crops are also responsible for *de novo* gene expression necessary for survival (Zandalinas *et al.*, 2016, 2018; Balfagón *et al.*, 2019). Though much emphasis has been given to the functional role of ABA under drought and salinity, the complex coordination with other hormone-signaling pathways cannot be ruled out. The high level of SA, ethylene, and JA are also associated with hyperthermia and salinity stress, highlighting their integrative action in regulating acclamatory response under stress combinations (Balfagón *et al.*, 2019; Devireddy *et al.*, 2021).

While the hormonal signaling processes ensue under stress combinations, the role of redox players cannot be ruled out, as revealed by several recent studies (Choudhury *et al.*, 2017; Mittler, 2017; Devireddy *et al.*, 2021). Different combination of multiple stresses like extreme temperature, drought, salinity, and excess photochemical energy (EPE) always results in different ROS signature under hormonal signaling, governing specificity of stress acclamatory response (Choudhury *et al.*, 2017; Devireddy *et al.*, 2021). The work of several other workers in the recent past (Choudhury *et al.*, 2017; Mittler, 2017; Zandalinas *et al.*, 2018) also corroborated strongly with the role of redox cues under stress combinations. The endogenous level of pro-oxidants, involvement of antioxidative defense system (ascorbate-glutathione cycle, flavonols, polyphenolic compounds, carotenoid and tocopherol, anthocyanin, betacyanin, and alkaloids), accumulation of redox osmolytes exhibit unique response pattern under stress combinations (Choudhury *et al.*, 2017; Devireddy *et al.*, 2021). In the backdrop of the intricate interplay of different phytohormones along with the involvement of ROS as the second messenger, the complexity of ROS-hormone interaction under multiple stress combinations is inherent. In order to make these signaling co-ordinations successful in regulating plant survival under stress combination, the combinatorial interaction must be flexible depending on stress types and their impact on specific plants (Suzuki *et al.*, 2016; Devireddy *et al.*, 2021). For example, the interaction between ABA, JA, SA, and ROS is required for the regulation of stomatal conductance under stress combinations. Previous studies based on genetic and molecular experiments reported that ABA-sensitive mutant (*abi1*), with impaired ABA and associated protein ABI1, become sensitive to stress combinations of hyperthermia and drought as well as hyperthermia and salinity (Zandalinas *et al.*, 2016; Suzuki *et al.*, 2016), substantiating the significance of ABA-ROS interaction for stress combinations. Independent studies have also shown that the hormones SA and JA also interact with H₂O₂ under the same stress combinations for influencing stomatal regulations. Further, the role of other hormone signaling is highlighted in influencing redox signature for stomatal regulation. Other studies of ROS-hormone interaction under stress combinations also revealed the role of JA and

CK in controlling redox cues under stress combinations. Although JA up-regulates the expression of the APX1 (ascorbate peroxidase 1) gene under the stress combinations of heat and drought, the impact seems to be on the accumulation of CK as well, which exhibits down-regulation (through the expression of CK degrading enzymes) (Lubovská *et al.*, 2014). Different recent works related to different integrative systemic signaling of ROS and plant growth under stress combinations revealed that the plant could simultaneously process and integrate different systemic signals under stress combinations depending on how efficiently they can relay the ROS signal and integrate the same with hormonal responses (Zandalinas *et al.*, 2016; Devireddy *et al.*, 2021). Exposure of plant leaves to hyperthermia and excess photochemical energy separately triggers the origin of efficient ROS signal that culminates in systemic acquired resistance to both hyperthermia and excess photochemical energy (EPE). On the contrary, imposition of both EPE and hyperthermia simultaneously to the leaves of the same plants inhibited the initiation of ROS waves or redox signals, thereby impairing systemic acquired acclimation under these stress combinations. Incidentally, this suppression of the origin of systemic acquired acclimation was found to be erased in JA *aos* mutant, strongly vouching for the synergistic interactions between JA and SA in determining systemic signaling under stress combinations (Zandalinas *et al.*, 2020b) through the specific ROS-hormone interactions. All such experimental evidence (Table 1) strongly corroborates the specific integration pattern between ROS-hormone signaling under stress combinations which play a pivotal role in the stress acclimation of plants (Fig. 1).

Reactive oxygen species-abscisic acid interaction determines acclamatory stress tolerance of plants

The physiological role of ABA ranges from the maintenance of normal physiological events, like promoting dormancy in seeds, regulating stomatal conductance, and root development to stress response (Xiong *et al.*, 2002). It is considered one of the important hormones whose biosynthesis is up-regulated under abiotic stresses (Sah *et al.*, 2016). While ROS has a crucial role in instigating ABA-mediated signaling cascades, ABA also instigates activation of NADPH oxidase and influences the photosynthetic electron transport system (Jiang and Zhang, 2003; Zhang *et al.*, 2006; Xia *et al.*, 2015). There are pieces of evidence that exhibited the role of ABA in maintaining the positive feedback system for ROS production and stress tolerance by regulating the production of H₂O₂ (Mohanta *et al.*, 2018). Core ABA signaling module PYR/PYL/RCAR-SnRK2-PP2C can positively regulate NADPH oxidase for ROS formation (Fig. 2). During ABA signaling, phospholipase D produces phosphatidic acid via the hydrolysis of phosphatidylcholine which binds to NADPH oxidase and activates it to produce ROS (Zhang *et al.*, 2009) (Fig. 2). Mutation in RBOH genes causes impairment in this ABA-induced of H₂O₂ formation. ROS produced by NADPH oxidase generates a ROS wave. This ROS wave can induce nitrate reductase to produce NO, which in turn can increase the level of divalent calcium (Ca²⁺) in the cytoplasm. Ca²⁺ can again produce ROS by

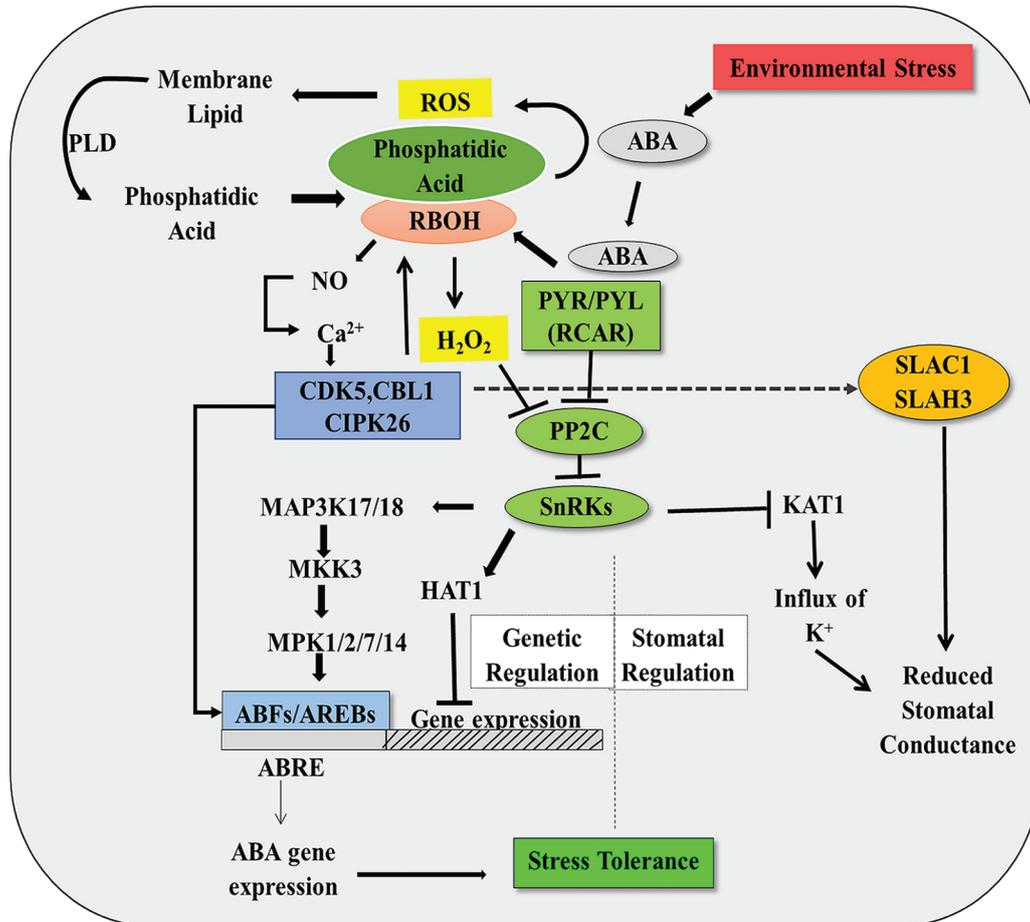


FIGURE 2. Core ABA signaling module that regulates the origin of redox cue associated with downstream signaling cascades involving NO, Ca²⁺, etc., in plants (detail in text).

invoking RBOH with the help of calcium-dependent CPK5, CBL1-CIPK26 (Pei *et al.*, 2000; Zhang *et al.*, 2001; Kwak *et al.*, 2003; Bright *et al.*, 2006; Mittler and Blumwald, 2015; Drerup *et al.*, 2013) (Fig. 2). There exist a positive feedback loop operating for ABA-mediated production of ROS (Raja *et al.*, 2017). ABA signaling can transduce changes through both Ca²⁺-independent and Ca²⁺-dependent pathways. The PYR/PYL/RACR-SnRK2-PP2C module controls the Ca²⁺-independent pathway (Kumar *et al.*, 2019). All PYR/PYL [pyrabactin resistance1 ((pyr1)/pyr1-like)] proteins can act as ABA receptors. These PYR/PYL/RCAR (PYR/PYL/regulatory components of aba receptors), when attached to ABA, can inhibit PP2C (type 2C protein phosphatase), which is a vital controller of calcium-independent ABA signaling (Ma *et al.*, 2009; Park *et al.*, 2009; Santiago *et al.*, 2009a, 2009b; Kumar *et al.*, 2019) (Fig. 2). Elevated level of H₂O₂ can inhibit these PP2C proteins (like ABI1) and thus negatively regulate ABA signaling (Fuji *et al.*, 2009; Kumar *et al.*, 2019) (Fig. 2). So, the ROS signaling independently influences ABA signaling through PP2C down-regulation and allowing SnRKs to down-regulate defense gene expression or inhibiting KAT1 necessary for osmolyte regulation and stomatal closure.

Reactive oxygen species-C₂H₄ interaction determines plant performance under abiotic stress

C₂H₄, a gaseous phytohormone, plays a significant role in the senescence of plants, flowering, fruit ripening, nodulation,

etc., and also regulates stress response under hostile environments. C₂H₄ invokes a prominent role in the abiotic stress tolerance of plants in particular (Reid, 1995; Lutts *et al.*, 1996; Thompson *et al.*, 1998; Pierik *et al.*, 2006; Masood *et al.*, 2012; Nazar *et al.*, 2014; Müller and Munné-Bosch, 2015; Thao *et al.*, 2015; Khan *et al.*, 2017). H₂O₂ works downstream of C₂H₄ signaling pathways for exerting tolerance to salinity-stressed plants (Jiang *et al.*, 2012, 2013). Actually, ET mediates stress response in rice through the action of the ROS signaling cascade under abiotic stresses like a flood (Steffens *et al.*, 2013). In salinity-stressed plants, TFs like *Lycopersicon esculentum* ethylene responsive factor (LeERF1), LeERF2, and MsERF8 can induce the biosynthesis of proline for conferring tolerance against stress, which can also reduce oxidative membrane lipid peroxidation (Fig. 3) (Cheng *et al.*, 2013; Hu *et al.*, 2014). C₂H₄ can also reduce ROS accumulation by activating ROS detoxification or an antioxidative defense maintenance system. For example, Arabidopsis AtERF98, an ERF (Ethylene responsive factor), can give a plant tolerance against salinity stress by controlling the biosynthesis of ascorbate, which is essential for ROS detoxification via ascorbate-glutathione pathway (Zhang *et al.*, 2012) (Fig. 3). Overexpressing mutants of CaPF1 (a TF) reduces oxidative stress by up regulating the antioxidative defense mechanism in plants in response to ROS-induced ERF activation (Youn *et al.*, 2008) (Fig. 3). Another ERF, JERF3 regulates the

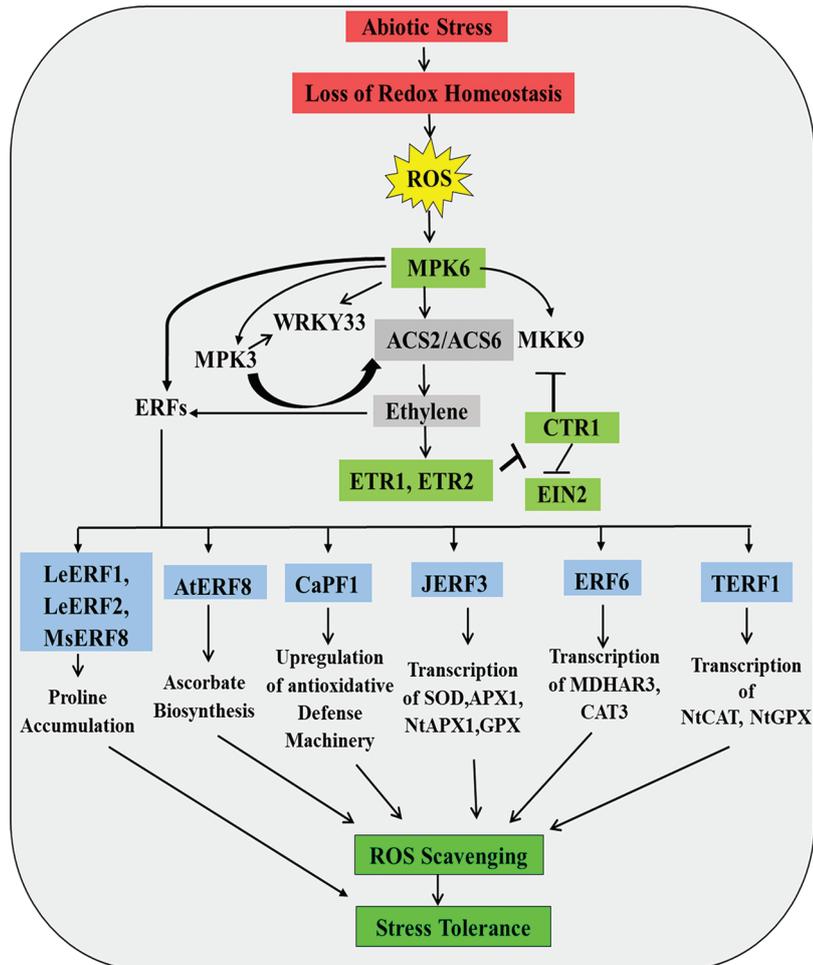


FIGURE 3. Role of ROS in ethylene biosynthesis and downstream signaling, showing regulation of diverse TFs associated with defense mechanism (detail in text).

transcription of many antioxidants machinery related genes like SOD, NtAPX2, APX1, glutathione peroxidase (GPx), etc. in tobacco plants in response to C_2H_4 signaling under salinity and drought stress, substantiating ROS- C_2H_4 interaction for stress tolerance (Wu *et al.*, 2008) (Fig. 3). Under oxidative stress, the expression of ERF6 is increased and the association between ERF6 and the reduction of stress by up-regulating the antioxidant levels has been established (Fig. 3). H_2O_2 treatment in tobacco is associated with increased expression of TERF1, indicating the ROS-mediated expression of ERFs under different stresses. TERF1 is also associated with the up-regulation of transcription of genes like NtCAT and NtGPX to several folds, which helps to maintain the redox homeostasis needed for the alleviation of stress (Zhang *et al.*, 2006; Sewelam *et al.*, 2013) (Fig. 3). In a mutant of ERF6, *erf6*, the level of several antioxidants was reported to be low. These findings can lead to the conclusion that ERF6 is associated with the maintenance of proper antioxidant activity in stressed plants. Further, it has been seen that ERF6 is linked with the expression of MDHAR3 and CAT3 as in *erf6* mutants, the level of these gene products was found to be significantly low (Fig. 3). Mutant NtCDPK2 (lacking auto-inhibitory domain) in *Nicotiana bethamiana*, led to generation of ROS, JA, C_2H_4 , and 12-oxo-phytodienoic acid (Ludwig *et al.*, 2005). However, it was noticed that elevated CDPK signaling compromised the activation of MAPK

signaling through the synthesis and perception of C_2H_4 (Ludwig *et al.*, 2005).

Reactive oxygen species–auxin interaction determines plant development performance under abiotic stress

ROS signaling can change auxin titer in a cell through several biochemical processes, like oxidative degradation of auxin, re-localization of PIN (PIN-formed) in certain tissues, conjugation of auxins, etc. (Fig. 4) (Kawano, 2003; Raeymaekers *et al.*, 2003; Minglin *et al.*, 2005; Junghans *et al.*, 2006; Park *et al.*, 2007; Santelia *et al.*, 2008; Tognetti *et al.*, 2010; Grunewald and Friml, 2010; Tognetti *et al.*, 2012). Auxin also plays an important role in responding to various abiotic stresses through interplay with ROS (Mohanta *et al.*, 2018). It has been seen in *Arabidopsis* that hypocotyl cutting results in respiratory burst oxidase protein D (RBOHD) and RBOHF-dependent up-regulation of ROS production, which can increase the endogenous titer of IAA. Excised seedlings showed increased expression of YUCCA and TAA1 [(YUC) family of flavin monooxygenases/tryptophan aminotransferase of *Arabidopsis* 1] expression. Expression of these genes, mediated by ROS, can up-regulate the synthesis of auxin in stressed plants (von Sonntag, 1987; Armstrong, 1990; Prakash and Prathapasenan, 1990; Uchida and Kawakishi, 1993; Schoneich, 2000; Bashandy *et al.*, 2010) (Fig. 4). In *AtRbohD* mutants, expression of these genes was hampered significantly. In salinity stress, *tir1* (Transport

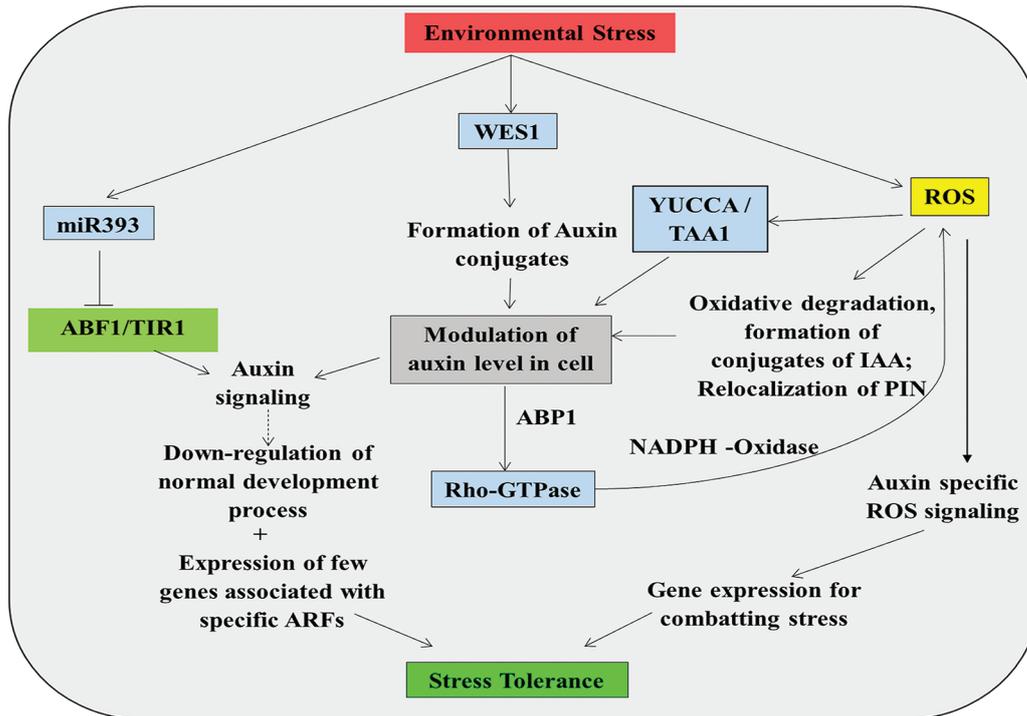


FIGURE 4. ROS-auxin interaction showing auxin-specific ROS signaling and subsequent modulation of endogenous titer of both the components in plants (detail in text).

inhibitor response 1) and afb2 (auxin-binding F-box protein) auxin-responsive mutants of Arabidopsis showed a significant decline in H₂O₂ level as compared to wild-type plants under stress. In these cases, the activities of different enzymes like ascorbate peroxidase (APX) and catalase (CAT) and transcription of glutathione S-transferase 1 (GST1) and APX1 in the mutants was enhanced, suggesting the involvement of ROS production by auxin (Iglesias *et al.*, 2010; Mohanta *et al.*, 2018). The level of ascorbic acid was increased significantly in mutants tir1 and afb2 (Iglesias *et al.*, 2010). This high accumulation of ascorbic acid level may be due to the down-regulation of ascorbate oxidase (AO) activity (Bashandy *et al.*, 2010). The lower concentration of H₂O₂ can be explained by the up-regulation of antioxidants. Under salinity stress, TIR1 and AFB2 activity are negatively regulated by a high level of miR393 (Fig. 4). The Arabidopsis triple mutants of ntra, ntrb, and cad2, which are involved in thioredoxin and glutaredoxin signaling-mediated redox regulation was found to affect auxin transport (Bashandy *et al.*, 2010). Another protein of Arabidopsis, which helps in auxin-mediated stress response, is Rho-GTPase, which are products of RAC/ROP genes. ABP1, after binding with auxin, can regulate the expression of different ROP genes. These Rho-GTPase can interact with NADPH-oxidase to produce ROS in turn, which can induce several signaling cascades (Xu *et al.*, 1994; Duan *et al.*, 2010; Tognetti *et al.*, 2012) (Fig. 4).

Reactive oxygen species-gibberellins interaction determines germination and other developmental performances under stress

The role of GA signaling under abiotic stresses is largely regulated by DELLA proteins, which are negative regulators of GA signaling pathway. During abiotic stress, the

endogenous level of GA decreases significantly, and as a result, the level of DELLA becomes high inside the cellular environment (Achard *et al.*, 2006; Colebrook *et al.*, 2014) (Fig. 5). GA deficit biosynthetic mutants show resistance even in severe salinity stress, whereas, plants with non-functional DELLA showed susceptibility to salt stresses. Experiments suggest that DELLA imposes tolerance to stressed plants by controlling the amount of ROS with the up-regulation of the antioxidative defense mechanism. It regulates the expression of genes expressing antioxidative enzymes and thus preventing oxidative damage in plants, thereby prolonging survival and enhancing fitness (Mohanta *et al.*, 2018) (Fig. 5). During salt stress, DELLAs also delay ROS-induced necrosis by inhibiting their accumulation (Achard *et al.*, 2008). In rice plants, expression of Submergence toleranace gene (Sub 1A) also restricts the ROS production through the activity of DELLA, SLR-1, and SLR-2 proteins, which are negative regulators of GA signaling (Fig. 5). This phenomenon reduces oxidative damage during the submergence of plants (Fukao *et al.*, 2006, 2011). Superoxide dismutase (SOD) plays a pivotal role in DELLA-mediated ROS scavenging (Kliebenstein *et al.*, 1998; Achard *et al.*, 2008). DELLA proteins showed prominent roles in the expression of CSD1,2, which are Cu/Zn SOD encoding genes suggesting the role of GA in regulating the antioxidative defense mechanism of plants (Achard *et al.*, 2008). Transcriptomic analysis with complete Arabidopsis microarray (CATMA) has revealed that DELLA can directly up-regulate the levels of Cu/Zn SOD, CAT, peroxidase (POD), GST1, indirectly hinting the role of GA-ROS interaction (Crowe *et al.*, 2003; Hilson *et al.*, 2004; Achard *et al.*, 2008) (Fig. 5). Both exogenous GA and NaCl can significantly increase the ROS level via NADPH-oxidase

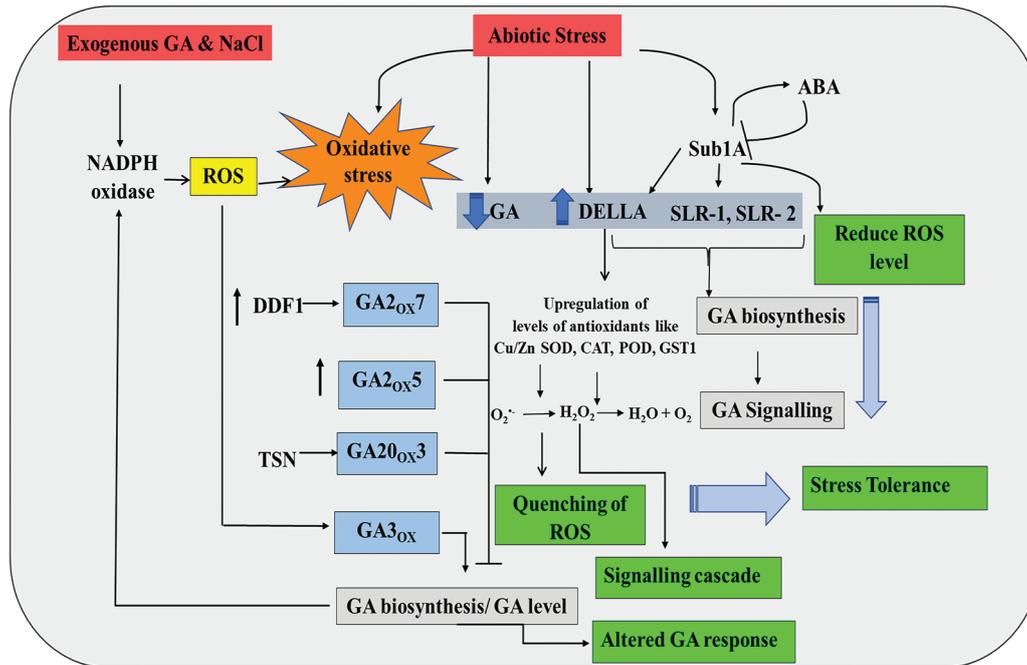


FIGURE 5. ROS-GA interaction showing the involvement of DELLA, NADPH-oxidase and other TFs in regulating physiology of plants under stress (detail in text).

activity (Apel and Hirt, 2004). In *Arabidopsis*, only *AtrbohD* was required for the production of ROS in salinity stress, and *AtrbohF* was not required. However, the activities of *AtrbohD* and *AtrbohF* activity are not controlled by DELLA (Achard et al., 2008). Quadruple DELLA mutants of *A. thaliana* also resulted in reduced ROS accumulation and enhanced expression of antioxidant enzymes-producing genes during salinity stress (Achard et al., 2009). In maize also, reduced GA levels and enhanced DELLA activity were observed during dehydration stress, which facilitated ROS scavenging (Wang et al., 2008). It is also noticed that *GA2ox7* (GA 2-oxidase) can reduce the level of bioactive GA under salinity stress by upregulating the synthesis of the C20-GA deactivating enzyme (Magome et al., 2008). Another experiment by Shan et al. (2014) revealed that overexpressed *GA2ox5* conferred high salt tolerance to plants but reduced GA levels (Shan et al., 2014). *GA20ox3* is an important enzyme in GA biosynthetic pathway that helps in bioactive GA4 synthesis. Tudor-SN (TSN), a very common protein of *Arabidopsis*, also plays important role in the maintenance of stress by controlling the level of *GA20ox3* mRNA. So, by modulating *GA20ox3* and TSN, one can reduce the concentration of bioactive GA, which in turn can confer greater stress tolerance (Yan et al., 2014) (Fig. 5). On the contrary, ROS produced during different abiotic stresses can induce GA synthesis with the help of enzymes like *GA3ox* (Kai et al., 2016) (Fig. 5). Therefore, the impact of ROS-GA interaction seems to be flexible depending on the signaling module and environmental stress, which ultimately regulate plant performance under stress.

Reactive oxygen species-salicylic acid interaction determines stress tolerance and the developmental process of plants

One of the key phytohormones, SA, confers tolerance to both abiotic and biotic stresses to plants (Drzewiecka et al., 2012; Li

et al., 2017; Thevenet et al., 2017). Exogenous application or endogenous biosynthesis of SA and accumulation both help in tolerance to abiotic stress like metal, salinity, drought, high temperature, ozone, etc. (Khan et al., 2015). Plants under salinity stress can show better tolerance to stress with the help of SA-mediated up-regulation of different stress-tolerant mechanisms (Azooz, 2009; Nazar et al., 2011; Palma et al., 2013; Nazar et al., 2014, 2015). ROS plays an important role in SA-mediated responses during abiotic stress and acts directly or indirectly on different stress tolerance mechanisms (Lee and Park, 2010; Herrera-Vásquez et al., 2015). During the early event of stress signaling, SA promotes ROS signaling using peroxidase (PRX) and acts as a key player in the plant defense system (Lee and Park, 2010; Garretón et al., 2002; Khokon et al., 2011; Miura et al., 2013). It has been found that ROS signaling, initiates primarily at the chloroplast of the guard cell under the influence of SA. SA is suggested to be associated with ROS generation in chloroplasts and peroxisomes (Apel and Hirt, 2004; Joo et al., 2005; Herrera-Vásquez et al., 2015). However, the exact mechanism of H_2O_2 production via SA signaling in the apoplast, peroxisome, and chloroplast remains unknown. Also, ICS1 (Isochorismate synthase 1) regulating transcription factors like SARD1, CBP60, WRKY8/28/48, CAMTA 3/SR1, and ZAT6 is associated with ROS-mediated signaling and biosynthesis of SA (Du et al., 2009; Zhang et al., 2010; van Verk et al., 2011; Shi et al., 2014) (Fig. 6). During different stresses, the redox homeostasis of plant cell is disrupted that causes overaccumulation of ROS, which in turn instigates oxidative damage of different cellular components (Mittler, 2002; Torres et al., 2002; Miller et al., 2008). SA helps to decrease the electron leakage from the photosynthetic electron transport chain and inhibits ROS generation (Khan et al., 2014). Again, SA can protect cells from oxidative

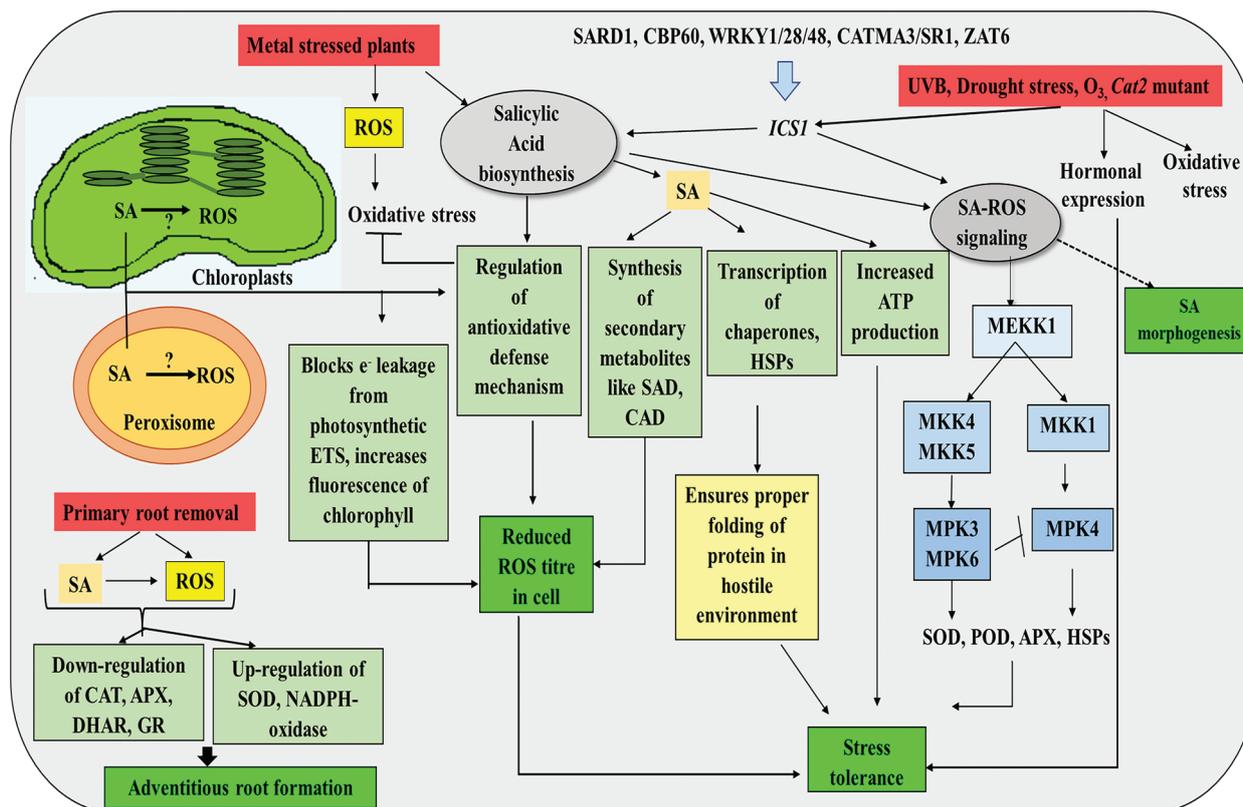


FIGURE 6. ROS-SA interaction in plant cell showing SA-induced changes in redox homeostasis, antioxidative defense and morphogenesis (detail in text).

damage caused by ROS by up-regulating different antioxidative defense mechanisms like APX, SOD, Glutathione peroxidase (GPO), glutathione peroxidase (GR), etc. (Janda *et al.*, 1999; Kang *et al.*, 2013; Li *et al.*, 2013) (Fig. 6). Different metal tolerant plants like *Linum usitatissimum* are tolerant to metal stress-induced oxidative stress due to SA-mediated detoxification of ROS like H_2O_2 (Belkadhi *et al.*, 2015) (Fig. 6). Application of exogenous SA in metal stressed plants have shown up-regulation of different enzymatic and non-enzymatic antioxidants, which helps to reduce lipid peroxidation due to ROS (Jing *et al.*, 2007; Zengin, 2014). Plants with heavy metal accumulation ability are associated with a high concentration of SA biosynthesis components and derivatives of those components, indicating that the biosynthesis of SA is up-regulated in those heavy metal hyperaccumulators (Freeman *et al.*, 2005). A proteomics study has revealed that SA treatment can enhance the expression of at least 37 proteins under drought stress. These proteins include antioxidants like GST, APX, etc., which can work for maintaining redox homeostasis. SA increases transcription of different antioxidant genes like GPX1/2, dehydroascorbate reductase (DHAR), mono-dehydroascorbate reductase (MDHAR), GST1/2, etc., under different abiotic stresses that strengthen the antioxidative mechanism and help to protect plants from environmental odds. Application of SA on plants under drought stress has also shown increased transcription of chaperones and heat shock proteins (HSPs) (Fig. 6). This indicates that SA can help in proper protein folding under stress. Plants under drought stress even can increase the

biosynthesis of different secondary metabolites like lignin-related cinnamyl alcohol dehydrogenase (SAD, CAD) and cryptochrome P450 for fighting against stress (Jumali *et al.*, 2011) (Fig. 6). It is assumed that MAPK cascades play an important role in SA-mediated abiotic stress tolerance by up-regulating transcription of different genes. MAP (Mitogen-activated protein) kinases like MPK3/4/6 play a crucial role in abiotic stress tolerance and are important components for SA-ROS signaling (Baier *et al.*, 2005; Kangasjärvi *et al.*, 2005; Fujita *et al.*, 2006). MEKK1, which is a kind of MAP kinase kinase, can be directly controlled by SA and ROS (Fujita *et al.*, 2006; Suarez-Rodriguez *et al.*, 2007). Two MAP kinases, MPK6 and MPK3 in Arabidopsis, can be controlled under the influence of MAP kinase kinase proteins like MKK4 and MKK5 (Baier *et al.*, 2005). MPK4 is seen to be activated in those plants, where the MPK6 is mutated; but under normal conditions, MPK6 is not associated with active MPK4. This indicates that MPK6 inhibits MPK4 activity in Arabidopsis in SA-mediated stress signaling, and there must be two different MAPK signaling cascades working together under the influence of MEKK1 (Menke *et al.*, 2004). Under the influence of these MAPK cascades, different antioxidant genes (SOD, HSP, APX, POD) are expressed, substantiating ROS-SA interaction, which helps to tolerate abiotic stress (Chini *et al.*, 2004; Gruhler *et al.*, 2005; Salzman *et al.*, 2005; Rajjou *et al.*, 2006) (Fig. 6). However, it has been reported that treatments with high concentrations ($>100 \mu M$) of SA cause higher SA production in plants leading to an oxidative burst and reduced tolerance to drought and salinity-stresses (Lee *et al.*, 2010; Miura and Tada, 2014).

SA has also been found to enhance adventitious root formation (ARF) via increasing endogenous titer of ROS (H_2O_2) (Babar Ali *et al.*, 2007; Yang *et al.*, 2013; Kora and Bhattacharjee, 2020). Explants incubated in SA after primary root removal showed the maximum concentration of H_2O_2 at 12 h. Combined treatment of SA and H_2O_2 resulted in higher adventitious roots than their individual treatment in mung bean explants (Yang *et al.*, 2013; Kora and Bhattacharjee, 2020). SA treatment down-regulates CAT activity and activities of enzymes of the central redox hub, the Halliwell Asada pathway (APX, DHAR GR), and simultaneously increases the activity of SOD and RBOH (NADPH-oxidase), suggesting the important role of ROS as a second messenger in SA-mediated ARF (Yang *et al.*, 2013; Kora and Bhattacharjee, 2020) (Fig. 6).

Reactive oxygen species-Brassinosteroid (BR) interaction in plant cell under stress

BR triggers many stress signaling pathways with the help of Ca^{2+} and ROS as a second messenger (Allen *et al.*, 2000). In response to stress, BR can regulate the ROS titer by modulating ROS generation as well as the ROS scavenging mechanism, thus changing the redox status of the cell for precise regulation of redox signaling for stress adaptations (Jakubowska and Janicka, 2017; Ahmad *et al.*, 2018). BR induces NADPH-oxidase-mediated ROS generation in the apoplast, and silencing of RBOH1 reduces BR-mediated ROS production (Nie *et al.*, 2013). MAPK cascades play an important role in BR-dependent ROS production (Zhang *et al.*, 2010b) (Fig. 7). A microtubule-associate protein MAP65-1a, whose transcription is dependent on BR, turns MAPK cascades on,

which ultimately regulates the expression of NADPH-oxidase genes (Zhu *et al.*, 2013) (Fig. 7). Experiments have proven that NADPH-oxidase activity is confluent with the activity of endogenous BR level (Xia *et al.*, 2009). Overly expressed BR biosynthesis gene CYP1 leads to ROS production and change in the redox status, which in turn produces ABA and evokes stress response. Biosynthesis modulation of BR is also observed by feedback repression of BR biosynthesis genes (Bancosí *et al.*, 2002). BR, along with ABA, plays an important role in stomatal regulation that includes ROS (Fig. 7). Low BR level is associated with ephemeral ROS production, which leads to stomatal opening, whereas a high BR level induces prolonged ROS generation through NADPH-oxidase activity which is subsequently associated with high ABA level and leads to stomatal closure (Xia *et al.*, 2014; Mohanta *et al.*, 2018) (Fig. 7). ABA might also induce NO synthesis along with ROS. Both of these can induce 8-nitro-cGMP, which promotes stomatal closing during abiotic stress conditions (Joudoi *et al.*, 2013). JA produced during stressed conditions interacts with ABA-mediated stomatal closure by stimulating the extracellular Ca^{2+} influx and/or by activating H_2O_2 /NO signaling pathways (Fig. 8). On the contrary, another finding by Desikan *et al.* (2006) provided much evidence that stomatal closure by ethylene is regulated via its signal transduction pathway, which stimulates the production of H_2O_2 and requires H_2O_2 synthesis (Fig. 8). Treatment with either ABA or methyl jasmonate (MeJA) for 10 min resulted in a reduction of stomatal aperture in turgid and excised leaves of Arabidopsis and suggested both ABA and MeJA interact in guard cells and induce the formation of ROS and NO (Wani *et al.*, 2016).

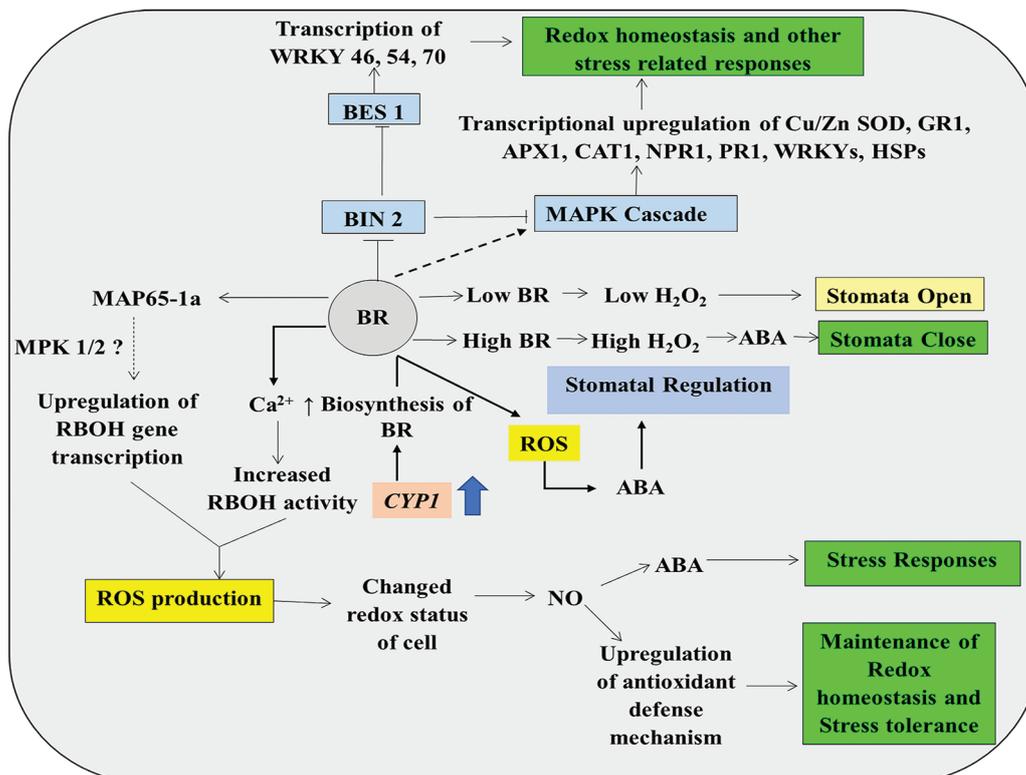


FIGURE 7. ROS-BR synergistic action in plant cell showing BR-induced induction of redox, NO and ABA signaling regulating stomatal conductance and plant defense processes (detail in text).

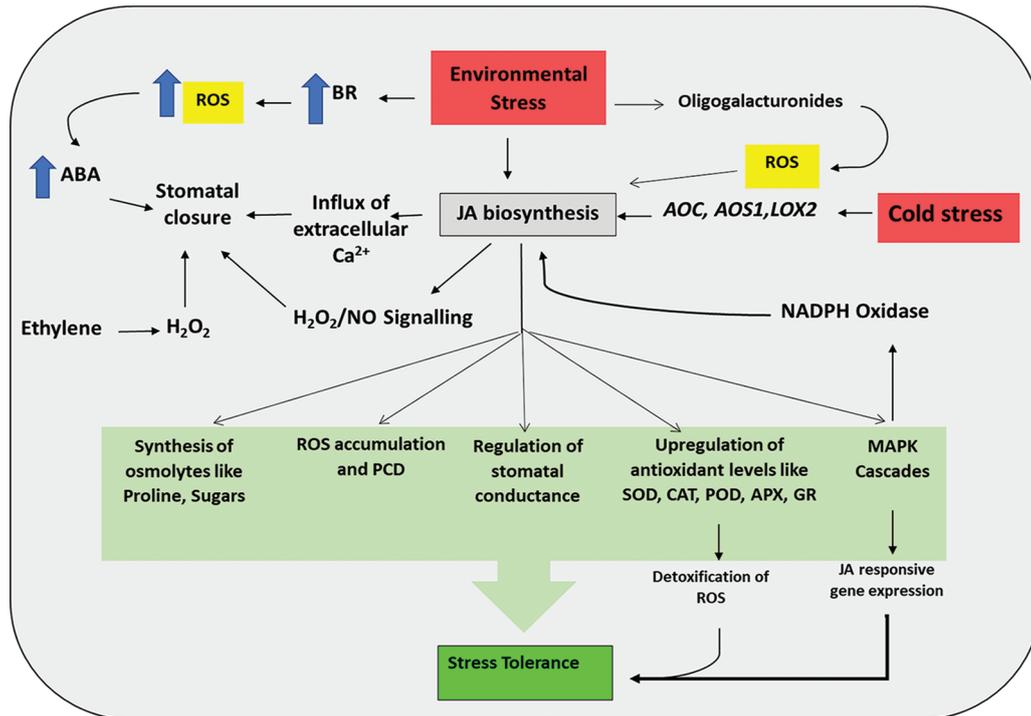


FIGURE 8. ROS-JA interaction under stress in plant cell showing both feed-forward and feed-backward and interactions for influencing their endogenous titres and regulation of stress tolerance mechanism (detail in text).

ABA levels in the BR biosynthetic mutants are found to be low, but the exogenous application of BR on the mutant might raise ABA levels (Zhou *et al.*, 2014). These findings suggest a significant link between ABA, GA, BRs, and ROS during abiotic stress in plants. The application of BR biosynthesis inhibitor brassinazole (BRZ) decreases the endogenous level of BR, which leads to decreased tolerance to different abiotic stresses (Xia *et al.*, 2009). Constitutive BR signaling mutant, *bes1-D*, resulted in constitutive activation of BR signaling that leads to stress tolerance in plants (Sun *et al.*, 2010). Kim *et al.* (2012) showed that BR could induce MAPK cascades by inhibiting BIN2 (BR-INSENSITIVE 2) and inhibition (Fig. 7). Silencing genes like RBOH1, MPK2 or MPK1/2 caused inhibition of BR-mediated stress signaling to some extent (Nie *et al.*, 2013). Silencing of MPK2 can give greater silencing of BR-mediated signaling than MPK1. This suggests that MPK2 plays a more important role as compared to MPK1 during stress tolerance. Also, MPK1/2 is seen to play an important role in ROS generation, and MPK2, ROS, and RBOH1 are assumed to work together in a positive feedback loop for facilitating BR-mediated signaling for environmental stress tolerance (Zhou *et al.*, 2014). MAPK cascades in plants can positively up-regulate many defenses related genes like Cu-Zn SOD, GR1, APX1, CAT1, NPR1, PR1, WRKY1 even HSPs like HSP90, in which transcription factors like WRKY plays an important role in conferring tolerance to plants under stress (Zhou *et al.*, 2014) (Fig. 7). Transcription factors like WRKY46, 54, and 70 assist in BR-mediated stress signaling with the help of Brassinosteroid signaling positive regulator (BZR1) family protein (BES1) (Banerjee and Roychoudhury, 2015; Chen and Yin, 2017) (Fig. 7).

Reactive oxygen species-jasmonate interaction in plant cells under stress

JA synthesis happens to be involved in wound and stress response. During mechanical injury, Ca²⁺ channels sense mechanical shear, and along with other signaling components, it induces several MAPK cascades that involve NADPH-oxidase for JA biosynthesis (Wolf *et al.*, 2012) (Fig. 8). Oligogalacturonides, which are produced from wound stress, can prompt the biosynthesis of JA (Doares *et al.*, 1995) (Fig. 8). Abiotic stresses like cold stress induces up-regulation of transcription of different JA biosynthetic genes like AOC, AOS1, and LOX2, leading to high accumulation of JA in the cold stressed plants (Hu *et al.*, 2017) (Fig. 8). The level of JA is increased initially during drought stress but in prolonged drought stress the level drops to a normal level as seen in unstressed plants (Wang *et al.*, 2020). Wounding or other abiotic stress can alter the redox status of cells, leading to the generation of different ROS in plants which is assumed to be associated with JA biosynthesis in plants (Parra-Lobato *et al.*, 2009) (Fig. 8). In return, JA helps in maintaining physiological responses under abiotic stress by activation of antioxidant machinery, accumulation of different amino acids like proline, accumulation of sugars, and regulation of stomatal conductance as a general response (Acharya and Assmann, 2009; Karpets *et al.*, 2014; Wasternack, 2014) (Fig. 8). On the other hand, Endogenous JA modulates the titer of ROS associated with salinity stress tolerance. It also increases the salinity stress tolerance by increasing photosynthetic rate, ABA concentration, proline content, the activity of enzymatic antioxidants, etc. (Bandurska *et al.*, 2003; Walia *et al.*, 2007; Khan *et al.*, 2012; Abouelsaad and Renault, 2018) (Fig. 8). Qiu *et al.* (2014) showed JA-induced

significant oxidative damage in salt-stressed wheat seedlings via up-regulation of gene expression of SOD, POD, CAT, and APX genes, indicating the role of JA in redox regulation (Qiu *et al.*, 2014) (Fig. 8). Exogenous application of MeJA could alleviate the adverse consequences of drought stress by up-regulating different enzymatic antioxidants like POD, SOD, CAT, APX, GR, and non-enzymatic antioxidants like proline, soluble sugar, etc. (Wu *et al.*, 2012). Several other studies done on different stressed plants have shown that JA and MeJA help to withstand by up-regulating the antioxidative defense mechanism and maintaining the redox status of the cell (Soares *et al.*, 2010; Manar *et al.*, 2013; Faghih *et al.*, 2017). Also, a very high level of JA seems to be associated with ROS accumulation in cells and programmed cell death under stress (Orozco-Cárdenas and Ryan, 2002; Xia *et al.*, 2015) (Fig. 8). Takahashi *et al.* (2007) have shown that in JA mediated stress signaling, MAPK cascade plays a significant role and MKK3 and MPK6 are the most important components in that signaling cascade.

Future outlook

ROS is an intrinsic part of the signaling network that plays a major role in the responses against abiotic stress in plants. Evidences are accumulating that suggests that ROS-hormone interplay forms an integrated signaling web that can act to attenuate environmental stresses. In those pathways, ROS itself can act as a signaling molecule or influence other *bona fide* hormonal signaling modules by changing the redox status of cells. ROS can modulate hormone biosynthesis and or influence hormonal signaling circuits. ROS can directly up-regulate several enzymes for the biosynthesis of phytohormones, and can also regulate the endogenous titer of several hormones by influencing their degradation or chelation for proper response under stress. These chemically reactive molecules are also involved in oxidative degradation and localization of various hormones for proper stress response of plants. ROS can also mediate hormone-hormone interaction under several situations. The reverse events are also noticed, wherein hormones can up-regulate the synthesis of ROS and subsequently recruit them as 'second messenger' in several stress acclamatory signaling events. ROS can operate several common MAPK cascades for different hormones; also, it can turn on hormone-specific MAPK cascades depending on the environmental stimulus. Gene expression in response to a hormone signaling up-regulates the expression of several stress-specific genes. Many important TFs like WRKY (WRKY 1, 46, 54, 70), ZAT, NAC, etc., are expressed as a result of redox-hormone interaction. Also, the transcription of many chaperones and HSPs are positively regulated by redox-hormone signaling.

As previously discussed, one of the cornerstones of starting these signaling cascades by various phytohormones and ROS itself involves a change in the redox status of cells under several environmental odds. These signaling cascades shoots up, and the ultimate motto of the signaling web is to bring the cell back to its original state where it can function properly, i.e., perform the normal physiological activity. Different ROS scavenging machinery, along with other responsive factors, gets turned on to alleviate stress and help

to perform physiological functions. Though the interaction between ROS-hormones is elucidated to some extent, detailed ROS-dependent hormone signaling pathways need to be deciphered for greater understanding to give us a clear picture of ROS-mediated converging pathways of hormone signaling under abiotic stress.

The present review tried to explore the central role of ROS-hormone interaction in defense signaling under environmental threats. The well-characterized role of redox signaling coupled with Ca⁺⁺ signaling with downstream kinase and phosphatase activities that form flexible, interactive roles were found to be extremely important and necessary for the amplification of signaling response and survival of plants under stress. The redox regulation of several molecular events, like activation of transcription factors, transporter proteins, enzymes activation associated with hormonal metabolism and signaling, etc., have been found to perform a key role in stress defense and developmental processes. In spite of all these evidences, the most challenging aspect of the ROS-hormone integrative defense signaling pathway is understanding this aspect from the point of view of stress combinations, where different individual specific signaling molecules interact and collide. Further, it will be more challenging to explore ROS-hormone interaction in view of the conflict of interest that arise under different stress combinations. Moreover, the mechanistic aspect of the spatio-temporal regulation of ROS and their relative subcellular activities to control and regulate hormonal signaling is yet to be understood. The technical backup needed to prove the detail of molecular redox regulatory events (redox impacted modification of target molecules and their functional changes) needs to be explored further.

Conclusion

In spite of unprecedented progress in plant redox biology and hormonal cell signaling process, the precise position of these two highly dynamic signaling components in the integrative signaling web largely remains obscured and hence necessitates further molecular genetic investigation along with physiological study for ascertaining their exact status, position, and the function in the plant cell. Taken as a whole, the process of redox regulation through ROS production and processing is found to be an integral part of hormonal physiology and the functioning of plant cells, and there exists a very complicated interactive signaling mesh to accomplish this function. Our understanding regarding this complex signaling network between ROS-hormone signaling is thus far from complete.

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