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Hormones and Plant Response

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Chapter 3
Seed Germination: Explicit Crosstalk Between Hormones and ROS

Arkajo Majumdar and Rup Kumar Kar

Abstract Life cycle of a plant (spermatophyte) sets off by germination of seeds that virtually transfer successfully genetic information from parents to off-springs across adverse environmental conditions. Considering the pivotal roles played by both hormones and ROS (especially H_2O_2 and $^{\bullet}OH$ radical) during seed germination, it appears most likely that they function in a coordinated manner having one or more signaling cross-talks. Overwhelming evidences embossed the process of germination diligently controlled by GA-ABA balance; ROS probably being proactive in this event by modulating their metabolism. Ethylene can also be accommodated in this network of regulation, again, through ROS intervention. On the other hand, involvement of PM H^+-ATPase in germination is also documented over time. Interestingly, both ROS and phytohormones (e.g. IAA, ethylene) have been reported to modulate PM H^+-ATPase activity. Based on its activity of energy-driven transport of H^+ across the PM, the H^+-ATPase activates cell wall loosening enzymes and proteins like expansins in the context of a redox milieu maintained primarily by NADPH oxidase activity. Nitric Oxide ($^{\bullet}NO$), another potential candidate to play a role in signaling, has been documented to regulate seed germination through modulation of hormonal metabolism in a ROS-mediated way. In this chapter, the probable signaling cross-talks among ROS and hormones during seed germination have been discussed with a special emphasis on the role PM H^+-ATPase and $^{\bullet}NO$.

Keywords NADPH oxidase · Phytohormones · PM H^+-ATPase · Reactive nitrogen species (RNS) · Reactive oxygen species (ROS) · Seed germination

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3.1 Introduction

From the earliest simple life forms long course of evolution, in compliance with the changing environment, led to the emergence of complex multicellular organisms having structurally and functionally distinct parts or organs to survive the challenges of habitat. Gradual development of such architectural complexity in terms of cellular and tissue patterning calls for subtle coordination and communication between cells and tissues, a concept that was envisaged long back by German botanist Julius von Sachs (1832–1897) breeding to the idea of chemical messengers (Kucera et al. 2005; Taiz et al. 2015). Thus in higher plants well-regulated growth and development, based on harmonized functioning of cells and tissues of different organs, is possible with the involvement of such chemical messengers, aptly called hormones (Weyers and Paterson 2001).

Plant hormones, analogous to animal hormones, act at extremely low concentration and often transported away from their site of synthesis to target tissues; but, unlike animal hormones, these are unexpectedly simple molecules, e.g. ethylene, an olefin of molecular weight 28 only (Gray 2004; Davies 2010). Moreover, although functional similarities exist between animal and plant steroidal hormones (Brassinosteroids), their respective perception and signal transduction mechanisms are completely different (Thummel and Chory 2002; Lozano-Elena et al. 2018). Parallel to the discovery of auxins as the first class of plant hormones rigorous research by the plant physiologists of several countries established other classes of hormones that too have important role in plant growth and development and this list is still growing (Taiz et al. 2015). All these hormones act as signaling agents throughout the plant body, from root tip to the leaves, and throughout the life cycle, right from seed germination to senescence (Weyers and Paterson 2001; Shu et al. 2016). Apart from intrinsic regulation, some of these hormones also mediate responses to external oscillating environment. These messenger molecules are synthesized by most of the plant cells with differential capacity and, interestingly, function through both local [paracrine e.g. Brassinosteroid (Lozano-Elena et al. 2018) or autocrine e.g. GA (Arteca 1996)] and long distance [endocrine e.g. cytokinin (Kudo et al. 2010)] signaling pathways. Both ABA and cytokinin demonstrate combination of local and long distance signaling systems (Wasilewska et al. 2008; Wang and Irving 2011). Thus, plant hormones do not strictly adhere to the characteristics of hormones in mammalian sense i.e. *transported* chemical messengers (Davies 2010).

3.2 Seed Germination: First Sign of Perceptible Growth and Hormonal Interplay

Seed is a very unique structure having independent existence, but a part of it (embryo) is finally transformed into a plant. Germination of a seed marks the earliest event of growth that initiates in the metabolically hyperactive embryo (or

embryonic axis) following a resting stage (Bewley 1997; Weitbrecht et al. 2011). Right from this stage hormones take over the control of well programmed developmental processes. However, truly speaking, hormones, particularly auxin and GA, set to work in cellular orientation of the axial embryo that already started growing, even before germination, following fertilization inside the developing seed, which is practically bridging two generations successfully transferring genetic information. During this seed maturation phase, when the seed is still attached with the mother plant, embryonic development is regulated by hormones from dual source – maternal and own. Although rapid growth of the embryonic axis occurs during the early stage of seed maturation under the guidance of set of hormones, when auxin is playing the pivotal role towards polarity, late stage of development is dominated by ABA and characterized by arrested growth and metabolism followed by dehydration (except viviparous seeds) entering into a resting break awaiting germination marked by a fresh spurt of growth.

New generation for a plant starts with the seed germination that passes through a set of complex developmental changes under the strict guidance of hormones. Quiescent seeds germinate upon receiving favorable conditions encompassing light, ambient temperature, oxygen and water. In case of dormant seeds, however, process of germination is suspended until receiving some extrinsic cue or after-ripening (endogenous). As orthodox seeds undergo maturation desiccation and generally contains less than 5–15% water by weight, rapid uptake of water (imbibition) ensues at the very commencement of germination (Bewley 1997; Weitbrecht et al. 2011). During this rehydration phase cellular structures are rebuilt with integrated membrane system with gradual water saturation. Along with, activities like respiration, protein and nucleic acid synthesis and other metabolic processes resume, either parallel or one by one to flag off embryonic growth. Strictly speaking, germination starts with imbibition and culminates in the protrusion of radicle through testa, radicle growth being relied mostly upon cell extension, not cell division (Barroco et al. 2005; Kucera et al. 2005).

Plant hormones that play a definite role in this earliest event of growth are most likely to influence the expression of several genes associated with seed germination process. Among the hormones, GA-ABA conflict is a well-known issue in this connection that has been dealt with seed biologists through ages (Taiz and Zeiger 2010). Most convincing evidence came up with elegant experiments done with mutants leading to the firm concept that GA and ABA act antagonistically- GA releases dormancy and promotes germination whereas ABA inhibits germination and maintains dormancy (Koornneef et al. 1982; Bentsink and Kooenneef 2002). In fact, ABA-GA balance behind dormancy/germination is a result of positive feedback loop involving transcription factors and DELLA proteins (Piskurewicz et al. 2008). Thus environmental factors influencing germination, like light (photoblastism) and cold temperature (stratification), act through modulation of GA metabolism and GA response (Sawada et al. 2008; Seo et al. 2009; Lee et al. 2018). Further studies also revealed the roles of other hormones, like ethylene, jasmonates, brassinosteroids and auxin (Taiz and Zeiger 2010; Linkies and Leubner-Metzger 2012; Shu et al. 2016) indicating for a complex signaling network with the possibility of crosstalk at

several points that finally control the 'commitment to growth of the next generation' (Taiz and Zeiger 2010).

Storage mobilization, often considered as a part of germination process, is practically an event subsequent to germination proper, whereby reserve polymers in the storage organs (endosperm or cotyledons) are hydrolysed to provide soluble substrates for embryonic growth. Most popularly studied material is barley endosperm, a classical model system, with its outer aleurone layer that secretes hydrolytic enzymes (dominated by α-amylase) to the non-living starch grain loaded thin walled cells of endosperm. Storage mobilization thus results from synthesis of hydrolytic enzymes, α-amylase as an example, and their subsequent secretion, both of which are conducted by GA that reaches the aleurone layer through diffusion after being synthesized by the growing embryo. Further molecular biological approaches elucidated GA action towards α-amylase synthesis and secretion in great details. Binding of GA with its receptor (possibly GID1 protein) results in ubiquitin-26S proteasome mediated degradation of downstream DELLA protein, which encourages up-regulation of a transcription factor (GA-MYB) that promotes α-amylase gene expression through binding with GA response elements, GARE (Gocal et al. 2001; Ueguchi-Tanaka et al. 2005; Xia et al. 2015). ABA, an antagonist of GA action, can block GA-induced α-amylase synthesis directly by repressing GA-regulated genes (Hoecker et al. 1995) and indirectly by repressing GA-MYB expression (Gómez-Cadenas et al. 2001).

3.3 ROS, an Inevitable Player – Signaling and/or Direct Action in Growth

For a long period, reactive oxygen species (ROS) have been traditionally considered as cytotoxic agents that cause oxidative damage of lipids, DNA and protein ultimately leading towards cell death (Garg and Manchanda 2009). However, extensive research over the last few decades has brought about a paradigm shift in outlook of plant redox biology studies, particularly exploring the monumental beneficial roles of ROS in plant life (Kocsy et al. 2013; Singh et al. 2016). Among the most studied varieties of ROS *viz.* superoxide radical ($O_2^{\bullet-}$), hydroxyl radical ($^{\bullet}OH$), hydrogen peroxide (H_2O_2) and singlet oxygen ($^1O_2$), H_2O_2 is the most stable one (half-life of 1 ms; Bienert et al. 2006) whereas $^{\bullet}OH$ is regarded as the most reactive form (cleaves wall polysaccharides; Schweikert et al. 2000). Numerous plant processes ranging from momentary phenomena e.g. chloroplast movements (Majumdar and Kar 2016, 2020) to plastic developmental events e.g. root growth (Gapper and Dolan 2006; Tsukagoshi 2016) have been identified to be mediated by ROS. The divergence of ROS-intervened plant processes justifies the wide distribution of ROS generators throughout the plant body in different intracellular organelles (e.g. chloroplast, mitochondria, peroxisome etc.) or plasma membrane and apoplast (Kar 2015). The strict adherence of ROS signaling events to their localization indicates presence of

delicate communication systems among different subcellular components giving rise to a complex ROS-network (Shapiguzov et al. 2012). Since the basic requirements of plant growth i.e. cell divisions (Livanos et al. 2012) as well as cell elongations (Huang et al. 2019) are found to be regulated by ROS homeostasis, involvement of ROS in plant growth and development is inevitable. Parallel to other plant events, ROS have been reported to be crucially involved in seed germination starting from the very early stage of after-ripening and acceleration of loss of dormancy to the weakening of endosperm cap and radicle protrusion (Schopfer et al. 2001; Bailly et al. 2008; Müller et al. 2009a; Gomes et al. 2014; Bailly 2019). Concomitantly, imbibition of seeds with exogenous ROS (H_2O_2) promoted germination in many species of monocot e.g. *Oryza sativa* (Hemalatha et al. 2017), *Triticum aestivum* (Wahid et al. 2007), *Hordeum vulgare* (Bahin et al. 2011), *Andropogon gerardii* (Sarath et al. 2007) and dicot plants e.g. *Arabidopsis thaliana* (Leymarie et al. 2012), *Pisum sativum* (Barba-Espín et al. 2011), *Vigna radiata* (Chaudhuri et al. 2013).

As metabolism is nearly stalled in a dry (desiccated) mature seed, enzymatic ROS production is greatly reduced and the limited amount of available ROS may come from non-enzymatic reactions e.g. lipid peroxidation (El-Maarouf-Bouteau and Bailly 2008; Gomes and Garcia 2013). However, in a hydrated germinating seed, mitochondria [through respiratory electron transport chain (ETC)] and peroxisomes (including specifically, glyoxysomes) are the most active cellular organelles involved in ROS production (both $O_2^{\bullet-}$ and H_2O_2) at high rates (Bailly 2004; El-Maarouf-Bouteau and Bailly 2008). Among the enzymatic sources of ROS, plasma membrane (PM) NADPH oxidase (NOX) [or respiratory burst oxidase homologs (RBOHs); homologs of $gp91^{phox}$ subunit of mammalian NOX complex] is the most prominent one which is almost universal in distribution in plants and functions as the prime source of ROS (Sagi and Fluhr 2006). Its importance is even more pronounced in skotomorphogenic organs (e.g. seed, root etc) which are devoid of photosynthetic electron transport chains (pETC) (operating in chloroplasts; one of the most active ROS producers in plants) (Li et al. 2017). NOX produces $O_2^{\bullet-}$ by one electron reduction of O_2 (Fluhr 2009), which is readily converted to H_2O_2 either spontaneously or by the activity of superoxide dismutase (SOD) enzyme. Treatment with DPI (specific NOX inhibitor) results in almost complete inhibition of germination and axis growth e.g. in *Arabidopsis thaliana* (Leymarie et al. 2012), *Vigna radiata* (Singh et al. 2014) and *Oryza sativa* (Li et al. 2017) highlighting the necessity of NOX-dependent ROS formation for successful completion of germination (Hu et al. 2020). Apart from NOX, cell wall located class III peroxidase (Prx) also plays key role in regulation of germination as it is the major enzymatic source of $^{\bullet}OH$ radical that relaxes the cell wall by cleaving wall polysaccharides (Schweikert et al. 2000; Singh et al. 2015). It is well reported that onset and progress of germination is accompanied by production of $^{\bullet}OH$ radicals (Schopfer et al. 2001; Müller et al. 2009a, b; Richards et al. 2015). Accordingly, the level of cellular Prx activity reached its peak at the time of axis emergence by rupturing the seed coat, whereas treatment with Prx inhibitors *viz.* salicylhydroxamic acid (SHAM) and $^{\bullet}OH$ scavenger (sodium benzoate) suppressed *V. radiata* germination (Singh et al. 2015). Other

sources of ROS that may mediate germination are also being explored. Chen et al. (2016) have reported that polyamine oxidase (PAO) regulates *O. sativa* seed germination by producing H_2O_2 and after studying gene expression patterns they have identified *OsPAO5* as the gene that encodes most of the PAO activity during germination. Expression and activity of apoplastic germin-like oxalate oxidase (gl-OXO) enzyme has been identified in germinating *T. aestivum* embryo (Caliskan and Cuming 1998). The authors suggested that H_2O_2 originating from gl-OXO activity is involved in "cell wall-restructuring" through cross-linking of wall polymers.

Among the different ROS forms, H_2O_2 appears to be responsible for most of the ROS signaling owing to its structural and chemical properties. Unlike $O_2^{\bullet-}$, $^1O_2$ or $^{\bullet}OH$, H_2O_2 is freely diffusible through aquaporins (Mubarakshina and Ivanov 2010; Bienert and Chaumont 2014) thereby being able to cross membranes. Thus it can accumulate either at apoplast or protoplast and function irrespective of the site of production (e.g. mitochondria, peroxisome or NOX). However, $O_2^{\bullet-}$ and $^{\bullet}OH$ also perform specific functions during germination in close proximity to their origin. Various modes of action are involved in ROS-mediated seed germination which are spatiotemporally differentiated. The accumulation of $O_2^{\bullet-}$ and H_2O_2 during after-ripening leads to protein carbonylation which has been suggested to underlie alleviation of dormancy (Oracz et al. 2007; Müller et al. 2009a; Bahin et al. 2011). Dormancy breaking and onset of germination are greatly dependent on the interactions between ROS and phytohormones. Thus, ROS signals are perceived by the nucleus and alterations in hormone metabolism take place following modified nuclear gene expression patterns. The germination-stimulatory role of H_2O_2 indeed involves promotion of GA biosynthesis and catabolism of ABA leading towards the establishment of low ABA/high GA content ratio necessary for germination (Liu et al. 2010; Gomes et al. 2014; Bailly 2019). The role of $^{\bullet}OH$ in relaxation of cell wall by cleaving wall polysaccharides is well established (Schopfer et al. 2002; Liszkay et al. 2004; Müller et al. 2009b). This allows the mechanically weakened cell walls (with relaxed tension) to stretch in response to turgor pressure which essentially results in cell expansion (Fry 1998; Gomes et al. 2014). ROS are also involved in reserve mobilization by mediating oxidative break down of stored polysaccharides, DNA, RNA, proteins and fatty acids (Schweikert et al. 2002; Buetler et al. 2004; Job et al. 2005) which provides nutrients to the growing embryo. In a strictly GA-favored (and ABA-inhibited) manner, ROS carry out programmed cell death (PCD) of aleurone layer cells stimulating the release of amylase and protease enzymes that facilitates the mobilization of stored materials (Fath et al. 2001, 2002; Gomes et al. 2014).

3.4 Cross-Talk Between Hormone and ROS During Seed Germination

Interactions between ROS and phytohormones are well known to underlie a large number of plant processes encompassing different growth and stress tolerance responses (Baxter et al. 2014; Xia et al. 2015). For instance, inhibition of NOX by treatment with dipheneyelne iodoinium (DPI; specific NOX inhibitor) resulted in impairment of ABA-induced stomatal closure (Zhang et al. 2001) which was further corroborated by obtaining similar effects from *Atrboh f* single mutant as well as *Atrboh d/f* double mutants (Kwak et al. 2003; Mignolet-Spruyt et al. 2016). Regulation of plastic root system architecture by H_2O_2 has been suggested to be dependent on modulation of polar auxin transport by H_2O_2 which results into alteration of auxin accumulation and redistribution (Su et al. 2016). Moreover, heat stress specific systemic acquired acclimation (SAA) has been reported to be regulated by spatio-temporal interactions between ROS and ABA in *Arabidopsis* (Suzuki et al. 2013). Interestingly, proteins (transcription factors, kinases, phosphatases etc) that are specifically involved in hormone signaling have been found to act also as ROS signaling factors thereby integrating the two different signaling pathways (Mignolet-Spruyt et al. 2016; Oracz and Karpiński 2016).

It is evident that seed germination is a complex process which involves intense hormonal regulation along with pivotal roles played by ROS. Efforts are being made since long to identify any possible cross-talks among the two signaling systems during germination (as already found in case of different plant responses) (Oracz and Karpiński 2016). As ABA and GA are the primary phytohormones that antagonistically regulate seed germination, responses of ROS to alteration in ABA/GA balance are crucial for alleviation of dormancy and onset of germination. As such, the typical ROS "burst" in the seed coat and embryo was inhibited by ABA in both seed parts (and inhibited germination) whereas GA reversed the inhibitory effect of far-red light on ROS production and maintained the ROS level during germination in dark (Schopfer et al. 2001). Direct interaction of H_2O_2 with ABA is greatly studied in stomatal closure where ABA induces ROS production and H_2O_2 stimulates ABA-dependent signaling (Zhang et al. 2001; Kwak et al. 2003; Taiz et al. 2015). However, on the contrary to stomatal movement regulation, ABA reduces ROS production in seeds (especially embryo) and inhibits germination (Ye et al. 2012) probably by activating antioxidant enzymes *viz.* catalase, ascorbate peroxidase (Fath et al. 2001; Xia et al. 2015). Inhibition of germination under ABA treatment has often been found to be reversed/overcome by H_2O_2 e.g. in *Panicum virgatum* (Sarath et al. 2007), *Vigna radiata* (Chaudhuri et al. 2013). This can be explained by the findings of Liu et al. (2010) that imbibition with H_2O_2 significantly increases the expression of four ABA catabolism genes encoding. ABA 8′-hydroxylase (*CYP707A1, CYP707A2, CYP707A3, CYP707A4*) and promote germination. In addition they also showed that treatment with DPI reduces the expression of those genes and inhibits germination, suggesting a role of NOX in the process. In *Nicotiana tabacu*m plants, H_2O_2 suppressed the expression of ABA biosynthesis genes encoding

9-cis-epoxycarotenoid dioxygenase (*NCED1 and NCED3*) and promoted *CYP707A1* and *CYP707A2* gene expression (Li et al. 2018). Similar effects were obtained on application of exogenous GA. Expression of ABA insensitive 3 and 5 [*ABI3 and ABI5*; central ABA signaling components] were significantly downregulated by H_2O_2 and GA whereas DPI and Uniconazole (Uni; GA biosynthesis inhibitor) promoted them (Li et al. 2018) depicting the synergistic effect of ROS and GA on repression of ABA signaling. Confirming the suggested involvement of NOX in ABA-dependent signaling in germination, Chaudhuri et al. (2013) reported that NOX activity was indeed repressed under the treatment of ABA and was stimulated when seeds were treated with ABA biosynthesis inhibitor (fluridone). Barba-Espín et al. (2011) has suggested that H_2O_2 may impair ABA transport from cotyledons to the embryo thereby promoting germination. Interestingly, Ishibashi et al. (2012) reported that H_2O_2 suppressed the expression and autophosphorylation of an ABA-responsive Ser/Thr protein kinase (PKABA) which is involved in inhibition of *GAmyb* expression (Gómez-Cadenas et al. 2001). In turn, reduced expression and activity of PKABA results in induction of α-amylase expression and promotes germination. Thus, the mode of action of H_2O_2 in antagonizing the ABA-dependent germination inhibition appears to correlate with GA signaling pathway. It is indeed observed that while ABA suppresses expression of GA biosynthesis genes e.g. *GA3ox*, H_2O_2 stimulated their expression and rescued germination (Liu et al. 2010).

Interactions between ROS and GA are found in different plant tissues which mostly involve the negative regulatory role played by DELLA proteins (Xia et al. 2015). It is reported by Achard et al. (2008) that DELLA proteins' content increases in *ga1-3* (GA deficient) mutant which promotes the expression and activity of SOD and catalase enzymes, resulting in inhibition of ROS accumulation. Extensive involvement of ROS in enhancement of GA biosynthesis and signaling during germination has also been reported (Leymarie et al. 2012; Xia et al. 2015; Li et al. 2018). During germination in *N. tabacum*, H_2O_2 promoted the expression of GA insensitive dwarf protein (*GID1* and *GID2*; a receptor of GA signaling) which would facilitate the formation of GA-GID-DELLA complex and would release transcription factors from DELLA-mediated suppression (Xia et al. 2015; Li et al. 2018). The GA-mediated PCD of aleurone cells (leading to mobilization of storage reserve) involves key roles played by ROS e.g. damage to membrane lipids (resulting in loss of membrane integrity), DNA and cellular proteins (Bethke and Jones 2001; Fath et al. 2001). GA reduces the rate of activity of ROS-metabolizing enzymes e.g. catalase, ascorbate peroxidase, SOD and, in effect, makes the aleurone layer cells progressively more sensitive to H_2O_2 which accelerates PCD and promotes germination. Stimulation of H_2O_2 production has also been found to be induced by GA in wheat aleurone cells (Wu et al. 2014). Conforming to this, inhibition of germination under treatment of GA biosynthesis inhibitor (paclobutrazole, PAC) was counteracted and reversed by H_2O_2 in *Vigna radiata* (Chaudhuri et al. 2013). On the other hand, imbibition with H_2O_2 enhanced the transcription level of five GA biosynthesis genes *viz.GA20ox1, GA20ox2, GA20ox3* (encoding GA 20-oxidase enzyme) and *GA3ox1, GA3ox2* (encoding GA 3-oxidase enzyme) during early seed germination (Liu et al. 2010; Li et al. 2018). Nonetheless, reduced

expression of GA catabolism gene *viz.GA2ox3* (encoding GA 2-oxidase enzyme) was inflicted by H_2O_2 treatment (Bahin et al. 2011). Interestingly, ABA suppressed the expression of *GA3ox* genes. In an ABA catabolism mutant (*cyp707a2*), *GA3ox* expression was greatly reduced whereas in its overexpression line i.e. *CYP707A2-OE*, increased level *GA3ox* expression was obtained. Although treatment with DPI reduced the expression of all the five GA biosynthesis genes, exogenous H_2O_2 was able to successfully reverse the DPI-mediated reduction in gene expression (Liu et al. 2010). Different combinations of treatments were utilized by Li et al. (2018) and it was found that H_2O_2 + Uni and GA + DPI could overcome the inhibition of germination caused by individual treatments of DPI and Uni. From the inhibitory role of DPI it can be assumed that NOX is involved in GA signaling during germination. Corroborating to the proposal, Chaudhuri et al. (2013) reported that in the germinated axes of PAC treated seeds, reduction in NOX activity were detected in native PAGE assay indicating the enzyme's positive involvement in GA signaling. Isocitrate lyase (ICL), a key enzyme of glyoxylate cycle that catalyzes irreversible aldol cleavage of isocitrate to glyoxylate and succinate, enhances mobilization of storage during germination. Treatment with DPI or Uni led to inhibition of ICL expression as well as activity which were efficiently counteracted by H_2O_2 and GA (Li et al. 2018).

Interestingly, expression of two GA-regulated proteins which are involved in cell wall loosening and cell expansion *viz.* xyloglucan endotransglucosylase (*XTH5*) and expansin (*EXP2, EXP11*) has been found to be upregulated by H_2O_2 (Yamauchi et al. 2004; Thiel et al. 2008; Liu et al. 2010; Bahin et al. 2011). Both the genes are down-regulated under DPI and c-PTIO [2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide; NO scavenger] treatments (Liu et al. 2010). This clearly depicts the interaction or co-activity among GA and NOX-produced ROS in the cell elongation process leading to seed germination. Another ROS form, $^{\bullet}OH$ radical mediates cell wall relaxation by cleaving wall polysaccharides e.g. pectin (Airianah et al. 2016). The $^{\bullet}OH$ radical can be important for mediation of germination as it can weaken the endosperm cap which would result in less force being needed for the radicle to protrude through the cap (Müller et al. 2009b). Indeed, Schopfer et al. (2001) have reported an increase in $^{\bullet}OH$ production in seed coat and embryo co-occurring during radish seed germination. The DPI treatment-induced reduction in $^{\bullet}OH$ production is mimicked by ABA, whereas H_2O_2, GA and ethylene promotes $^{\bullet}OH$ radical production and counteracts ABA signaling (Graeber et al. 2010; Barba-Espín et al. 2011; Richards et al. 2015).

Apart from ABA and GA, ethylene also plays important role in germination. Involvement of ethylene in germination is based on its cross-talks with ABA and GA (Oracz et al. 2008, 2009; Linkies et al. 2009). When seeds were imbibed with GA and $AgNO_3$ (ethylene action inhibitor), germination could commence, while a combined treatment of PAC and ethrel could not restore germination depicting that ethylene alone cannot signal germination when GA is absent (Chaudhuri et al. 2013). Supportive molecular evidences show that GA could induce germination even in *etr1* mutant seeds; however ethylene was unable to do the same in *gib-1* mutant (Groot and Karssen 1987; Bleecker et al. 1988). It has been reported that

ethylene counteracts ABA effects and promotes germination (Kucera et al. 2005). On the other hand, interaction of ethylene with ROS has also been observed during seed germination indicating towards a common signaling system involving ROS, ethylene and GA. Treatment with ethylene biosynthesis inhibitor repressed germination, which could be reversed when supplemented with exogenous H_2O_2 (Chaudhuri et al. 2013). However, when germination was stalled under treatment of propyl gallate (PG; general ROS scavenger), addition of ethylene was little effective (Chaudhuri and Kar 2008). In *Helianthus annus*, ethylene and cyanide release the seeds from dormancy and the mechanism involves cyanide-dependent stimulation of ethylene response factor1 (*ERF1*) expression which was sensitive to DPI treatment (Corbineau et al. 1990; Oracz et al. 2008, 2009). The cyanide-dependent dormancy alleviation was found to be mimicked by ROS generators e.g. MV (methyl viologen) and menadione and was counteracted by ROS scavengers e.g. Tiron ($O_2^{\bullet -}$ scavenger), DMTU (H_2O_2 scavenger), sodium benzoate ($^{\bullet}OH$ scavenger), ascorbic acid. Moreover, MV induced the expression of *ETR2* and *ERF1* genes significantly (Oracz et al. 2008, 2009). Supporting results were reported by Ishibashi et al. (2013) where a cross-talk among ROS and ethylene signaling pathways was reported during germination in *Glycine max*. Treatment with N-acetylcysteine (NAC, an antioxidant) counteracted the effects of ROS and suppressed germination. In addition, NAC treatment lowered cellular ethylene content by reducing the expression of ACC synthase genes viz. *GmACS2e* and *GmACS6a*. Addition of ethophen (which is converted to ethylene) reverses the effects of NAC on germination. Interestingly, the expression of ACS genes have been found to be promoted by H_2O_2 in both *Vigna radiata* (*VrACS1* and *VrACS6*; Song et al. 2007) and *Glycine max* (GmACS6a; Ishibashi et al. 2013) during germination. Therefore it is evident that coordinated action of ROS and ethylene is underlying seed germination process.

3.5 ROS – PM H^+-ATPase – Hormones: Extension of the Signaling Network

Being an electrogenic proton (H^+) pump in nature, PM H^+-ATPase is primarily responsible for conduction of H^+ from cytosol across the PM to the apoplastic space utilizing the energy released from hydrolysis of ATP. The trans-membrane electrochemical gradient (negative at cytosolic side, positive at apoplastic side) arising from active H^+-transport along with tight regulation of pH homeostasis (high at intracellular and low at extracellular sides) is instrumental in the apoplastic events including the activity of several enzymes and proteins like expansin involved in cell wall relaxation (Falhof et al. 2016). Besides, they also provide driving force for ion and metabolites transport (Palmgren 2001; Gévaudant et al. 2007). Consequently, involvement of PM H^+-ATPase in several plant processes is known for decades which includes, but not limited to, dormancy alleviation and seed germination (De

Bont et al. 2019), organ growth (Janicka-Russak 2011), stomatal responses (Kinoshita et al. 2003) and stress tolerance (Zhang et al. 2017).

One of the most important growth promoting roles of PM H^+-ATPase is its ability to enable cell elongation mediated by cell wall loosening (Hager 2003; Janicka-Russak 2011). As germination is defined by radicle protrusion through seed coat which mostly depends on embryo cell elongation rather than cell division (Gimeno-Gilles et al. 2009; Sliwinska et al. 2009), PM H^+-ATPase activity is indispensable for the process (Obroucheva 2017; Obroucheva et al. 2018). Interestingly, selective localization of the enzyme at certain regions of embryo has been observed during germination. These regions are predominantly involved in either secondary nutrient transport or cell elongation (Enríquez-Arredondo et al. 2005). Analyzing the effects of Vanadate (specific PM H^+-ATPase inhibitor) and fusicoccin (a toxin that activates PM H^+-ATPase) treatments on seed germination, De Bont et al. (2019) suggested crucial involvement of PM H^+-ATPase in dormancy alleviation. Reduced germination (and root growth thereafter) of aged seeds has been co-related with inhibition of PM H^+-ATPase activity too (Sveinsdóttir et al. 2009). Tissue-specific expression patterns of different isoforms of the enzyme have been studied and AHA10 (*Arabidopsis* PM H^+-ATPase 10) has been found to be expressing exclusively in developing seeds (in the integument tissues surrounding the embryo sac) (Harper et al. 1994). Disruption of AHA10 gene resulted in severe reduction of production of proanthocyanidin in the seed coat endothelium in *Arabidopsis* (Baxter et al. 2005). However, AHA1 an AHA2 are expressed almost in every tissue and organs demonstrating the importance of the enzyme in different plant processes (Janicka-Russak 2011). Overexpression of PM H^+-ATPase gene commonly results in enhancement of the enzyme activity. Gévaudant et al. (2007) selectively excluded last 103 amino acids (corresponding to the C-terminal auto inhibitory domain) from NpPMA4 (*Nicotiana plumbaginifolia* PM H^+-ATPase 4) and created a constitutively active ΔPMA4. Under salt stress, overexpression of the ΔPMA4 (ectopically) in tobacco (*N. tabacum*) plants exhibited higher seed germination in contrast to the wild type PMA4, further corroborating the efficiency of H^+-ATPase in promotion of germination.

Although operating through different modes of action, both apoplastic ROS and PM H^+-ATPase enable cell elongation by loosening/relaxing the cell wall thereby playing pivotal roles in early seed germination (radicle emergence; depends on cell elongation only). The relationship between ROS and PM H^+-ATPase is a matter of curiosity and significance and is being studied under different physiological conditions. Recently, involvement of PM H^+-ATPase in a functional synchronization with NOX (initiator of apoplastic ROS cascade) has recently been identified during root growth in *Vigna radiata* (Majumdar and Kar 2018). This is in complete agreement with earlier studies exhibiting positive interplays between these enzymes. PM H^+-ATPase activity was promoted, under different physiological conditions, by application of exogenous H_2O_2 and was repressed under the treatment of NOX inhibitor e.g. DPI or ROS scavengers (Zhang et al. 2007; Li et al. 2011; Zhao et al. 2015). Conversely, inhibition of PM H^+-ATPase was found to be detrimental for NOX activity (Majumdar and Kar 2018). Moreover, H_2O_2 can promote activity as well as

gene expression of PM H^+-ATPase (Janicka-Russak et al. 2012) and NOX (via MAPK cascade pathway) (Yoshioka et al. 2016; Liu and He 2017; Hu et al. 2020). Since Ca^{+2} can activate both NOX (Sagi and Fluhr 2006; Kurusu et al. 2015) and PM H^+-ATPase (Lang et al. 2014), threshold $[Ca^{+2}]_{cyt}$ also serves as a potent mediator, apart from H_2O_2, of the enzymatic loop (Majumdar and Kar 2018). The hyperpolarization-activated Ca^{+2} channels (HACC) are crucial gates for Ca^{+2} entries into the cytosol. By definition HACCs require membrane hyperpolarization caused by PM H^+-ATPase activity, whereas their activation depends on H_2O_2 (Michelet and Boutry 1995; Demidchik et al. 2003, 2007; Foreman et al. 2003; Mori and Schroeder 2004). Apparently, Ca^{+2}influxes across PM into the cytosol are regulated by both ROS and PM H^+-ATPase. Therefore, it can be presumed that during germination, PM H^+-ATPase and NOX work co-operatively in a Ca^{+2}-regulated manner and maintain PM electrical (charge) balance while mediating cell expansion. Interestingly, enzymatic production of apoplastic H_2O_2 by SOD is dependent on activities of both NOX and PM H^+-ATPase simultaneously as the products of the latter enzymes ($O_2^{\bullet -}$ and H^+, respectively) are substrates of SOD (Majumdar and Kar 2019). Thus a feed-forward relationship is established among the three enzymes as H_2O_2, being produced by SOD, activates both NOX and PM H^+-ATPase either directly or through facilitating Ca^{+2} entry into the cell. Furthermore, cell wall located class III peroxidase (Prx) utilizes apoplastic H_2O_2 as substrate and produces $^{\bullet}OH$ radical which cleaves wall polysachharides and relaxes cell wall (Schweikert et al. 2000; Liszkay et al. 2004; Müller et al. 2009b; Airianah et al. 2016). It has been found that H_2O_2 coming from the NOX-PM H^+-ATPase-SOD loop is crucial for Prx activity since inactivation of the enzymatic loop inhibits Prx too (Majumdar and Kar 2019). Therefore, it appears that PM H^+-ATPase is necessary for production of $^{\bullet}OH$ radical. Additional support comes from Liszkay et al. (2004) who demonstrated that fusicoccin (a stimulator of PM H^+-ATPase) could increase the production of $^{\bullet}OH$ radical in *Zea mays* root.

On the other hand, varying relationships of PM H^+-ATPase with different phytohormones have been documented time and again. Strikingly, the responses have been found to be location (tissue/organ) or condition (normal growth/stressful) dependent. The best example of such is ABA-PM H^+-ATPase. ABA-induced inhibition of PM H^+-ATPase in guard cells has been extensively reported (Taiz et al. 2015). In *Arabidopsis*, ABA induces the attachment of VAMP711 (vesicle-associated membrane protein; a R-SNARE family protein) to the C-terminal autoinhibitory domain of AHA1 and AHA2 and inhibits the enzyme (Xue et al. 2018). On the contrary, ABA has been found to stimulate PM H^+-ATPase in developing apple fruit, especially in phloem cells (Peng et al. 2003). Moreover, a specific CDPK *viz.* ABA-stimulated calcium-dependent protein kinase (ACPK1; ABA stimulates autophosphorylation and kinase activity) is identified in grape berry mesocarp, which acts on the C-terminal domain of PM H^+-ATPase and activates the enzyme by phosphorylation (Yu et al. 2006). However during germination, ABA appears to inhibit PM H^+-ATPase activity. Gimeno-Gilles et al. (2009) reported that ABA targets the process of cell wall loosening to restrict germination and inhibits the expression of several genes that are crucial for wall loosening (and resultant cell

expansion) e.g. alpha-expansin, extensin, xyloglucan endotransglycosylase, cellulose synthase etc. Concomitantly, during seed germination in *Arabidopsis*, prominent non-transcriptional inhibition of PM H^+-ATPase (AHA2) was induced by ABA via activation of SnRK2.2 kinase which phosphorylates unidentified amino acids at C-terminal domain of the enzyme (Planes et al. 2015). On the other hand, IAA-induced activation of PM H^+-ATPase is known for long (Rayle and Cleland 1992; Hager 2003) and it is crucial for elongation of plant cells following increase in plastic extensibility of cell wall. IAA has been reported to stimulate PM H^+-ATPase activity either by inducing phosphorylation of Thr947 (Chen et al. 2010; Takahashi et al. 2012; Haruta et al. 2015) or by indirectly inhibiting dephosphorylation of the enzyme [by inhibiting protein phosphatases (PP2C-D)]. IAA accelerates gene expression of SAUR19 (Small Auxin Up-RNA) which, in turn, interacts and inhibits PP2C-D (Spartz et al. 2014). Auxin up regulates PM H^+-ATPase gene expression and increases exocytosis of the enzyme too (Hager et al. 1991; Du et al. 2020), which eventually results in an increased density of the enzyme at the PM (Xia et al. 2019). Although GA increased phosphorylation of the conserved Thr947, thereby promoting AHA1 and AHA2 activity, jasmonic acid (JA) and kinetin (cytokinin) significantly dephosphorylated the site (Chen et al. 2010). Additionally in *Solanum tuberosum* stolons, GA treatment was found to induce expression of PHA1 and PHA2 (potato PM H^+-ATPase) (Stritzler et al. 2017). While exogenous polyamines (spermine and spermidine) have been found to promote 14-3-3 binding to PM H^+-ATPase thereby increasing the enzyme activity (nearly two-fold), treatment with polyamine synthesis inhibitor reduced the enzyme's activity (Reggiani et al. 1992; Garufi et al. 2007). The role of ethylene in promotion of H^+-efflux and activation of expansin protein leading to enhanced petiole elongation in completely submerged *Rumex palustris* (Vreeburg et al. 2005) may be considered as its stimulatory effect on PM H^+-ATPase. In agreement to this, Waters et al. (2007) have reported that ethylene induces enhancement of PM H^+-ATPase (*CsHA1*) gene expression in Fe-deficient *Cucumis sativus* plants, whereas treatments with ethylene inhibitors [Co and AOA (aminooxyacetic acid)] resulted in inhibition of the gene's expression and reduced extracellular acidification.

Considering the large cross-talks between ROS/hormones, ROS/PM H^+-ATPase and hormones/PM H^+-ATPase, it seems justifiable to presume a common signaling system working among them that mediates seed germination. Conforming to the hypothesis, De Bont et al. (2019) have suggested that the observed dormancy alleviation under treatments of ethylene and MV (ROS generator) may involve promotion of PM H^+-ATPase activity (as indicated by membrane hyperpolarization) by both the agents. Delayed germination under treatment of ROS scavengers was accompanied by membrane depolarization indicating inhibition of PM H^+-ATPase activity. Thus it is evident that a close relationship of PM H^+-ATPase with ROS and phytohormones exists and regulation of seed germination process is governed by the signaling system.

3.6 Reactive Nitrogen Species (RNS): Another Potential Candidate to Play for Signaling

Apart from ROS, different other types of free radicals are also generated in living systems which can be broadly classified as reactive nitrogen species (RNS), reactive chlorine species (RCS), reactive bromine species (RBS) etc. Among these, RNS have been reported to play vast signaling roles in different aspects of plant life under both physiological and adverse conditions (Gupta and Igamberdiev 2015). As a collective term, RNS incorporates both free radicals [e.g. nitric oxide ($^{\bullet}NO$), nitrogen dioxide ($^{\bullet}NO_2$), nitrate radical ($^{\bullet}NO_3$)] and non-radicals [e.g. nitrous acid (HNO_2), nitrosyl cation (NO^+), nitroxyl anion (NO^-) etc] (Halliwell and Gutteridge 2015). Involvement of $^{\bullet}NO$ in cellular signaling has been identified long back (Palmer et al. 1987; Laxalt et al. 1997) and extensive research is being carried out since then to further explore its functions and modes of operation. Consequently, $^{\bullet}NO$ is now established to mediate diverse plant processes ranging from seed germination to stress tolerance (Šírová et al. 2011; Hancock and Neill 2019; Kohli et al. 2019).

In germinating seeds, $^{\bullet}NO$ may be produced by both enzymatic [e.g. nitrate reductase (NR) and nitric oxide synthase (NOS)] and non-enzymatic sources (Corpas et al. 2009; Moreau et al. 2010; Šírová et al. 2011). It has been observed that treatment of seeds with sodium nitroprusside (SNP; a potent $NO^{\bullet}$ donor) promotes early seed germination in *Lupinus luteus*. Moreover, SNP could counteract the negative effects of heavy metals (e.g. Pb and Cd) and NaCl and reinstate germination (Kopyra and Gwóźdź 2003). Conforming to this, Bethke et al. (2004, 2006a) have reported that exogenous application of $NO^{\bullet}$ donors break dormancy of *Arabidopsis* seeds. On the other hand, treatment with c-PTIO [$^{\bullet}NO$ scavenger; 2-[4-carboxyphenyl]-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide] enhanced seed dormancy (Liu et al. 2010). The signalling process through which $^{\bullet}NO$ regulates germination is complex and involves cross-talks with hormones and ROS. In different studies, SNP promoted germination by enhancing the positive effect of norflurazon (ABA synthesis inhibitor) while cPTIO negated the effects of fluridone and prevented germination (Bethke et al. 2006b; Piterková et al. 2012; Arc et al. 2013). $^{\bullet}NO$ antagonizes the ABA-induced dormancy maintenance by promoting post-translational degradation of ABI5 (ABA insensitive 5) protein through *S*-nitrosylation of Cys153 residue (Albertos et al. 2015). As found in case of H_2O_2, treatment with SNP also induces the expression of ABA catabolism gene *CYP707A2*. Interestingly, SNP could reverse the DPI-induced reduction of gene expression; however, H_2O_2 was unable to overcome the inhibitory effects of cPTIO (Liu et al. 2010). On the other hand, expressions of GA biosynthesis genes (*GA20ox* and *GA3ox*) are enhanced by SNP and down-regulated by cPTIO. While SNP reversed the down-regulation induced by DPI, H_2O_2 was able to counteract the negative effects of cPTIO and enhance GA synthesis leading to germination. Exogenous H_2O_2 could also reverse the negative effects of cPTIO on expressions of two GA-regulated genes *viz. XTH5* and *EXP2* which are involved in cell wall loosening

and cell expansion (Liu et al. 2010). Thus, it is evident that seed germination involves intrinsic cross-talks among ROS, $^{\bullet}$NO (or RNS), and hormones.

Interestingly, $^{\bullet}$NO has been found to be involved in regulation of ion homeostasis in a ethylene-dependent manner, which is mediated through the stimulation of PM H^+-ATPase activity (Wang et al. 2009). While NaCl repressed PM H^+-ATPase activity in *Arabidopsis* callus both individually as well as in combined treatments with AOA [aminooxyacetic acid; ethylene biosynthesis inhibitor] and L-NNA [N_ω-nitro-L-arginin; nitric oxide synthase (NOS) inhibitor], the inhibitions could be overcome with treatments of ACC (1-aminocyclopropane-1-carboxylic acid; an ethylene precursor) and SNP. Nonetheless, the SNP-mediated stimulation of PM H^+-ATPase was abolished by both PTIO [$^{\bullet}$NO scavenger; 2-Phenyl-4,4,5,5-tetramethylimidazoline-1-oxyl 3-oxide] and AOA treatments, depicting an interplay between $^{\bullet}$NO and ethylene that precedes PM H^+-ATPase promotion. Further, Zhang et al. (2007) have reported that SNP-induced promotion of PM H^+-ATPase activity in *Populas euphratica* callus could be eliminated by DPI whereas the positive effect of H_2O_2 on PM H^+-ATPase was not reversed under treatments of NMMA (N^G-monomethyl-L-Arginine acetate; NOS inhibitor) and PTIO. Thus, it appears that $^{\bullet}$NO promotes PM H^+-ATPase activity through ethylene and (NOX-dependent) ROS homeostasis. Since PM H^+-ATPase is closely associated with ROS/hormone cross-talks that regulate seed germination, it can be hypothesized that a functional ROS – $^{\bullet}$NO – PM H^+-ATPase – hormone signalling network is governing the process.

3.7 Conclusion

Seeds, if otherwise not in a dormant state, experience the first spell of growth upon germination (under a set of congenial environmental conditions) by radical protrusion as dictated by subtle levels of hormonal combination mainly dominated by GA. Ethylene has also been demonstrated to promote the process while ABA is recognized for inhibition of germination. These hormones exert their action through specific signaling pathways with purported crosstalk. ROS (generated through NOX-dependent apoplastic cascade) integrates with such signaling network along with a transmembrane H^+ gradient inflicted by PM H^+-ATPase. NO$^{\bullet}$ modulates GA/ABA ratio and PM H^+-ATPase activity in a ROS and ethylene-dependent way and thereby regulates seed germination process. A working model portraying the combined mode of action of hormones, ROS, $^{\bullet}$NO and PM H^+-ATPase during seed germination has been depicted in the Fig. 3.1.

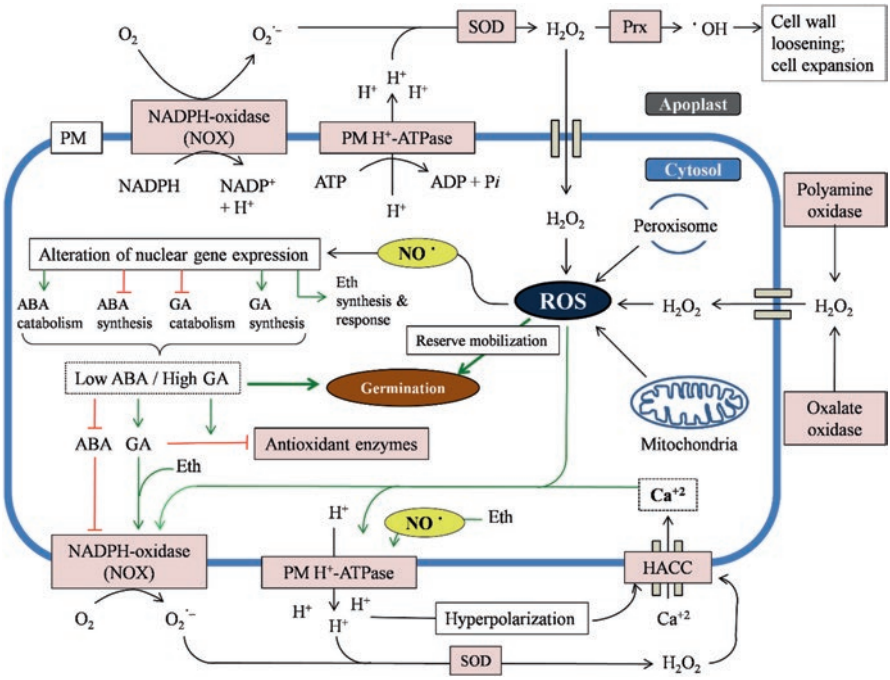

Fig. 3.1 An integrated working model demonstrating the cross-talks between hormonal signaling network, ROS homeostasis and PM H^+-ATPase activity during seed germination. NOX-dependent ROS production cascade is the major source of apoplastic ROS in plants. The $O_2^{\cdot -}$ being generated from NOX activity is readily converted (disproportionated) to H_2O_2 either by spontaneous reactions or by SOD activity. Co-activity of PM H^+-ATPase with NOX ensures adequate supply of H^+ at the apoplast, which is essential for SOD activity. *De novo* generated H_2O_2 is utilized by class III Prx enzyme and is converted to ·OH radical that cleaves wall polysaccharides thereby mediating cell wall relaxation. Other apoplastic enzymes *viz.* polyamine oxidase and oxalate oxidase also produce H_2O_2 during germination. H_2O_2, from all the sources, diffuses across the plasma membrane and accumulates into cytosol. Mitochondrial respiratory electron transport chain (ETC) and peroxisome are the primary intracellular sources of ROS (both $O_2^{\cdot -}$ and H_2O_2) in germinating seeds and they contribute effectively in building a cytosolic ROS pool. PM H^+-ATPase mediated hyperpolarization of plasma membrane and H_2O_2 together activate HACC channels that facilitate Ca^{+2}influxes into cytosol from apoplast. Threshold $[Ca^{+2}]_{cyt}$, in turn, stimulates both the enzymes either by directly binding to the EF-hand motifs (of NOX) or by phosphorylating different amino acids. The cytosolic ROS signal is perceived by nucleus and alterations in gene expression pattern take place. ROS specifically up-regulate GA synthesis and ABA catabolism genes whereas down-regulate ABA synthesis and GA catabolism genes. Thus, a low ABA/high GA concentration ratio is established which stimulates germination. While ABA-induced inhibition of NOX is reduced in this condition, high GA concentration activates NOX and simultaneously deactivates antioxidant enzymes. Ethylene synthesis and response genes are also up-regulated by ROS. In a GA-dependent manner, ethylene promotes NOX activity and increases ROS production. ROS mobilize the storage reserves by breaking down polysaccharides, DNA, RNA, proteins and fatty acids and facilitating the release of amylase and protease enzymes and, in effect, promote seed germination

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