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Review article

Implications of reactive oxygen and nitrogen species in seed physiology for sustainable crop productivity under changing climate conditions

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ABSTRACT

Reactive oxygen species (ROS) and reactive nitrogen species (RNS) incessantly produced as by-products of metabolism play significant roles in seed physiology. ROS (hydroxyl, superoxide radical and hydrogen peroxide) and RNS (nitric oxide, nitric dioxide, nitrous acid and dinitrogen tetroxide) content changes in all phases of seed life cycle that influence seed germination, dormancy and longevity. Recent studies illustrate that ROS and RNS are performing oxidative and nitrosative signaling to induce seed germination within oxidative window level. Besides, ROS/RNS-mediated post-translational modifications (PTM) like carbonylation, S-nitrosylation and nitration are gaining interest in promoting seed germination. Understanding the signalling pathways, cross-talk with plant hormones and their role in promoting seed germination and dormancy alleviation could pave way for hormone engineering that help in crop productivity, particularly under climatic changing conditions. In addition, role of antioxidants and glutathione thiols in protecting from oxidative damage indicate that these compounds can be used for seed viability/quality markers that aid in monitoring of crop establishment. In this review, sources of ROS and RNS, their cross-talk with plant hormones (prospects for hormone engineering), signalling functions pertaining to seed germination, dormancy and deterioration have been illustrated. In addition, seed quality markers under climatic changing conditions for effective monitoring of crop stand establishment and diagnostics development have been elucidated.

Abbreviations: ABA, abscisic acid; ABI5, abscisic acid insensitive 5; ACC, 1-aminocyclopropane-1- carboxylic acid; ACO, ACC oxidase; ANT, adenine nucleotide translocator; APX, ascorbate peroxidase; ASC, ascorbate; ASK-1, apoptosis signal-regulating kinase; BiP, binding protein; CAT, catalase; CDT, controlled deterioration treatment; CK, cytokinins; *cnu1*, continuous NO-unstressed-1; CO_2, carbon dioxide; $_C$PTIO, 2-4-carboxyphenyl-4,4,5,5-Tetramethylimidazoline-1-oxyl-3-oxide; CuAO, Copper Amine Oxidase; CYP707A, cytochrome P450 ABA 8'-hydrolase; DHAR, dehydroascorbate reductase; ER, endoplasmic reticulum; ET, ethylene; GA_3ox, gibberellic acid oxidase; GAs, gibberelins; Gifu, Gifu Komugi; GPX, glutathione peroxidase; GSH, glutathione; GSNO, S-nitrosoglutathione; H_2O_2, hydrogen peroxide; $^{\bullet}$HO, hydroxyl radical; HS, heat stress; ISTA, International Seed Testing Association; LC–MS/MS, Liquid Chromatography-Mass Spectrometry; MAPK, mitogen activated protein kinase; MAPKs, mitogen activated protein kinases; MC, moisture content; MoCo, molybdenum cofactor; MT, metallothionein; NADPH, nicotinamide adenine dinucleotide phosphate (Reduced Form); NO^-, nitroxyl anion; NO, nitric oxide; NO^+, nitrosonium; NOOMoCo, nitrated molybdenum cofactor; $^{\bullet}$O2-, superoxide radical; $ONOO^-$, peroxynitrite; PAs, polyamines; PHS, pre-harvest sprouting; PPP, pentose phosphate pathway; PR, pathogenesis related genes; PRX, Peroxiredoxin; PTM, post-translational modifications; PTP, permeability transition pore; qRT-PCR, quantitative real time PCR; RFO, raffinose family saccharides; RH, relative humidity; RNS, reactive nitrogen species; ROS, reactive oxygen species; SNAP, S-nitroso-*N*-acetyl-DL-pencillamine; SNO ABI5, S-nitrosylated abscisic acid insensitive 5; SNO, SnRKS-nitrosylated sucrose non-fermenting 1 (SNF1)-related protein kinases; SNO, S-nitrosothiol; SNP, sodium nitroprusside; SnRK, sucrose non-fermenting 1 (SNF1)-related protein kinases; SOD, superoxide dismutase; S-S, disulfide bonds; TRX, thioredoxin; Trx-ASK 1, thioredoxin-apoptosis signal regulating kinase 1; UPR, Unfolded Protein Response; VDAC, voltage dependent anion channel; Zn, zinc.

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1. Plant growth and development

Plant growth and development are important features that are incessantly regulated by genotypic and environmental signals. Owing to its sessile habitat, plants are endowed with diverse metabolic pathways that allow them to grow and develop in highly variable environments [1]. Reactive oxygen and nitrogen species (ROS, RNS) products are few examples that govern the plant growth and development [2–4]. Recent studies substantiate that the seed quality traits such as germination vigour (uniform and rapid seedling emergence under a wide range of environmental conditions), seed dormancy and longevity are regulated by ROS and RNS [4,5] (Supplementary Fig. 1). Moreover, studies on free radicals that favouring seed germination by regulating ABA and GAs through transcriptional and post-translational modifications is gaining great interest [6]. In contrary, ROS accumulation for prolonged periods coupled with decline of antioxidants governs seed deterioration in inappropriate stored seeds [7–9].

Climate changing factors such as heat stress, availability of ozone and atmospheric carbon dioxide (CO_2) perturbs redox imbalance and have a profound effect on photosynthetic metabolism and environmental stress responses [10]. For instance, over the decades, increase in 0.2 °C of average temperature has been predicted and greatly influence in fall of crop productivity. HS during flowering, results in complete loss of grain production [11]. Wang et al. [12] reported decrease of cereal productivity at an extent of 4–10 % occurred owing to an increase of annual seasonal temperature of 1 °C [12]. Thermo tolerance can be attained in plants through synthesis of heat shock proteins that are mediated by ROS signalling [13]. Similarly, at elevated CO_2, activation of pathogenesis related (PR) genes and defense mechanisms are activated with concomitant increase ROS production [14].

ROS formed during varied abiotic and biotic stresses are regulated through plant antioxidant machinery, which includes enzymatic [ROS detoxifying enzymes namely, catalase (CAT), superoxide dismutase (SOD), glutathione peroxidase (GPX), ascorbate peroxidase (APX) and peroxiredoxin (PRX)] and non-enzymatic antioxidants (ascorbic acid, glutathione, phenols). In additions to these antioxidants, nitric oxide (NO) plays an important signalling role in photosynthesis, osmolyte accumulation, gene expression and protein modifications under HS [15]. NO regulate ROS concentration and restores the balance between ROS, GSNO, GSH and ascorbate. At higher concentration of ROS, NO induces the transcription of APX, SOD and CAT activities. In contrary, when ROS are required for pathogen resistance, NO may inhibit NOX, CAT and APX activities through S-nitrosylation of cysteine residues [16]. Owing to these intricate networks, gaining deeper insights on ROS and RNS in seed physiology is necessary.

Understanding the signal transduction pathways driven by ROS and RNS for specific physiological traits is essential, which helps to address the problem of pre-harvest sprouting in wheat, quality seed production, field weathering of soybean and resurgence of recalcitrant species [17]. Further unravelling these signal transduction pathways in the seed could enable to develop an eco-friendly and cost effective techniques for seed germination, seed longevity and diagnostic tools for determination of physiological seed quality. So far, reviews have focused on ROS and RNS production and their role in seed physiology; but in this review, elucidation of signal transduction pathways, their interactions with plant hormones and implications in crop productivity (translational research), future prospects of genome editing with new variants of CRISPR/Cas-9 for sustainable agricultural productivity have been discussed.

2. Dynamics of reactive oxygen species in seed life cycle

ROS such as hydrogen peroxide (H_2O_2), superoxide radical ($O_2^{\cdot-}$) and hydroxyl radical (HO·), are incessantly produced in seeds as by-products of various metabolic pathways [18,19]. Generally, orthodox seeds undergo significant changes in moisture content during various stages of seed life cycle. For example, during imbibed stage the metabolic activity is higher, which requires water for translocation of metabolites and cell division. Several studies reported that mitochondria, glyoxysomes and NADPH oxidases of the plasma membrane are the major sources for ROS [20–24] (Fig. 1a). In contrary, at maturation and after ripening conditions the orthodox seeds minimize their metabolic activity and require less water. During these conditions, the predominant sources for ROS are Amadori, Maillard and lipid peroxidation mechanisms, respectively [23,25,26] (Fig. 1b).

ROS and RNS have been considered detrimental due to oxidative stress imposed on plants/seed. However, recent studies on the role of RNS and ROS have changed the paradigm-from toxicity molecules to important regulators of cellular functions [27,28]. Evidences are emerging that ROS and RNS coupled with plant hormones have become a part of signalling networks that regulates the seed germination, dormancy alleviation, development and ageing [29–33]. Topical studies pertaining to ROS have been reported that they play dual functionality, which implies that they act not only as a signalling molecule (at oxidative window limits) but also cytotoxic due to oxidative stress [34,35].

3. Role of ROS in seed germination and dormancy

Germination is an intricate network regulated by genetic and environmental cues. According to Bewley and Black [36] germination starts with uptake of water by a non-dormant and quiescent dry mature seed and ends with elongation of embryonic axes. During dormancy release process to germination capacity, H_2O_2 production has been observed during transition of seed from dormant state to a metabolically active state in jasmine rice (*Oryza sativa* L. cv. KDML 105), garden pea, sunflower seeds, soybean, maize, wheat and radish [3,37–39]. In addition, some more studies on increase in ROS content during seed germination implies that they have oxidative signalling function, which triggered for seed germination (Table 1). Here, an intriguing question is, how does the ROS influence the germination?

To explain the phenomenon, it has been proposed that ROS either acts as a secondary messenger or directly involve in triggering a cascade of events that result in germination. After imbibition, the ROS levels shoots up and accumulation of these molecules, particularly H_2O_2 (more stable than other oxidants) could trigger the oxidation of protein (carbonylation including seed storage protein) that inhibits glycolysis and promotes the activation of pentose phosphate pathway (PPP) [48]. This pathway provides NADPH and supplements to thioredoxin (TRX) enzyme, which reduces the disulfide (S-S) bonds of proteins including enzymes favouring the germination [3,27,49–52]. Another mechanism pertaining to accumulation of H_2O_2 and its interaction with plant hormones by mitogen activated protein kinases (MAPKs) have been illustrated in Fig. 2.

Barba-Espın et al. [53] had reported positive correlation with abundance of PsMAPK2 transcript and endogenous levels of H_2O_2 and seed germination. Activation of MAPKs by phosphorylation could promote germination by decreasing the ABA and 1-aminocyclopropane-1--carboxylic acid (ACC) contents with simultaneous increase in GAs [53,54]. Liu et al. [55] observed up-accumulation of H_2O_2 during imbibition in *Arabidopsis* sp. seeds showed increasing ABA catabolism genes and GA biosynthesis that favoured seed germination. In another study, dormancy alleviation of apple was done with cyanide, where decrease in ABA level and increase in H_2O_2 has been observed [56–58]. This study showed that the H_2O_2 influenced the regulation of GA biosynthesis and ABA catabolism during seed imbibitions, which regulate seed germination and dormancy. Further, quantitative RT-PCR (qRT-PCR) studies showed that the H_2O_2 has up-regulated the ABA catabolism genes (*e.g. CYP707A*) and decreased ABA content was observed during imbibition. On the other hand, H_2O_2 mediated up-regulation of GA biosynthesis genes is also observed through qRT-PCR studies. To perform this action, nitric oxide (NO) is also required. Evaluation of ABA catabolism mutant (*cyp707a2*) and an over-expressing *Arabidopsis* plant (*CYP707A2-OE*)

has been done, where the GA biosynthesis is negatively correlated with ABA content. GA applied exogenously is able to over-come the inhibition of germination at meagre concentrations of ABA; however, no significant effect of GA was exerted when ABA concentrations are high.

Here, the interactions between ABA and H_2O_2 is significant; since, the latter (H_2O_2) inactivates the ABI1 and ABI2 type 2C protein phosphatase enzymes that are essential for ABA signalling [59–61]. Chauffour et al. [62] reported that ABA deficient (*nced-2569*) seeds released more H_2O_2, O_2^- and NO than ABA over-accumulator and showed higher protein oxidation in *nced2569* than wild-type seeds. In contrary, the rate of protein oxidation was very low in *cyp707ala2* seeds, which implies a negative correlation between ABA content and protein oxidation.

4. Role of reactive nitrogen species in seed germination

Nitric oxide (NO) is a gaseous free radical, which can react with transition metal ions and radicals that influence the cellular redox status [63,64]. NO upon losing or gaining an electron forms nitroxyl anion (NO^-) or nitrosonium (NO^+), which is a part of RNS [65]. In the plant life cycle, particularly seed germination and seedling establishment process, tight control of NO concentration is an essential physiological event [66,67]. Plants possess effective sensing mechanisms for NO, which trigger specific responses in their life cycle. NO signal in plants is mainly sensed through S-nitrosylation reaction, which is a most relevant post-translational modification, occurs in the plants [65,68–70]. Covalent reaction of NO with free thiols of cysteine residues in proteins leads to the formation of S-nitrosothiol (SNO), which induces the conformational changes of the protein that ultimately influence its stability, interactions, localization and function [68,71]. Through S-nitrosylation reaction, NO regulates hormonal regulatory processes, which influence in seed germination.

Studies have revealed that NO play an important physiological role in seed germination and dormancy alleviation in several species [72] (Table-1). Pharmacological studies have been done using NO donors such as sodium nitroprusside (SNP), S-nitrosoglutathione (GSNO) and S-nitrosothiol (SNAP; S-nitroso-*N*-acetyl-D,L-pencillamine) to mimic the effect of gaseous radical in *Arabidopsis* [73]. Studies showed that these NO donors promoted seed germination and dormancy release; whereas the NO scavenger cPTIO maintained the seed dormancy [74,75]. Moreover, studies on C4-grasses confirmed the role of NO as potential regulator of seed germination [76].

To understand the role of testa, aleurone layer and embryo in sensing NO signal, several studies have been conducted. Bethke et al. [79] has observed that the seeds devoid of testa has responded to NO indicate that it has no role in NO sensing, either aleurone layer cells or embryo could sense N. Further, the embryo and aleurone cells were treated with cPTIO (NO scavenger) and found that the growing isolated embryos were insensitive to cPTIO; while, the isolated aleurone layers have showed the inhibition of vacuolation. It is a general agreement that GAs favours vacuolation in cereals; whereas ABA inhibits the vacuolation process. Treatment of isolated aleurone cells with GAs restored the vacuolation, which indicates that the aleurone cells sense the NO for dormancy release [85].

Apart from NO, nitroxyl anion (NO^-) and nitrosonium (NO^+) species, peroxynitrite ($ONOO^-$) is one of the important RNS species that play an important role in seed germination. Reaction between NO with superoxide (O_2^-) gives rise to peroxynitrite that acts as oxidizing and nitrating agent [86]. Tyrosine nitration (ie. addition of nitro group to tyrosine amino acid) is predominantly observed in simultaneous release of ROS and NO, which alters diverse protein functions [72].

5. Nitric oxide and phytohormones crosstalk during germination

Crosstalk of phytohormones with NO, particularly GAs, ethylene and ABA have prominent role in seed germination [72]. Maintenance of hormonal homeostasis to environmental cues is the key either to activate seed germination or dormancy maintenance [72]. NO induces seed germination through activation of GA synthesis and inhibition of ABA metabolism and signalling [72,89]. Decrease of endogenous NO levels has been observed with exogenous ABA application in tobacco and *Arabidopsis* [90–92]. Negative regulation of NO and ABA has been noticed in aleurone cell layer during barley seed germination [74]. These studies indicate that the NO accumulation is associated with decrease of ABA level [90].

Okamoto et al. [93] have studied that during seed germination NO induces ABA catabolism genes through upregulation of *CYP707A* (cytochrome P450 ABA 8'-hydrolase) gene family that encode ABA 8'-hydroxylases. In *cyp707a* mutant, ABA levels has been increased, which indicates that NO regulates ABA through expression of *CYP707A* gene family [93]. Furthermore, SNP treatment in *Arabidopsis* showed enhanced protein levels of *CYP707A* but decreased with cPTIO treatment, which substantiate the NO-induced ABA decrease [90]. In addition, NO alters proteins involved in ABA biosynthesis and signalling pathways through nitration and S-nitrosylation post-translational modifications [89]. Molybdenum cofactor (MoCo) sulfurase, ABA3 (At1g16540) is an enzyme involved in sulfurylation of desulfo form of MoCo. This sulfurylated MoCo functions as co-factor for the abscisic

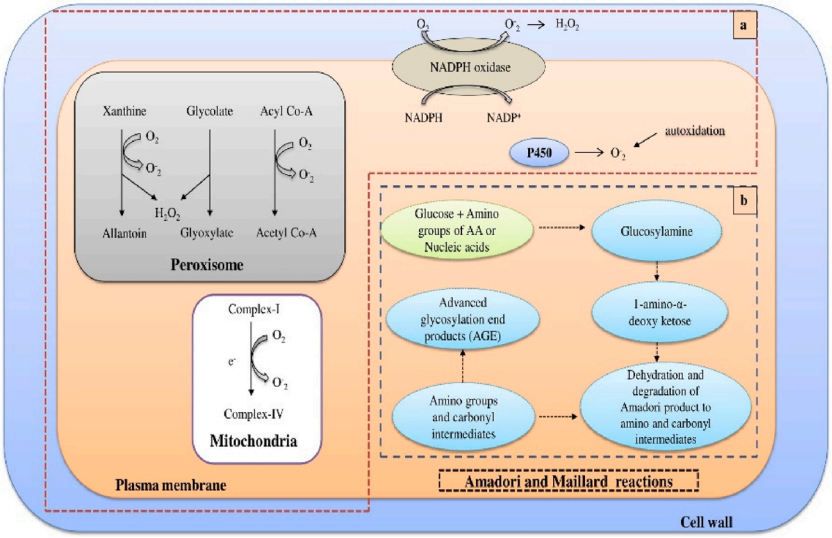

Fig. 1. a) ROS production sites after transition from dormancy to germination stage. After imbibition of seed, leakage of electrons from mitochondria and glyoxysomes, peroxisomes, singlet oxygen from chloroplast are important sources. b). ROS production sites during dry/after ripening stage. In this physiological state, glucose and amino groups derived from amino acid and nucleic acids are condensed to form Amadori and Maillard products, which are major sources for ROS production in addition to lipid peroxidation. [Adapted Bailly et al. [23]].

Table 1
Role of reactive oxygen/nitrogen species and antioxidants in seed germination.

S. No	Radical/donor molecule/ Antioxidant	Physiological trait	References
1.	H_2O_2	Hydrogen peroxide produced in response to Zn stress and strict control by antioxidants resulted germination in *Dimorphandra wilsonii*	[40]
2.	H_2O_2	Barley seeds were exposed to γ radiation and observed seedling development *via* ROS production.	[41]
3.	H_2O_2	In pepper (*Capsicum annuum*), interaction and spatial differences of ROS and RNS lead to seed establishment.	[42]
4.	H_2O_2	Proposed to oxidize RNA and protein for dormancy release.	[24,43]
5.	$O_2^{\cdot-}$	Increased levels of super oxide radical during germination in pea seeds (*Pisum sativum*) results in hydroxyl radical (O'H) production. The later radical loosens the cell wall and promotes cell elongation.	[44,45]
6.	$O^{\cdot-}{}_2$	Superoxide radical alleviated dormancy release and favoured germination in barley	[46]
7.	·OH	Break down of cell wall polysaccharides resulting seed germination.	[47]
8.	H_2O_2 and $O_2^{\cdot-}$	In sunflower seeds, alleviation of dormancy associated with ROS in embryonic axes. ROS accumulation is mainly triggered by protein carbonylation and lipid peroxidation.	[27]
9.	H_2O_2 and $O_2^{\cdot-}$	In *Arabidopsis thaliana*, Columbia (Col) accession showed higher ROS content in non-dormant seeds than in dormant seeds after 24 h of imbibition	[28]
10.	H_2O_2 and $O_2^{\cdot-}$	In jasmine rice, increased levels of $^{\cdot-}O_2$ radical was observed in nano-primed seeds at 0 h. After imbibitions, H_2O_2content has been shoot up from 24 h and observed the radicle emergence.	[37]
11.	NO	NO is involved in the process of dormancy release in Arabidopsis. NO scavenger c-PTIO strengthened dormancy but did not inhibit germination	[74]
12.	NO	NO and ROS induced promotion of seedling parameters and α- amylase activity of maize seeds	[76]
13.	NO	The seed germination and growth are linked with NO and ROS levels	[77]
14.	NO	NO induced *Arabidopsis* seed germination and determined that aleurone cells are responsible for NO sensing	[78]
15.	NO	*S*-nitrosylation triggers ABI5 transcript degradation to promote seed germination and seedling growth	[79]
16.	SNP	The nitric oxide (NO) donor sodium nitroprusside (SNP) significantly promoted germination of switchgrass (*Panicum virgatum* L. cv Kanlow) in the light and in the dark at 25 °C	[80]
17.	SNP	SNP alleviates the inhibition on wheat seed germination imposed by salt stress	[81]
18.	SNP	SNP at low concentration induced germination in *Lycopersicon esculentum* MILL. However, at high concentrations SNP has been inhibitory in nature	[82]
19.	SNP and SA mixture	SNP and SA induced germination in pea seeds and secreted enzymes to alleviate salt stress	[83]
20.	NO_2	NO_2 induced germination in *Caulanthus heterophyllus*, *Emmenanthe penduliflora*, *Phacelia grandiflora,* and *Silene multinervia*	[84]
21.	SOD	Study revealed SOD gene over expression in *Nicotiana* resulted protection against seed deterioration during aging	[139]
22.	MT	Expression of the PsMTA1 gene, encoding a metallothionein-like protein from *Pisum sativum*, confers protection against oxidative stress in the nucleus and also reduced oxidative DNA damage	[140]
23	MT and SOD	*Silene acaulis* grown at low altitude conditions showed up-regulation of SOD and MT2 genes in rehydrated seeds	[25]
24.	ASC and glutathione	Increased levels of glutathione and ascorbate were observed during germination in wheat and *Pinus pinea* seeds	[141,142]
25.	APX	Ascorbate peroxidase levels increased during seed imbibition and germination	[143]
26.	DHAR	Silver maple (*Acer saccharinum* L.) recalcitrant seeds were treated with glutathione resulted higher germination and parallel enhanced dehydroascorbate reductase activity	[144]
27.	Alpha-tocopherol	Increased alpha-tocopherol content was observed in isolated soybean embryonic axes during storage and imbibition phases.	[145]
28.	CAT	Higher activity of catalase was observed in non-dormant barley cultivar- Harrington during germination and also found reduction of H_2O_2 levels	[83]
29.	SOD, CAT and APX	Increased superoxide dismutase activity observed during germination in neem seeds. Further, APX and CAT levels were increased from 9 to 12 weeks after anthesis.	[146]
30.	APX	Ascorbate peroxidase protects hydrogen peroxide produced in differentiating peroxisomes	[147]

aldehyde oxidase that converts abscisic aldehyde to ABA [87]. Proteomic analysis has showed that MoCo is the target for the tyrosine nitration to inactivate ABA synthesis during germination [72,87]. Thus, protein nitration might contribute in controlling the dormancy release and germination vigour. In addition, protein nitration is a biological marker for nitrosative stress and participates in signal transduction and protein turnover in plants [88].

S-nitrosylation is an important post-translational modification, where the thiol groups (SH) of cysteine amino acids are altered by NO to form S-nitrosothiols. NO during germination process modifies SNF1-related protein kinase (SnRK) 2.2/SnRK2.3 through S-nitrosylation, which are involved in ABA signalling pathway [94] (Fig. 3). Studies on *snrk2.2/2.3/2.6* triple-mutant plants showed complete insensitivity to ABA, which suggest the importance of SnRK2s-mediated phosphorylation in ABA signalling [95]. In *Arabidopsis* seedling development, GSNO treatment had inactivated the SnRK2.2 kinase proteins by S-nitrosylation and further the S-nitrosylated ABI5 (abscisic acid insensitive 5) has been degraded by proteasome pathway [80]. Therefore, it is clearly evident that the NO promote germination through inactivation of ABA synthesis and signalling proteins by post-translational modifications [72]. On the contrary, Bethke et al. [79] studies on cell vacuolation with GAs and NO donors demonstrate that the NO promotes GAs biosynthesis through upregulation of GA_3ox1 and GA_3ox2 that encode gibberellic

oxidases 1 and 2 [79]. Thus, these studies corroborate that NO promotes germination by enhancing GAs with reduction in ABA-imposed dormancy [89].

In addition to GAs, ethylene (ET) also favours seed germination through crosstalk between NO and ET biosynthesis [96,97]. Gniazdowska et al. [98] had observed in apple embryos that the NO has induced germination through ET biosynthesis. Further, it has been reported that the mechanism for signalling of NO and ethylene occurs through S-nitrosylation of proteins such as ACC synthase (ACS) and ACC oxidase (ACO), respectively [99,100]. However, it is unknown how this S-nitrosylation reaction could affect the ACS and ACO enzymes for seed germination.

NO and its role with cytokinins (CK) and polyamines (PAs) are limited. However, as observed in few studies, both the phytohormones exhibit antagonistic behaviour with NO [101]. Liu et al. [102] had observed elevated levels of cytokinin in *Arabidopsis* NO-insensitive mutant *cnu1* (continuous NO-unstressed-1). Furthermore, they had treated peroxynitrate (derivative of NO) with zeatin (predominant cytokinin) and found that the CK suppressed the NO that lead to decrease in endogenous NO levels [102]. Polyamines are reported to regulate seed germination negatively [103]. Wimalasekera et al. [104] had reported NO biosynthesis through enzyme copper amine oxidase involved in PA catabolism. Loss-of-function mutants for *CuAO1* showed lower NO production in response to exogenous PA application [104]. Interestingly, NO action on mutual regulation of ABA and GAs in seed germination shows similarity with ROS and other external factors mechanisms that promote seed germination.

6. Seed deterioration

During storage conditions, seeds are prone to oxidative damage that is mediated by ROS. Depending upon the type of seed (orthodox, intermediate and recalcitrant) properties, the extent of damage would be during storage conditions [105]. Recent studies support two putative mechanisms responsible for seed deterioration, which are illustrated in subsequent sections.

Seed longevity is defined as the ability of seed to remain viable after dry storage condition. Unlike developed countries, conventionally, in developing countries the farmers save some of their farm produce (as seeds) for next season sowing and store the produce in uncongenial atmosphere. As a result, seeds tend to deteriorate at a faster rate particularly in soybean and peanut/groundnut (oilseeds) [106]. On the other hand, the farmers are unaware of the quality of seeds and sow the seed in the next season. Consequently, the productivity is low and indulges the farmers in debt drudgery. This phenomenon shows that the seed longevity is an important parameter for maintenance of seed quality. Generally, studies on seed ageing have been conducted predominantly either by accelerated ageing (CDT, controlled deterioration treatment) or natural ageing by increasing moisture content (MC) and relative humidity (RH).

Studies unravelled that ageing mechanism is mainly orchestrated by ROS accumulation in the seed (prolonged storage or improper storage of seed). However, to maintain the seed viability, ROS homeostasis and DNA/RNA/protein repair mechanisms should operate at optimum levels in the embryo [25,37,107,108]. This implies that under storage/stress conditions ROS accumulates in the cells, which are controlled by antioxidants (enzymatic and non-enzymatic). Transcriptomics study on pea (*Pisum sativum*) has revealed that seed deterioration under ageing conditions begins with ROS accumulation and simultaneous decline of antioxidant potential of the cell [109].

In addition, during this process, thiol based reducing conditions have shifted to oxidizing conditions that could have triggered the cascade of events. As per the study, two possible mechanisms for seed deterioration governed by ROS have been elucidated (Fig. 4). In the first mechanism, ROS formed at ageing conditions were scavenged by glutathione-s hydrolase that increases the ratio of $E_{GSSG/2GSH}$ (oxidizing condition). Under these conditions, the thioredoxin-apoptosis signal regulating kinase 1 (Trx-ASK 1) complex splits. Further, the ASK-1 triggers the MAPK cascade that leads to breakdown of nucleic acids, structural and nuclear proteins [109].

In the second mechanism of seed deterioration, programmed cell death (PCD) has been manifested, which is mainly triggered by calcium release from endoplasmic reticulum (ER). Study on transcriptome mapping of pea seed in ageing conditions revealed declined antioxidant potential and imbalance of thiol based redox couple ($E_{GSSG/2GSH}$). Increase of GSSG has been associated with PCD and indicative of chain of events such as loss of mitochondrial integrity, cytochrome c release and caspase-3 activation [109–111]. Under oxidative stress conditions, protein folding is hampered in the ER lumen; consequently, the misfolded and unfolded proteins accumulate and trigger unfolded protein response (UPR). This UPR response further up-regulate the chaperones for protein folding machinery and mitigate stress in endoplasmic reticulum [55]. Derlins are other proteins that help in targeting of misfolded proteins to cytosol for ubiquitination.

Transcriptome study in pea demonstrated up-regulation of stress marker binding protein (BiP) and two derlin 2.2 genes during ageing. This indicates that the misfolded proteins are degraded by ubiquitin/26S proteasome system during ageing in pea [109]. Increase in cytosolic calcium release, cytochrome-c protein from mitochondria by activation of permeability transition pore (PTP), which include adenine nucleotide

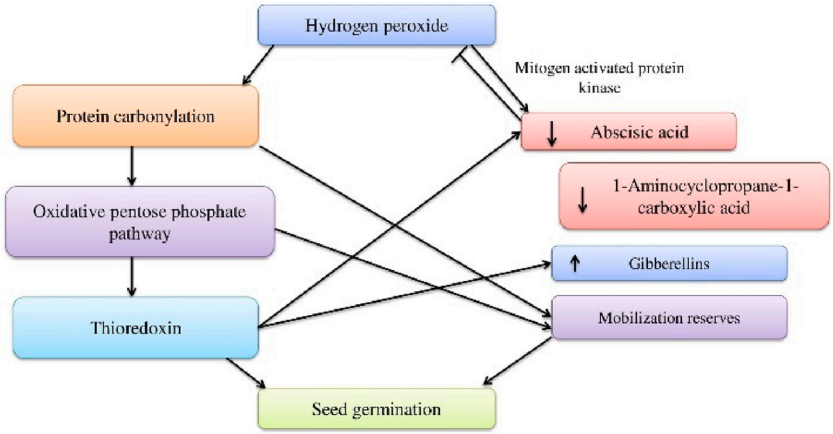

Fig. 2. Putative signal transduction pathways during germination stages. Seed dormancy can be maintained with high ABA content and the GAs content should be high for germination [55]. In germination process, NADPH is supplemented by Pentose phosphate pathway, which is activated by protein carbonylation. Thioredoxin triggers ACC and ABAs decrease with increase GAs biosynthesis, which leads to seed germination [4].

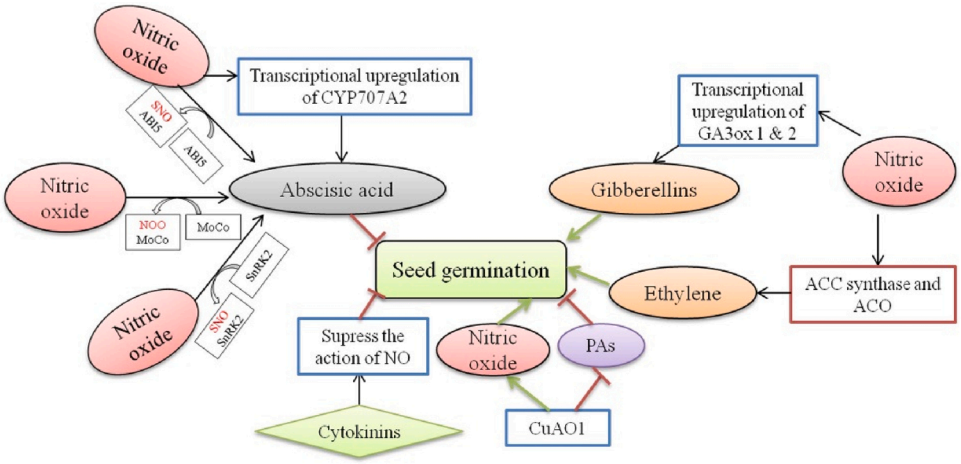

Fig. 3. Role of reactive nitrogen species in regulation of seed germination.
Arrow in red colour indicates negative regulation; Arrow in green colour indicates positive regulation ABI5- abscisic acid insensitive 5; SNO ABI5- S-nitrosylated abscisic acid insensitive 5; MoCo- molybdenum cofactor; NOO-MoCo- Nitrated molybdenum cofactor; SnRK- sucrose non-fermenting 1 (SNF1) related protein kinases; SNO SnRKS-nitrosylated sucrose non-fermenting 1 (SNF1)-related protein kinases; PAs- polyamines CYP707A2 : cytochrome P450 ABA 80 –hydrolase; GA_3ox- gibberellic acid oxidase ; ACC- 1-aminocyclopropane-1- carboxylic acid; ACO-ACC oxidase ; CuAO- copper amine oxidase.

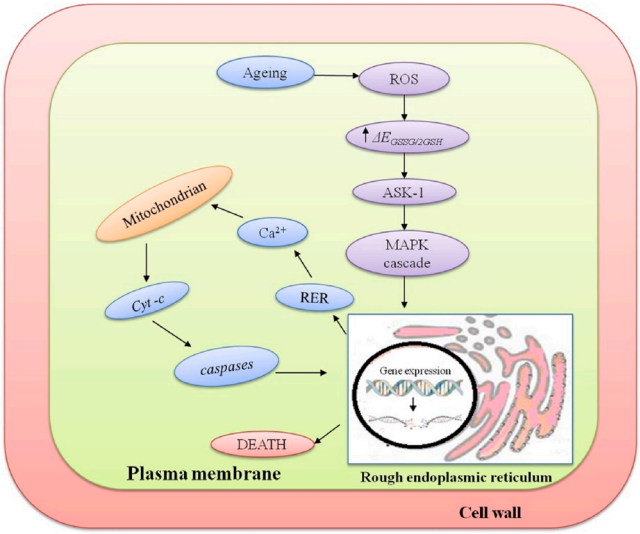

Fig. 4. Putative seed deterioration pathways elucidated from microarray studies.
MAPK cascade: mitogen activated protein kinase cascade; RER: Rough endoplasmic reticulum; ROS: reactive oxygen species. Adapted from Chen et al. [109].

translocator (ANT) and voltage dependent anion channel (VDAC). Further, in this study, it was observed that caspases such as papain and RD21 have been up-regulated, which indicates their involvement in degradation of structural and nuclear proteins and activation of nucleases [109–111]. Nucleases degrade the RNA and fragment DNA, which is the hallmark for programmed cell death [112,113].

7. Biotechnological applications in agricultural research

Among the factors for crop production, quality seed is one of the pivotal components that determines around 15–20 % of crop production [114]. Climate change has adverse effects on crop phenology, reproduction and flowering pattern, pollen viability, pollen germination, pattern pertinent to pollination, seed yield, seed size, seed quality, seed length and seed dormancy [115,116]. Moreover, environmental conditions coupled with soil-borne diseases have unpredictable seedling emergence rate that ultimately reduces the crop productivity [116].

To circumvent these problems, seed priming has been showcased as a viable, cost-effective technique in enhancing uniform seed germination rate, stress resistance and crop yield [31]. Seed priming with bio-agents (bio-priming) [117], osmo-priming [118], halo priming [119], ROS priming (H_2O_2) [120], hydro priming [118], antioxidant priming [121], hormonal and growth promoting rhizobacteria priming [122,123] have showed significant results. Besides, plasma technique particularly non-thermal plasma has shown promising results in increasing the seed quality parameters under varied abiotic and biotic stresses [124,125]. In addition, we will focus on some major issues, such as the germination of recalcitrant species and thermotolerance, the ROS control and their implications in pre-harvest sprouting, the seed quality markers to monitor crop performance, seed production, seed longevity/storability, seed priming and germination and prospects of genome editing for sustainable seed production.

7.1. Germination of recalcitrant species and thermotolerance

Population increase and decrease in natural resources (arable land and fresh water) coupled with climatic changes imposed challenges to meet the food and nutrition security. At this juncture, to cater the food demand, translation of seed agronomic traits from lab-to-field conditions is essential. Green Revolution is one of the classic examples attained due to introduction of *semi-dwarf1* (*sd1*) gene in rice breeding programs [126–128]. Considering the potential of ROS/RNS in favouring seed germination, these may be applied to enhance germination of recalcitrant species (unorthodox seeds) like lychee, coconut, horse chestnut, avocado, coffee and cacao; while for lettuce and spinach seeds at suboptimal temperatures [129].

Mutual regulation of ABA and GAs through oxidative signalling could be applied in inducing seed germination at low temperature [129]. For example, Kashiwakura et al. [130] studied the dormancy breaking and inducing germination in wheat pre-harvest sprouting (PHS) tolerant variety such as Gifu komugi (Gifu). Results show that the Gifu variety germinated at 15 °C but remained dormant at 20 °C after imbibition. Pharmacological and hormone analyses demonstrated that in Gifu variety, incubation at low temperatures (15 °C) triggered ABA catabolism genes (*TaABA8'OH1*, *TaABA8'OH2*) and increase in GAs biosynthesis gene (*TaGA30 × 2*) and *vice versa* at 20 °C incubation. This temperature dependent dormancy mechanism is mutually regulated between ABA and GAs controlled by ROS has huge scope for engineering the hormone metabolism in seeds either to suppress or enhance germination [131]. Technically, manipulation of proteins involved in signal transduction might be difficult, but the expression levels of hormone metabolism genes could be altered. Hence, realizing the mutual regulation of hormones and their judicious application could alleviate thermo-tolerance stress [13].

7.2. ROS control and their implications in pre-harvest sprouting

In agriculture, seed dormancy is an important trait to control precocious germination and vivipary imparted from maternal plant. In cereal crops, PHS influences the grain quality and yield. For instance, in wheat grains precocious germination degrades starch by triggering α-amylase activity, which mobilizes the reserve for germination [132, 133]. Subsequently, grain quality is reduced because of premature starch digestion that amounts to significant loss to the farmers. In China, around 80–83 % of the wheat production regions are prone to sprouting damage [134].

Another phenomenon associated with ROS is field weathering of soybean (*Glycine max* L.). In this process, soybean seeds deteriorate due to accumulation of ROS even when remaining in pods while associated with mother plants [17]. This is more intense, because of unexpected rains during harvest (precipitation shift) of soybean and envisages devising mechanisms that control ROS in weathering process. In both of these mechanisms, apart from ROS signal, thioredoxin enzyme is the key for germination process and could be targeted for development of potential technology to reduce the pre-harvest sprouting (PHS) and field weathering. Li et al. [135] have developed antisense PTrx h gene from sunol grass (*Phalaris coerulescens*) that has close resemblance with wheat and expressed the gene in controlled fashion under gliadin promoter (Supplementary Fig. 2). The controlled expression has reduced the Trx h content in seeds and suppressed the PHS [135]. In another study, seed deterioration has been reduced by targeting thioredoxin enzyme located in mitochondria. Ortiz-Espin et al. [136] over expressed the mitochondrial thioredoxin *TRXO1* gene and observed not only the decrease of cellular H_2O_2 and NO levels but also in delaying the cell death. Interestingly, these features increased cellular glutathione pool and catalase activity to maintain in a highly reduced state.

7.3. Seed quality markers to monitor crop performance

In seed industry, seed quality markers are essential to monitor the crop performance and quality control measures. Microarray study on seed ageing in pea seeds revealed two significant events such as decline of antioxidant potential (enzymatic and non-enzymatic) coupled with shift in oxidizing conditions from reducing atmosphere ($E_{GSSG/2GSH}$) in the cell [109]. Dona et al. [25] showed antioxidant potential of seeds is one of the reliable markers to monitor seed ageing process. To enhance seed longevity, seeds need effective antioxidant systems that protect from excessive oxidation of macromolecules [137,138]. Antioxidants are compounds that have the capability of scavenging the ROS either by enzymatic cascades (detoxify, active mechanism) or neutralization of pro-oxidants (passive mechanism). To remove ROS accumulated during resurgence of metabolism upon imbibition and inappropriate seed storage conditions, seeds utilize a battery of enzyme based antioxidant systems such as catalases, glutathione and ascorbate peroxidases, superoxide dismutases, monodehydroascorbate and glutathione reductase, respectively. Several studies reported metallothionein, glutathione, alpha-tocopherol, phenolics (flavonoids) and ascorbic acid as antioxidants during ageing [7,23] (Table-3).

In addition to enzymatic and non-enzymatic antioxidants, carbohydrates [raffinose family saccharides (RFO), sucrose] and seed storage proteins are also reported to act as antioxidants [148–150]. Recent studies suggest that reduced glutathione play a major role in regulating the intracellular redox environment and serve as quality marker for viability [151]. Kranner et al. [110] had demonstrated that the measurement of reducing capacity of redox couple ($E_{GSSG/2GSH}$) and its half-cell reduction potential ($E_{GSSG/2GSH}$) based on Nernst equation is an effective tool for cell viability and seed ageing [110]. Further, Nagel et al. [132] reported a strong correlation between glutathione redox and total germination in 26 barley genotypes, which implies that the variations in the EGSSG/2GSH can be used as a reliable marker for seed deterioration.

Development of microfluidic/nanofluidic device that readily estimate the half-cell potential of $E_{GSSG/2GSH}$ ratio could give an indication about seed viability [152]. Besides, antioxidant profiling with fabricated chips serve the function of quality determination and further, it is essential to enlist these parameters as quality seed markers in International Seed Testing Association (ISTA) procedures. Moreover, farmer friendly-technologies like seed priming with ROS, antioxidants, non-thermal plasma and rhizo bacteria could help in maintaining the uniform germination and rapid seedling emergence as these features are key determinants for successful crop stand establishment.

7.4. Scope for genome editing for sustainable seed production

Targeted mutagenesis with Cas9 has been interesting but limitations of non-targeted mutagenesis have triggered to look after new options [153]. New variants of Cas9 enzyme such as Cpf1 from *F. novicida*, *Acidaminococcus*, C2c2 from *Leptotrichia shahii*, and Cas9 derived from *Francisella novicida*, *Streptococcus thermophiles* and *Staphylococcus aureus* induced targeted mutagenesis in wheat [154], soybean [155], maize [156] apple and grape [130] without transgenesis in plant cell. Targeting α- amylase and *Trx-h* genes in wheat using genome editing can reduce the pre-harvest sprouting [130]. Further, embracing such new techniques could accelerate research in seed science and breeding domains [157–158].

8. Conclusions

Producing crops with enhanced resilience to perturbation is urgent in the view of an increasing world population, predicted climate change and agro-ecological transitions. Although knowledge on radical metabolism (ie., ROS and RNS) related to stress tolerance is available for model species and some crops, there is still currently no integrated model of the combined interaction of pre- and post-harvest environmental conditions and the cellular basis of radical metabolism influencing the response to stresses in seed. Genetic-based models have to be applied to develop a model of the impact of maternal and post-harvest environments on changing seed quality related to radical metabolism and to improve seed management from farm production to trade through the global seed industry market. The integration of the genetic-based data and radical metabolism data will provide a theoretical understanding of the heterogeneity in seed physiological quality traits within genetic diversity under fluctuating climate conditions. Besides, this study would pave way for hormone engineering through ROS/RNS changes that influences the seed physiology.

Author contributions

SPJK conceptualized, analysed data and drafted the paper, ADC edited and drawn the figures, YMR edited the text and formatted the text and references, LR conceptualized, meticulously edited the MS, GVK edited the paper, DKA meticulously checked the content and edited the grammar, JSG meticulously edited the English and content of the MS, SRP conceptualized and analyzed the data, SK edited the grammar meticulously.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.cpb.2021.100197.

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