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REVIEW

Reactive oxygen and nitrogen species (RONS) signalling in seed dormancy release, perception of environmental cues, and heat stress response

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Abstract

Seed germination is a crucial plant-life process whose success depends largely on the seed's ability to germinate under favourable environmental conditions. Through molecular signalling, a seed is able to perceive environmental information, assimilate it, and transmit signals that determine its destiny. Reactive Oxygen and Nitrogen Species (RONS) function as signalling molecules that influence multiple phases of plant development. In the process of seed germination, their presence generally promotes germination completion, though not to the same extent in all species and environments. As signalling molecules, they participate in the sensing of light and temperature fluctuations as favourable germination cues, but they also play a role in inhibiting germination when temperatures exceed the optimal range, preventing seedling exposure to heat. Depending on environmental conditions, RONS set up crosstalk with the major phytohormones involved in germination, ABA, GA, and even auxin, regulating their biosynthesis and signalling. Here, we show relevant studies on how RONS exert seed germination control on multiple levels, such as through protein oxidation, epigenetic control, promotion of phytohormone key-metabolism genes expression, post-translational protein modifications, and redox interactions with DOG1. This review summarises the current understanding of the role of RONS in the seed, from its maturation to the transduction of environmental conditions. Special consideration is given to the RONS-mediated germination response to favourable stimuli, such as light or temperature fluctuations, and to conditions that inhibit germination, such as high temperatures.

Keywords ROS · RNS · Environment variation perception · Seed development · Seed germination signalling in wild species · Abiotic stress · High temperature

Introduction

Seed germination is a plant-life process of crucial importance for the successful development and establishment of a new generation. For a mature seed, the principal factors that control its germination behaviour are soil temperature and water availability. In the presence of water, a specific temperature pattern, i.e., large temperature fluctuations, may indicate a favourable seasonal window for a dormant seed for germination (Footitt et al. 2013; Buijs et al. 2020). On top of that, for light-sensitive seeds, the presence of a specific photoperiod irradiance, comprised within a certain wavelength range, might provide useful information on soil position and terminate or maintain dormancy.

Accurate sensing of environmental variables is also critical for abiotic strain detection in order to avoid germination or activate certain tolerance mechanisms. Global climate change causes a variety of abiotic pressures that have a significant impact on sustainable agriculture and food security (Altieri et al. 2015). Among abiotic stresses, most global climate change models imply a rise in mean air temperatures and the frequency of high temperatures (HT), such as heat waves (Schiermeier 2018). Thus, improving our understanding of how seeds perceive and distinguish favourable environmental cues from adverse conditions by sensing temperature changes and can safely tolerate them is critical to

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combating the effects of global climate change on crop and wild species preservation.

Heat stress (HT stress), which is defined as heat beyond physiological threshold values, impairs metabolic functions including respiration and photosynthesis or lowers a cell's capacity to scavenge oxygen radicals, all of which lead to oxidative damage (Barnabás et al. 2008). This promotes the accumulation above physiological thresholds of Reactive Oxygen Species (ROS) and Reactive Nitrogen Species (RNS), hereafter referred to as RONS, and is the cause of the initiation of oxidative stress. Increased RONS levels can cause rapid lipid and protein peroxidation, higher membrane permeability, and nucleic acid damage (Choudhury et al. 2017). HT, depending on its intensity and duration, can either inhibit seed germination or promote their death. Because of a seedling's vulnerability, plants have evolved unique methods for limiting seed germination under unfavourable conditions. Germination at high temperatures is prevented by thermoinhibition when it is imposed transiently and by secondary dormancy (thermo-dormancy) when a specific pattern of dormancy-breaking patterns is required for its release (Hills and Van Staden 2003).

In addition to the cell-damaging effects of uncontrolled RONS growth, it is widely recognised that RONS play a function as signalling molecules in the regulation of germination response to specific environmental stimuli, such as light and temperature (Bailly et al. 2008; Krasuska and Gniazdowska 2012), and in plant development processes (Considine and Foyer 2021). During HT, for example, drought or UV radiation stimulate the production of RONS that trigger molecular networks that promote downstream responses to mitigate stress-related adverse effects (Choudhury et al. 2017; Medina et al. 2021; Gupta et al. 2022). Concerning seed biology, even under physiological conditions, multiple oxidative bursts occur from seed dispersal up to the completion of germination. Their appearance is regulated by specific scavenging systems and serves as a signalling mechanism (Bailly 2019). The addition of specific RONS at certain concentrations results in seed dormancy release in many crop and wild species (Bailly et al. 2008; Leymarie et al. 2012; Ciacka et al. 2022), and they are nowadays widely used as seed dormancy breakage treatments (Arc et al. 2013; Grainge et al. 2022). RONS action mechanisms are still not completely understood, but many investigations in the last decades showed that they can regulate seed germination at different levels: interplaying with hormones, mainly abscisic acid (ABA), possibly with auxin involvement, and gibberellins (GAs); activating or repressing entire transcriptional programmes through chromatin remodelling; and post-translationally through the redox modification of the dormancy hub and interaction with cell wall proteins.

Despite the importance of RONS and their ability to regulate each other through a constant ROS-RNS interplay, most of the scientific literature in recent decades has always treated the effects of ROS and RNS on germination separately. In fact, to date, only a very few studies have focused on both ROS and RNS, considering their synergistic action at different levels: gene transcription, epigenetics, and post-translational regulation. In addition, our understanding of RONS' role in the germination regulatory signalling associated with temperature perception and tolerance in natural populations as well as in crops is still in its infancy. Thus, the current review focuses on the physiological and molecular mechanisms that regulate seed germination and dormancy release via RONS, with a particular emphasis on three aspects: (1) provide a viewpoint that integrates the role of RNS and ROS by treating them as components of a unique signalling system in germination. This provides a starting point on which to hypothesise relationships and links between the different regulatory pathways involving these compounds; (2) analyse the various effects of RONS on seed germination acting on protein and gene regulation associated with model species as well as in crops and wild species; and (3) review the RONS signalling role in germination response to optimal seasonal cues, such as light and alternate temperatures, and to abiotic stress, such as HT.

Generation and homeostasis of RONS in seed germination

ROS production and regulation

ROS are a group of extremely reactive, oxygen-containing molecules that include superoxide anion ($O_2^{\cdot-}$), hydrogen peroxide (H_2O_2), the hydroxyl radical ($^{\cdot}OH$), and singlet oxygen ($^1O_2$) (Bano et al. 2022; Medina et al. 2021). From the final stages of seed development in the mother plant up to germination completion, the orthodox seeds start desiccating, reaching a very low moisture content, which is a peculiar trait of mature seeds. After shedding, seed drying will go on with the onset of the after-ripening process. During the desiccation phase, the seed faces extreme drought stress, which is associated with the appearance of ROS (Fig. 1). At this stage, ROS are produced by the autooxidation of lipids, which is a non-enzymatic reaction (Bewley and Black 1985). Upon seed imbibition, when the water content reaches 50%, the generation of ROS starts its shift from the non-enzymatic system to the enzymatic system (Kibinza et al. 2006; Bazin et al. 2011; Basbouss-Serhal et al. 2016). The mitochondrion is the first and main source of ROS production in the seed through the reduction of O_2 to $O_2^{\cdot-}$ at the respiratory electron transport chain (Bailly 2004).

Cu Superoxide Dismutase (Cu-SOD) or Mn/Zn-SOD convert the $O_2^{\cdot-}$ to H_2O_2. Chloroplasts are also an key site for the generation of ROS in plants, as the illumination of

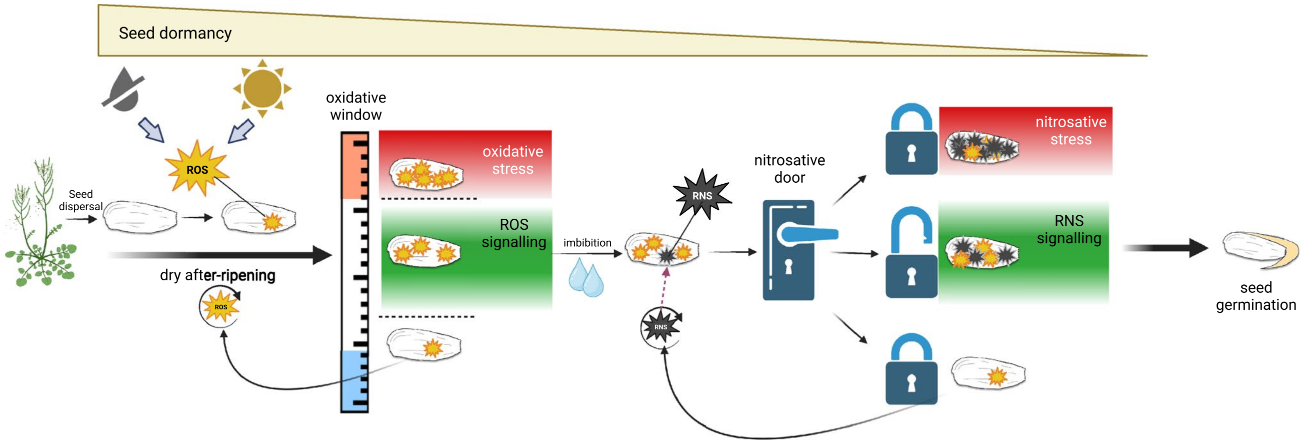

Fig. 1 A schematic representation of RONS generation from seed shedding to imbibition. The models of "oxidative window" (Bailly et al. 2008) and "nitrosative door" (Krasuska and Gniazdowska (2012) and Krasuska et al. (2015) are presented together in a temporal sequence

photosystem I and II produces $O_2^{\cdot-}$, $^{\cdot}OH$, and $^1O_2$ (Richards et al. 2015), and the $O_2^{\cdot-}$ is converted into H_2O_2 by Cu/Zn-SOD or Fe-SOD (Waszczak et al. 2018). Production of ROS can also take place in the extracellular space, the apoplast, through the activation of NADPH oxidases, also known as Respiratory Burst Oxidase Homologues (RBOHs), or Polyamine Oxidases (PAOs), which were also proposed to participate in nitric oxide (NO) generation (Tun et al. 2006; Moschou et al. 2008; Gilroy et al. 2014). Class III heme peroxidases are also important sources of $O_2^{\cdot-}$ and H_2O_2 in this extracellular space (Janku et al. 2019). $O_2^{\cdot-}$ generated by NADPH oxidases is also converted to H_2O_2 by apoplastic SODs, and $^{\cdot}OH^-$ is converted from Cu^+ and H_2O_2 by ascorbate and directly cleaves wall polysaccharides (Fry 1998; Schopfer et al. 2001). Since its localization, the apoplast is ideal to transmit redox signals from cell to cell, 'ROS waves', probably through plasmodesmata (Considine and Foyer 2021).

Peroxisomes are cell organelles with multiple functions ranging from ROS metabolism, H_2O_2 signalling, photorespiration, phytohormone biosynthesis (Jasmonic Acid, Auxin, and Salicylic Acid), fatty acid biosynthesis, and the glyoxylate cycle, among the most investigated (Sandalio et al. 2021). They are characterised by metabolic plasticity modulated by different physiological stages, tissue or organ conditions, and environmental conditions (Corpas 2015; Corpas et al. 2020). Their number, shape, and protein content can vary in a plant cell depending on the environmental conditions and developmental stage (Sandalio et al. 2021, 2023). For example, in light-exposed leaves, these organelles change shape from spherical to elliptical (Oikawa et al. 2015), and the peroxisomal H_2O_2 increases together with the peroxisomal catalase (CAT) activity to regulate ROS homeostasis (Corpas 2015). Whereas, proteomic analysis of peroxisomes in dark-induced senescent leaves showed an increase in proteins involved in the detoxification of ROS and proteins involved in fatty acid metabolism (Pan and Hu 2018). Under drought stress, peroxisomal production of H_2O_2 was observed in both guard cells and subsidiary cells, determining stomatal closure consistently with the increase in ABA levels (Yao et al. 2013). In germinating seeds, β-oxidation pathway has a central role in providing energy through oil storage mobilisation and acquiring germination potential (Pinfield-Wells et al. 2005; Khan and Zolman 2010). A recent investigation in soybean seeds showed that a peroxisomal *ATP-BINDING CASSETTE 7* (*GmABCA7*) transporter gene facilitated β-oxidation pathway as its overexpression increased enhanced succinate and malate levels and improved germination rate (Li et al. 2022b). In the peroxisomal β-oxidation pathway, the acyl-CoA oxidase (AOX) breaks down the fatty acids stored as triacylglycerides into acetyl-CoA (Baker et al. 2006). The subsequent conversion of acetyl-CoA to succinate via the glyoxylate cycle provides germinating seeds with both carbon skeletons and energy before the seedlings are able to photosynthesize. This pathway is a major source of H_2O_2, and its buildup is controlled by the complementary kinetic properties of CAT, which is found in the peroxisome lumen, and ascorbate peroxidase (APX), which is found in peroxisomal membrane proteins (Yamaguchi et al. 1995). They both have the capacity to decompose H_2O_2 in O_2 and water, but with different affinities (Corpas 2015). Xiang et al. (2023) demonstrated an additional mechanism responsible for the control of ROS formed by β-oxidation during the process of seed germination in *A. thaliana*. Their findings indicated a regulatory loop wherein the expression of *CYTOCHROME P450 A4*

(CYP77A4) is modulated by ROS, hence contributing to the maintenance of ROS homeostasis through fatty acid epoxidation. In addition to H_2O_2, the $O_2^{\cdot -}$ accumulation in plant peroxisomes is enzymatically regulated by different SODs, including CuZn-SOD, Mn-SOD, and Fe-SOD, especially in stressful conditions (Houmani et al. 2022a, b).

RNS production and regulation

In the time between full seed imbibition and radicle protrusion, the oxygen in dry seed tissues rapidly depletes, respiration is reduced, and seed metabolism becomes primarily anaerobic (Narsai et al. 2017). This phase is characterised by fermentation and NO synthesis in mitochondria via anaerobic nitrate (NO_3^-) and nitrite (NO_2^-) reduction (Dębska et al. 2013). The generation of NO leads to a family of molecules termed as RNS, such as dinitrogen trioxide (N_2O_3), peroxynitrite ($ONOO^-$), nitrogen dioxide (NO_2), S-nitrosothiols (SNOs) or S-nitrosoglutathione (GSNO), which may affect protein, nucleic acids and lipid activity (Dębska et al. 2013). Indeed they can, for example, regulate protein function through post-translational modifications (Corpas et al. 2021 and references therein). As in the case of salinity stress, NO is released in the cytosol, allowing the generation of $ONOO^-$ which leads to the nitration of the protein tyrosine residues, affecting its activity (Corpas et al. 2009a). Another post-translational modification is S-nitrosation*,* in which an NO group is covalently attached to the thiol (–SH) side chain of cysteine (Cys) residues (Corpas et al. 2021). This reaction is reversible, so it can be used as a fine-tuned mechanism for redox regulation of specific hub proteins that trigger seed dormancy release (Arc et al. 2013). The generation of NO in plant cells is currently thought to take place both through enzymatic and non-enzymatic routes. Slow and spontaneous (non-enzymatic) liberation of NO can be observed with nitrite at neutral pH, which can be improved at low pH in the presence of a reductant agent, such as ascorbic acid (AsA) (Yamasaki 2000). Non-enzymatic generation of NO via nitrite reduction was reported to occur in the apoplast of barley aleurone layers (Bethke et al. 2004). Enzymatic production of NO takes place through the oxidative or reductive pathways (Gupta et al. 2011; Janku et al. 2019). At present, the best-characterised source of enzymatic NO generation is through NO_3^- to NO_2^- reduction by nitrate reductase (NR). This finding was indirectly proven since NR inhibitors have been shown to inhibit the generation of endogenous NO (Arc et al. 2013; Berger et al. 2020), even though no NR was reported in plant peroxisomes. The oxidative pathway responsible for enzymatic NO production in mammals is NO synthases (NOS), which catalyse its production from L-arginine in the presence of NADPH and O_2 (Corpas et al. 2009b). In peroxisome organelles, a putative NO synthase activity was demonstrated in Barroso et al. (1999), and it is likely to take place in the later stage of seed germination sensu stricto. However, the absence of a confirmed identification of a nitric oxide synthase plant homologue makes this enzymatic route of NO generation still questionable. L-arginine NOS activity has been documented to take place in chloroplast and peroxisome cell organelles (Jasid et al. 2006; Corpas et al. 2009b), but the lack of a plant NOS gives credit to the hypothesis that not a single protein, but protein complexes could work together to generate NO (Corpas and Barroso 2017). RNS produced after seed imbibition (anaerobic phase) can be scavenged by the interaction of $O_2^{\cdot -}$ and NO to form peroxynitrite (Wulff et al. 2009; Ma et al. 2016), while ROS are indirectly regulated by NO through the control of scavenging enzymes involved in ROS metabolism. For example, APX activity is inhibited by tyrosine nitration and enhanced by S-nitrosation (Begara-Morales et al. 2016). These findings show how much ROS and RNS interact with each other, affecting their own concentration and activity (Radi 2018; Mandal et al. 2022).

RONS critical ranges control seed maturation and germination

Both reactive oxygen and nitrogen species are known to cause oxidative damage when they are produced in excess (Mandal et al. 2022). However, their centrality as signalling factors releasing seed dormancy has been widely demonstrated so far (Bailly 2004; Oracz et al. 2007; Krasuska et al. 2016). In particular, ROS trigger complex cellular processes by acting as a primary messenger by oxidising compounds that will in turn act as second messengers (Møller and Sweetlove 2010; El-Maarouf-Bouteau et al. 2013). Moreover, they are regarded as essential electron sinks to properly adjust the cell redox state (Meyer et al. 2021). However, uncontrolled ROS accumulation can lead to the formation of a dangerous oxidative environment (Bailly 2004). Therefore, maintenance within a safe critical range of oxidative stress, namely the "oxidative window of germination", is of pivotal importance, and it is carried out by enzymatic and non-enzymatic mechanisms, avoiding extensive lipid peroxidation, membrane permeability, defective proteins, and nucleic acids damage (Kurek et al. 2019). Glutathione reductases (GR), CAT, and SOD form the antioxidant enzymatic repertoire, while non-enzymatic antioxidants include the reduced form of glutathione, AsA, and tocopherols. Similarly to the ROS model, the"nitrosative door" concept was conceived to identify a threshold of minimum RNS accumulation level that unlocks the signalling and regulation features of RNS: gene expression, protein nitration, S-nitrosation (often referred to as S-nitrosylation), lipid nitration and oxidation, ROS level and metabolism, redox potential, and hormone cross-talk (Krasuska et al. 2014). Above the safe range, the overproduction of RNS leads to damage to cellular components that prevents or delays germination. RNS scavenging is exerted by S-nitrosoglutathione reductase and uric acid, while phytoglobin (Pgb) is responsible for the regulation of NO metabolism through the Pgb-NO cycle (Ma et al. 2016; Corpas et al. 2021; Nie et al. 2022). In Fig. 1, the "oxidative window" and "nitrosative door" models are presented together, highlighting the different timing of the two processes, the role of RONS, and safe critical ranges.

RONS affects seed germination cross-talking at multiple levels

The ABA and GA serve as crucial regulators of germination

Physiological dormancy is a block of seed germination that can be released when specific conditions are met. The balance of the antagonistic phytohormones GAs and ABA can drive the seed towards completion of germination or the maintenance of dormancy, respectively (Fig. 2).

ABA is a sesquiterpenoid synthesised from the carotenoids pathway that promotes reserve storage accumulation during seed maturation, the set of seed dormancy, and its maintenance (Sano and Marion-Poll 2021). In the biosynthetic pathway, 9-cis-epoxycarotenoid dioxygenases (NCED) is the first committed enzyme and the main target for ABA biosynthesis regulation. *NCED* mutants, *vp14*, showed viviparous germination in *Zea mays* due to impaired ABA synthesis (Tan et al. 1997). Afterwards, the *ABA2* gene transcription provides the intermediate reaction for the final step of ABA biosynthesis carried out by the *ABA3* that encodes a molybdenum cofactor sulfurase (Sano and Marion-Poll 2021). *Arabidopsis thaliana aba3* mutants showed that this step leads to activation of the molybdenum enzymes aldehyde oxidase and xanthine dehydrogenase (Bittner et al. 2001). On the other hand, the ABA accumulation can also be controlled by the activation of its catabolism through 8'-hydroxylation, carried out by an enzyme belonging to the CYP707A subfamily of P450 monooxygenases (Sano and Marion-Poll 2021). The expression of *CYP707A2* was observed to take place from late-maturation to mature dry seed, while *cyp707a2 A. thaliana* mutant seeds exhibited an increase in ABA levels in dry condition and after imbibition (Okamoto et al. 2006). Beside structural genes, transcription factors play a crucial role in ABA regulation. *LAFL* genes, namely *LEAFY COTYLEDON1 (LEC1), ABSCISIC ACID INSENSITIVE 3 (ABI3)*, and *FUSCA3 (FUS3)*, encode B3 domain transcription factors that are master regulators of seed development, reserve storage, and inhibit seed

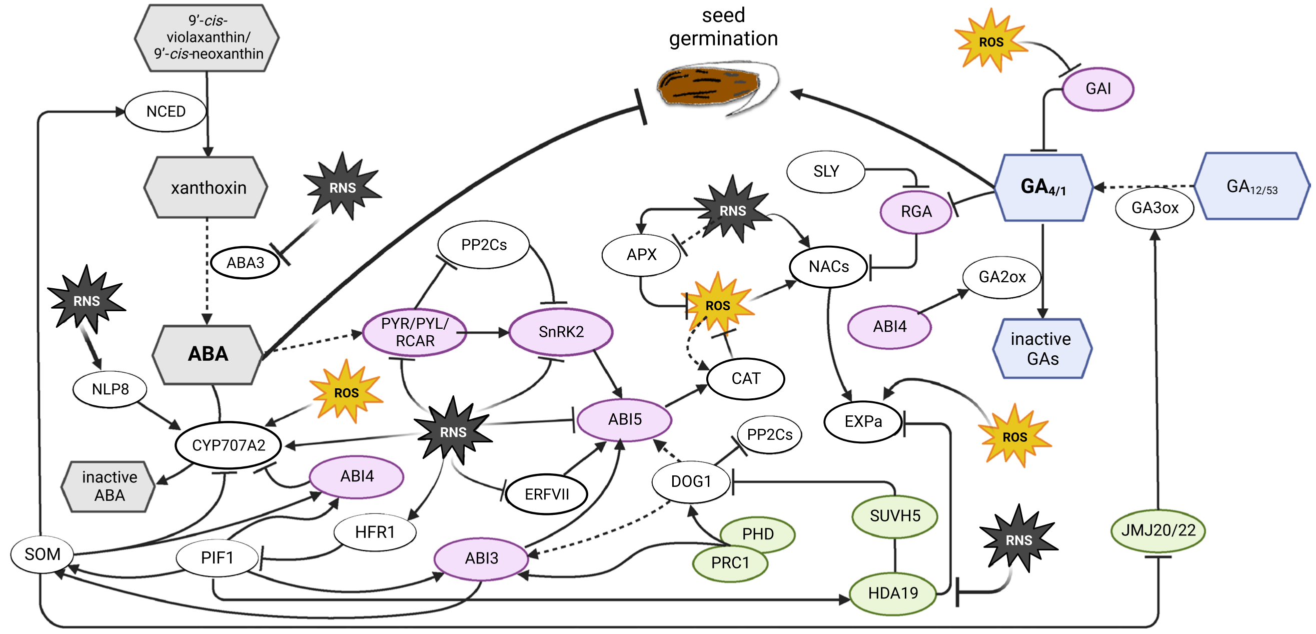

Fig. 2 Simplified model showing RONS's role in the regulatory network of ABA/GAs metabolism and signalling to trigger or repress seed germination. ROS controls the ABA/GAs ratio mainly by promoting ABA catabolism and cell wall remodelling proteins. RNS can lower ABA levels by upregulating *CYP707A2*. However, RNS can also inhibit ABA signalling or biosynthesis through post-translational modifications such as tyrosine nitration, S-nitrosation, or via N-end rule degradation proteolysis. Compounds are depicted with hexagons, while proteins are represented with ellipses. Pink ellipses represent signalling control, while green ones are related to epigenetic control. Arrows indicate positive regulation, and T-bars indicate negative regulation. Dashed lines represent multiple steps or unconfirmed direct interactions

germination and vegetative growth (Lepiniec et al. 2018; Baud et al. 2022). Mutations of *LAFL* are associated with misexpression of embryonic characteristics, resulting in arrested seedling development, while their action is antagonised by VIVIPAROUS1/ABI3-LIKE (VAL) proteins that repress *LAFL* transcription during the final stage of germination (Jia et al. 2013). Among *LAFL*, *FUS3* represses GA biosynthesis, affecting ABA/GAs balance by promoting ABA accumulation (Gazzarrini et al. 2004). While *ABI3* binds the promoter of *REVERSAL OF RDO* (*ODR*) and hinders its expression. ODR was shown to interact with bHLH57, a transcription factor that facilitates *NCED* expression, blocking the binding of bHLH57 to the *NCED* promoter region and leading to dormancy reduction (Liu et al. 2020). Moreover, *ABI3* interacts with either the PHYTOCHROME-INTERACTING FACTOR (PIF1) or ABI5, a bZIP transcription factor, in the dark or at high temperature, respectively, activating expression of *SOMNUS* (*SOM*), encoding for a CCCH-type Tandem Zinc Finger (TZF) protein, and contributing to the inhibition of seed germination through the PIF1-SOM-JMJ20/JMJ22 module, as afterwards discussed (Park et al. 2011). *ABI5* is positively regulated by group VII Ethylene Response Factors (ERFVIIs) that induce *ABI5* expression, enhancing ABA signalling, and it is modulated by NO (Gibbs et al. 2014; Albertos et al. 2015). Moreover, ABI4 is able to bind *CYP707A1* and *A2* promoters, blocking their expression and positively regulating dormancy induction by repressing ABA catabolism and promoting the expression of *GA2OX* and, possibly, *NCED* (Shu et al. 2013, 2016). ABA signal transduction takes place also through a cascade mechanism involving the PYRABACTIN RESISTANCE1 (PYR1)/PYR1-LIKE (PYL)/REGULATORY COMPONENTS OF ABA RECEPTORS (RCAR) interacting with protein kinases, SnRKs. In fact, PYR/PYL/RCAR receptors function at the apex of a negative regulatory pathway to directly regulate PP2C phosphatases, ABI1 and ABI2, which in turn directly regulate SnRK2 kinases that interact with ion channels, transcription factors, and other factors (Cutler et al. 2010).

Oppositely, GAs antagonise ABA action, resulting in dormancy release and completion of germination. Biosynthesized GAs induce hydrolytic enzyme production that weakens the seed testa and mobilises reserves in the endosperm sustaining seedlings during heterotrophic growth. The activity of each gibberellin is highly specific for each organ or tissue, and the most important biosynthetic genes for seed-active GAs are *GIBBERELLIN 3-OXIDASE 1 (GA3OX1)* and *GA20ox3* (Mitchum et al. 2006). *A. thaliana ga3ox* and *ga1* mutants cause GA deficiency and abolish seed germination in the absence of exogenous GAs (Mitchum et al. 2006; Shu et al. 2013). GAs catabolism is carried out by *GA2OXs*. As a proof of that, a loss-of-function *ga2ox2* mutation led to a higher level of GA_4, the active GA form in the seed, and suppressed germination inability during dark imbibition in the presence of inactive phytochrome in *A. thaliana* seeds (Yamauchi et al. 2007). Moreover, GAs signalling is negatively mediated by DELLA (Asp, Glu, Leu, Leu, Ala motif containing) proteins encoded by *REPRESSOR OF GA1-3 (RGA), RGA-LIKE 1 and 2, GIBBERELLIN INSENSITIVE (GAI)* genes. When these genes simultaneously lose function, *A. thaliana* seeds germinate without light or gibberellin (Cao et al. 2005). Substantial DELLA GAI down-regulation was observed during after-ripening, which is associated with the ROS increase (Nelson et al. 2017).

ABI4, which is stabilised by ABA, directly triggers *GA2OX7,* lowering GAs levels, whilst GAs can suppress the expression of *NCED6* via ABI4 (Shu et al. 2016). This continual interaction between GAs and ABA occurs during seed germination in addition to the regulation of each hormone's metabolism. Further examples of Gas–ABA interaction are provided in the next section in the context of environmental conditions and perceptions.

RONS and ABA/GAs cross-talk during seed germination

Cross-talk between RONS and ABA/GAs balance allows for control of germination with respect to environmental factors. The mediation of RONS in the ABA or GA metabolism is dispersed across multiple control levels (Fig. 2). In the presence of favourable conditions, different RONS affect ABA and GAs metabolism depending on the specific germination phase or environmental factors. Upon imbibition, ROS increase and control ABA metabolism to promote germination. Non-dormant barley seed embryos spontaneously produced higher H_2O_2 levels than dormant seeds after imbibition, while the addition of H_2O_2 was associated with a higher expression of *ABA-8'-hydroxylase* (*HvCYP707A*) and lower ABA content in the embryos (Ishibashi et al. 2017). Similarly, H_2O_2 was shown to up-regulate ABA catabolism during imbibition in *A. thaliana* seeds through activation of *CYP707A* expression and nitric oxide mediation, resulting in a decreased ABA content (Liu et al. 2010). This mechanism is balanced, though, by the activation of the enzymatic scavenging system. This happens because *HvABI5* controls the promoter region of *HvCAT2* and enhance its transcription (Ishibashi et al. 2017). Further evidences of this interaction was observed also for *CAT1* in *A. thaliana* seed germination, as *abi5* mutants were more sensitive (lower germination percentages), while ABI5-overexpression transgenic lines were less sensitive (higher germination percentages) suggesting the *CAT1* transcription activation by ABI5 to scavenge ROS accumulation (Bi et al. 2017). On the other hand, ROS interacts with GAs at several levels. As observed in radish plants (Schopfer et al. 2001), GAs increases the production of ROS, primarily $O_2^{\cdot -}$ and H_2O_2, and in cress (Muller et al. 2009), while, in turn, H_2O_2 enhances the expression of *GA3OX1* in tomato seeds (Anand et al. 2019). Bahin et al. (2011) suggested that exogenously applied H_2O_2 has a pronounced effect mainly on GA signalling. The association between exogenous GAs and the production of endogenous ROS has been recently investigated in an old crop, *Brassica parachinensis.* Authors observed that $O_2^{\cdot-}$ addition determined quick germination completion (Chen et al. 2021). Additionally, the study conducted by Dey and Bhattacharjee (2023) shown a strong correlation between hormonal homeostasis and internal redox cues that regulate germination physiology in two indica rice cultivars. This correlation was observed by the utilisation of GAs or ABA in combination with redox modulating agents.

Oxidative bursts can also be controlled by non-enzymatic scavenging systems, which can, in turn, affect germination behaviour. The presence of coumarin, a plant secondary metabolite with antioxidant properties, delayed germination by decreasing gibberellins accumulation in *B. parachinensis* (Chen et al. 2021). Thus, ROS scavenging can limit germination enhancement by acting on the ABA/GAs balance. In fact, coumarin was shown to also act on ABA metabolism, as imbibition in the presence of this compound remarkably reduced *OsABA8'ox2/3* (*OsCYP707A2/3*) expression and increased the ABA content of germinating rice embryos (Chen et al. 2019). Differently from *B. parachinensis*, coumarin addition in rice embryos enhanced the scavenging activity of SODs and catalase (Chen et al. 2019).

A recent study of two wild palm species with different levels of desiccation tolerance showed that when the operculum was removed, $O_2^{\cdot-}$ accumulated faster in *Attalea speciosa* (desiccation-tolerant) than in *Mauritia flexuosa* (desiccation-sensitive) (Santos et al. 2022). This was seen along with a drop in ABA levels suggesting that the haustorium could be a hub region for dormancy-breaking signalling mediated by $O_2^{\cdot-}$ associated with an increase of APX in the first stage of germination (aerobic phase) and GR during both the removal of the operculum and the emergence of the cotyledonary petiole (Santos et al. 2022). So the APX can be involved in the production of $O_2^{\cdot-}$ from H_2O_2, while the GR is involved in regenerating the glutathione pool to prevent oxidative injuries. Aside from non-deep physiological dormancy, ROS were reported to have a role in the completion of germination in morphophysiological dormancy as well. The morphophysiologically dormant seeds of *Ferula ovina* needed a long seed stratification period to completely morphologically develop, and during this period an increase in H_2O_2 was observed. However, the $O_2^{\cdot-}$ radical was supposed to be the active signalling molecule within the embryonic axes of *Ferula ovina* (Fasih and Afshari 2018). To date, only one report has investigated the RONS effect on seed secondary dormancy (Hourston et al. 2022). In a wild secondary dormant *Brassica oleracea* accession, ROS was reported to increase during seed imbibition; the addition of nitric oxide and karrikin 1 (KAR1) was found to induce seed germination through ROS content augmentation, in parallel to catalase and glutathione reductase activity (Sami et al. 2019).

After seed full imbibition, under anoxic conditions, the NO signalling route prevails. As observed in rice, *A. thaliana*, and barley (Gibbs et al. 2014; Loreti et al. 2016), oxygen deprivation activates hypoxia-responsive genes, including *ABI5*, via the stabilisation of ERFVIIs, which undergo a series of N-terminal alterations and cysteine oxidation under aerobic conditions. ERFVIIs positively regulate *ABI5* triggering ABA inhibitory effects on seed germination. ERFVIIs, on the other hand, are controlled by NO, which promotes their degradation through the destabilization of N-terminal residues (Gibbs et al. 2014; Albertos et al. 2015). Therefore, *ABI5* transcription is suppressed, ABA responses are inhibited, and seed germination is promoted by NO-mediated degradation of group ERFVIIs. Moreover, ABI5 can be modified by NO S-nitrosation at cysteine-153, which promotes its degradation. Collectively, these mechanisms limit germination completion at the start of the anaerobic phase, setting the path for NO-ABA interaction later on.

Aside from ABA signalling during late imbibition phases, RNS were recently shown to promote directly ABA catabolism by activating a NIN-like protein 8 (NLP8) transcription factor that promotes *CYP707A2* expression (Yan et al. 2016; Duermeyer et al. 2018). Its presence has been shown to be essential for *A. thaliana* germination via nitrate signalling since *nlp8* loss-of-function mutants do not respond to nitrate and accumulate ABA (Yan et al. 2016). On the other hand, other reports show that the perception of NO takes place in specific areas of the *A. thaliana* seed, as when it is supplemented by the aleurone layer cells that start vacuolation of protein storage vacuoles, which has been used as a semiquantitative marker for GA-dependent events (Bethke et al. 2007). Most notably, NO, ABA, GA, and temperature all regulate this process, but NO acts upstream of GA in the signalling that results in vacuolation (Bethke et al. 2007). In a recent study, the basis of the interplay of NO and GA signalling in *A. thaliana* seedlings exposed to salt stress was postulated (Chen et al. 2022). Researchers discovered that NO S-nitrosylated the RGA DELLA protein at Cys-374, inhibiting the RGA-SLEEPY1 (SLY1) interaction and, as a result, stabilising the RGA repressor protein and, consequently, arresting plant growth and improving salt stress tolerance, most likely by altering the ABA/GAs ratio. This interaction has yet to be demonstrated in the context of seed germination. Its presence would provide NO with a new regulatory role in terms of GA signalling.

Beyond the nitric oxide, the addition of a scavenger of NO, the 2-4-carboxyphenyl-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide (cPTIO), to a herbaceous crop, *Amaranthus retroflexus*, antagonised the stimulatory effect of GA_3, ethephon, and 1-aminocyclopropane-1-carboxylic acid (ACC), an ethylene biosynthesis precursor, on seed germination (Kępczyński et al. 2017). Altogether, these findings suggest that NO may be involved in the modulation of gibberellins action not only upstream but also downstream. ABA and GA continuously regulate NO concentration, forming a strong connection between NO and ABA/GAs balance. GA supplementation increased the production of α-amylase and NO scavenger phytoglobins (Pgb1 and Pgb3) in barley (*Hordeum vulgare* L.) aleurone cells (Nie et al. 2022). ABA addition, on the other hand, removed the GA stimulating effects on both α-amylase and Pgb1 and Pgb3 expression, indicating that ABA and GA regulate the Pgb-NO cycle (Nie et al. 2022). On the other hand, ROS and RNS interplay each other, regulating their own biosynthesis (Zhao 2007). In switchgrass (*Panicum virgatum* L.) seeds, for example, H_2O_2 addition enhances the endogenous production of NO, while a scavenging action on NO affects the peroxide-responsive stimulation of seed germination (Sarath et al. 2007). Collectively, these findings suggest that RONS actively regulate germination by controlling ABA and GA metabolism through several interaction routes.

Effect of NO-related compounds on seed germination

Researchers have been using several compounds, such as sodium nitroprusside (SNP) or hydrogen or potassium cyanide (HCN or KCN), which can elicit NO signalling and were proposed to play significant functions in the regulation of germination. For example, SNP induced the accumulation of DELLAs repressors and PIF expression to promote photomorphogenesis in *A. thaliana* seedlings (Lozano-Juste and León 2011). The addition of SNP, cyanide, nitrite, or nitrate triggers germination in dormant *A. thaliana* seeds, while the supplementation of cPTIO results in dormancy maintenance (Bethke et al. 2006). However, SNP not only enhances nitric oxide concentration but also increases cyanide in plants supplemented with SNP (Keisham et al. 2019). Furthermore, cyanide action mechanisms in the regulation of seed germination are not well-defined. It is associated with the synthesis of ethylene and phospholipids (Keisham et al. 2019) and has been shown to promote germination in a dose-dependent manner. In sunflower (*Helianthus annuus*) embryos, the cyanide dormancy alleviation effect was demonstrated to involve the mediation of ROS as expression of genes related to ROS production (*NADPHox*, *POX*, *AO1*, and *AO2*) and signalling (*MAPK6*, *Ser/ThrPK*, *CaM*, and *PTP*) was enhanced after cyanide treatment (Oracz et al. 2009). HCN was also proposed as a signalling factor cross-talking with ROS and RNS and playing an important role in their modulating systems, as after hydrogen cyanide addition, authors observed accumulation of ROS in apple seeds (Krasuska and Gniazdowska 2012). Germination of tomato (*Solanum lycopersicum* L., A. Craig cultivar) was stimulated by treating seeds with 10 µM of KCN for 12 h, and it up-regulated the expression of genes related to storage protein and late embryogenesis abundant proteins, glycolytic metabolism, and GAs biosynthesis while inhibiting expression of ABA biosynthetic related genes (Yu et al. 2022). Similar behaviour has been observed in wild cardoon (*Cynara cardunculus* var. *sylvestris*) dormant achenes, whose germination levels were enhanced with increasing KCN concentration (Huarte et al. 2014; Puglia et al. 2022). Collectively, these findings suggest that cyanide stimulates seed germination in a dose- and time-dependent manner within a safe range of concentration.

Moreover, polyamines are ubiquitous polycationic compounds that mediate fundamental aspects of eukaryotic and prokaryotic cell proliferation, differentiation, and cell death (Baron and Stasolla 2008). Their levels may influence the synthesis of heat shock proteins (HSPs) that play crucial roles in maintaining the integrity and properties of cell membranes under HT stress (Pooja et al. 2019). Polyamines maintain the thermostability of thylakoid membranes exposed to heat, thereby increasing photosynthetic efficiency (Kusano et al. 2008). PAs are plant regulators and share arginine, as a precursor of their biosynthesis, with NOS-like production of NO and ethylene (Baron and Stasolla 2008). NO-dependent stimulation of ethylene formation was demonstrated during the germination of apple embryos (Gniazdowska et al. 2010). Moreover, the addition of putrescin (Put) and spermidine (Spd) polyamines increased ROS (H_2O_2 and $O_2^{\cdot-}$) production in apple embryos, both at the beginning of this process (after 2 days of imbibition) as well as during termination of sensu stricto germination (Sun et al. 2023). A recent study by Sun et al. (2023) confirmed at the transcriptional level that the addition of Put is associated with the biosynthesis-related genes of the NOS-dependent pathway and with endogenous NO generation in *Anthurium andraeanum* seedlings.

In Table 1, several recent reports were categorised according to the reported RONS effect on seed germination and investigated species at different treatment conditions.

RONS and auxin cross-talk

Auxins are important phytohormones involved in many aspects of plant growth and development. Their role in seed germination has been associated with the inhibition of germination and promotion of primary dormancy, as the addition of IAA (indole-3-acetic acid) delays germination in soybean seeds, and this is associated with the increasing of the ABA/GAs ratio (Shuai et al. 2017). In *A. thaliana*, Liu et al. (2013) demonstrated that auxin controls seed dormancy by triggering ABA signalling through the promotion of *ABI3*

Table 1 Reported effects of ROS interaction with ABA, GA, temperatures and antioxidant system during seed germination

Species	ROS mostly involved	Seed district mainly involved in ROS production	Effect on germination	Treatment triggering ROS production	Interaction with GA	Interaction with ABA	Scavenger system involved	Study
M. flexuosa and A. speciosa	$O_2^{\cdot -}$	Haustorium	+	Operculum removal	N.D	Decrease of ABA	SOD and CAT	Santos et al. (2022)
F. ovina	H_2O_2 and $O_2^{\cdot -}$	Embryonic axis	+	Cold stratification	N.D	N.D	N.D	Fasih et al. (2018)
Z. tubispatha	$O_2^{\cdot -}$	Embryonic axis	-	High temperature	±	Increased sensitivity to ABA	Peroxidases (APX and GPOX)	Acosta et al. (2022)
Oryza sativa L	$O_2^{\cdot -}$ and H_2O_2	N.D	-	High temperature	-	Increased biosynthesis of ABA	Decreased SOD and CAT	Liu et al. (2019)
B. oleracea	H_2O_2 and $O_2^{\cdot -}$	N.D	+	NO and karrikin (KAR1)	Accumulation of GA	Decrease of ABA	CAT and GR	Sami et al. (2019)
C. cardunculus var. sylvestris	H_2O_2 and $O_2^{\cdot -}$	Embryonic axis	+	Alternating temperatures/cyanide	Up-regulation of GA biosynthetic genes	Down-regulation of ABA signalling and biosynthetic genes	Up-regulation of *CAT*	Puglia et al. (2022); Huarte et al. (2020a, b)
S. lycopersicum cv. A. Craig	H_2O_2	N.D	+	Cyanide	Up-regulation of GA biosynthetic genes	Down-regulation of ABA biosynthetic genes	Up-regulation of GPX and POD	Yu et al. (2022)
H. vulgare	H_2O_2	Aleurone cells and embryo	+	Non-dormant seeds	N.D	activation of *CYP707A*	Promotion of *CAT2*	Ishibashi et al. (2017)
L. sativa	H_2O_2	Embryo	+	Non-dormant seeds	N.D	N.D	N.D	Zhang et al. (2014)
O. sativa	H_2O_2	Coleorhiza and radicle	+	Non-dormant seeds	N.D	Catabolism through *CYP707A*	Promotion of CAT	Chen et al. (2019)
H. annuus	H_2O_2	Embryonic axis tip	+	Methyl viologen	N.D	Down-regulation of ABA signalling genes	CAT	El-Maarouf-Bouteau (2015); Bailly (2004); Bazin (2011)
H. vulgare	H_2O_2	Embryo	+	H_2O_2	Inhibition of *HvGA2ox3* expression	ABA upregulated *HvCAT* expression	CAT	Bahin et al. (2011)
P. virgatum	NO	N.D	+	H_2O_2	N.D	ABA inhibited NADPH-oxidase activity	cPTIO	Sarath et al. (2007)
R. sativus cv Eterna	$O_2^{\cdot -}$	Aleurone cells and embryo	+	Germination in darkness	Promotion of ROS	Lowering of ROS	N.D	Schopfer et al. (2001)
B. parachinensis	$O_2^{\cdot -}$	Radicle and endosperm cap	+	Non-dormant seeds	Promotion of ROS	N.D	Promotion of CAT	Chen et al. (2021)
M. sieversii	N.D	N.D	+	Cold stratification/addition of ascorbic acid	Promotion of ROS	N.D	N.D	El-Maarouf-Bouteau et al. (2013)

Table 1 (continued)

Species	ROS mostly involved	Seed district mainly involved in ROS production	Effect on germination	Treatment triggering ROS production	Interaction with GA	Interaction with ABA	Scavenger system involved	Study
M.s domestica	NO	Embryo axes	+	Addition of Put and Spd	N.D	N.D	cPTIO	Krasuska et al. (2014)
M. sativa	H2O2	N.D	+	Addition of ascorbic acid	Promotion of ROS	N.D	Promotion of POD and CAT	Chen et al. (2021)
L. sativum	·OH	Radicle and endosperm cap	+	Non-dormant seeds	Promotion of ROS	Inhibition of ROS accumulation	N.D	Muller et al. (2009)

APX ascorbate peroxidase, *CAT* catalase, *GPX* guaiacol peroxidase, *GPOX* glutathione peroxidase, *GR* glutathione reductase, *POD* peroxidase, *SOD* superoxide dismutase, *cPTIO* 2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide, *ND* not described

expression by recruiting AUXIN RESPONSIVE FACTOR (ARF) 10 and 16. Under low auxin concentrations, ARF10 and 16 are inactivated by AUXIN REPRESSOR (AXR) 2 and AXR3, while when the auxin reaches high concentrations, the phytohormone binds auxin receptor Transport inhibitor response 1 (TIR1)/Additional F box protein (AFB) and promotes the degradation of AXR2 and AXR3, releasing ARF10 and 16 that can promote *ABI3* expression and enhance ABA signalling. A recent investigation revealed that *ABI3* is down-regulated by the auxin signalling repressor Aux/IAA8 protein in *A. thaliana* seeds, and this interaction was promoted in the presence of ROS, resulting in a synergistic effect on germination (Hussain et al. 2020). Moreover, transcriptomic investigation on dormant *Capsella bursapastoris* seeds exposed to histone deacetylase inhibiting treatment showed that an epigenetic control might occur on histone deacetylases that are implicated in the regulation of auxin pathways and signals also associated with the regulation of seed germination processes, such as SWI-INDEPENDENT 3 (SIN3)-LIKE 1 (SNL1) and SNL2 (Gomez-Cabellos et al. 2022). Further investigations on TIR1/AFB have shown that they physically interact (Iglesias et al. 2010), and this plays a role in triggering ROS generation, as *tir1 afb2* mutants showed significantly reduced ROS accumulation, higher antioxidant enzymatic activities, and enhanced levels of antioxidant activity. A similar effect was documented in the roots of tomato seedlings, for which the addition of H_2O_2 caused the repression of the expression and activity of CuZn-SOD, peroxidase, and catalase (Tyburski et al. 2009). Thus, the regulation of ROS homeostasis through the control of the scavenging system might represent the bridge between auxin and ROS. Concerning the RNS, several investigations have shown the positive interplay between NO and auxin through the degradation of the phytohormone by inhibiting IAA oxidase activity in *Medicago truncatula* seedlings under cadmium stress (Xu et al. 2010). Furthermore, NO positively regulates auxin signalling through S-nitrosylation of the auxin receptor protein TIR1. This post-translational modification improves TIR1 binding to auxin response repressor proteins, AXRs, resulting in their degradation and thus promoting transcription of auxin-responsive genes, *i.e., ARFs* (Terrile et al. 2012). Iglesias et al. (2018) reported that this NO-post-translational modification occurs by S-nitrosylation and S-glutathionylation in cysteine (Cys) 37 and Cys 118 residues, respectively, and it enhances the correct assembly and efficiency of the auxin co-receptor. The presence of multiple redox modifications might be part of a fine-tuning regulation of the co-receptor for proper auxin signal transduction (Iglesias et al. 2018). Furthermore, *ARF* genes were shown to be targeted at the post-transcriptional level by the microRNA160, miR160 (Liu et al. 2013; Lin et al. 2018). Repression of *ARF10* and *ARF16* by miR160 has been shown to negatively affect *ABI3* expression, hampering ABA signalling in *A. thaliana* (Liu et al. 2013). Also, it was shown that miR160, through the genes it controls, affects hypocotyl elongation in light or in the presence of a GA biosynthesis inhibitor. This makes miR160 a hub between many factors that affect plant development, such as auxin, light, and GA (Dai et al. 2021). These evidences provide a complex picture of auxin interplay both with RONS and with the ABA/GAs ratio. This multi-level interaction might represent the way this phytohormone can affect several stages of plant growth and development.

Aside from ABA, GAs, and auxin, other plant hormones such as brassinosteroids, ethylene, and jasmonic acid have also been demonstrated to have a role in the control of dormancy and germination by interacting with RONS. For relevant information, recent reviews can be referred to (Li et al. 2021, 2022a; Bailly et al. 2023).

RONS interact with cell wall proteins and polysaccharides to control germination

Plant cell walls are made of a diverse set of polymers, including polysaccharides (cellulose, hemicellulose, and pectin) and small amounts of proteins, mostly glycoproteins. Cell wall loosening is considered a major process required for radicle elongation growth driven by water uptake and for the weakening of the covering envelopes (Cosgrove 2022). In vivo scission of specific cell wall polysaccharides in endosperm caps of germinating cress seeds was documented to be caused by $^{\cdot}$OH production in the apoplast, and this process is controlled by the ABA/GAs ratio (Muller et al. 2009).

Although plant cell walls contain only small amounts of protein, cell wall-remodelling proteins (CWRP), *i.e.*, expansins (EXPs) and xyloglucan endotransglycolases/hydrolases (XTHs), are important components in the endosperm (cap) weakening process (Samalova et al. 2022). Expansins mediate pH-dependent cell wall enlargement through wall stress relaxation (Tenhaken 2015). They are activated in response to various stresses associated with ROS production. It was hypothesised that the accumulation of $^{\cdot}$OH induces the cleavage of polymer chains, resulting in cell wall weakening and enabling further growth (Han et al. 2015). Expansins can also mitigate ROS effects by upregulating specific cell-wall-bound peroxidases that maintain oxidative stress within an optimal range (Han et al. 2015; Samalova et al. 2022). Through the use of Gas Plasma-Activated Water (GPAW), Grainge and colleagues (Grainge et al. 2022) have recently demonstrated in the *A. thaliana* model that the generated ROS caused endosperm weakening by direct chemical action (scission of backbone polysaccharides) and by inducing CWRP genes, such as those encoding expansins (*EXPA2*, *EXPA8*) and xyloglucan endotransglycolases/hydrolases (*XTHs*; *XTH5*). ROS accumulation has also determined changes in the expression patterns of key genes in GA and ABA biosynthesis, as shown in previous investigations on tomato (Chen et al. 2002) and *L. sativum* (Graeber et al. 2014). In addition, a direct link between gibberellins and expansins has been provided by Sánchez-Montesino et al. (2019). Within the NAC (NAM, ATAF, and CUC) transcription factor family, they proposed NAC25 and NAC1L as upstream regulators of *EXPA2* expression. According to their study, DELLA (Asp, Glu, Leu, Leu, Ala motif containing) RGL2 proteins, repressors of GA signalling activity, sequester NACs that cannot bind to a conserved cis-element within the *EXPA2* promoter, repressing its activation. Moreover, ANAC089, another NAC family transcription factor, sorted within the group of *OsNAC08*-related NACs together with *ANAC060* and *ANAC040*, has been shown to be directly affected by changes in the cellular redox status regulated by RONS balance and to have an essential role in the regulation of redox-related homeostasis genes, such as *EXPAs* and *XTH* (Albertos et al. 2021).

DOG1 and RONS interplay

DELAY OF GERMINATION-1 (DOG1) controls a molecular network implicated in the control of germination response in temperature-dependent *A. thaliana* seed germination (Graeber et al. 2014). Transcriptomic analyses on *A. thaliana dog1-1* mutant have shown that the DOG1 protein regulates the transcription of hundreds of genes involved in seed maturation and dormancy maintenance (Dekkers et al. 2016; Sall et al. 2019). Control of *DOG1* expression can occur through several regulatory pathways, such as chromatin remodelling, alternative splicing, selective polyadenylation, and non-coding RNAs (Katsuya-gaviria et al. 2020; Tognacca and Botto 2021). The SUVH family of histone H3 lysine 9 N-methyltransferases is responsible for DNA methylation of *DOG1* in *A. thaliana*, as *SUVH* mutants showed up-regulation of *DOG1* and *ABI3* and exhibit higher levels of dormancy (Zheng et al. 2012; Ding et al. 2022).

Alternative splicing of the *DOG1* gene can potentially produce five different transcript variants, which differently affect dormancy levels and the accumulation of DOG1 protein (Nakabayashi et al. 2015). Moreover, the transcriptional elongation factor TFIIS enhances *DOG1* expression, as the non-dormant *A. thaliana tfIIs* mutants phenotype points out (Mortensen and Grasser 2014), but it also affects alternative splice site selection (Brzyżek and Świeżewski 2015). Moreover, as a post-transcriptional modification, the mRNA of *DOG1* can undergo alternative polyadenylation that produces two *DOG1* transcripts: a shorter two-exon short *DOG1* (*shDOG1*), which is a key player in the establishment of seed dormancy, and a longer three-exon long *DOG1* (*lgDOG1*) (Cyrek et al. 2016; Kowalczyk et al. 2017). On top of that, during transcription, several non-protein-coding RNAs can be generated, among which an antisense transcript originating from the *DOG1* proximal termination silences *DOG1* with a cis-interaction, hampering seed dormancy strength (Fedak et al. 2016).

DOG1 protein interacts physically with ABA-*HYPERSENSITIVE GERMINATION 1 (AHG1)* and *AHG3,* which encode PP2C protein phosphatases, which are negative regulators of ABA signalling and dormancy (Née et al. 2017; Nishimura et al. 2018). Moreover, DOG1 interacts with two ABA signalling-related transcription factors: ABA-responsive element BINDING FACTOR 4 (ABF4) and ABI5. They regulate the transcription of ABA-responsive genes responsible for the germination inhibition or triggering through RONS action (Kim et al. 2013; Li et al. 2023). In fact, ABF4 was recently shown to promote the expression of *PYRUVATE DECARBOXYLASE 1 (PDC1),* enhancing fatty acid β-oxidation and ROS accumulation that ultimately determines inhibition of seed germination (Li et al. 2023). While, the NO S-nitrosation of ABI5 at cysteine-153 and NO-mediated degradation of group ERFVIIs via the N-end rule limit ABI5 signalling, inducing germination and seedling development (Gibbs et al. 2014; Albertos et al. 2015).

DOG1 regulation has primarily been investigated at the transcriptional level; however, our inquiry into its epigenetic and post-transcriptional modification has only recently begun, and only a few specialised reviews provide a thorough grasp of the state of the art (Katsuya-gaviria et al. 2020; Ding et al. 2022). More research on the exact set of genes regulated by changes in DNA methylation and chromatin remodelling is needed to better understand the significance of this epigenetic regulation.

RONS induces chromatin remodelling through histone modification

Chromatin is a complex of DNA and proteins that form the chromosomes found in the cells of higher organisms. Chromatin proteins, *i.e.,* histones, package the huge amount of genomic DNA into a highly compact form that can fit into the nucleus. Remodelling of chromatin alters this compact form, changing the accessibility of genes by transcriptional machinery and thereby regulating gene expression at the epigenetic level. RONS can act on chromatin state directly, through the generation of RONS-induced histone marks such as carbonylation or glutathionylation, or indirectly, by influencing the enzymatic activity of DNA methyltransferases and DNA glycosylases or S-adenosyl methionine (SAM) availability, thereby impacting histone and DNA methylation (Shen et al. 2016). Histone deacetylases (HDAs) regulate seed-setting and dormancy by lowering the acetylation levels of target genes, inhibiting their expression (Mengel et al. 2017). HDA19 interacts with the histone methyltransferase SUVH5 during seed germination to regulate dormancy in *A. thaliana*, since mutations of both *SUVH5* and *HDA19* increase histone H3 acetylation (H3ac) and reduce H3K9me2, boosting *DOG1* expression and seed dormancy (Zhou et al. 2020). Moreover, HDAs are regulated by NO S-nitrosation, which inhibits their deacetylation activity (Mengel et al. 2017). As a result, histone acetylation is enhanced, and chromatin is in a more accessible state for genes' transcriptional machinery when NO is added (Ageeva-Kieferle et al. 2019). Treatment of *A. thaliana* seedlings in the presence of a NO donor increased the abundance of several histone 3 and histone 4 acetylation marks, while the addition of the NO scavenger, cPTIO, strongly lowered the abundance of these histone marks (Mengel et al. 2017). Histone methylation and demethylation are also important epigenetic modifications that regulate the chromatin state. Methyltransferases or demethylases are regulated by NO modification (Ageeva-Kieferle et al. 2019). Jumonji C (JmjC) domain-containing histone demethylases JMJ20 and JMJ22 act redundantly as positive regulators of seed germination. When PIF1 binds the zinc-finger protein SOM, it directly suppresses *JMJ20* and *JMJ22*, and the repression will be released upon PIF deactivation by phytochrome B (phyB) (Wang et al. 2021). Derepressed *JMJ20/JMJ22* promote seed germination by removing repressive histone arginine methylations at *GA3OX1* and *GA3OX2* (Cho et al. 2012). These findings imply that distinct regulatory pathways for chromatin remodelling occur during germination. The extent to which RONS compounds cause specific alterations in the epigenome profiles of germinating seeds is still largely unknown.

RONS role in the environment perception

Light perception

Light and temperature are two major environmental factors that fluctuate throughout the day and seasons. For many plant species, germination can only proceed after exposure to light and/or alternating temperatures, which, consequently, represent dormancy termination factors (Marin et al. 2019; Yan and Chen 2020). As environmental factors, they can provide important information about soil burial depth that can make a substantial difference in seedlings fate (Cristaudo et al. 2014; Fernández-Pascual et al. 2015). In changeable habitats across the year, their fluctuation can form a specific seasonal pattern that is associated with favourable conditions related to temperature and water availability and is perceived by the seed as a germination cue (Cristaudo et al. 2016; Puglia et al. 2018). Light and temperature information are integrated into the circadian clock system to generate biological rhythms that are finely regulated.

Light is perceived by the plants through specific photoreceptors depending on the wavelength: phytochromes (phy) for the red/far-red light sensing and the blue light-sensing cryptochrome (cry). Among phytochromes, Phytochrome A (phyA) and phyB are the main ones responsible for light perception, as mutations of them alter the clock period in a light intensity-dependent manner (Somers et al. 1998). PhyB is present in two inter-convertible forms, switching from one to another according to intensity and quality of light. In the far-red region of the electromagnetic spectrum, it is in the inactive form (Pr), while when phyB Pr is exposed to red light, it changes to the active form (Pfr) (Sweere et al. 2001; Klose et al. 2015). Phytochrome light sensors modulate the clock period by conveying light input signals to the circadian clock through the regulation of *PIF1* expression (Somers et al. 1998; Tóth et al. 2001; Nusinow et al. 2011). The *PIFs* gene family encodes for transcription factors with a basic helix-loop-helix (bHLH) DNA binding domain and includes *PIF1* (also named *PIF3-LIKE 5* or *PIL5*), *PIF3*, *PIF4,* and *PIF5* (*PIL6*). When the phytochrome is in the Pr form (dark or HTs), PIF can bind target genes, promoting their expression, while in the Pfr form (light or low temperatures), it enters the cell nucleus, sequesters PIF1, and is degraded by 26 proteasomes through ubiquitination (Sakamoto and Kimura 2018). Thus, changes in the form of phytochrome affect the expression of PIF1, which acts on the transcription of multiple genes, called PIF1-Direct Target Genes (DTGs). These are regulated to prevent seeds from germinating in the dark (Zhang et al. 2020), as *pif1* mutants can sprout without light (Kim et al. 2016) (Fig. 3). The most known downstream PIF1 regulation module repressing seed germination in dark conditions is *SOM*, which encodes a CCCH-type tandem zinc finger protein that inhibits the promotion of *GA3OX1 and GA3OX2* expression through inhibition of JMJ20/22 histone demethylases (Dong et al. 2008; Cho et al. 2012). In addition, *SOM* expression was associated with the activation of *GA2OX2*, a GA catabolic gene, and both *ABA1* and *NCED,* which allow ABA biosynthesis (Dong et al. 2008). Another PIF1 downstream regulation module controls the histone acetylation levels of seed-germination-related genes.

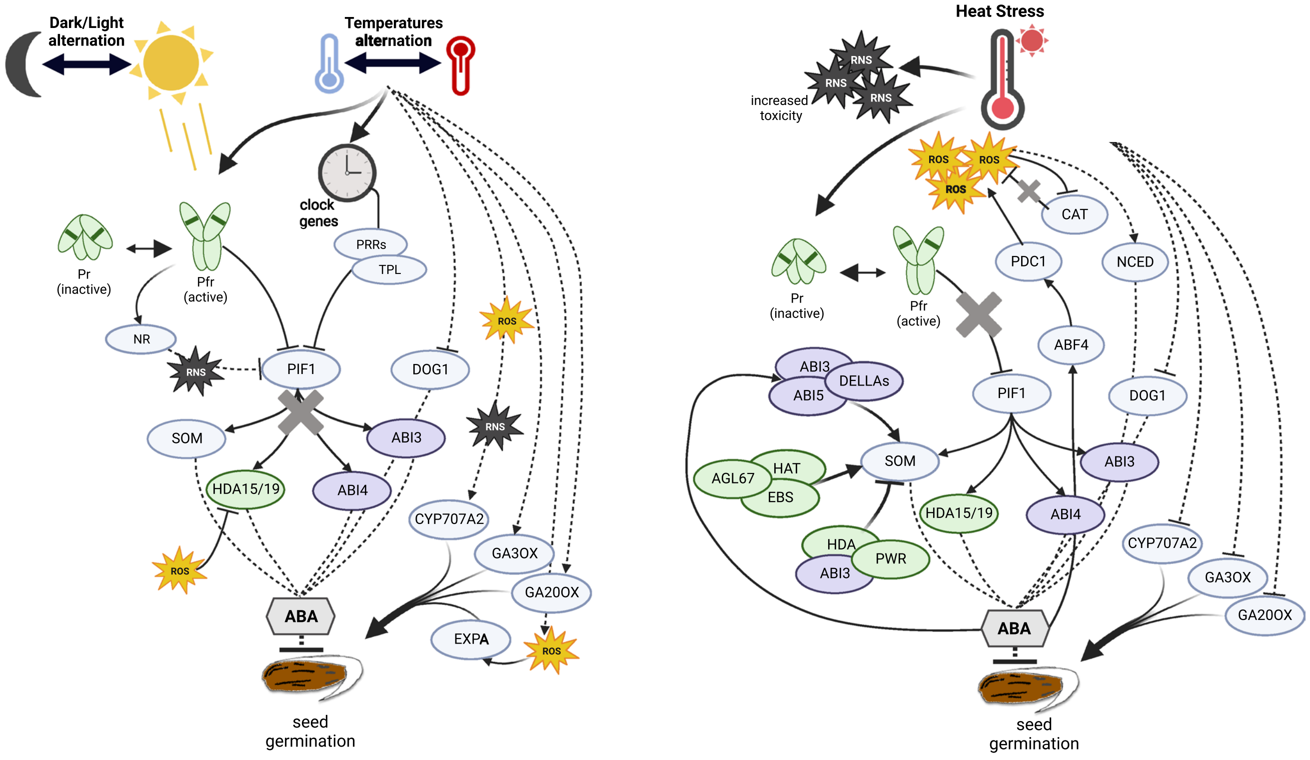

Fig. 3 Model presenting the RONS signalling role within the molecular routes related to light and temperature changes in perception and response. In the presence of light, active Pfr sequesters PIF1 and activates NR (nitrate reductase) that generates RNS. Both actions ultimately inhibit PIF1-DTG binding and promoting germination. At fluctuating temperatures, activated clock components form a protein complex (PIF1-PRRs-TPL) repressing transcriptional activation activity of PIF1 protein. ROS produced at fluctuating temperatures upregulate *EXPAs* expression. Heat stress determines inhibition of Pfr, similar to the dark condition. Generated ABA produces reinforcing germination-repressive loops: one with the ABI5-ABI3-DELLAs complex, and another one promoting ROS production through ABF4-PDC. However, PWR can reverse this mechanism through deacetylation (by HDA) at the *SOM* level to repress its expression. The role of the latter module needs to be demonstrated in the HT condition. Dashed lines represent hypothesised interactions. Regulative modules are indicated with arrowed rectangles. Arrows indicate positive regulation, and T-bars indicate negative regulation. Pink ellipses represent signalling control, while green ones are related to epigenetic control

According to a report by Gu et al. (2017), PIF1 recruited HDA19 to lower H3 acetylation levels in the dark condition (Pr form), which interfered with the transcription of *EXPAs* and other seed germination-related genes. In fact, HDA19 and PIF1 mutants had higher levels of H3 acetylation in the promoter and first exon regions of *EXPAs* than wild-type. This supports the idea that HDA-PIF1 stops its target genes from being expressed by lowering the levels of histone acetylation. On the other hand, HDA19 deacetylation activity has been shown to be inhibited by NO S-nitrosation modifications (Mengel et al. 2017). Thus, the NO-driven HDA19 inactivation paves the way to the *EXPAs* expression and completion of germination. Furthermore, *EXPA* is also directly regulated by ROS, as in morphologically dormant celery seeds, the content of $O_2^{\cdot-}$ and H_2O_2 in light increased and was correlated to *EXPA* expression (Li et al. 2022c). In addition, PIF1 directly influences ABA signalling by binding *ABI3* and *ABI4*, affecting ABA and GA metabolism. ABI3, in turn, promotes expression of *ABI5,* whose corresponding protein can interact with PIF1 to form a protein complex that binds G-boxes, or the GCE of target genes (Kim et al. 2013). NO mediates ABI5 activity at the post-translational level by cysteine S-nitrosation or by affecting its expression through degradation via the N-end rule proteolysis route of ERFVII that promotes ABI5 transcription.

On the other hand, Shi et al. (2013) showed that there is an opposing pathway for PIF1 to stop seed germination in *A. thaliana*. In this pathway, the LONG HYPOCOTYL IN FAR-RED1 (HFR1), a bHLH subfamily 15 transcription factor, plays a key role in forming heterodimers with PIF1 and locking it away. Interestingly, the molecular basis of HFR1-PIF1 heterodimer binding was proposed to lie in stabilisation NO, which is generated in light conditions by phyB-activated NR (nitrate reductase) in *A. thaliana* seeds (Li et al. 2018). As a matter of fact, the addition of NO promoted light-initiated seed germination, while the scavenging of exogenous NO by the cPTIO treatment suppressed seed germination regardless of the activation form of phyB, and the *phyB nox1* (NO overproducer) mutant seeds still showed relatively higher germination rates than did the *phyB* mutant, which did not germinate under either Pr or Pfr conditions (Li et al. 2018). In addition, direct interaction between HFR1 and PIF1 was revealed in *Brassica napus*, as yeast cells bearing the *BD-BnaPIL5* and *AD-BnaHFR1* constructs grew abnormally and proportionally to the *BnaPIL5-BnaABI3* interaction (Boter et al. 2019). By creating a fail-safe mechanism to appropriately regulate seed germination, the HFR1-PIF1 module ensures quick adaptability to environmental changes.

Mérai et al. (2019) looked at how light affects germination in natural populations of plants and found that PIF1 may act as a hub, even in light-inhibited *Aethionema arabicum* accessions. Researchers found that the expression of key regulator genes changes in this case, which leads to opposite hormone regulation compared to positive photoblastic *A. thaliana* seeds. This suggests that the basic parts of light perception are the same across Brassicaceae species, but they are linked in a different way (Mérai et al. 2019). On the other hand, studying negative photoblastic species or accessions would help us understand how the RONS-mediated regulation modules described for *A. thaliana* can also apply to these plants. For example, further research on naturally occurring mutants of *A. arabicum* revealed that phytochromes can play a role in mediating germination inhibition under red, far-red, and white light, allowing the fine-tuning of many propagation parameters in adaptation to habitat conditions (Mérai et al. 2023).

Fluctuating temperatures as an environmental cue promoting germination

The temperature fluctuation can be perceived by a sensitive seed as a favourable seasonal pattern for germinating; however, only a few studies have investigated the role of the circadian clock in this process (Penfield and Hall 2009; Arana et al. 2017). The plant circadian clock controls many processes that facilitate plant developmental and environmental adaptive responses, such as leaf movement, stomatal opening and closing, hypocotyl growth, subcellular localization of organelles, photoperiodic control of flowering induction (Covington et al. 2008), and seed germination (Penfield and Hall 2009). This system is composed of multiple genes that are regulated by several transcription-translation feedback loops (Gil and Park 2019). The main feedback loop contains *CIRCADIANCLOCK-ASSOCIATED 1* (*CCA1*), its functional ortholog *LATE ELONGATED HYPOCOTYL (LHY), TIMING OF CAB EXPRESSION 1 (TOC1*, also known as *PSEUDO-RESPONSE REGULATOR1 (PRR1)),* and some additional clock components, such as the evening complex (*PRR* and *GIGANTEA, GI,* genes) (Tóth et al. 2001; Gil and Park 2019). In the morning, the CCA1 and LHY transcription factors repress in a negative feedback loop the transcription of the *TOC1* gene, whereas the TOC1 transcription factor forms a second interlocking feedback loop with *GI* that represses the transcription of the *CCA1* and *LHY* genes in the evening (Alabadí et al. 2002; Gendron et al. 2012). By contrast, CCA1 and LHY transcription factors form a third interlocking loop that activates the *PRR7* and *PRR9* genes (Harmer and Kay 2005), whose gene products in turn repress the *CCA1* gene transcription. Meanwhile, TOC1 represses the transcription of the Evening Complex components (Nagel and Kay 2012). On top of that, the E3 ubiquitin ligase ZEITLUPE (ZTL) in conjunction with HSP90 interacts with the circadian clock, providing stabilisation during high temperatures (Gil et al. 2017).

Besides perceiving light presence, phyB has also been proposed as a temperature sensor that is activated by cool temperatures and red light, while it is inactivated by far-red light and HTs (Legris et al. 2016; Sakamoto and Kimura 2018). The interaction between clock components and phytochrome takes place through PIF-TOC1-TOPLESS (TPL), a transcriptional corepressor family protein, an interaction mediated by PRRs that repress expression of PIF1-DTGs (Zhang et al. 2020) (Fig. 3). Thus, PRRs function as direct outputs from the core circadian oscillator to regulate the expression of PIF1-DTGs through modulation of PIF1 transcriptional activation activity (Zhang et al. 2020). Among the *PRRs* genes, *A. thaliana* seeds require the expression of *TOC1* and *PRR7* to germinate at alternating temperatures (Arana et al. 2017). Authors have shown that *prr7-3* and *toc1-1* mutant seeds showed a similar percentage of germination regardless if they were incubated at constant 15 °C or 17.5 °C or at 15/23 °C alternating temperatures. Moreover, alternating temperature incubation was associated with the expression of ABA catabolic (*AtCYP707A2*) and GA biosynthetic (*AtGA3OX1* and *AtGA20OX3*) genes. On top of that, DOG1 plays a role in this regulation, as *dog1* mutants germinated and accumulated *AtTOC1* transcripts at the same rate regardless of the temperature regime, so it inhibits seed germination under constant temperatures by repressing *AtTOC1* expression. Thus, it indicates that alternating temperatures promote germination through the main components of the clock, TOC1 and PRR7, while DOG1 interacts with them to inhibits germination at constant temperature (Arana et al. 2017). Moreover, as aforementioned, DOG1 was proposed as a thermal sensing mechanism for seed because the H3K4me3 and H3K27me3 mark levels in the DOG1 region vary in response to seasonally changing soil temperature in a soil seed bank (Graeber et al. 2014; Footitt et al. 2015). Aside from *A. thaliana*, in *Sysimbrella dentata* (Brassicaceae) natural populations, alternating temperatures significantly promoted germination even in non-after-ripened seeds, and nitrate addition neutralised ABA addition, promoting germination and an earlier testa rupture (Puglia et al. 2018), though the molecular basis of this mechanism remains to be unravelled. In *Cynara cardunculus* var. *sylvestris*, another wild species with a fluctuating-temperature-sensitive germination, achenes require alternating temperatures to terminate dormancy, and this is associated with a decrease in the ABA/GAs ratio by decreasing the content and sensitivity to ABA and involving a reduction in the expression of *NCED* and *ABI5* (Huarte et al. 2014). Later studies showed that imbibition at fluctuating temperatures was also associated with ROS generation and up-regulation of ABA catabolism, cell wall-remodelling proteins expression as *EXPAs*, and catalases (Huarte et al. 2020a, b; Puglia et al. 2022). These findings provide a new avenue for research into seed germination responses to environmental cues in wild species. Beyond the interplay between ABA/GAs ratio and clock, the latter was demonstrated to regulate auxin signal transduction in *A. thaliana* plants. In this study, Covington and Harmer (2007) demonstrated that the addition of IAA, even at high had no effect or only transiently affecting the expression of *TOC1, CCA1, GI, CCR2* and *ELF3*. However, the auxin responsive genes were, instead, gated by the circadian clock control, as peak IAA responsiveness coincided just before subjective dawn.

Thermoinhibition in the HT stress condition

When seeds are imbibed at supraoptimal temperatures, their germination potential can be reduced (thermoinhibition), which is critical for *A. thaliana* to establish vegetative and reproductive growth in appropriate seasons (Fig. 3). Earlier investigations in *A. thaliana* seeds showed that high temperature (HT) induces abscisic acid biosynthesis through the up-regulation of zeaxanthin epoxidase gene (*ABA1/ZEP*) and *NCED,* and represses GA synthesis and signalling by the suppression of *GA20OXs*/*GA3OXs* and DELLA proteins activation (Toh et al. 2008; Park et al. 2017). The GA biosynthesis would be most probably mediated by JMJ20/22, while the suppression of GA signalling route might be occurring via SLY-RGA interaction, as above described. Following studies found that ABA signalling was also involved in the inhibition of germination via *SOM* expression, as *som* mutants germinated more frequently than the wild type at high temperatures (Lim et al. 2013). The *SOM* promoter is the target of ABI3, ABI5, and DELLA transcription factors, as chromatin immunoprecipitation assays revealed (Lim et al. 2013). Thus, at HT, the proteins ABI3, ABI5, and DELLAs bind with each other to create a complex on the *SOM* promoter that activates its expression. In parallel to this controlling mechanism, seed germination thermoinhibition has been demonstrated in *A. thaliana* via epigenetic regulation at *SOM* locus. The MADS-box transcription factor AGAMOUS-LIKE67 (AGL67) affects seed dormancy, since the *agl67* mutant has reduced seed dormancy. It interacts with *EARLY BOLTING INSHORT DAY (EBS)*, which has a bivalent bromo-adjacent homology (BAH)-plant homeodomain (PHD) and works as a histone mark reader (Narro-Diego et al. 2017; Li et al. 2020). Under HT stress, AGL67 and EBS bind *SOM* promoter and recruit H4-specific acetyltransferases (HATs) initiating H4K5 acetylation and opening the chromatin at the *SOM* locus altering ABA/GAs balance, subsequently inhibiting germination (Li et al. 2020). However, this controlling pathway can be counterbalanced by the POWERDRESS (PWR) epigenetic factor that negatively controls *SOM* expression promoting seed germination at high temperature in PWR overexpressing lines (Yang et al. 2019). To change the level of nucleosome histone H2A.Z incorporation and the histone acetylation state in the target loci, PWR interacts with the ABI3 and HDA proteins. The complex enhances the thermotolerance of seed germination by decreasing H4 acetylation and increasing nucleosome H2A.Z at the *SOM* locus, which limits *SOM* expression. In wild-type seeds, under HT, the PWR expression lowered, causing *SOM* to be released from the repression state (Yang et al. 2019), possibly via PIF1 binding.

Aside from direct ABA/GAs balance perturbation, the temperature increase was reported to promote ROS levels. Expressing a cotton (*Gossypium hirsutum*), which germination is temperature-sensitive, Heat Shock Protein *GhHSP24*.7 localized in the mitochondrial matrix in *A. thaliana* and tomato, ROS levels increased at warm condition between 20 and 36 °C, while at 44 °C (HT condition) germination was suppressed (Ma et al. 2019). Under warm condition HSP24.7 interacts with a CytC maturation protein Fc (CcmF) inhibiting the COX pathway through the block of the electron transport in mitochondria, and inducing ROS generation. This, led higher ROS levels and accelerate endosperm rupture to promote seed germination. When the COX pathway is reduced, the AOX pathway is activated and it lowers ROS levels (Ma et al. 2019). However the increase of ROS above a certain threshold causes thermoinhibition. This association was observed in rice germination, in which the HT induced thermoinhibition and ROS burst (Liu et al. 2019). This rapid increase can be explained mostly by diminishing of activity of all ROS-scavenging enzymes (for example, POD activity fell by 32.1%) and deduced from the lower expression of *OsCATb* in seeds exposed to HT. At the same time the expression of *OsNCED3*, a key gene in the ABA biosynthetic pathway, was enhanced (Liu et al. 2019). In the monocotyledon *Zephyranthes tubispatha* seed germination, the increase of ROS, mostly $O_2^{\cdot-}$, was directly associated with the induction of germination at the radicle pole (Acosta et al. 2022). However, this study demonstrates the presence of a thermoinhibition effect of the peroxidase activity and antioxidant capacity when *Z. tubispatha* seeds were imbibed at supraoptimal temperatures for longer periods. The HT treatment caused localized alterations in ROS homeostasis and enhancement of ABA metabolism to maintain thermoinhibition in *Z. tubispatha* seeds (Acosta et al. 2022). Aside from affecting scavenging system, the ROS burst at HT can be explained via ABA. In fact consequently to *SOM* expression ABA metabolism and signalling is promoted. It was recently shown that the PYRUVATE DECARBOXYLASE 1 (PDC1) responsible for fatty acid β-oxidation and consequent ROS accumulation in peroxisomes, was strongly induced by ABA during seed germination (Li et al. 2023). Seed germination of PDC1-deficiency, *pdc1* mutants, were higher, whereas those of PDC1-overexpression lines were lower, than those of wild-type plants in the presence of ABA demonstrating the association between ABA-PDC. While as the levels of free fatty acids were lower in *pdc1–1* mutants, but higher in the PDC1-overexpression lines, than WT plant provide evidence of PDC-ABA function (Li et al. 2023). This represents a new route to control germination via ABA-ROS. However, despite this germination control was demonstrated in *A. thaliana*, its involvement in the thermoinhibition by HT still remains to be proven.

Another system by which HT stress reduces seed germination is by lowering the mobilisation and utilisation efficiency of seed stores via RNS participation (Blum and Sinmena 1994). SNP, a NO donor compound, was shown to stimulate seed germination in *M. sativa, A. thaliana*, and *T. aestivum* by promoting α-amylase activity upon seed germination onset (Zhang et al. 2005; Parankusam et al. 2017). However, a study suggests that thermoinhibition of *A. thaliana* seed germination is caused by abnormal NO generation under heat stress since the toxicity of RNS may increase such conditions (Hossain et al. 2010). Furthermore, *A. thaliana* T-DNA insertion mutant *glb3* seeds exhibit significant HT sensitivity during germination at 32 °C due to their inability to eliminate heat-induced excess NO, whereas cPTIO, a NO scavenger, partially restored germination (Hossain et al. 2010). Likewise, via a NO-dependent manner, nitric oxide donors such as Fe(III)CN, SNP, and acidified nitrite limited the seed germination thermoinhibition effect in *L. sativa*, but cPTIO addition reversed their action (Deng and Song 2012). Moreover, under HT condition auxin signalling was shown to play a role, as overexpressing miR160, targeting ARF 10 and 16, enhanced seed germination and seedling vigour under HT (Lin et al. 2018). In addition, it was shown that miR160 gates HSPs under HT, which are crucial for the stabilisation of stressed-out proteins and the upkeep of precision in early protein folding (Lin et al. 2018). Therefore, miR160 induction has an impact on plant development and HSP gene expression, which increases plant thermotolerance. However, whether this effect can be observed in seed germination exposed to heat stress remains to be documented.

Collectively these findings suggest a cross-talk between ABA metabolisms/signalling (also mediated by auxin) and RONS that, at warm temperatures, promotes germination via ROS enhancement within the oxidative window level range, whereas at high temperatures, ABA signalling repression blocks activation of the ROS enzymatic scavenging system via ABI5, allowing ROS accumulation above the safe range. Thus during HT the ABA synthesis are restored via SOMNUS–JMJ20/JMJ22 de-repression through epigenetic modification at *SOM* locus by AGL67-EBS-HAT. Consequently to the rapid increase in ABA, it can trigger ROS burst in the peroxisomes, possibly, via ABF4-PDC1 module. This situation may be sustained temporarily by the imbibed seed as a thermoinhibition condition, but if extended, it may induce cell damage and seed death. It is currently unclear to what extent and how the seed may handle it during thermoinhibition, and further scientific research is needed to unravel it.

Conclusions and future perspectives

Seed germination behaviour in response to environmental stimuli represents a sophisticated process finely shaped by nature. Substantial research efforts have been carried out so far to understand this process and provide new solutions to face environmental challenges associated with global climate change threats. Scientific investigations in the last two decades have demonstrated that reactive oxygen and nitrogen species play a signalling role in the regulation of germination physiology, from seed development to radicle emergence. The increasing scientific community's attention to the role of reactive oxygen and nitrogen species in the regulation of the seed germination process in the last decades has provided new evidence to explain how these molecules contribute to the switch of dormancy release in many species. Overall, the latest advances attained so far provide new information for modelling ROS and RNS involvement in the perception of environmental cues. ROS are generated during seed maturation, but soon after imbibition, the oxygen is rapidly depleted, paving the way for the anaerobic phase when the RNS starts to accumulate. At this step, the enzymatic machinery for RONS homeostasis is activated, and the stimulation by specific environmental factors, such as light or alternating temperatures, drives the RONS signalling towards seed dormancy release and completion of germination. In fact, this gives rise to a first oxidation burst directed to seed reserves, chaperones, and CWRPs and probably stimulates DOG1 (mediated by RNS), or homologous proteins, to modulate ROS homeostasis. Afterwards, the cell could activate apoplast ROS production for signal transmission and exert ROS-mediated chromatin remodelling that determines a transcriptional programme change.

Throughout the many seed physiological states discussed here, the presence of RONS signalling provides an additional control level that allows the seed to fine-tune its response to external stimuli. This control occurs at various levels, influencing gene expression through direct gene regulation, epigenetic alterations, and post-translational modifications. They play a signalling role in all the processes here described. From promotion of ABA catabolism and GA-related genes to post-translational protein modifications and epigenetic control influencing ABA and GA signalling and seed germination fate. Moreover, the presence of enzymatic and non-enzymatic systems gate their activity to maintain homeostasis. Thus, the availability of this rich gamma of regulatory terminations enables rapid modification of the prevailing physiological pathway when conditions improve, providing a quick response to beneficial environmental changes.

Hitherto, the presence of a mainly distinct scientific literature for ROS and RNS function in seed germination physiology has limited the possibility of conceiving the reciprocal interplay and synergic actions within the molecular signalling. The new omics technologies nowadays available are providing precious, boundary-free information that needs to be integrated in order to fill this knowledge gap and to treat ROS and RNS as an interconnected signalling system mediating the various physiological states of the seed. Epigenetic control is certainly one of the research fields providing new interpretation scenarios to major questions and improving our understanding of wild populations in the environment. Furthermore, auxin interplay with the ABA/GAs ratio through epigenetic and RONS-mediated interactions is an exciting field for future integrative research. In this regard, how the circadian clock gates auxin-related gene responses and if this can be observed in fluctuating temperature-sensitive seed germination remains to be explored. Thus, future research efforts on epigenetics should be encouraged to try to disentangle the basis of the perception of a favourable season to germinate in a natural population. To this end, the role of other phytochromes and Phy-interacting-proteins should be taken into consideration. Moreover, another interesting field of research would be the understanding of microevolutive processes driven by epigenetics that have a role in response and tolerance to abiotic stresses such as drought, salinity, heat, or cold waves. Can we take advantage of new tolerant genotypes to be used for agricultural purposes? Within this path, other research efforts on thermomorphogenesis in seed and seedling maturation would be desirable, especially in crop species. This advancement would, in fact, enhance our understanding of how heat and cold waves can affect seed maturation and seedling establishment under the threat of global climate change.

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Declarations

Conflict of interest The author declares that there is no conflict of interest.

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