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Regulation of abscisic acid metabolism in relation to the dormancy and germination of cereal grains

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Abstract

Seed dormancy is of particular importance in the cultivation of cereals, as it directly affects the quality of crop yield. If the dormancy period is too short, this may lead to pre-harvest sprouting, whereas a dormancy period that is too long may cause uneven germination; both of these scenarios are associated with economic losses. Most enzymes engaged in the metabolism of abscisic acid (ABA) have been identified, and significant progress has been made in understanding the role of this phytohormone in the induction and maintenance of dormancy, mainly as a result of research conducted in *Arabidopsis*. Much less is known about the metabolism and function of ABA in cereal grains, especially in relation to dormancy and germination. This review focuses on the regulation of ABA metabolism in dormant and non-dormant cereal grains, in both the dry state and upon imbibition. Moreover, this review describes the influence of factors such as after-ripening, light, temperature, nitric oxide, and reactive oxygen species (ROS) on the dormancy and germination of cereal grains. These factors, with the exception of ROS, appear to affect the level of dormancy and germination of grains through regulation of ABA metabolism.

Keywords: 9-*cis*-epoxycarotenoid dioxygenase; ABA 8′-hydroxylase; abscisic acid; abscisic acid metabolism; dormancy; germination

Introduction

Dormancy is one of the most intensively studied aspects of seed biology. Primary dormancy of seeds is initiated during the seed maturation period, and it is characterized by the inability of intact viable seeds to germinate under favorable conditions [1–4]. The level of seed dormancy in many species of cultivated plants, cereal grains in particular, directly affects the quality of crop yield. Short and shallow dormancy, which is characteristic of numerous varieties of cereal species that are important for agriculture, may result in the harmful phenomenon of pre-harvest sprouting, in which the seeds gain the ability to germinate while they are still on the mother plant [5,6]. Wheat, rye, and triticale are particularly prone to this unfavorable process. In contrast, the dormancy of barley at harvest can be too strong, which disrupts the fast and uniform germination required in the malting process; as a result, the technological costs are increased due to the long after-ripening period (dry storage of mature seeds after harvest). Seed dormancy and germination are collectively controlled by numerous genes and environmental factors, particularly the prevailing conditions during seed development and storage after harvest [7]. The environmental factors that are of particular importance include light quality, temperature, soil moisture, and the length of the after-ripening period. Although the mechanisms associated with release and breaking of dormancy still remain largely unexplained, it is now generally accepted that abscisic acid (ABA) is the primary mediator of seed dormancy; however, other participating hormones, such as gibberellins, ethylene, and brassinosteroids, are also very important [6,8]. ABA plays a central role not only in the acquisition of primary dormancy during seed maturation but also in maintaining dormancy in imbibed seeds. Dormancy release is accompanied by a decrease in embryo ABA content and/or a decrease in the sensitivity of embryos to ABA in parallel with a simultaneous increase in gibberellin levels. However, gibberellins are increasingly considered to promote germination after dormancy release, rather than to participate in breaking seed dormancy [6,9–13].

Recently, there have been reports suggesting that the capacity of seeds to metabolize ABA, as a result of the regulation of synthesis and catabolism of this phytohormone, undergoes changes during the after-ripening period, and this may be one of the key factors that determines the breaking of cereal grain dormancy [14–16]. Additionally, factors such as the quality of light, temperature, and donors of nitric oxide (NO) present during imbibition of seeds appear to

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regulate the state of dormancy and germination via changes in ABA content and modifications in the expression of genes participating in its metabolism. Most information regarding the regulation of ABA metabolism and its effect on dormancy has been obtained from studies on *Arabidopsis*. However, due to the immense economic significance of cereals, the intensification of research that would enhance understanding of the mechanisms responsible for breaking dormancy in cereal grains becomes necessary. This paper presents a review of the available literature regarding identification of genes participating in the biosynthesis and catabolism of ABA in cereals as well as the literature exploring the effect of factors such as after-ripening, light, and temperature on ABA content and metabolism in dry and imbibed grains of cereals.

ABA metabolism

The ABA biosynthesis and catabolism pathways have been clarified to a large extent mainly through the genetic modifications that caused ABA deficiency or ABA accumulation in *Arabidopsis* plants (Fig. 1), and are summarized in many earlier and recent reviews [17–23]. However, only some of the potential genes participating in ABA biosynthesis and catabolism have been identified so far in cereals (Tab. 1). Although the expression products of these genes have not yet been characterized biochemically, the phenotypic analyses of mutants and transgenic plants, have proved that the potential genes encoding two ABA biosynthetic enzymes, zeaxanthin epoxidase (ZEP) and 9-*cis*-epoxycarotenoid dioxygenase (NCED), and an enzyme catalyzing the predominant ABA catabolic pathway, ABA 8′-hydroxylase (ABA8′OH), are involved in regulation of the seed ABA content and dormancy also in cereals (Tab. 2). In imbibed seed, the expression of these genes is also influenced by factors such as after-ripening, light quality, temperature, nitric oxide, and is described in subsequent sections.

Effect of after-ripening on ABA metabolism

In cereals, after-ripening does not alter ABA content or ABA metabolism in dry grains in most experiments; however, the situation changes diametrically when dormant and after-ripened grains undergo imbibition. Freshly harvested mature dry grains of wheat or barley that were still dormant (D grains) had ABA content similar to those of grains that underwent 3–4 months of after-ripening to release dormancy (AR grains, after-ripened grains). Although no differences

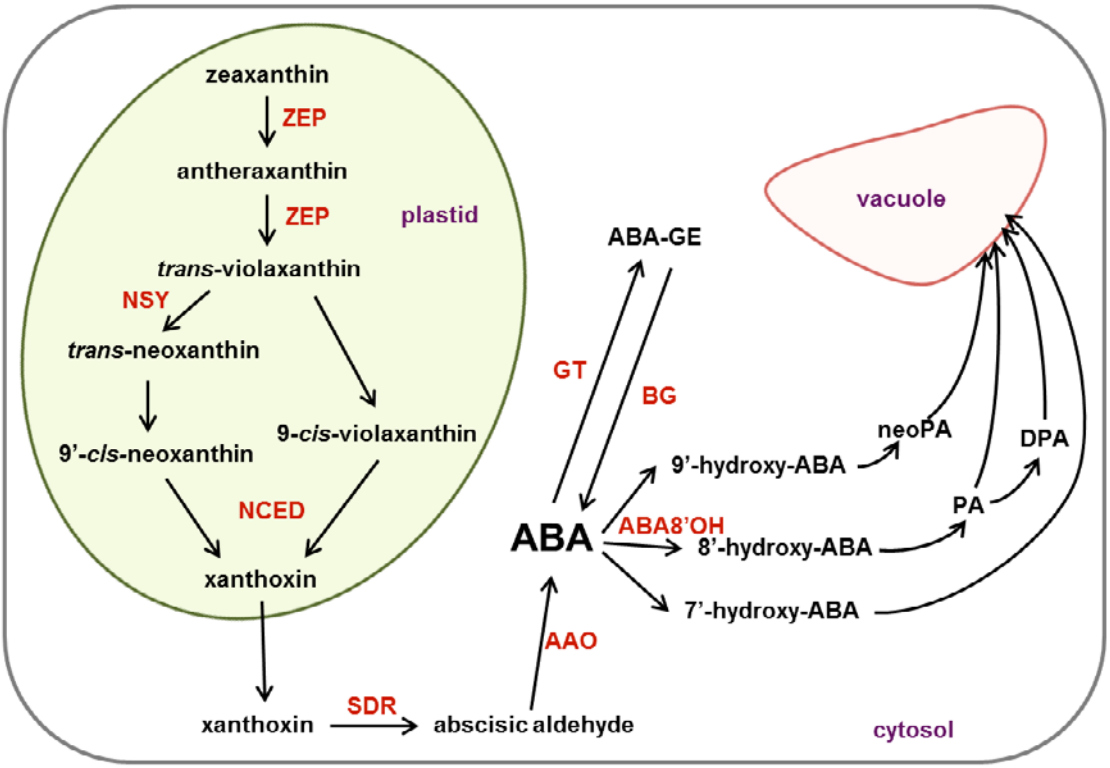

Fig. 1 Abscisic acid biosynthesis and inactivation pathways in higher plants. In plastids, the immediate precursor of ABA, zeaxanthin, is converted to trans-violaxanthin in reactions catalyzed by zeaxanthin epoxidase (ZEP). Trans-violaxanthin is then converted, to cis-violaxanthin by an unknown isomerase and to cis-neoxanthin in reaction catalyzed by neoxanthin synthase (NSY). Oxidative cleavage of cis-violaxanthin and cis-neoxanthin to xanthoxin is catalyzed by 9-*cis*-epoxycarotenoid dioxygenase (NCED). Xanthoxin is transported to the cytosol and is then converted into abscisic acid in reactions catalyzed by a short-chain dehydrogenase/reductase (SDR) and an abscisic aldehyde oxidase (AAO). ABA catabolism occurs by either hydroxylation or conjugation. The 8′-hydroxylation of ABA is catalyzed by ABA 8′-hydroxylase (ABA8′OH), a cytochrome P-450 monooxygenase. ABA hydroxylation may also take place at the C-7′ and C-9′ positions. ABA and its oxidative catabolites, phaseic acid (PA), neophaseic acid (neoPA), and dihydrophaseic acid (DPA) are the potential targets for conjugation. The conjugation of ABA with glucose is catalyzed by glucosyltransferases (GTs). ABA conjugation is reversible, and the hydrolysis of ABA glucosyl ester (ABA-GE) is catalyzed by β-glucosidases (BG).

Tab. 1 Potential genes participating in ABA synthesis and catabolism in cereals. The complete coding sequences are shown in bold.

Enzyme	Species	Gene	References
Zeaxanthin epoxidase	*Oryza sativa*	***OsABA1***	[63]
	Hordeum vulgare	***HvZEP1*** *HvZEP2* *HvZEP3* *HvZEP4* *HvZEP5*	[66]
	Triticum aestivum	*TaZEP1*	[67]
	Zea mays	*ZEP1* *ZEP2*	[68,69]
Nine-*cis*-epoxycarotenoid dioxygenase	*Zea mays*	***vp14/ZmNCED1*** ***ZmNCED2*** ***ZmNCED3*** ***ZmNCED4*** ***ZmNCED5*** ***ZmNCED6***	[69,70]
	Hordeum vulgare	***HvNCED1*** ***HvNCED2***	[14,25]
	Oryza sativa	***OsNCED1*** ***OsNCED2*** ***OsNCED3*** ***OsNCED4*** ***OsNCED5***	[32]
	Brachypodium distachyon	***BdNCED1*** ***BdNCED2***	[28]
	Triticum aestivum	***TaNCED1*** ***TaNCED2***	[16,65]
Short-chain dehydrogenase/ reductase	*Hordeum vulgare*	***HvSDR1*** ***HvSDR2*** *HvSDR3* *HvSDR4* *HvSDR5* *HvSDR6* *HvSDR7*	[66]
	Oryza sativa	*SDR1* *SDR2* *SDR3*	[71]
Abscisic aldehyde oxidase	*Hordeum vulgare*	*HvAO1* ***HvAO2*** ***HvAO3*** *HvAO4* *HvAO5a* *HvAO5b* *HvAO6* *HvAO7*	[66]
	Oryza sativa	*AAO1* *AAO2* *AAO3*	[71]
β-glucosidase	*Hordeum vulgare*	***HvBg1*** ***HvBg2*** ***HvBg3*** ***HvBg4*** *HvBg5* *HvBg6* ***HvBg7*** ***HvBg8*** ***HvBg9*** *HvBg10*	[66]
ABA 8′-hydroxylase	*Hordeum vulgare*	***HvCYP707A1/HvABA8′OH1*** ***HvABA8′OH2*** *HvABA8′OH3*	[14,25,66]
	Triticum aestivum	***TaCYP707A1/TaABA8′OH1*** *TaABA8′OH2*	[16,31,72]

Tab. 1 *(continued)*

Enzyme	Species	Gene	References
	Triticum monococcum	***TmABA8′OH2***	[73]
	Oryza sativa	***CYP707A5***	[74]
		CYP707A6/ OsCYP707A5	[32]
		OsCYP707A6	
		OsCYP707A7/ OsABA8ox1	[75]
		OsABA8ox2	
		OsABA8ox3	
	Zea mays	***ABAOx1a***	[68]
		ABAOx1b	
		ABAOx2	
		ABAOx3a	
		ABAOx3b	
	Brachypodium distachyon	***BdABA8′OH1***	[28]
		BdABA8′OH2	

Tab. 2 Mutants and transgenic lines in which the potential genes involved in ABA metabolism in cereal grains are silenced or overexpressed.

Source of the gene	Gene	Mutant/transgenic line	Phenotypic effects	References
Oryza sativa	*OsABA1(ZEP)*	*Oryza sativa Osaba1* mutant	A strong viviparous mutant with wilty phenotype, precocious germination.	[63]
Zea mays	*vp14 (NCED)*	*Zea mays vp 14* mutant	Lower ABA content in embryos of developing seeds, reduced seed dormancy.	[64]
Oryza sativa	*OsNCED3*	Overexpression of *OsNCED3* in *Arabidopsis thaliana*	Higher seed ABA content, delayed seed germination.	[33]
Triticum aestivum	*TaNCED1*	Overexpression of *TaNCED1* in *Nicotiana tabacum*	No obvious differences in germination rates between the transgenic and WT plants, however higher germination rate in transgenic lines under drought treatment.	[65]
Hordeum vulgare	*HvABA8′OH1*	*Hordeum vulgare HvABA8′OH1* RNAi transgenic lines	Higher ABA level in embryos of dry seeds, increased seed dormancy.	[15]
Triticum aestivum	*TaABA8′OH1*	A double *Triticum aestivum* mutant in *TaABA8′OH1* on the A and D genome	Higher ABA content in embryos of developing and mature seeds, lower germination rate.	[31]

in embryo ABA content were found between dry D and AR grains, the AR grains germinated much earlier [10,14–16,24]. In turn, significant differences in ABA levels were observed between D and AR embryos after the imbibition. During the early hours of imbibition, the ABA content rapidly decreased in both D and in AR grains; however, in the subsequent hours, the decrease was observed only in AR grains, whereas in D grains the ABA content stabilized or even increased in certain varieties [10,14–16,25]. Thus, the direct indicator of the depth of dormancy is not always the level of ABA in the grains before imbibition, but rather the varied capacity of grains to catabolize and synthesize ABA upon imbibition [26]. It is assumed that the decrease in ABA content observed during grain imbibition results from intensified catabolism of this phytohormone, as it was accompanied by an increase in phaseic acid (PA) content, an oxidative catabolite of ABA [10,13]. On the other hand, studies using norflurazon, which disturbs the synthesis of ABA, due to inhibition of carotenoid synthesis, revealed that de novo ABA synthesis is responsible, in some extent, for maintaining the dormancy of imbibed grains of deep dormant rice cultivar. It has been observed that dehusked grains of deep dormant, medium dormant and non-dormant rice cultivars, in the presence of norflurazon, showed similar germination rates [27]. However, inhibitor of ABA biosynthesis did not change germination rate of the intact grains of deep dormant

rice cultivar, which suggests that not only ABA biosynthesis during imbibition but also some compounds in the husk might affect seed dormancy [27].

Analysis of the expression of genes potentially encoding regulatory enzymes involved in ABA metabolism in correlation with ABA level and dormancy release during imbibition of monocots seeds was conducted for barley, *Brachypodium distachyon*, wheat, and rice [14–16,25,27,28]. In barley, an increase in *HvNCED1* and *HvNCED2* transcripts, either transitory or stabilizing after a few hours following the start of imbibition, was observed in embryos of both D and AR grains [14,15]. However, the expression profiles of these genes observed upon imbibition as a result of after-ripening differ and in the case of *HvNCED1* it also depends on the variety. In Proctor barley variety, the increase in the *HvNCED1* transcript level was more obvious in imbibed D grains than in AR grains, while there were no significant differences between D and AR grains during imbibition of Betzes variety [15]. Surprisingly, the *HvNCED2* transcript level was higher in the embryos of AR than D grains in all varieties, analyzed so far [14,15,25]. Thus, the expression of genes participating in the biosynthesis of ABA seems not to affect (or has a limited effect on) the differences in the ABA content between D and AR grains observed during imbibition of barley grains. Although after-ripening has ambiguous effect on the expression of genes participating in ABA biosynthesis, it always considerably increases the expression of *HvABA8′OH1*, the gene engaged in ABA catabolism. The expression of *HvABA8′OH1* increased in both AR and D grains within the first few hours after the start of imbibition and decreased thereafter; however, it was always considerably higher in the embryos of AR versus D grains [14,15,25]. The *HvABA8′OH2* expression level was very low during the imbibition of both D and AR grains. It is therefore suggested that the higher decrease in ABA content, observed in the embryos of AR versus D barley grains during first hours of imbibition is due to increased ABA catabolism, through increased expression of *HvABA8′OH1*. RNAi silencing of *HvABA8′OH1* expression in barley plants supported an involvement of *HvABA8′OH1* in dormancy release. Reduced expression of *HvABA8′OH1* in RNAi plants resulted in higher ABA content of embryos isolated from dry as well imbibed grains, and increased dormancy compared to grains of wild-type and null segregant plants [15]. However, silencing of *HvABA8′OH1* only slightly affected the after-ripening time compared to wild-type grains, which indicates that the loss of seed dormancy due to after-ripening is not solely caused by increased ABA catabolism; rather, it may also result from decreased sensitivity of embryos to ABA in AR grains [15,29]. In situ localization of *HvABA8′OH1* in imbibed D and AR grains of barley revealed that in the embryos of AR grains, expression was observed only in the coleorhiza (tissue surrounding the primary root of the cereal embryo), whereas in the embryos of D grains, the expression of this gene was undetectable [14]. The authors suggest that the coleorhiza plays a crucial role in the regulation of grain dormancy, and the control mechanism may be based on the fact that a high ABA level prevents the coleorhiza from weakening and growing, leading to a blockage of radicle elongation, whereas intensive ABA catabolism removes this limitation [14,30].

Changes in the expression level of the genes engaged in ABA metabolism during imbibition were analyzed with reference to changes in the content of this phytohormone also in the embryos of wheat grains. In imbibed grains of wheat, after-ripening not only increased the expression of genes engaged in ABA catabolism but also resulted in significant changes in the expression of genes participating in ABA biosynthesis [16]. During the first few hours of imbibition, a considerable increase in the *TaNCED1* transcript level was observed in the embryos of both D and AR grains. Subsequently, the expression of this gene in AR embryos rapidly decreased, while in the embryos of D grains, it was stably maintained at a relatively high level. *TaNCED2* expression did not demonstrate any clear correlation with the ABA content in the embryos of D grains, whereas in the embryos of AR grains, despite the initial relatively high level, it rapidly decreased after six hours following the start of imbibition [16]. The *TaABA8′OH1* transcript level increased in the embryos of both types of grains, although it increased to a significantly higher level in the embryos of AR grains. Similar to what was observed in imbibed barley grains, *TaABA8′OH2* expression remained at a very low and stable level in both in D and AR grains [16]. The above expression analysis conducted upon imbibition of AR and D grains of wild wheat as well as the examination of the double wheat mutant in the *TaABA8′OH1* gene demonstrates that research involving manipulation of the *TaABA8′OH1* gene may contribute to solving the problem of pre-harvest sprouting of cereal grains [15,31]. However, recent report indicate that AR mediated wheat dormancy release might be associated with changes in ABA signaling and sensitivity without affecting the metabolism of this phytohormone, since there were no significant differences in expression of ABA metabolic genes between D and AR wheat grains, even after imbibition [24]. Differences in the results obtained by different research groups may arise from analysis of the different varieties of wheat, various tissues (grains/separated embryos), as well as various conditions of after-ripening. However, it should be assumed that the resolution of dormancy by after-ripening is rather the result of both, changes in the metabolism of ABA and in the grain responsiveness to ABA. Perhaps, depending on the tissue and the conditions of after-ripening, one of these processes might be more or less substantial.

Similarly to the results obtained for other cereal species, which showed differences in the content of ABA in imbibed D and AR grains, in imbibed grains of deep dormant rice cultivar ABA accumulation had been observed, while in medium dormant and non-dormant rice cultivars increasing in ABA content had not been observed [27]. It is also suggested that genes engaged in the synthesis and catabolism of ABA in rice, *OsNCED3* and *OsCYP707A5*, respectively, participate in the regulation of seed dormancy and germination. *OsNCED3* expression in embryos of dry grains was obviously higher, and *OsCYP707A5* expression was much lower in the *PA64s* cultivar, which exhibited stronger dormancy than the *9311* cultivar with weaker dormancy [32]. Differences in the expression of potential regulatory genes of ABA metabolism reflected higher ABA content in the embryos of *PA64s* grains compared with those of *9311*

grains. In addition, *OsNCED3* overexpression in *Arabidopsis thaliana* resulted in increased accumulation of ABA and a delay in germination of transgenic seeds compared to wild-type seeds [33].

Effect of light on ABA metabolism

Light quality is a key environmental factor that regulates dormancy and germination of numerous species of plants, including cereals and other Poaceae [34,35]. White light, similarly to blue light, represses the germination of barley, *Lolium rigidum*, and *Brachypodium distachyon*, whereas red light stimulates the germination of *Brachypodium distachyon* but does not affect the dormancy of barley [15,28,36–38]. In barley, imbibition of primary dormant grains in the dark resulted in considerable dormancy release, similarly to the results of after-ripening, and in both cases it was associated with a significant, similar decrease in ABA content as well as an increase in PA in the embryos over the initial 12-h period of imbibition [10].

The expression of genes encoding enzymes engaged in ABA metabolism was examined to determine whether the decrease of the embryo ABA content, and the consequent dormancy release during imbibition in the dark, is due to the differential expression of these genes. It appeared that imbibition for 24 hours under white light or blue light strongly induced *HvNCED1* expression in the embryos of both D and AR barley grains, whereas after-ripening had a limited effect on expression of this gene. Expression of a gene encoding ABA 8′-hydroxylase, *HvABA8′OH1*, was strongly induced by AR; however, it was not affected by white or blue light [14,15]. It have been also shown, that longer incubation (more than 24 hours) of primary dormant barley grains at low temperature, under blue light inhibits germination, which was associated with an increase in expression of both *HvNCED1* and *HvNCED2*, while expression of *HvABA8′OH1* was not significantly changed [38]. These results indicate that the effect of white or blue light on maintaining dormancy of D barley grains are correlated with increase in embryo ABA content and is the result of intensified biosynthesis of this phytohormone rather than reduced ABA catabolism. However, this effect might also result from changed sensitivity of embryos to ABA in response to white or blue light [15,38]. In barley, blue light significantly increased embryo sensitivity to abscisic acid [38]. Such a situation may occur during germination of *Brachypodium distachyon* grains in white light [28]. Exposure to white light during imbibition had very little effect on the grain ABA concentration as well as on the expression of ABA metabolism genes, despite the fact that a reduction in the *BdNCED1* transcript level and an increase in *BdABA8′OH* were observed as a result of after-ripening [28]. The results indicate that after-ripening considerably affects ABA metabolism in *Brachypodium distachyon* grains, although the effect of white light on grain germination in this species cannot be explained by changes in ABA metabolism [28].

It have been suggested that inhibition of germination under blue light is cryptochrome (blue light photoreceptor) dependent, and this was recently confirmed by Barrero et al. [36]. RNAi silencing of cryptochrome 1 (CRY1) expression in barley resulted in increased mRNA level of *ABA8′OH1* in first few hours after imbibition under blue light and significant reduction of *NCED1* expression after 18 hours imbibition, which was consistent with lower embryo ABA content. These results indicate that Hv-CRY1 is engaged in blue light dependent maintenance of high ABA content in barley [36].

Effect of temperature on ABA metabolism

In cereals and other Poaceae growing in moderate climates, a germination temperature above 15–20°C gradually deepens the primary dormancy observed in mature grains [7]. For example, primary dormant grains of barley germinated easily at 20°C, while imbibition at 30°C resulted in almost complete suppression of grain germination [39,40]. Incubation of primary dormant grains at 30°C can even induce thermodormancy; i.e., after incubation of primary dormant grains at high temperatures the grains lose the ability to germinate at lower temperatures (e.g., 20°C) [40,41]. This phenomenon may be considered as an induction of secondary dormancy, and it was correlated with maintaining a relatively high embryo ABA content, increased sensitivity of the embryos to ABA, and changes in the expression of genes engaged in the metabolism of this phytohormone [42–45].

In barley, relatively high embryo ABA content during imbibition of primary dormant grains at 30°C and during imbibition of secondary dormant grains at 20°C, was correlated with the maintenance of a high *HvNCED1* transcript level. Instead, during imbibition of primary dormant grains at 20°C, the *HvNCED1* expression level was considerably lower in comparison to that in dry grains, which in turn was correlated with a sudden decrease in embryo ABA content [39,40]. *HvNCED2* expression in embryos was constantly decreasing during imbibition of primary dormant grains at 30°C; however, interestingly, it increased when grains with induced by 30°C secondary dormancy were imbibed at 20°C [40]. The *HvABA8′OH1* expression level did not change significantly in the embryos of primary dormant grains imbibed at 30°C; however, its expression increased in the embryos of grains after induction of secondary dormancy. Therefore, participation of this gene in the induction and regulation of secondary dormancy induced by temperature is rather dubious [40–44]. It seems that in barley, regulation of ABA synthesis during secondary dormancy takes place with the participation of *HvNCED1* and *HvNCED2*, while *HvABA8′OH1* can be considered as a key gene regulating primary dormancy.

H_2O_2 and ABA have antagonistic effects on germination

Reactive oxygen species (ROS) are constantly produced in plants, as by-products of many metabolic pathways. Beside their well-documented toxicity, they are considered as important signaling molecules in many processes related to plant growth, development, and stress responses. In

seed biology, they are believed to participate in regulation of dormancy, after-ripening, and germination [46–48]. In dry seeds, ROS are probably generated in non-enzymatic reactions such as lipid peroxidation or Amadori and Maillard reactions. In hydrated seeds, ROS may originate from mitochondria, peroxisomes, glyoxysomes and chloroplasts, or can be produced through the activity of NADPH oxidase, amine oxidase, peroxidase or cytochrome P450 [46,48]. The production of hydrogen peroxide, which is one of the reactive forms of oxygen, primarily with the participation of NADPH oxidase was observed during the early imbibition stages in the grains of wheat and barley [49,50].

Exogenously applied H_2O_2 promotes seed germination of many plant species, including cereals [51,52]. It has been demonstrated that H_2O_2 may stimulate germination by participating in programmed cell death of the aleurone layer in cereal grains, and its production is accelerated by gibberellins and inhibited by ABA [53,54]. Despite the fact that H_2O_2 stimulates germination, a slight increase in ABA content was observed in the embryos of barley treated with exogenous H_2O_2. This increase was associated with the induction of expression of genes participating in the biosynthesis of this phytohormone, *HvNCED1* and *HvNCED2*, whereas no changes in the expression level of the gene encoding ABA 8′-hydroxylase were observed [55]. It is assumed that the increase of ABA in embryos under the influence of exogenous H_2O_2 may be related to the role of this phytohormone in activation of the antioxidative system, thus preventing oxidative stress; this phenomenon was observed in vegetative tissues of *Cynodon dactylon* grass [55,56]. Moreover, germination in the presence of H_2O_2 with simultaneous high ABA content may be explained by changes in the balance between ABA and gibberellins [55].

Is NO involved in the regulation of ABA metabolism in cereal grains?

Treatment of seeds with a NO donor, such as sodium nitroprusside (SNP), results in reduction or release of the dormancy of *Arabidopsis thaliana*, barley and wheat seeds, whereas the use of c-PTIO [2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3 oxide], an NO scavenger, effectively promotes the maintenance of seed dormancy [16,57,58]. In imbibed *Arabidopsis thaliana* seeds, NO induces a rapid ABA decrease, which is correlated with an increase in the transcript level of one of the genes encoding ABA 8′-hydroxylase, *CYP707A2*. In addition, the germination rate of the *cyp707a2* mutant seeds was not elevated by SNP treatment, contrary to what was observed in the wild-type seeds [59,60]. These results indicate a significant role for the *CYP707A2* gene in the NO-mediated control of ABA levels during seed germination of *Arabidopsis* seeds; however, it has yet to be determined whether NO also affects seed dormancy in cereal grains through the regulation of genes participating in ABA metabolism.

Conclusions and perspectives

The length and depth of seed dormancy plays a key role in crop cultivation, thus affecting the economic aspect of agricultural production. Weak seed dormancy in plants such as cereals is important from an economic perspective, as it causes pre-harvest sprouting, which is a serious problem for growers in many regions of the world. Because of the scale and scope of pre-harvest sprouting, improving cereal resistance to this phenomenon has become one of the most difficult tasks that breeders are currently facing. Recently, there have been numerous reports exploring seed dormancy and germination at the molecular level. Many of these studies provided very promising results, which may be important for cultivation of plants in the future. However, most of the studies conducted thus far have been performed using a model plant, *Arabidopsis thaliana*, and the published data regarding cereals are still limited. Incomplete knowledge about the molecular mechanisms regulating dormancy and germination of cereals results primarily from difficulties in methodology and problems caused by the complexity of genome and polyploid nature of these plants [4]. Use of the wild grass *Brachypodium distachyon* in molecular studies seems to be promising, as it may become a diploid model of cereals. *Brachypodium distachyon*, apart from its mentioned diploidy, is also characterized by a small genome size and a short life cycle, which makes it a perfect model for studies at the molecular level [61,62]. Expanding our knowledge of mechanisms regulating dormancy and germination of cereal grains is therefore becoming one of the most important directions of research in the upcoming years.

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Authors' contributions

The following declarations about authors' contributions to the research have been made: created the concept, searched the literature and wrote the manuscript (contributed equally to the preparation of this article): JF, EZZ; critically reviewed the paper and proposed some useful suggestions: WB.

Competing interests

No competing interests have been declared.

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