Chapter 4

Seed Dormancy: The Complex Process Regulated by Abscisic Acid, Gibberellins, and Other Phytohormones that Makes Seed Germination Work

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http://dx.doi.org/10.5772/intechopen.68735

Abstract

Seed dormancy is one of the most important adaptive mechanisms in plants, which protects seeds from precocious germination in the presence of the inappropriate conditions for growth continuation. Numerous environmental and molecular signals regulate seed dormancy. Maintenance or release of seed dormancy is dependent on light, temperature, and water availability. Precise response of seeds to environmental factors is mediated by different phytohormonal pathways. ABA is considered as a main phytohormone regulating seed dormancy induction and maintenance. ABA- and GA-responsive components, ensure crosstalk between the GA and ABA pathways and enable seed response adequate to the environment. Phytohormonal regulation mechanism of seed dormancy is similar in dicot and monocot plants. Recently, it is suggested that other phytohormones, such as auxin, jasmonates, brassinosteroids, and ethylene, also take part in seed dormancy regulation. Auxin regulators, enhance ABA action and positively influence seed dormancy. However, jasmonates, brassinosteroids, and ethylene reduce seed dormancy level. Here, we describe recent advances in understanding the complex process of seed dormancy regulated by many phytohormonal pathways and their components. Seed dormancy studies can help obtain crop varieties producing seeds with the most desirable timing of germination.

Keywords: seed dormancy, germination, abscisic acid, gibberellic acid, phytohormone crosstalk

1. Introduction

Seed dormancy is defined as the inability of seeds to germinate under favorable conditions. The quiescent stage of seeds enables their survival during the adverse period for further seedling development. The high level of seed dormancy is considered as a negative trait due to germination retardation and reduction in the length of the growing season. On the other hand, low level of seed dormancy leads to preharvest sprouting (PHS) and yield loss. Thus, the varieties with medium value of seed dormancy are the most desirable [1–4]. Seed dormancy is considered as a quantitative trait under the control of the genetic and environmental signals. The primary dormancy is induced during seed maturation, and its expression occurs mainly in freshly harvested seeds in order to prevent precocious seed germination. After-ripening, which is dry seeds' storage at room temperature, can reduce primary seed dormancy [1]. The secondary dormancy can be induced in the presence of unfavorable conditions even in initially nondormant seeds [5–7]. Environmental conditions such as cold or heat temperature (stratification), light, nitrate (NO^{3-}), and nitric oxide (NO) can break the dormancy stage [1, 3, 6, 8, 9]. The level of seed dormancy depends on the season of a year. Deep dormancy is associated with sensing slow seasonal changes in winter. Shallow dormancy senses rapid condition changes in summer [10].

Induction and release of seed dormancy is mainly under the control of abscisic acid (ABA) and gibberellic acid (GA). ABA promotes seed dormancy and germination inhibition. Action of ABA is counteracted by GA, which promotes seed germination at appropriate time. The balance between ABA and GA is regulated by environmental conditions (light, temperature) and endogenous signals [4, 6, 7, 11]. Other phytohormones, such as auxin, brassinosteroids, and ethylene, modulate the interaction between ABA and GA in the regulation of seed dormancy [2, 4, 12].

Seed dormancy in cereals is established during seed development; however, the time of seed dormancy release can be different. Some varieties loose dormancy when the harvest maturity is reached. There are also varieties ready for germination after seed physiological maturity (fully developed, but not dried seeds). In cereals, such as barley (*Hordeum vulgare*), wheat (*Triticum aestivum*), and sorghum (*Sorghum bicolor*), the switch between physiological and harvest maturity is related to ABA decrease [7].

Here, we discuss the genetic and molecular bases of seed dormancy entrance and breaking in Arabidopsis and monocot plants, considering the action of components belonging to ABA, GA, and other phytohormone pathways. Additionally, the influence of environmental cues on ABA- and GA-related genes is described.

2. Role of ABA metabolism and signaling in maintaining seed dormancy

ABA is considered as a crucial phytohormone for seed dormancy establishment and maintenance. Many of the ABA metabolism- and signaling-related genes play a crucial role in the control of seed dormancy.

http://dx.doi.org/10.5772/intechopen.68735

2.1. ABA biosynthesis and catabolism activity in the regulation of seed dormancy

ABA produced in the embryo is fundamental for the promotion of seed dormancy. ABA synthesized in maternal tissues or ABA applied externally is not able to induce seed dormancy [13]. However, Kanno et al. [14] showed that ABA produced by maternal tissues can be transported to the embryo in order to take part in seed dormancy induction. ABA biosynthesis is catalyzed in several steps, and the rate-limiting reaction is mediated by carotenoid cleavage dioxygenase (NCED) [15, 16].

Many ABA biosynthesis genes are implicated in the regulation of seed dormancy in Arabidopsis. *NCED6* and *NCED9* are considered as the key ABA biosynthesis genes for induction of seed dormancy. They are expressed specifically during seed development. Double mutant *nced6*/*nced9* shows reduced seed dormancy [17]. Additionally, overexpression of *NCED6* results in an increase in the ABA content in seeds and in the inhibition of precocious germination [18]. *NCED5* is also described as a seed dormancy regulator (**Figure 1**) [19]. Other enzymes necessary for ABA biosynthesis and seed dormancy are encoded by *ABA deficient 2* (*ABA2*) and *abscisic aldehyde oxidase 3* (*AAO3*). *aba2-2* and *aao3* mutants show a reduced ABA content and similar disorders in seed dormancy as *nced6*/*nced9* (**Figure 1**) [14, 20]. ABA level in seeds depends also on degradation process. The catabolism of ABA is mediated by ABA8'hydroxylase encoded by *cytochrome P450* (*CYP707A*) genes [15, 16]. The activity of *CYP707A* genes is related to the loss of seed dormancy. *CYP707a* mutants show higher level of seed dormancy than the wild type (WT), especially the *CYP707A2*. The expression of *CYP707A2* is induced in seeds during imbibition. Furthermore, *CYP707A2* activity and after-ripening show a positive relationship. Therefore, *CYP707A2* is proposed to be responsible mainly for ABA degradation during release of seed dormancy and the germination process (**Figure 1**) [21, 22]. The other *CYP707A* genes, *CYP707A1* and *CYP707A3*, also take part in ABA catabolism in seeds; however, their role in breaking dormancy is minor [22, 23].

The regulation of ABA metabolism genes plays also a very important role in seed dormancy of monocot plants. In rice (*Oryza sativa*), the expression of *OsNCED2* is activated at the early or the late stage of seed development, in dormant and nondormant cultivars, respectively. The different times of ABA biosynthesis in seeds could result in a high or low dormancy level [24]. In barley, the expression pattern of *HvNCED* genes in developing grains shows the higher level of *HvNCED2* transcript in comparison to *HvNCED1* [25–27]. Moreover, *HvNCED2* activation in the field is independent of weather conditions, in contrary to *HvNCED1* and *HvABA8'OH1*/*HvCYP707A1*. On the other hand, the induction of *HvABA8'OH1* expression occurs in after-ripened seeds, but not in the dormant seeds during imbibition. Thus *HvNCED2* seems to play a more significant role in ABA biosynthesis and in the preventing of preharvest sprouting than *HvNCED1*. Furthermore, *HvABA8'OH1* activity mediates dormancy breaking [25].

Barley seed dormancy is associated with the presence of glumellae (lemma and palea). It was shown that dehulled grains have no induction of *HvNCED1*, *HvNCED2*, and *HvABA8'OH1* genes. The contrary reaction was observed in whole, dormant grains [28]. The induction of secondary dormancy in barley is also dependent on ABA metabolism genes. While *HvNCED1*

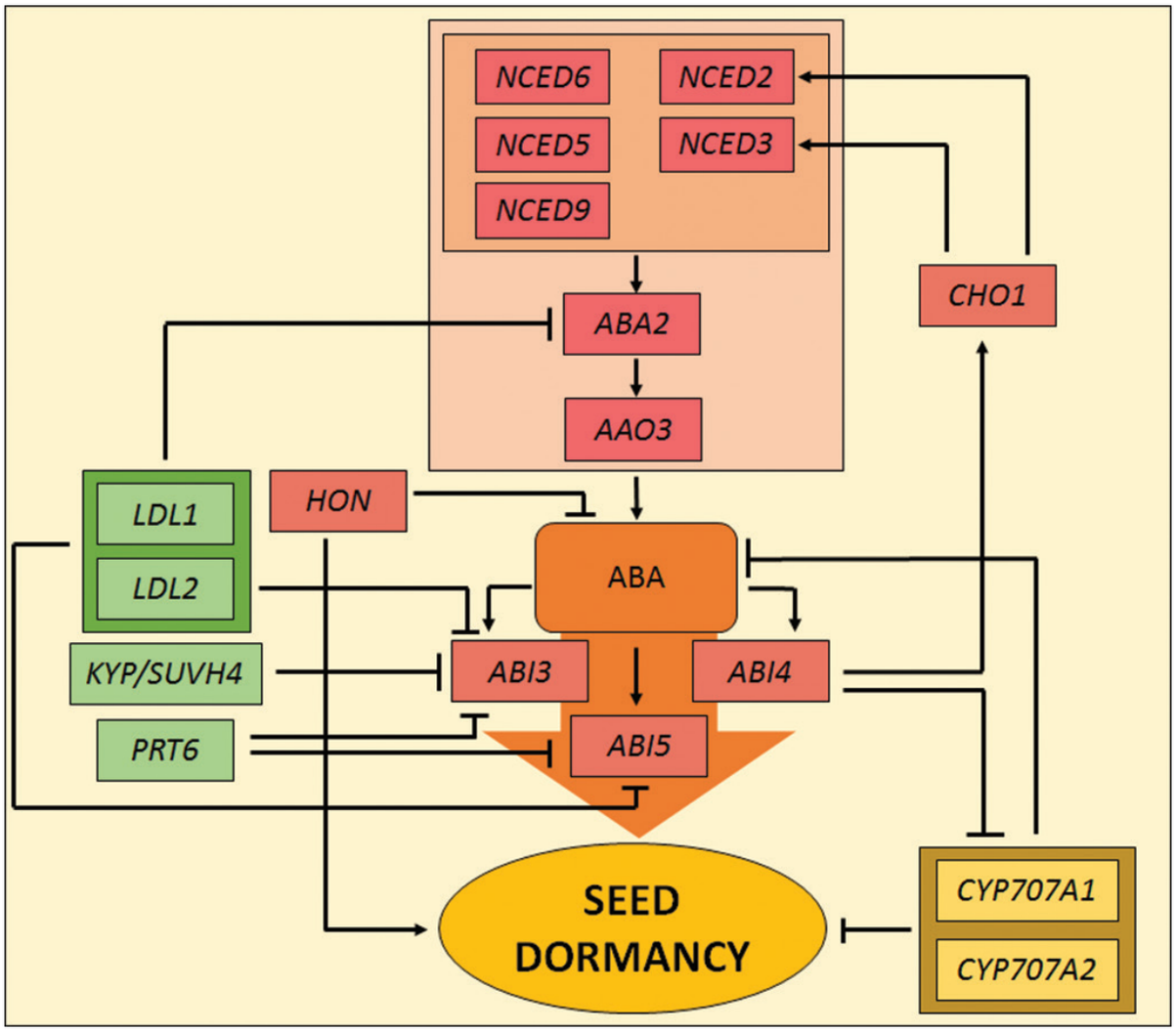

Figure 1. Probable function of ABA-related genes in seed dormancy promotion. Seed dormancy is positively regulated by ABA biosynthesis genes: *carotenoid cleavage dioxygenase 2 (NCED2)*, *NCED3*, *NCED5*, *NCED6*, *NCED9*, *ABA2 ABA deficient 2* (*ABA2*), and *abscisic aldehyde oxidase 3* (*AAO3*). Genes encoding ABA-related transcription factors, *ABA insensitive 3* (*ABI3*), *ABI4*, and *ABI5*, also promote seed dormancy. *HONSU* (*HON*) is a positive regulator of seed dormancy, but it represses ABA signaling. ABA catabolism genes, *cytochrome P450* (*CYP707A1*) and *CYP707A2*, are responsible for seed dormancy release. Other regulators like, *lysinespecific demethylase 1* (*LDL1*), *LDL2*, *kryptonite/SU(VAR)3-9 homolog 4* (*KYP/SUVH4*), *proteolysis6 (PRT6)* negatively regulates the ABA pathway and seed dormancy. ABI4 modulates the expression of ABA biosynthesis genes (*NCED2*, *NCED3*) probably via *CHOTTO1* (*CHO1*) and ABA catabolism genes (*CYP707A1*, *CYP707A2*).

shows higher activation at 30°C, the transfer of grains to 20°C is associated with *HvNCED2* and *HvABA8'OH1* induction. Probably, the expression of secondary dormancy depends mostly on *HvNCED2*, whereas the promotion of *HvABA8'OH1* may be a response to immediate increase in the ABA level in seeds [26]. *HvNCED2* is also mostly expressed during hypoxia-related seed dormancy [29]. The after-ripening process is associated with the increased expression of *HvABA8'OH1* in coleorhizae [30–32]. The barley lines with silenced *HvABA8'OH1* expression show the increased ABA accumulation and seed dormancy level [31]. In *Brachypodium*

distachyon, the higher expression of *BdNCED1* was observed in dormant grains in comparison to after-ripened grains. Contrarily, after ripening promoted the induction of *BdABA8'OH-1* at the second day of imbibition. Probably, *BdABA8'OH-1* plays a prominent role in the after-ripening process [33].

2.2. Regulation of seed dormancy via ABA signaling components

The core ABA signaling is mediated by pyrabactin resistance proteins/PYR-like proteins/regulatory components of ABA receptor (PYR/PYL/RCAR), phosphatase 2C (PP2C), SNF1-related protein kinase 2 (SnRK2), and abscisic acid responsive elements-binding factor (AREB) basic leucine zipper (bZIP) transcription factors [34–36]. In Arabidopsis, ABA signaling genes are also implicated in seed dormancy regulation. *ABA insensitive 1* (*ABI1*) encodes PP2C phosphatase, which acts as the negative regulator of ABA signaling [37]. *abi1* was described as the mutant with decreased seed dormancy level and better germination in the presence of ABA [38]. The other PP2C phosphatase, HONSU (HON), also represses ABA signaling, specifically in seeds. However, its role in seed dormancy is inconclusive. *HON* expression is associated with both, dormancy establishment and release (**Figure 1**) [39]. *ABI* genes, such as *ABI3*, *ABI4*, and *ABI5* encode crucial ABA-dependent transcription factors expressed in seeds. Expression of *ABI3, ABI4*, and *ABI5* is higher in dormant seeds than in seeds with reduced seed dormancy level (**Figure 1**) [40–42]. Among *ABI* genes, *ABI3* is the most substantial for seed dormancy establishment. *ABI3* is expressed in developing seeds. It regulates the accumulation of chlorophyll, anthocyanins, and storage proteins together with two other seed-related regulators, *FUSCA3* (*FUS3*) and *leafy cotyledon 1* (*LEC1*) [43, 44]. *abi3* mutant shows no seed dormancy, and immature seeds are able to germinate [45]. ABI3 is under direct regulation of WRKY DNA-binding protein 41 (WRKY41) during the establishment of primary seed dormancy. WRKY41 binds directly to *ABI3* promoter and induces its expression [46].

ABI4 is another ABA-activated transcription factor with APETALA 2 (AP2) domain, expressed in seeds. It takes part in the regulation of abiotic stress responses and different aspects of plant development [47]. *abi4* mutant germinates faster than the wild type without stratification. The expression analysis showed decreased activation of *NCED2* and *NCED3* in *abi4* seeds. Moreover, ABI4 binds to *CYP707A1* and *CYP707A2* promoters and represses their expression. It indicates the important role of ABI4 in seed dormancy maintenance (**Figure 1**) [41]. It is worth noting that *ABI4*, *NCED2*, and *NCED6* are under positive regulation of a common ABA-dependent regulator, myeloblastosis 96 (MYB96). The activation of *NCED2* and *NCED6* ensures ABA biosynthesis and seed dormancy promotion, whereas *ABI4* induction inhibits lipid breakdown and further seed germination [48]. One of the downstream target of ABI4 is *CHO1* (*CHOTTO 1*), encoding a transcription factor with double AP2 domain. *CHO1* acts also as a positive regulator of primary seed dormancy (**Figure 1**) [49, 50]. ABI5 is a bZIP transcription factor regulating ABA signaling in seeds [42]. The role of *ABI5* in seed dormancy regulation is not clear. *abi5* mutant shows a normal dormancy level [51]. However, many studies described below showed a distinct relationship between *ABI5* and seed dormancy [40, 52–54].

In monocot plants, the activation of ABA signaling is also associated with seed dormancy. The maize (*Zea mays*) ortholog of *ABI3*, the *viviparous 1* (*VP1*), is a crucial regulator of seed dormancy. *vp1* mutant shows premature embryo germination (vivipary) and reduced ABA sensitivity [55]. The overexpression of maize *VP1* in wheat induces increased seed dormancy and prevents preharvest sprouting [56]. Some rice varieties produce truncated versions of *OsVP1* transcript. There is a relation between incorrect transcripts' amount and preharvest sprouting. This phenomenon is associated with developmental stage: immature embryos accumulate a higher number of truncated transcripts than mature embryos [57]. Another gene, the *seed dormancy 4* (*SDR4*) is a rice quantitative trait locus (QTL) responsible for seed dormancy promotion in ABA-dependent manner. The *japonica* varieties have reduced dormancy and possess only SDR4-n allele, whereas more dormant varieties of *indica* type include SDR4-n and SDR4-k alleles. OsVP1 was shown to positively promote *SDR4* expression [58]. Other ABA-related genes also take part in seed dormancy maintenance. Expression analysis of sorghum grains with various dormancy level identified a set of differentially regulated ABA signaling genes. A dormant inbred line of sorghum showed increased expression of *SbABA-responsive protein kinase* (*SbPKABA1.1*), *SbABI1*, *SbVP1*, *SbABI4*, and *SbABI5* during grain imbibition. However, no induction of these genes in a nondormant inbred line was observed [59]. In barley, dormancy expression is associated with increased induction of *HvPKABA*, *HvVP1*, and *HvABI5* [28]. Probably, the general ABA-related mechanism of seed dormancy induction is similar in dicots and monocots.

2.3. Environmental cues and epigenetic modifications in the regulation of the ABA pathway

The expression of Arabidopsis ABA metabolism and signaling genes is regulated through environmental factors. The red (R) light pulse irradiation applied to the far-red (FR) light pulse pretreated, dark-imbibed seeds inhibits and induces the expression of *NCED6* and *CYP707A2*, respectively. It suggests that the ABA metabolism genes are under the control of PHYB (phytochrome B), which regulates germination in response to FR and R pulse light [60]. On the other hand, the blue light has a negative impact on the germination of dormant grains in cereals. The blue light–associated secondary dormancy induces *HvNCED1* and *HvNCED2* and weakly reduces *HvABA8'OH-1* expression in grains [61]. The activation of *HvNCED1* is under the regulation of phytochrome photoreceptor, cryptochrome 1 (HvCRY1). It indicates that ABA biosynthesis and catabolism take part in blue light–dependent regulation of seed dormancy [62, 63]. The temperature and NO also exert an impact on ABA pathway in Arabidopsis seeds. The high temperature promotes the expression of ABA biosynthesis genes in imbibed seeds, whereas NO positively regulates ABA signaling during seed dormancy breaking [52, 64]. NO action may be associated with N-end rule pathway, leading to degradation of proteins with destabilizing amino acid residues. NO and oxygen are sensed by N-end rule pathway with the participation of many protein regulators [65]. The components of N-end rule pathway, proteolysis 6 (PRT6) and arginyl-tRNA:protein arginyltransferase (ATE), regulate after-ripening, inhibit ABA signaling, and finally promote seed germination. PRT6 is E3 ligase promoting protein degradation via 26S proteasome. Some PRT6 substrates belong to the ABA pathway. As a result, ABA signaling is inhibited, and the activation of ABI3 and ABI5 is detained (**Figure 1**) [52].

http://dx.doi.org/10.5772/intechopen.68735

The ABA metabolism and signaling genes are also regulated at epigenetic level during the establishment of seed dormancy. Kryptonite/SU(VAR) 3-9 homolog 4 (KYP/SUVH4) is responsible for histone H3 lysine 9 dimethylation. Repression of *ABI3* by KYP/SUVH4 is required to release seed dormancy (**Figure 1**) [66]. Moreover, the expression of *ABA2*, *ABI3*, and *ABI5* is downregulated through the action of two histone demethylases, lysinespecific demethylases 1 and 2 (LDL1 and LDL2). Thus, the activity of LDL1 and LDL2 ensures decrease in primary seed dormancy via negative regulation of ABA response (**Figure 1**) [67].

3. Gibberellins-mediated control of seed dormancy release and germination

A high level of gibberellins (GA) is needed for the counteraction of ABA activity in seeds. GA promotes seed dormancy release and radical protrusion during seed germination. The activation of GA-responsive genes induces cell wall–remodeling enzymes, such as endo-β-mannase, xyloglucan endotransglycolase, expansin, and β-1,3-mannase. Their activity leads to the weakening of the embryo-surrounding layers. Additionally, GA ensures the high-growth potential of the embryo [68].

3.1. Role of GA metabolism in seed dormancy break

GA biosynthesis takes place mainly in the radicle of the embryo, which in turn ensures germination progression [69]. Arabidopsis seed germination is associated with the regulation of GA metabolism genes. The highest expression of GA-biosynthesis genes, *gibberellin 3-oxidase 1* (*GA3ox1*), *GA20ox3*, and *ENT-kaurene oxidase 1* (*KO1*), was shown during the first 8 hours of imbibition [68]. The crucial role of GA in the breaking of seed dormancy was presented using a *ga requiring 1* (*ga1*) mutant in GA biosynthesis gene, *CPP synthase* (*CPS*). Interestingly, *ga1* capacity to germinate was renewed after removing testa and endosperm, without exogenous GA application. It was concluded that dormancy release and germination promotion was dependent on GA-ABA balance in the embryo and the embryo-surrounding layers of the seed [70]. The environmental factors, such as light and temperature, interact with GA biosynthesis and signaling, which in turn promotes seed germination. The expression of *GA3ox1* is activated by red light and cold. Additionally, the low temperature determines the *GA3ox1* expression localization in the embryonic axis and the aleurone layer [71, 72]. Contrarily, low temperature represses the expression of GA catabolism gene, *GA2ox2* [71]. Two bHLH (basic helix-loop-helix) transcription factors, spatula (SPT) and phytochrome interacting factor 3-like 5 (PIL5), regulate seed germination after cold stratification, including GA biosynthesis pathway. SPT represses germination before stratification, whereas PIL5 also acts as an inhibitor of germination, but after cold stratification in darkness. Both, SPT and PIL5, act through negative regulation of *GA3ox1* and *GA3ox2* [73]. Another transcription factor, DOF affecting germination1 (DAG1) was found to mediate PIL5 negative regulation of *GA3ox1*. PIL5 promotes the expression of *DAG1* in darkness. Furthermore, DAG1 protein binds directly to *GA3ox1* promoter, inhibits its expression, and blocks germination [74]. Contrary to cold, high

temperature represses the expression of *GA20ox1*, *GA20ox2*, *GA20ox3*, *GA3ox1*, and *GA3ox2* during seed imbibition and blocks germination [64]. Similar to ABA-related genes, the expression of GA metabolism genes is regulated seasonally. *GA3ox2* activation is associated with summer, whereas *GA2ox2* is expressed in winter [10].

In barley and wheat, the expression of GA biosynthesis genes occurs during imbibition of nondormant seeds [31, 72]. The rapid increase in *HvGA3ox2* involved in GA biosynthesis was observed in the after-ripened grains during imbibition. The high expression level of *HvGA3ox2* is associated with *HvGA2ox2* activation [31]. The hypoxia-related secondary dormancy in barley is associated with the modulation of the GA pathway. Low oxygen concentration causes induction of *HvGA2ox3* and repression of *HvGA3ox1* and *HvGA20ox1* in dormant grains. The activity of GA-responsive gene, *HvEXPANSIN11* (*HvEXPA11*), is also repressed [29]. Similar reaction was observed during seed dormancy imposed by blue light. The negative regulation of the GA pathway occurred through the promotion of *HvGA2ox3* and *HvGA2ox5* and the repression of *HvGA3ox2* [61]. The relationship between the expression of GA metabolism genes and the induction of secondary dormancy at 30°C was also shown; however, the particular expression pattern depended on the embryo water content in barley. The embryo with high-water content (1.60–1.87 g H_2O g^{-1} DW) shows the higher expression of GA catabolism and signaling genes than the embryo with lower water content (0.45 g H_2O g^{-1} DW) [75].

GA metabolism genes are involved in seed dormancy regulation in other monocot species. In wheat, after-ripening causes induction of *GA20ox1* and *GA3ox2* [72]. The regulation of expression of GA synthesis and catabolism genes is more complex in rice. *OsGA20ox1*, *OsGA2ox5*, and *OsGA2ox6* expression pattern showed higher variability in a nondormant than in a dormant variety during seed development. Furthermore, the dormant variety accumulated less-active GA in seeds in comparison to the nondormant variety. It resulted in appropriate dormancy phenotype of analyzed cultivars [24]. Similar analysis was conducted in terms of immature grains of sorghum inbred lines with contrasting dormancy level. Higher expression of *SbGA20ox1* and *SbGA20ox3* was observed for a less-dormant line, whereas a strong induction of *SbGA2ox1* and *SbGA2ox3* was found in the line with higher dormancy [76]. To summarize, a proper regulation of GA biosynthesis and catabolism genes ensures the regulation of seed dormancy dependent on environmental conditions, both in dicot and monocot plants.

3.2. Action of GA signaling components in seed dormancy regulation

In Arabidopsis, GA signaling is mediated by GA insensitive dwarf1 (GID1) receptor. Overexpression of *GID1* promotes the release of seed dormancy. The impact of cold stratification and after ripening on *GID1* expression showed that imbibition at 4°C promoted expression of three *GID1* transcript forms: *GID1a*, *GID1b*, and *GID1c,* while after-ripening storage induced only *GID1b*. Thus, both mechanisms of seed dormancy loss seem to be regulated differently [77]. In sorghum, exogenous GA represses *SbGID1* in immature grains. It suggests the role of SbGID1 in negative feedback regulation of the GA pathway [76]. The sleepy1 (SLY1) is a F-box protein which enables 26S proteasome-mediated degradation of

DELLA proteins in the presence of active GA [78]. DELLA proteins act as repressors of GA signaling. *sly1* mutant shows reduced germination, even after the application of exogenous GA. It indicates that SLY1 is the crucial regulator of seed germination [79]. Another mutant related to GA signaling, *cts* (*comatose*), maintains seed dormancy even after stratification or after ripening. CTS functions as a peroxisomal ABC transporter and seems to be crucial for seed dormancy release [80]. The proper regulation of DELLA proteins is crucial for seed germination. Simultaneous deactivation of *repressor of GA* (*RGA*), *RGA-like 1* (*RGL1*), *RGL2*, and *gibberellic acid insensitive* (*GAI*) results in insensitivity to GA and light during germination. It indicates that DELLA proteins integrate environmental cues into GA signaling [81]. Among them, RGL2 seems to play a more important role in seed germination than other DELLAs. Thermoinhibition of seed germination demands activity of *RGL2,* which suggests its crucial role in the regulation of GA signaling in seeds [64]. Moreover, *GID1* transcripts are under control of RGL2 during cold stratification and after ripening. The RGL2 can promote or inhibit *GID1* expression according to a particular *GID1* transcript form and surrounding conditions during dormancy loss [77]. *RGL2* activity associates with the regulation of shallow dormancy. Its expression is promoted during summer time [10]. Another negative regulator of GA signaling is *spindly* (*SPY*). The *spy* mutant demands the lower amount of GA to break seed dormancy and continue germination. *SPY* encodes *O*-linked *N*-acetylglucosamine (*O*-GlcNAc) transferase which probably glycosylates components of GA signaling. SPY acts upstream of RGA through the modulation of its activity through *O*-GlcNAc modification [82].

3.3. The role of essential seed dormancy regulator, DOG1, in GA pathway regulation

Delay of germination 1 (*DOG1*) is considered as the crucial, positive regulator of seed dormancy with unknown function. Expression of *DOG1* is seed specific, and *dog1* mutant shows disturbed seed dormancy in Arabidopsis [83]. Similar to ABA-related genes, *DOG1* is under negative epigenetic regulation mediated by KYP/SUVH4, LDL1, and LDL2, which as a result reduces primary dormancy [66, 67]. *DOG1* expression is related to deep dormancy during winter season [10]. Recently, the role of DOG1 in temperature-dependent coat dormancy through GA metabolism regulation was shown. DOG1 differently regulates the expression of GA biosynthesis genes, such as *GA3ox1* and *GA20ox*, at 18 and 24°C. This leads to the inhibition of genes encoding cell wall remodeling enzymes: *expansin 2* (*EXPA2*), *EXPA9*, *xyloglucan endo-transglycosylase 19* (*XTH19*) but only at 24°C. Therefore, DOG1 regulates the appropriate time of germination according to environment temperature [84].

4. ABA and GA crosstalk during seed dormancy

The seed dormancy maintenance or release and further promotion of the seed germination process are regulated by ABA and GA balance [1, 2, 12]. ABA-mediated repression of GA biosynthesis enables the positive regulation of seed dormancy [60]. Many molecular interactions between ABA and GA pathways enable precise regulation of seed response according to environmental conditions.

4.1. Activity of ABA and GA metabolism genes ensures the ABA-GA interaction

There is the relationship between ABA and GA biosynthesis in Arabidopsis. ABA-deficient mutant, *aba2-2*, shows the higher expression of *GA3ox1* and *GA3ox2* than the wild type [60, 64]. Interestingly, *AAO3* and *ABA2* expression were detected in a radicle, whereas *GA3ox2* in hypocotyl. It suggests that the places of ABA and GA biosynthesis are different in seeds [60]. *aba2-2* shows also the reduced expression of *SPY* during seed imbibition in the presence of high temperature. Therefore, the negative regulator of GA signaling, *SPY*, is under the positive action of ABA (**Figure 2**) [64]. NCED9 negatively influences GA biosynthesis. The application of paclobutrazol, GA biosynthesis inhibitor, causes better germination of *nced9* than the wild type. It is an evidence that ABA biosynthesis modulates GA pathway in seeds [85].

4.2. ABA-GA crosstalk depends on ABI transcription factors and DELLA proteins in seeds

ABA and GA signaling components are involved in the ABA-GA crosstalk in Arabidopsis seeds. ABI4 exerts action on GA biosynthesis genes. In *abi4* mutant, the expression of *GA3*,

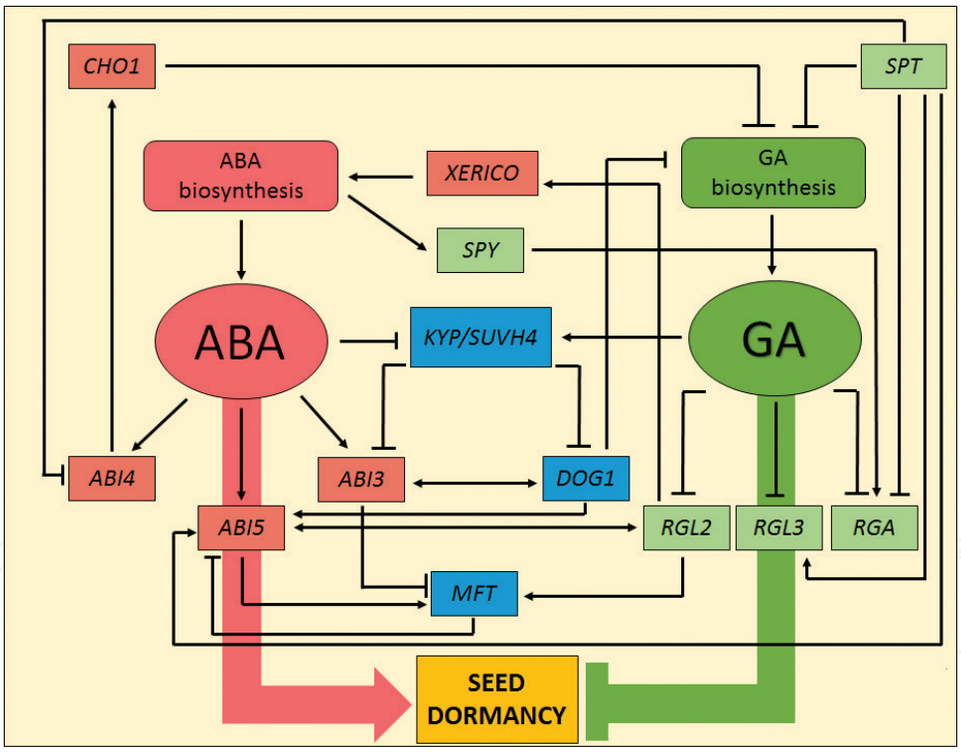

Figure 2. Model for seed dormancy regulation by ABA-GA crosstalk. ABA-mediated promotion of seed dormancy and GA-related release of seed dormancy are possible through ABA-GA interactions. The seed dormancy regulator, *mother of FT and TFL 1* (*MFT1*), is promoted by ABA insensitive 5 (ABI5) and RGA-like 2 (RGL2), but ABI3 downregulates its expression. ABI5 and RGL2 positively regulate reciprocal expression. RGL2 also promotes *XERICO* and ABA biosynthesis. Repressor of GA biosynthesis, delay of germination 1 (DOG1), activates *ABI3* and *ABI5*. GA biosynthesis is inhibited by spatula (SPT) and ABI4 via chotto1 (CHO1) activity. SPT also represses the expression of *ABI4* and *RGA repressor of GA (RGA)* but promotes *ABI5* and *RGL3*. *Spindly* (*SPY*), a negative regulator of GA signaling, is promoted by ABA. Modulation of ABA and GA responses also includes an epigenetic regulator, kryptonite/SU(VAR)3-9 homolog 4 (KYP/SUVH4).

http://dx.doi.org/10.5772/intechopen.68735

GA3ox1, *GA20ox1*, *GA20ox2*, *GA20ox3*, *ENT-kaurenoic acid oxydase 1* (*KAO1*), and *KAO2* genes is upregulated in imbibed seeds. The *abi4* seeds also accumulate more GA [41]. *CHO1* acts downstream of *ABI4* in seed dormancy regulation, and its activity leads to the repression of GA biosynthesis genes (**Figure 2**) [49]. RGL2 seems to be one of the most important GA-related component acting in ABA-GA crosstalk in seeds. The positive interaction between RGL2 and ABA biosynthesis through *XERICO* was described (**Figure 2**) [86]. Moreover, *RGL2* and *ABI5* positively regulate reciprocal expression during seed germination (**Figure 2**) [87]. Recently, the cooperation of NF-YC transcription factor with RGL2 was identified during the regulation of *ABI5* expression in seeds [88].

Coat-mediated dormancy is also related to RGL2 action. RGL2 promotes ABA biosynthesis in endosperm, then coat-derived ABA is released to the embryo, where it ensures the expression of *ABI5* and in consequence germination inhibition [40]. ABA and GA signaling genes are under the control of the negative regulator of GA biosynthesis, SPATULA (SPT): *ABI5* and *RGL3* are promoted, whereas *ABI4* and *RGA* are repressed by SPT. It suggests the universal role of SPT in seed dormancy induction and release through complex influence on ABA and GA pathways (**Figure 2**) [89]. Induction of secondary dormancy through seed imbibition in darkness at 25°C is associated with changes in GA content and signaling. However, this process also includes positive action of RGL2 on *ABI5*. It suggests that ABA-GA crosstalk is also important for entrance into secondary dormancy [90]. Epigenetic modifications are implicated in ABA-GA interaction. *KYP*/*SUVH4* is promoted by GA and repressed by ABA. Regarding the role of KYP/SUVH4 in the regulation of *ABI3* and *DOG1* expression, this histone methylotransferase is also a part of ABA-GA interaction (**Figure 2**) [66].

The interaction between ABI transcription factors and GA catabolism genes was described in monocot plants. In sorghum, SbABI4 and SbABI5 are able to bind with coupling element 1 (CE1) and ABA responsive element (ABRE), respectively, that are present in *SbGA2ox3* promoter and subsequently promote its expression. ABA-dependent activation of GA catabolism can promote seed dormancy in grains [53].

4.3. Seed dormancy regulators, MFT and DOG1, are a part of the ABA-GA crosstalk

Mother of FT and TFL 1 (MFT) is one of the crucial regulators of seed dormancy enabling the interaction between ABA and GA signaling in Arabidopsis. MFT negatively regulates ABA signaling and seed dormancy, which in turn leads to germination. Its expression is repressed by ABI3 but promoted by RGL2. MFT also ensures a negative feedback loop in ABA signaling through the repression of *ABI5* transcription, whereas ABI5 induces *MFT* expression (**Figure 2**) [91]. However, the role of MFT is not completely clear. The wheat ortholog of MFT, TaMFT, acts in an opposite way in seed dormancy regulation. The increased expression of *TaMFT* is related to the lower germination index, and *TaMFT* overexpression causes inhibition of precocious germination of isolated embryos. Low temperature during seed development is associated with a higher level of dormancy. Under such environmental conditions, the activation of *TaMFT* was observed during seed development [92]. Probably, the precise role of MFT in seed dormancy is different in dicots and monocots.

The role of DOG1, the GA-related regulator of seed dormancy, was also described in ABA signaling in seeds. *ABI5* is positively promoted by DOG1, which in turn leads to the regulation of many *late embryogenesis abundant* (*LEA*) and *heat shock protein* (*HSP*) genes. Moreover, the double-mutant *abi3-1/dog1-1* shows the lower sensitivity to ABA than *abi3-1*, and in control condition, it produces mature dry green seeds. It suggests the positive relationship between *DOG1* and *ABI3; therefore,* DOG1 may be responsible for ABA-GA interactions in seeds (**Figure 2**) [54].

5. The emerging role of auxin, jasmonates, brassinosteroids, and ethylene in seed dormancy regulation

ABA and GA are not the only phytohormonal regulators of seed dormancy establishment and release. Their action is modulated by other phytohormones, such as auxin, jasmonates (JA), brassinosteroids (BR), and ethylene.

5.1. Action of auxin pathway components in seeds

Auxin promotes seed dormancy release and germination. Constitutive induction of auxin biosynthesis in *iaaM-OX* line inhibits precocious germination in Arabidopsis. Contrarily, the switched off activity of *auxin response factor 10* (*ARF10*) and *ARF16*, auxin-dependent transcription factors, in *arf10/arf16* double mutant, causes faster precocious germination than in the wild type. The role of auxin in the control of seed dormancy includes the action of *ABI3*. The double mutants, *abi3-1/iaaM-OX* and *abi3-1/99999mARF16* (line resistant to miR160), show the reduced dormancy phenotype. Therefore, the activation of auxin signaling promotes *ARF10* and *ARF16*, which in turn induces *ABI3* and seed dormancy (**Table 1**) [93]. Analysis of after-ripened wheat grains showed increased expression of *TaIAA-alanine resistant 3* (*TaIAR3*) encoding hydrolase releasing IAA from conjugates. It was observed in parallel with the higher IAA level in seeds during imbibition. Probably, seed dormancy release may be associated with the increased auxin content in seeds of monocot plants. Furthermore, *TaAuxin-resistant 1* (*TaAXR1*), *TaUbiquitin-related protein 1* (*TaRUB1*), and *TaARF2* were also upregulated in after-ripened wheat grains. TaAXR1 is associated with AUX/IAA proteasome-mediated degradation, whereas TaRUB1 is related to ubiquitin action. The higher expression of *TaAXR1* and *TaRUB1* can exert a negative impact on auxin signaling (**Table 1**) [72].

5.2. Dual role of jasmonic acid in seed dormancy regulation

The role of JA (Jasmonic Acid) in seed dormancy is ambiguous. The increased JA content was detected in nondormant Arabidopsis seeds. Probably, the decrease of JA content during imbibition in nondormant seeds is associated with germination promotion [94]. Application of JA precursor, 12-oxo-phytodienoic acid (OPDA) promotes the expression of *ABA1*, *ABI5*, and *RGL2* in after-ripened seeds and inhibits seed germination. OPDA also exerts a regulatory action on the crucial seed dormancy component, *MFT* [95]. The opposite effect of JA on seed

Phytohormonal pathway	Regulator	Function	Role in seed dormancy regulation	References
Auxin	ARF10 ARF16	Auxin-related transcription factors	Promotion of *ABI3* expression and seed dormancy	[93]
	TaIAR3 TaARF2 TaAXR1 TaRUB1	Releasing auxin from conjugates Auxin-related transcription factor Aux/IAA proteasome degradation-associated protein Ubiquitin pathway-associated protein	Seed dormancy release	[93]
Jasmonic Acid	TaAOS TaKAT3 TaLOX5	JA biosynthesis	Seed dormancy release	[93]
	TaAOC TaAOS	JA biosynthesis	Seed dormancy release via repression of *TaNCED1* and *TaNCED2*	[96] [97]
Brassinosteroids	TaBIN2	Negative regulator of BR signaling with kinase activity	Seed dormancy promotion via ABI5 activation	[99, 100]
	TaDET2 TaDWF4 TaBSK2	BR biosynthesis Positive regulator of BR signaling with kinase activity	Seed dormancy release	[100]
Ethylene	ACO ETR1 EIN2	Ethylene biosynthesis Ethylene receptors	Seed dormancy release Seed dormancy release through the regulation of ABA metabolism genes	[101] [104]

Note: auxin response factor (ARF), IAA-alanine resistant 3 (IAR3), auxin-resistabt 1 (AXR1), ubiquitin-related protein 1 (RUB1), allene oxide synthase (AOS), 3-ketoacyl coenzyme A (KAT3), lipoxygenase 5 (LOX5), allene oxide cyclase (AOC), brassinosteroid insensitive 2 (BIN2), de-etiolated 2 (DET2), DWARF 4 (DWF4), br signaling kinase 2 (BSK2), 1-aminocyclopropane-1-carboxylic acid oxidase (ACO), ethylene triple response 1 (ETR1), ethylene insensitive 2 (EIN2).

Table 1. Regulators of auxin, jasmonic acid, brassinosteroid, and ethylene pathways in seed dormancy promotion or release.

dormancy exists in wheat. JA was shown to reduce the promoting effect of blue light on seed dormancy in a nitrate-dependent way [96]. Additionally, after ripening promotes expression of JA biosynthesis genes: *TaAllene oxide synthase* (*TaAOS*), *Ta3-ketoacyl coenzyme A* (*TaKAT3*) and *TaLipoxygenase 5* (*TaLOX5*) in wheat grains. However, the level of JA decreases during imbibition (**Table 1**) [72]. The cold-induced release of seed is associated with the increase in JA endogenous content. Cold stratification process promotes the expression of *TaAOS* and *TaAllene oxide cyclase* (*TaAOC*). Furthermore, JA positively regulates *TaNCED1* and *TaNCED2* activity and thus enables seed germination through ABA biosynthesis repression in wheat (**Table 1**) [96, 97].

5.3. Brassinosteroids promote seed germination via repression of ABA signaling

Brassinosteroids (BR) act opposite to ABA signaling in the regulation of seed dormancy and germination. In Arabidopsis, the crucial regulator of seed dormancy, *MFT*, is under BR regulation in seeds. Therefore, MFT acts as a mediator of ABA and BR pathways in seeds [98]. Brassinosteroid insensitive 2 (BIN2) is a GSK3-like kinase playing a negative role in BR signaling, and furthermore, it ensures the communication with ABA signaling. BIN2 interacts with ABI5 and phosphorylates it, which in turn promotes ABI5 activity during seed germination [99]. *TaBIN2* activity is downregulated in the after-ripened wheat seeds (**Table 1**) [100]. Expression analysis also showed the induction of genes encoding the positive components of BR pathway: *TaDE-etiolated 2* (*TaDET2*), *TaDWARF 4* (*TaDWF4*), and *TaBR signaling kinase 2* (*TaBSK2*) in wheat after-ripened grains. *TaDET2* and *TaDWF4* encode crucial enzymes for BR biosynthesis, whereas *TaBSK2* promotes BR signaling (**Table 1**) [100].

5.4. Ethylene represses ABA accumulation and promotes seed dormancy release

Ethylene (ET) is positively related to seed dormancy release and germination promotion. In Arabidopsis, the expression of ET biosynthesis gene, *1-aminocyclopropane-1-carboxylic acid oxidase* (*ACO*), is associated with imbibition; however, cold stratification reduces its expression (**Table 1**) [101]. Ethylene receptors, ethylene triple response 1 (ETR1) and ethylene insensitive 2 (EIN2) play a role in seed dormancy regulation. *etr1* and *ein2* mutants show the increased level of r seed dormancy associated with the increased level of seed ABA content [102, 103]. The higher expression of *NCED3* and lower activation of *CYP707A2* were observed in *ein2* and *etr1* mutants, respectively, compared to the wild type. It suggests a negative role of ethylene in the modulation of ABA pathway in seeds (**Table 1**) [104]. In wheat, after-ripened grains express *TaACO* at a higher level than in dormant grains. Thus, the increased ET content in seeds is associated with dormancy loss also in wheat [100]. The role of ethylene in seed dormancy regulation includes regulation at epigenetic level. *SIN3-like 1* (SNL1) and SNL2 reduce acetylation level of histone 3 lysine 9/18 and histone 3 lysine 14. The double mutant *snl1 snl2* shows reduced seed dormancy together with the increased expression of ethylene biosynthesis genes (*ACO1*, *ACO4*) and ABA catabolism genes (*CYP707A1*, *CYP707A2*). Therefore, SNL1 and SNL2 promote seed dormancy through simultaneous modulation of ethylene and ABA content in seeds [105].

6. Conclusions

Proper regulation of seed dormancy is crucial for appropriate timing of germination. Many environmental factors, including light and temperature, exert action on switch from dormancy to germination stage. Their action is mediated by phytohormones: ABA and GA. ABA is a master player for the entrance to and the establishment of seed dormancy. Many ABA-related genes are necessary for the quiescent stage of seeds. Contrary to ABA, GA-mediated pathway promotes germination under favorable conditions. Similar mechanism of seed dormancy regulation exists in monocot plants. The seed response is dependent on the ABA and GA balance.

The ABA-GA crosstalk ensures the precise seed response according to developmental stage, environmental factors, and seasons. Many components of the ABA and GA pathway, for example ABI3, ABI4, ABI5, RGL2, MFT, and DOG1, are responsible for the proper regulation of seed dormancy. Additionally, auxin, jasmonic acid, brassinosteroids, and ethylene modulate the ABA pathway in seeds. Furthermore, epigenetic control of dormancy-related components also occurs. Therefore, seed dormancy regulation appears to be a very elaborate process. In monocot plants, a part of the seed dormancy regulatory mechanism acts in a different manner. Action of MFT and JA pathway seems to be reverse in comparison to dicot plants. A better understanding of precise phytohormonal regulation of seed response of cereals can help in obtaining new varieties with the appropriate seed dormancy level.

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