

Review Article

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Seed Dormancy at Molecular Level

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ABSTRACT

The seed containing an embryo, a miniature of new plant, structurally and physiologically equipped to sustain the growing seedling until it establish as new plant. Some traits are acquired during evolution for capacity to survive under unfavourable condition. One of such trait is 'dormancy', an intrinsic/extrinsic block to germination. The ABA and GA are involved in induction and release of dormancy and it also showed the involvement and complex interaction with other plant hormones such as ethylene, brassinosteroids and reactive oxygen species. The use of transcriptomic and proteomic analysis refined the variation and similarities of the pathways affected by dormancy and germination. It provides a basis for studying the role of individual genes in these pathways. Advances in molecular technology, especially next-generation sequencing, will make it possible to study non model species in depth at the molecular level. Genetic and molecular mechanisms like silencing and over expression help us to induce and release of seed dormancy in many agricultural crop species which enables to farmers to take up sowing at any time.

Keywords

Seed dormancy,
Seed germination,
ABA and GA.

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Introduction

Dormancy is a genetically inherited trait whose intensity is modified by environment during seed development. Seed dormancy is a condition, where failure of an intact, viable seed to complete germination under favourable conditions (Bewley, 1997). A seed will germinate in an appropriate environmental condition only after it has lost dormancy. Dormancy and germination are complex traits that are controlled by a large number of genes, which are affected by both developmental and environmental factors. Seed dormancy is an important component of plant fitness (Donohue *et al.*, 2005; Huang *et al.*, 2010) that causes a delay of germination until the arrival of a favourable growth

season. Too low seed dormancy levels can lead to germination before the start of a favourable growth season, risking seedling mortality. In contrast, high seed dormancy levels delay germination and reduce the length of the growing season (Donohue *et al.*, 2010). Several of the tissues comprising a seed contribute to its final dormancy level. The roles of the plant hormones abscisic acid and gibberellin in the regulation of dormancy and germination have long been recognized. The last decade saw the identification of several additional factors that influence dormancy including dormancy specific genes, chromatin factors and non-enzymatic processes.

Site of dormancy

Dormancy resides in seeds in the two distinct sites. 1. Exogenous dormancy (Embryo coverings) is caused by physical factor: testa, pericarp, perisperm, and endosperm. 2. Endogenous dormancy: Embryo itself, caused by physiological and bio chemical factors.

Advantages of seed dormancy

As a means of survival to escape adverse or extreme conditions. (Frost, freezing cold temp, prolonged wet or dry periods, desert or drought conditions not fit for survival). As an escape mechanism to ensure distribution and survival in time and space. It is required in certain crops as it prevents vivipary (Groundnut, Maize, Wheat, Soybean *etc*). Dormant seeds will have longevity (longer shelf life).

Disadvantages of seed dormancy

Causes practical problems for immediate sowings in crops from freshly harvested seeds (Sunflower, Groundnut) *etc*. Gives rise to uneven field emergence, plant population and yield *etc*. Contributes to the occurrence of volunteer plants, weed plants, unwanted crop seeds, leads to field problems. Problem for seed analysis for germination. Seed dormancy breaking treatments are to be imposed.

This review gives overall mechanisms that control seed dormancy at the molecular level. Here, the induction and release of dormancy will be discussed along with some case studies in different plant species.

Induction of Seed Dormancy

The induction of seed dormancy is controlled by a diverse group of regulators that act at various levels and that also show different degrees of specificity. It includes different

levels, seed maturation, hormonal action, dormancy and chromatin regulation.

Seed maturation regulators

The stage in seed development and maturation at which dormancy develops varies between species (Bewley and Black, 1994). Seed dormancy can be initiated in mature non-dormant seeds by environmental conditions that do not favor germination (*e.g.* high temperature and anoxia). Seed development comprises the two major phase's embryogenesis and seed maturation. Seed dormancy is induced during the seed maturation phase simultaneously with the accumulation of storage compounds, the acquisition of desiccation tolerance and, finally, the quiescence of metabolic activity. Concerted actions of 4 transcription factors, *viz.*, Abscisic Acid Insensitive 3 (ABI3), Fusca 3 (FUS3), Leafy Cotyledon 1 (LEC1) and LEC2, play a central role in the regulation of seed maturation and the phase transition from embryo to seedling. Several factors, which control seed dormancy indirectly by regulating ABI3, FUS3, LEC1 and LEC2, have recently been identified. Maize *Viviparous 8 (VP8)* has been shown to regulate these transcription factors and a mutation in this gene causes a viviparous seed phenotype with pleiotropic developmental changes (Suzuki *et al.*, 2008). All 4 *abi3*, *lec1*, *lec2* and *fus3* mutants are severely affected in seed maturation and share some common phenotypes, such as decreased dormancy at maturation (Raz *et al.*, 2001). It has been shown that ABI3, FUS3, LEC1 and LEC2 interact as a network to control various aspects of seed maturation (Fig. 1). LEC1 was shown to regulate the expression of ABI3 and FUS3 (Kagaya *et al.*, 2005), FUS3 and LEC2 have been shown to act in a partially redundant manner to control gene expression of seed specific proteins, and LEC2 was shown to locally regulate FUS3 expression in

regions of the cotyledons (Kroj *et al.*, 2003). The indication of redundant regulation within this group of genes was recently shown (To *et al.*, 2006). It was found that one of the major roles of LEC2 was to up-regulate FUS3 and ABI3. The *lec2* mutation leads to a dramatic decrease in ABI3 and FUS3 expression, and most *lec2* phenotypes can be rescued by ABI3 or FUS3 constitutive expression. LEC1 positively regulates ABI3 and FUS3 in the cotyledons (To *et al.*, 2006).

Hormonal regulation

Several lines of evidence have established that abscisic acid (ABA) induces dormancy during embryo maturation (reviewed in Feurtado and Kermode 2007, Finch-Savage, 2006, Kermode, 2005). In particular, the balance between the levels of ABA and GA hormones and their respective signalling pathways are important in regulating both induction and maintenance of dormancy, and promotion of germination. A recent epoch-making finding concerning ABA was the identification of PYR/PYL/RCAR ABA receptors (Ma *et al.*, 2009; Park *et al.*, 2009). 14 members of this protein family in *Arabidopsis* function redundantly in mediating the ABA response by interacting with type 2C protein phosphatase (PP2C) negative regulators and antagonizing their action. However, it is not known yet whether any of these PYR/PYL/RCAR proteins are specifically involved in ABA signalling during the seed maturation stage. The PP2Cs ABA-Insensitive 1 (ABI1) and ABI2 were originally identified in ABA-insensitive mutant screen. The *abi1-1* and *abi2-1* mutants show reduced dormancy phenotypes and are caused by dominant-negative mutations that lead to abi proteins that are unable to bind to the ABA receptors (Ma *et al.*, 2009; Park *et al.*, 2009). In the presence of ABA, these abi-PP2Cs remain active and repress downstream ABA-activated protein kinases belonging to

the SNF1-related protein kinase subfamily 2 (SnRK2). Three *Arabidopsis* SnRK2s (SnRK2.2, SnRK2.3 and SnRK2.6) have been shown to act redundantly in the transmission of an ABA signal during seed development and dormancy induction (reviewed by Nambara *et al.*, 2010). The triple mutant of these kinases is nearly blind to ABA and exhibits abnormal seed development, produces ABA-insensitive green seeds similar to severe alleles of *abi3* and germinates early under high humidity conditions (Nakashima *et al.*, 2009).

Major targets of these kinases have been shown to be a group of bZIP-type transcription factors including ABI5 and Abscisic acid Responsive Elements binding Protein 3 (AREB3). Surprisingly, mutants of these transcription factors generally do not show strong dormancy phenotypes. Antagonistic to ABA action, GA, ethylene and other hormones have been shown to promote germination. Environmental signals such as light and temperature during imbibition and germination are integrated into GA biosynthesis and signalling by transcription factors like Phytochrome Interacting Factor 3-Like 5 (PIL5) and Spatula (SPT). These observations further reinforce the importance of the coordinated interaction of various hormones in the regulation of dormancy and germination.

Seed dormancy is an important agronomic trait in cereals. Liu *et al.*, 2014 correlated seed dormancy phenotypes with abscisic acid (ABA) and gibberellin (GA) metabolism gene expression profiles and phytohormone levels during seed development and imbibition. A time course analysis of ABA and GA content during seed development showed that N22 had a high ABA level at early and middle seed developmental stages, while at late developmental stage it declined to the level of ZH11, G46B had the lowest ABA content

during seed development though at early developmental stage its ABA level was close to that of ZH11, and its ABA/GA ratio peaked at late developmental stage that was at the same level of ZH11.

Analysis of gene expression in imbibed barley grains shows that the different ABA metabolism genes are targeted by white light and after ripening. Of the genes examined, white light promotes the expression of an ABA biosynthetic gene, *HvNCED1*, in embryos. Enzyme linked immunosorbent assays (ELISA) showed that dormant grains imbibed under white light have higher embryo ABA content than grains imbibed in the dark. After ripening has no effect on expression of ABA biosynthesis genes, but promotes expression of an ABA catabolism gene (*HvABA8'OH1*), a GA biosynthetic gene (*HvGA3ox2*), and a GA catabolic gene (*HvGA2ox3*) following imbibition (Gubler *et al.*, 2008). Chono *et al.*, 2013 cloned the wheat ABA 8'-hydroxyase gene which was highly expressed during seed development (*TaABA8'OH1*) and screened for mutations that lead to reduced ABA catabolism.

Peach genomic sequencing was accomplished in 2013 (Verde *et al.*, 2013); however, the functions of most of the genes are not clear. Some few genes relating to ABA synthesis and catabolism have been identified. Endo's method (2014) to deduce the *NCEDs*, *CYP707As*, *AAOs*, *ZEP*, *SDR1* genes in the peach genome sequence (Endo *et al.*, 2014).

Seed dormancy-specific genes

Only some few genes regulating dormancy have been identified that are not directly involved in hormone metabolism or seed maturation. Two examples are *Histone Monoubiquitination1 (HUB1)* and *Reduced Dormancy 2 (RDO2)* in *Arabidopsis*. The 1st cloned dormancy QTL in *Arabidopsis*, *Delay*

of Germination 1 (DOG1), encodes a protein of unknown function (Bentsink *et al.*, 2006). The absence of dormancy with no obvious pleiotropic phenotypes in the *dog1* mutant indicates that *DOG1* is a main player specific for the induction of seed dormancy; *dog1* mutants are completely nondormant and do not show any obvious pleiotropic phenotypes, apart from a reduced seed longevity. The *DOG1* protein belongs to a small family in *Arabidopsis* that was recently shown to be conserved in other plant species. *DOG1* homologs have been found in the *Arabidopsis* related species *Lepidium sativum* and *Brassica rapa* (Graeber *et al.*, 2010) and in the monocot rice (*Oryza sativa*; Sugimoto *et al.*, 2010)

Extensive QTL mapping has been performed for dormancy/pre-harvest sprouting traits in crop species. Recently, *Seed dormancy 4 (Sdr4)* has been identified as one of the major determinants for dormancy in rice. *Sdr4* is localized in the nucleus and that it affects the expression of several *DOG1-LIKE* genes (rice genes similar to *Arabidopsis DOG1*). Its mechanism of action is still not understood because *Sdr4* encodes a novel protein with unknown function (Sugimoto *et al.*, 2010). Characterization of the function of these novel factors and the molecular identification of additional dormancy QTLs will provide us with more solution on the mechanisms that control the induction and maintenance of dormancy. The molecular mechanisms of seed dormancy are not well understood. *Delay of Germination1 (DOG1)* was recently identified as a major regulator of dormancy in *Arabidopsis thaliana*. Nakabayashi *et al.*, in 2012 showed that the *DOG1* protein accumulates during seed maturation and remains stable throughout seed storage and imbibition. The levels of *DOG1* protein in newly harvested seeds highly correlate with dormancy. The *DOG1* protein becomes modified during after ripening, and its levels

in stored seeds do not correlate with germination potential.

Genes involved in the ABA signal transduction pathway also influence seed dormancy. In particular, members of the Protein Phosphatase 2C (PP2C) family were identified as components of ABA signaling from work with the *aba insensitive1-1 (abi1-1)* and *abi2-1 mutants* (Koornneef *et al.*, 1984; Rodriguez *et al.*, 1998). In a mutagenesis screen of a highly dormant *Arabidopsis* line, the *reduced dormancy5 (rdo5)* mutant was isolated based on its strongly reduced seed dormancy. The cloning of RDO5 showed that it encodes a PP2C phosphatase. Several PP2C phosphatases belonging to clade A are involved in abscisic acid signaling and control seed dormancy (Xiang *et al.*, 2014).

Regulation of dormancy at chromatin level

Epigenetics

Study of changes in organisms caused by modification of gene expression rather than alteration of the genetic code itself. Change in phenotype without a change in genotype.

Molecular basis of epigenetics: Histone modifications

Is a covalent post-translational modification (PTM) to histone proteins which includes acetylation, methylation, phosphorylation and ubiquitylation. The PTMs made to histones can impact gene expression by altering chromatin structure the organization of chromatin influences gene expression and important for all developmental processes in the plant, including seed dormancy and bud dormancy (Cooke *et al.*, 2012).

Histone monoubiquitination 1 and reduced

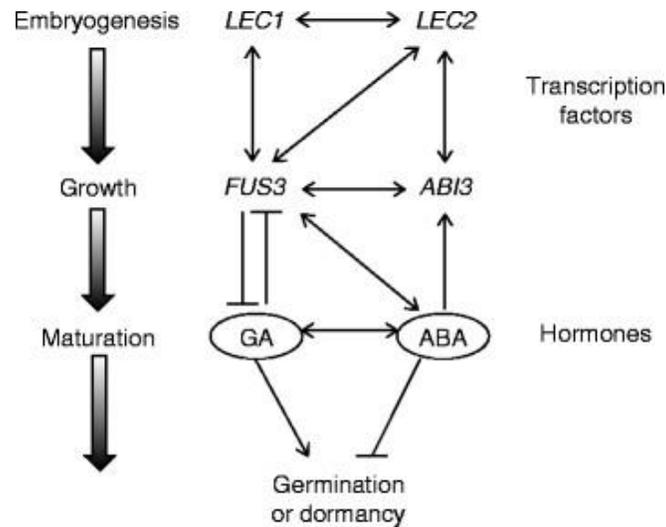
Dormancy 2 have been identified in a screen for reduced dormancy mutants (Peeters *et al.*, 2002). Both proteins probably influence seed dormancy by regulating transcription elongation of seed dormancy genes during maturation (Liu *et al.*, 2011). Two other chromatin factors, SIN3-LIKE1 (SNL1) and SNL2, positively regulate seed dormancy by modifying the ABA ethylene antagonism through histone acetylation (Wang *et al.*, 2013). A role for histone acetylation in seed dormancy was recently demonstrated by the reduced dormancy phenotype of the histone deacetylase9 mutant (Van Zanten *et al.*, 2014).

The *Early Flowering in Short Days (EFS)* gene has been selected as a phase transition regulator during seed germination in a transcriptional network modelling study (Bassel *et al.*, 2011). *EFS* codes for a histone H3 methyltransferase involved in histone H3 lysine 4 trimethylation (H3K4me3), it is a transcription activating histone mark. The *KRYPTONITE (KYP)/SUVH4* and *SUVH5* genes encode histone methyltransferases that mediate H3K9 dimethylation (Jackson *et al.*, 2002). The *kyp-2* and *suvh5* mutants show enhanced dormancy and increased expression of several dormancy genes, including *DOG1* and *ABI3* (Zheng *et al.*, 2012).

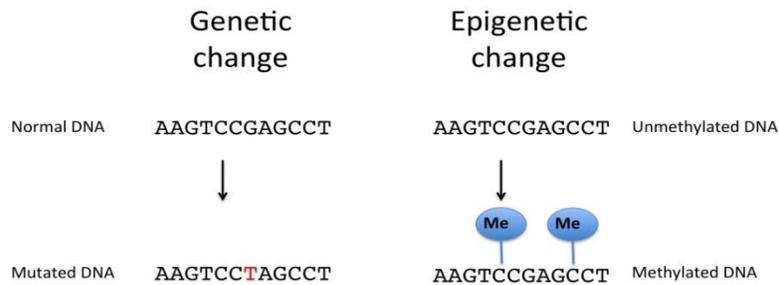
Release of seed dormancy

Dormancy can either be quickly released in imbibed seeds (within a couple of days) or relatively slow in dry seeds (within weeks or months). The molecular mechanisms controlling dormancy release are less well understood compared to that controlling dormancy induction. The fast release of dormancy requires imbibition at species specific temperatures and is called stratification.

Fig.1 Interactions in the regulatory network involving LEC1, LEC2, FUS3, and ABI3 genes in the control of seed development and maturation



Regulation of dormancy at chromatin level



In general, imbibition at low temperatures releases dormancy in seeds of summer annuals, while high temperatures release dormancy in seeds of winter annuals.

It is largely unclear how stratification drives the release of seed dormancy, and, especially, the temperature sensing mechanism is unknown, but a few genes with a role in this process have been identified. The basic helix-loop-helix transcription factors SPT and PIL5 have a role in cold stratification (Pinfield-Wells *et al.*, 2005). SPT is a negative regulator of germination that loses its repressive activity after stratification, whereas PIL5 is not responding to low

temperatures, but represses germination in the dark after a cold treatment.

Gibberellins (GAs), ethylene, strigolactone, and brassinosteroids influence seed dormancy and germination (Finkelstein *et al.*, 2008; Nelson *et al.*, 2011; Graeber *et al.*, 2012). In general, these hormones reduce seed dormancy and promote seed germination. For example, mutants defective in GA biosynthesis such as *ga requiring1* show deep seed dormancy and fail to germinate in the absence of exogenous GA (Debeaujon and Koornneef, 2000; Ogawa *et al.*, 2003). GA treatment alone does not stimulate germination in all species or in fully dormant

Arabidopsis seeds (Ali-Rachedi *et al.*, 2004). A decrease in ABA levels may be required before GA levels and sensitivity can increase (Jacobsen *et al.*, 2002). However, sensitivity to both GA and light increases as after ripening progresses in *Arabidopsis* and increased GA levels mediate the dormancy relieving effect of moist chilling in *Arabidopsis*. Light promotes GA synthesis, and light and GA promote the degradation of ABA in imbibing lettuce seeds. The accumulation of the GA biosynthetic gene *GA3ox2* (*Gibberellin 3 Oxidase*) transcript increased 40-fold in after ripened seeds whereas the GA-deactivating enzyme *GA2ox1* (*Gibberellin 2 Oxidase*) was expressed at the highest levels in the highly dormant seeds of *Arabidopsis* ecotype Cvi (Finch-Savage *et al.*, 2007). Stratification led to increased expression of the GA biosynthesis genes *GA20ox1* (*Gibberellin 20 Oxidase*), *GA20ox2*, and *GA3ox1* and decreased expression of the GA catabolic gene *GA2ox2* (Yamauchi *et al.*, 2004).

Studies using inhibitors of ethylene biosynthesis or of ethylene action and analysis of mutant lines altered in genes involved in the ethylene signaling pathway (*etr1*, *ein2*, *ain1*, *etr1*, and *erf1*) demonstrate the involvement of ethylene in the regulation of germination and dormancy. Ethylene enhances dormancy breaking through interactions with ABA signaling. Ethylene can regulate dormancy by affecting ABA levels and signal transduction (Linkies *et al.*, 2009). For example, induction of thermodormancy at high temperatures is associated with a reduced ethylene production in chickpea (*Cicer arietinum*; Gallardo *et al.*, 1991), sunflower (Corbineau *et al.*, 1988), and lettuce (Prusinski and Khan, 1990). This decrease in C₂H₄ production may result from an increase in ACC (1-aminocyclopropane-1-carboxylic acid)-malonyltransferase activity, thus from a decrease in ACC content as

demonstrated in chickpea (Martinez-Reina *et al.*, 1996), an inhibition of ACO activity (Corbineau *et al.*, 1988; Gallardo *et al.*, 1991), or a reduced expression of ACS (acyl-CoA synthetase) and ACO (Argyris *et al.*, 2008). Numerous data also suggest that ethylene stimulates seed germination by affecting the GAs biosynthesis or signaling pathway. GA₁, GA₄, and GA₇ strongly accumulate in dry mature seeds of the *etr1-2* *Arabidopsis* mutant relative to wild type, and both GA₄ and GA₇ contents remain higher than in wild type during the two first days of imbibition (Chiwocha *et al.*, 2005). The changes in GA content during germination suggest that lack of ETR1, i.e., of ethylene signaling pathway, results (i) in alteration of GAs biosynthesis pathway, and (ii) in a requirement for higher levels of GAs than wild type, to promote germination (Chiwocha *et al.*, 2005). In *Arabidopsis*, Achard *et al.*, (2007) reported that a part of ethylene action on hypocotyl growth and floral transition was mediated via its effects on the DELLA proteins.

Ethylene has shown to regulate endosperm cap weakening and rupture in *Lepidium sativum*, counteracting the action of ABA (Linkies *et al.*, 2009). Very recent reports have demonstrated the roles of strigolactones and karrikins (germination promoting compounds in smoke) in dormancy and germination. Strigolactone signalling is mediated by the F-box protein Karrikin Insensitive 1 (KAI1), strigolactone is allelic to More Axillary Branches 2 (MAX2). The *kai1/max2* mutant shows increased primary dormancy (Nelson *et al.*, 2011). It has been shown that strigolactones modulate the ABA/GA ratio in secondary dormancy control (Toh *et al.*, 2012).

Brassinosteroids (BRs) are plant steroid hormones involved in stem elongation and leaf unfurling (Clouse, 2001) that also

promote seed germination. In *Arabidopsis*, epibrassinolide (EBR) and brassinolide (BL) application overcomes nongermination of GA biosynthetic and *sleepy 1 (sly1)* GA signaling mutants, but BR and GA stimulate tobacco seed germination by different mechanisms (Leubner-Metzger, 2001).

The role of reactive oxygen species (ROS) in seed biology has progressively emerged and evolved this last decade. Originally considered as harmful compounds, causing deleterious reactions toward a wide range of biomolecules and to seeds, ROS are now widely acknowledged as signaling compounds regulating the germination process through an hormonal network. Oracz *et al.*, 2007 reported that after-ripening period a progressive accumulation of ROS, namely superoxide anions and hydrogen peroxide, in cells of embryonic axes. Accumulation was investigated at the cellular level by electron microscopy, occurred concomitantly with lipid peroxidation and oxidation (carbonylation) of specific embryo proteins. Incubation of dormant sunflower seeds for 3 h in the presence of hydrogen cyanide (a compound that breaks dormancy) or methylviologen (a ROS-generating compound) also released dormancy and caused the oxidation of a specific set of embryo proteins. Ishibashi *et al.*, (2013) have proposed that ROS produced in soybean (*Glycine max*) embryonic axes during imbibition induces ethylene production, which promotes cell elongation in the radicle.

Nitric oxide (NO), nitrite, and nitrate may stimulate the pentose phosphate pathway, and therefore germination, by increasing oxidation of NADPH to NADP⁺, a limiting electron acceptor. NO inhibition of catalase may lead to increased accumulation of H₂O₂ from the β -oxidation of stored fatty acids in seeds. Accumulated H₂O₂ may stimulate germination by acting as a substrate for

peroxidases, leading to oxidation of NADPH to NADP⁺ or by causing breakdown of ABA (Bailly, 2004). In *Arabidopsis*, NO may stimulate germination by causing vacuolation and cell wall weakening of the aleurone layer (Bethke, 2007).

Dormancy and germination are very complex traits under the control of a large number of genes. By understanding seed dormancy at molecular level, we can come to some of the genes which are involved in seed dormancy induction. As we are seed technologist we know that induction of seed dormancy is important in some crops like wheat, barley, ground nut *etc.* and release of seed dormancy in most of the crops. So genetic and molecular mechanisms create a path to achieve our goal. Genetic and molecular mechanisms like silencing and over expression help us to induce and release of seed dormancy in many agricultural crop species.

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