The release of dormancy, a wake-up call for seeds to germinate

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Seed dormancy determines the timing of germination, thereby contributing to successful seedling establishment and plant fitness. The induction and release of dormancy are controlled by various regulators like plant hormones and dormancy proteins. The relative strengths of these regulators are influenced by environmental factors during seed maturation and storage. In the last few years additional processes have been identified to be involved in the release of dormancy during seed storage with an important role for non-enzymatic oxidative reactions. However, the relations between the different dormancy regulators are not fully understood yet. Finally, all accumulated information will be processed in the seed during early seed imbibition and lead to the decision to germinate or not.

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Introduction

Plants need to be optimally adapted to their environment to obtain a high fitness. Therefore, developmental transitions should be properly timed to coincide plant growth stages with their favourable seasons. It is especially important that plants start their life cycle at the beginning of the growth season. In order to establish seedlings at the right time, seeds of most plant species have evolved the ability to time their germination. This is controlled by seed dormancy, which is defined as the incapacity of an intact viable seed to complete germination under favourable conditions [1,2]. Dormancy is particularly important to prevent germination during short spells of favourable conditions in an unfavourable season for plant growth. Seed dormancy is an unwanted trait for crops that require rapid and uniform germination after sowing. During the domestication of most crop species low dormancy levels have been selected. This level has to be well balanced because very low dormancy can cause pre-harvest sprouting and reduce the quality of harvested seeds [3,4]. A good understanding of dormancy will benefit ecological understanding of plants and lead to practical applications in crops. Several types of seed dormancy have been described based on the physiological state and physical structure of the seed [5]. Here, we will discuss its most prevalent form, physiological dormancy. This review is focussed on processes occurring during dry seed storage and early imbibition, as well as on dormancy cycling in the soil, because important progress has been obtained in these areas during the last few years.

The influence of the environment

The induction of seed dormancy occurs during seed maturation and is developmentally regulated. Environmental factors experienced by the mother plant during seed maturation like temperature, light, and soil nitrate influence the level of dormancy [6•]. Assuming that these conditions are predictive for the following growth season, this mechanism can support the next generation to adapt to the local environment. Especially temperature was shown to be an important factor. In the model plant Arabidopsis low temperatures during seed maturation enhance dormancy levels [7,8]. Surprisingly, it was recently shown that low temperature could even enhance seed dormancy levels when experienced by the mother plant before flowering, indicating the existence of a memory mechanism [9•]. Seeds harvested from a single plant usually show variation in their dormancy levels. This enables bet hedging, preventing all seeds from germinating simultaneously and reducing the mortality risk of the entire progeny. Probably, environmental variation during seed maturation leads to different levels of dormancy between individual seeds [10,11].

Freshly harvested seeds have a relatively high dormancy level that is gradually released during subsequent dry seed storage (so-called after-ripening). During this release of dormancy, the window of environmental conditions at which the seed can germinate is slowly opening [2]. Seeds stored in the soil under natural conditions monitor their

environment to adjust their dormancy level. For instance, dormancy can be lost in imbibed seeds after a short exposure to low temperatures (stratification) [2] or by compounds present in smoke [12].

The molecular regulation of seed dormancy

The genetic and molecular regulation of seed dormancy has been studied using both induced and natural variation in several species with an emphasis on the model plant Arabidopsis. This revealed its complex regulation by multiple semi-independent pathways. The main regulators can be grouped as follows:

Hormones

The roles of the plant hormones abscisic acid (ABA) and gibberellins (GA) in dormancy and germination were identified over 50 years ago [13,14] and have been confirmed by genetic, physiological and molecular experiments since then. ABA is required for the induction of dormancy during seed maturation and GA for germination. These two hormones negatively influence each other's biosynthesis and signalling pathways. It is especially the balance between both hormones that determines germination capacity [15–17] (Figure 1a). More recently, additional hormones have been demonstrated to contribute to dormancy and germination. Among them, an important role has been identified for ethylene, partially by counteracting ABA effects as reviewed previously [16,18].

Dormancy-specific regulators

A few genes have been identified that exclusively regulate dormancy and germination. These regulators have a seed-specific expression pattern and show strong dormancy mutant phenotypes. The main representative genes of this group are *DELAY OF GERMINATION 1* (*DOG1*) and *REDUCED DORMANCY 5* (*RDO5*) [19,20•]. These two genes also play important roles in natural variation for dormancy and have been identified as quantitative trait loci for dormancy in Arabidopsis [19,21,22]. DOG1 is involved in the enhancement of dormancy by low temperatures during seed maturation [7,8,23] (Figure 1b). The role of DOG1 is conserved throughout the plant kingdom and encodes a protein with unknown function [19,24,25,26•]. RDO5 is a pseudophosphatase that influences the phosphoproteome during early seed imbibition [21]. RDO5 and DOG1 protein levels in freshly harvested seeds correlate with seed dormancy levels and apparently act independent from ABA [20•,23]. Both ABA and DOG1 are absolutely required to induce seed dormancy [8,19,23,25] suggesting that their signalling pathways converge at a critical downstream step. The DOG1 protein amount is stable during seed storage and still present in imbibed non-dormant after-ripened seeds suggesting that it loses its activity during storage [23] (Figure 2a).

Another gene in this group is *MOTHER OF FT AND TFL1* (*MFT*), which encodes a member of the plant phosphatidyl ethanolamine binding protein (PEBP) family. MFT regulates germination in both Arabidopsis and wheat [27,28]. Its function has not been clarified, but it was shown to have a negative feedback role in ABA signalling [29]. Additional dormancy regulators were recently identified by cloning quantitative trait loci for dormancy in crops. Some of these are seed-specific, like

Figure 1
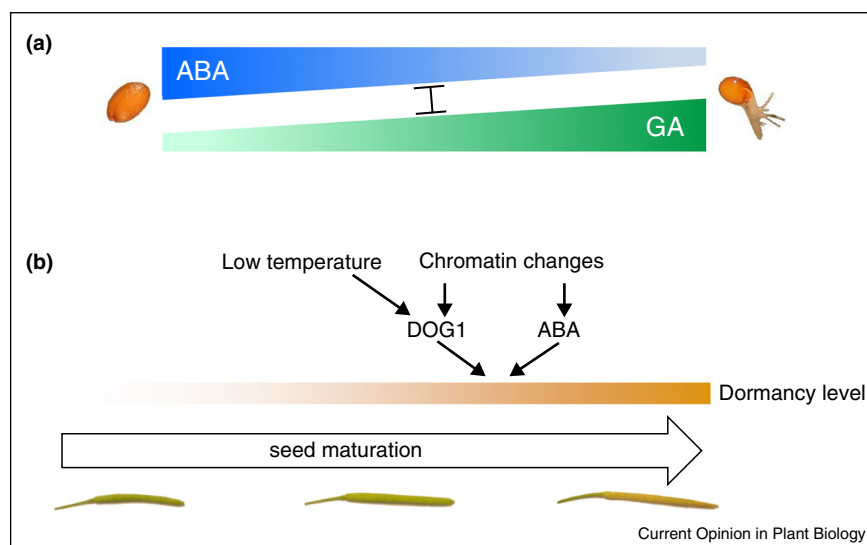
The roles of environmental and endogenous factors in seed dormancy. **(a)** Dormancy and germination are regulated by the balance between ABA and GA. **(b)** Factors controlling the induction of dormancy during seed maturation. Both environmental (temperature) and developmental (chromatin changes) factors regulate the dormancy protein DOG1 and the hormone ABA. Representative siliques are shown below the seed maturation arrow. The intensity of the colours in the bars indicates the strength of the indicated processes and factors. Arrows indicate positive and stop bars negative effects.

Figure 2
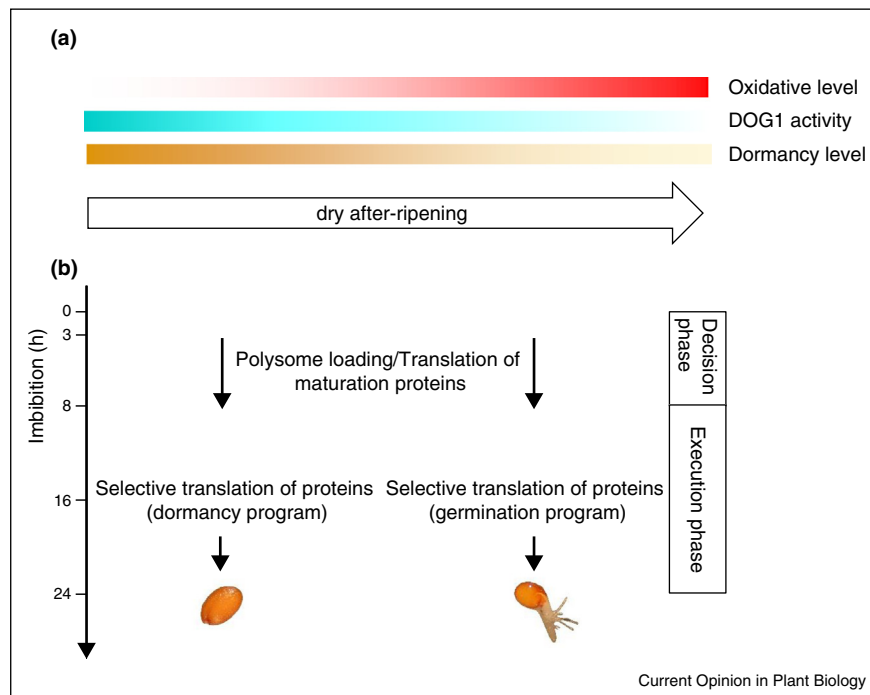
Processes occurring in seeds during dry after-ripening and imbibition. **(a)** An increase in oxidative level during dry storage of seeds correlates with reduced DOG1 activity and reduced dormancy level. The intensity of the colours in the bars indicates the strength of the indicated processes and factors. **(b)** Selective translation in fresh and after-ripened seeds during imbibition leads to different developmental outcomes. Increased after-ripening time is indicated from left to right, increased imbibition time is indicated from top to bottom.

Alanine Aminotransferase (*AlaAT*) in barley [30] and *Seed dormancy 4* (*Sdr4*) in rice [31]. Others are more generally expressed, like *Mitogen-Activated Protein Kinase Kinase* (*MKK3*), which was identified in barley [32] and wheat [33]. The relation of these genes with known dormancy pathways still has to be determined, although *Sdr4* was shown to influence the expression level of a rice homolog of *DOG1* [31].

Chromatin modifiers
The developmental transitions that occur during seed development, dormancy and germination are associated with major transcriptional changes and chromatin restructuring [34,35], suggesting epigenetic regulation. During the last ten years an increasing number of studies on chromatin regulation in seeds has indeed revealed a role for chromatin modifiers in seed dormancy and germination. In particular, seed dormancy phenotypes have been described for a number of chromatin mutants influencing acetylation, methylation, or ubiquitination of histone tails as reviewed previously [17,36]. These mutants showed pleiotropic phenotypes in accordance with their general role in the transcriptional regulation of genes. In addition, changes in dormancy levels have been shown to correlate with changes in repressive (histone H3 lysine27 trimethylation) and activating (histone H3 lysine4 trimethylation)

chromatin marks at dormancy genes [37,38,39•]. Overall, these studies showed that transcription levels of dormancy genes are regulated by chromatin modifications (Figure 1b).

The release of seed dormancy
After the induction of dormancy during seed maturation, its level is relatively high in fully matured seeds. Changes in seed dormancy continue to happen after seeds have been shed from their mother plant and become apparent upon imbibition by the ability of the seed to germinate or not. Evolution of dormancy acted on seeds stored in the seed bank experiencing fluctuating environmental conditions, including changes in temperature and humidity. Seed storage under agricultural or lab conditions usually take place in controlled dry environments. We should therefore separate events that occur during dry (controlled) storage from those happening in the soil seed bank.

Dry seed storage
Relative humidity and temperature are critical parameters that determine the nature of the reactions occurring during seed storage. For Arabidopsis seeds a moisture content (MC) of 0.06 g H_2O g^{-1} dry weight corresponds to the threshold above which the free available water can allow catalytic reactions. Dormancy release at high MC

has similarities to that of (partially) imbibed seeds in the soil seed bank. Below this critical MC (i.e. lab/agricultural storage conditions) the nature of the reactions is non-enzymatic [40•].

Several works have shown that transcription/translation, degradation of metabolites (i.e. ABA), as well as enzymatically catalysed post-translational modifications of proteins do not occur in the fully dry state [41,42••,43–46]. Consequently, the molecular events occurring in dry seeds are limited to passive reactions such as oxidation and Amadori–Maillard reactions. Interestingly, reactive oxygen species (ROS) are produced during dry storage of orthodox seed species [47] causing oxidative reactions and the formation of peroxy-lipids, carbonylated proteins, and oxidized mRNA [48–53]. Although 'passive', these oxidative reactions seem to selectively target a subset of proteins and mRNAs as reviewed previously [54]. This suggests an evolutionary mechanism that increased the sensitivity to oxidation of some molecular components related to the control of dormancy. The selective oxidation of mRNAs and proteins that gradually occurs during storage (oxidative imprinting) will turn into effect during the first few hours of imbibition leading to the maintenance or release of germination inhibition (Figure 2). The levels of ROS and nitric oxide (NO) further increase during early imbibition of non-dormant seeds and have been demonstrated to contribute to the release of seed dormancy [55–58]. This function of ROS and NO is at least partially mediated by the N-end rule pathway through degradation of group VII ethylene response transcription factors indicating a role of protein degradation in dormancy release [59–61].

Three pioneering studies [42••,44,62••] have revealed the importance of translational control for germination. In sunflower and Arabidopsis the association of mRNA with polysomes (active state of translation) is absent in dry seeds. After 3 h imbibition in the dark the loading of mRNA on polysomes increased gradually and translation metabolism is fully active after 16 h imbibition [42••,44]. In agreement, proteomics analysis of radiolabelled neo-synthesised polypeptides in Arabidopsis seed revealed that *de novo* protein synthesis started at low rates during the first 8 h of imbibition and that the 8–24 h imbibition window coincides with the highest rate of polypeptide production [62••]. The absence of correlation between transcriptome and translatome in the same seed material suggested that the regulation of germination is mainly controlled by translation instead of transcription [42••]. The identity of mRNAs loaded into polysomes in the 16–24 h imbibition window shows significant differences between dormant and non-dormant seeds [42••]. Surprisingly, in non-dormant seeds the proteins synthesized during the first hours of imbibition are associated with the seed maturation program, the germination program being activated only later during the 8–24 h imbibition window [62••]. This suggests a maintenance of the non-germination metabolism during the first hours of imbibition, which opens a short decisional window. Altogether, these recent advances indicate that after an early 'decision phase', a selective translation of mRNA occurs depending on the outcome of the selected developmental program, germination or dormancy (Figure 2b). Features of the 5′-UTR of mRNA have been proposed to play a role in this selective recruitment [42••,62••].

The precise mechanism by which oxidative imprinting in dry seeds is converted to molecular signals has still to be discovered. It has been hypothesized that damaged mRNA might fail to be translated and that stored carbonylated proteins will be degraded by the 20S proteasome [54]. The pro-oxidative environment in after-ripened seed raises the hypothesis that redox regulation of protein in early steps of imbibition might be part of the mechanism. This is of particular interest since reversible redox modifications of proteins are considered as molecular switches controlling developmental processes as reviewed previously [63–65].

Dormancy cycling in the seed bank

Dormant seeds that are shed from their mother plant in the field accumulate in the soil to form a soil seed bank (SSB). Seeds stored in the SSB will alternate between dry and imbibed states imposed by annual and temporal changes in soil humidity. Therefore, metabolic reactions can take place including transcription and translation, which are not considered in lab experiments with seeds stored under dry conditions. Seeds in the SSB are able to sense changes in the local soil environment and continually adjust their dormancy levels to complete germination and seedling establishment in their preferred time of the year [2]. Especially soil temperature and moisture indicate a temporal window for germination and affect the depth of dormancy and the sensitivity to spatial sensing signals, such as light and nitrate [66–68]. If these signals are not perceived, the seeds acquire dormancy again. This secondary dormancy can be induced and relieved in the same seed for several cycles until the environment is favourable for seedling establishment [69].

In a pioneering study, dormancy genes identified in laboratory experiments were analysed for their expression in Arabidopsis seeds stored in the SSB in a temperate climate [69]. Dormancy of these seeds increased during winter as soil temperature declined, coinciding with an increase in expression of ABA synthesis and GA catabolism genes. This was linked to an initial increase in endogenous ABA. A further increase in dormancy was correlated with enhanced transcript levels of ABA signalling genes. Dormancy declined in spring and summer. At the same time, endogenous ABA levels decreased along with transcript levels of positive ABA signalling genes, whereas ABA catabolism and GA synthesis genes

Figure 3
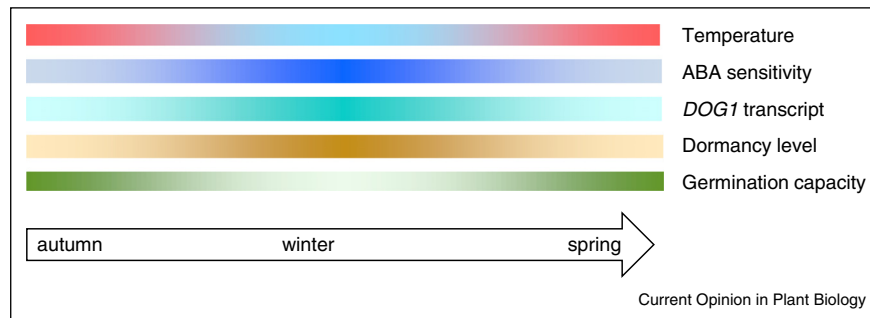
Processes occurring in buried seeds. Gradual changes in environmental and seed factors during the year correlate with dormancy cycling in the soil seed bank in a temperate climate. The intensity of the colours in the bars indicates the strength of the indicated processes and factors.

increased in expression [69] (Figure 3). Therefore, the roles of ABA and GA in dormancy identified in lab experiments are consistent with changes in transcript levels of their biosynthesis and signalling genes in the SSB.

DOG1 transcript levels showed a strong correlation with both dormancy levels and soil temperature in buried seeds [69]. These changes in transcript levels correlated with changes in repressive histone marks at the *DOG1* locus [39•]. This suggests an important role for *DOG1* as temperature sensor in seeds and is consistent with its identified role as a major regulator of seed dormancy in lab experiments (Figure 3). *MFT* expression also showed a strong correlation with dormancy in the field, although its relation with temperature seemed genotype dependent [70]. During the low dormancy period in spring and summer, environment sensing becomes more important to detect the proper spatial signals for germination. This was reflected by changes in nitrate sensing and expression levels of genes involved in light and nitrate detection [70,71].

Conclusions and future perspectives

The main factors involved in dormancy induction have probably been identified. However, their interactions and their regulation by developmental and environmental signals need further elucidation. The release of seed dormancy during dry seed storage and its cycling in the seed soil bank is less understood, although some regulatory processes have been identified in the last few years. We foresee important progress in this area in the near future, especially concerning the relations between identified regulators. For instance, it might be expected that major dormancy regulators, like DOG1, play a central role in the integration of oxidative imprinting during early imbibition. In addition, we anticipate that the identification of proteins at the convergence point of different dormancy pathways will be instrumental for our further understanding of dormancy. Finally, future research should be directed at the events that take place during early imbibition of seeds when all available information is combined, accumulating in the binary decision to germinate or not.

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