Seed Dormancy and Germination

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Seed dormancy, defined as the inability of seeds to undergo germination under optimal conditions, played a crucial role in the evolution of flowering plants.

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1. Introduction

Indeed, dormancy prevents early germination and vivipary, thus enabling seeds' dispersal in the environment. Dormancy is established during seed maturation and is finely regulated by a plethora of transcription factors interacting in a complex molecular network which in turn controls hormonal levels and signaling. Abscisic acid (ABA) and gibberellic acid (GA) are the phytohormones mainly involved in the induction, maintenance and release of seed dormancy. These hormones act in an antagonistic manner: ABA promotes the establishment of dormancy and is required for dormancy maintenance while GA triggers dormancy release. Seed germination will then take place properly as for place and time. Indeed, this process only occurs when a special combination of environmental optimal conditions such as light, temperature and water availability are present[1]. Seed germination, in *Arabidopsis* and most plant species, needs a pulse of red light to activate the photoreceptor, which for this process is mainly represented by phytochrome B (phyB)[2]. Active phytochromes promote seed germination also through the control of ABA and GA levels[3][4][5]; indeed, light induces GA biosynthesis and ABA catabolism while repressing GA catabolism and ABA biosynthesis, resulting in increased GA levels and reduced ABA levels. Therefore, the ABA/GA ratio, rather than ABA and GA levels, establishes whether the seed germinates or remains quiescent.

2. Light Control of Seed Dormancy and Germination

Seed germination is influenced by various environmental cues, the main being temperature, water and light. In particular, red light is an essential requirement for germination of seeds of *Arabidopsis* and most annuals. Among the phytochromes, phyB plays a key role in the promotion of seed germination[6].

3. Hormonal Control of Seed Dormancy and Germination

Dormancy and germination of seeds are two processes finely regulated by several phytohormones; indeed, although ABA and GA play the main role, auxin, cytokinins (CKs), and jasmonate (JA) have been shown to partly contribute to seed germination[7][8][9][10]. As for brassinosteroids (BRs), the involvement of this class of molecules in the promotion of germination has been shown since a long time[11]. Interestingly, it was recently proved that the transcription factor BRI1-EMS-SUPPRESSOR1 (BES1), which is part of the BR signaling pathway, physically interact with the ABA-responsive bZip transcription factor ABA INSENSITIVE5 (ABI5)[12], to restrain ABI5 from binding the promoters of target genes, thus promoting seed germination[12].

Additionally, the gaseous hormone ethylene plays a role in the control of both dormancy and germination of seeds[13][14][15]. Previous studies have shown that ethylene stimulates dormancy release and seed germination in dicot species, while inhibition of ethylene synthesis is related with repression of germination[13][14]. Consistently, inactivation of the membrane-associated receptor *ETHYLENE RESPONSE1* (*ETR1*) and the downstream factor *ETHYLENE INSENSITIVE 2* (*EIN2*) results in more dormant mutant seeds compared to wild-type seeds[16][17][18]. It has been recently demonstrated that the *reduced dormancy 3* (*rdo3*) loss-of-function mutant[19] is an *etr1* mutant allele[20]. *rdo3* was isolated for its reduced dormancy; further analysis revealed that *rdo3* mutant seeds were not altered in ABA sensitivity or endogenous ABA levels[21]. The recent study by Li et al.[20] proved that ETR1 promotes the establishment of seed dormancy in Arabidopsis, and its function requires DELAY OF GERMINATION1 (DOG1), which has been previously identified as a major quantitative trait locus controlling seed dormancy[22]. The activity of DOG1 in the promotion of seed dormancy is strictly dependent on ABA signaling; indeed, DOG1 controls dormancy at least in part through the control of *ABI5* expression[23]

[24]. Analysis of transcriptomic data of the *rdo* mutant led to identify ETHYLENE RESPONSE FACTOR12 (ERF12) as a downstream element; indeed, lack of ETR1 results in an increased *ERF12* transcript level, suggesting that ERF12 is involved in the ETR1-mediated dormancy, and it is likely to represent a link between ETR1-ethylene and the DOG1 pathway in the regulation of seed dormancy in *Arabidopsis*. ERF12 belongs to the ERF subfamily of repressors[25], which interact with the TOPLESS (TPL)/TPL-related (TPR) corepressors[26][27][28]. TPL does not bind directly DNA, but is required for DOG1 repression mediated by ERF12, as demonstrated by luciferase assay[20]. Although the molecular elements between the ETR1 receptor and ERF12 are still unidentified, these findings uncovered, at least in part, the molecular pathway which controls seed dormancy, linking ethylene to ABA signaling through ETR1-ERF12/TPL and DOG1. Interestingly, ETR1 is likely to be involved also in the repression of seed germination; indeed, a previous study revealed that *etr1* mutant seeds exposed to far-red light or in darkness, showed increased germination rate compared to wild type seeds[29]. Surprisingly, this germination behavior was not dependent on altered endogenous ethylene levels between mutant and wild-type seeds, but on increased GA and reduced ABA levels in *etr1* mutant seeds following far red light treatment[29].

4. Translational Control of Seed Dormancy and Germination

The seed is an autonomous structure in which a fully developed embryo is spread in the environment, allowing the establishment of an autotrophic organism. In *Arabidopsis*, seed development is divided in two major phases: embryo and endosperm development (or morphogenesis), and maturation[30][31]. Once embryogenesis is completed, seeds enter the maturation phase, dormancy is established, storage compounds and mRNAs are accumulated, and seeds become desiccation tolerant[32][33]. Once dormancy is released and the environmental conditions are permissive, seeds can germinate; this step represents a programmed transition from a quiescent to a metabolically active state. Since in the presence of the transcription inhibitor α-amanitin germination can occur, whereas cycloheximide blocks this process, germination of seeds is not strictly dependent on transcription of newly synthetized mRNAs, whilst it requires de novo protein synthesis[34][35][36][37][38][39][40]. The presence of stored mRNAs in dried seeds was discovered 50 years ago[41][42], and so far, they have been detected in a large number of seed species[43][44][45]; nevertheless, only in the last decade many open questions on the seed-stored mRNAs and on the translational control underlying dormancy release and seed germination have been, at least in part, addressed[46].

Genome-wide analysis showed that Arabidopsis mature dry seeds hold more than 12,000 transcripts, whereas rice dry seeds have about 17,000 different stored mRNAs[43][47]; it is assumed that not all these stored mRNAs are required for seed germination and a large number should represent housekeeping genes. Among the transcripts specifically required for seed germination, there are mRNAs related to the translation machinery, as well as ubiquitin and proteasome system, thus corroborating the importance of protein synthesis, and suggesting there should be a dynamic regulation and selective proteolysis during early seed germination[43]. A combined approach based on two-dimensional gel-based differential proteomics and dynamic radiolabeled proteomics demonstrated that germination starts when storage and desiccation tolerance-related proteins are synthesized, to guarantee that germination occurs only under favorable conditions[48]. Interestingly, among the translated mRNAs during the transition phase from seed-to-seedling, there are transcripts from hypoxia stress-related genes, thus pointing out the importance of a molecular control of low-oxygen conditions during germination[49]. ABA and GA control dormancy and germination antagonistically, with the former promoting dormancy and inhibiting germination, and GA inducing release of dormancy and germination; therefore, it is not surprising that, among the most represented stored mRNAs in dry seeds, there are transcripts from ABA-related genes, as they have ABA-regulated motifs or ABA responsive elements (ABREs), suggesting that they are accumulated during the maturation stage[43].

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