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Reviews and Progress **Open Access**

Research Progress on the Mechanism of GA and ABA during Seed Germination

Zuo Yue Xu Yonghua ✉
Jilin Agricultural University, College of Traditional Chinese Medicine, National Engineering Research Center of Ginseng Breeding and Application, Changchun, 130118, China
✉ Corresponding author Email: xuyonghua777@yeah.net

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Abstract The dormancy and germination of seeds are determined by the balance between the embryo growth potential and the binding force imposed by the seed coat. The germination of different seeds is not synchronized, and the stimulus required to promote germination varies greatly. Before germination, the seeds need to undergo water absorption, reactivate metabolic activities and redifferentiate embryonic tissues to mobilize nutrients stored in seeds and initiate meristematic activities. The transition from dry seeds to seedlings is highly sensitive to different environmental conditions, especially light, temperature and water. This response to environmental signals is regulated by one or more hormones. Various plant hormones regulate seed germination through highly complex interactions. Among them, the role of GA (gibberellin) and ABA (Abscisic acid) in regulating seed germination is particularly critical. This article reviewed the mechanisms by which GA and ABA control seed dormancy at the molecular level, and discussed the way they interact with other hormones. Finally, the development direction of plant hormone research on seed germination is prospected.

Keywords GA; ABA; Seeds; Dormancy; Germination

Plant hormones are natural signal molecules that regulate plants physiology, development, and to adapt to environmental stimuli, and have a wide range of physical and chemical properties. With the development of modern biochemical technology, more and more plant hormones have been discovered and recognized, currently including (but not limited to) abscisic acid, AX (auxin), BR (brassinosteroid), CTK (cytokinin), GA, ethylene, JA (jasmonic acid), SA (salicylic acid), and strigolactone, which play a pivotal role in regulating the developmental processes and signaling networks of plants in response to a wide range of biological and abiotic stresses. Plant life begins with seed formation, which is the carrier of the next generation of plant life cycle. Seed germination is affected by many factors, such as external temperature and humidity conditions, internal hormone changes. Hormone research during seed germination will help to understand the growth and development process of plants, thus guiding plant breeding and cultivation methods.

1 The Role of ABA in Seed Germination

ABA plays an important role in maintaining seed dormancy and regulating seed germination. It controls seed germination by controlling the germination of the radicle and inhibiting the loosening and expansion of the cell wall (Gimeno-Gilles et al., 2009). NCED (9-cis-epoxycarotenoid dioxygenase) and ABA8'OH (ABA 8'-hydroxylase) are the key enzymes in ABA metabolism. NCED is mainly involved in the synthesis of ABA, and ABA8'OH is a key enzyme in ABA catabolism, which is encoded by *CYP707A* (Millar et al., 2006). Overexpression of NCED delayed the germination of seeds, *Arabidopsis cyp707a2* mutant seeds increased the ABA level and delayed germination (Zheng et al., 2015). ABA can be synthesized both in dormant seeds and non-dormant seeds, however, ABA catabolism is stronger in non-dormant seeds, and dormant seeds are more conducive to ABA synthesis, that is, dormancy induces changes in ABA metabolism (Millar et al., 2006).

ABA signaling is mainly composed of ABA receptor proteins PYR (pyrabactin resistence)/PYL (PYR1-Like)/ RCAR (regulatory component of ABA receptor), PP2C (phosphatase 2C), SnRK2 (SNF1-related protein kinase 2), transcription factor ABFs (ABRE binding factors)/AREBs (ABA responsive element binding proteins) and ABA-responsive element ABRE (Figure 1) (Klingler et al., 2010). ABA can enhance the expression of many genes related to dormancy. For example, AtPr1 is involved in improving the dormancy ability of seeds. Atper1-1 mutants were shown to inhibit seed dormancy and the deletion of *CYP707A* gene can reduce the dormancy inhibition of *atper1-1* seeds (Chen et al., 2019).

2 The Role of GA in Seed Germination

GAs is a class of diterpene carboxylic compounds widely found in higher plants. Among the more than 100 types of GAs that have been found, only few GAs have biological activity, which can promote the expansion and development of organs, and the most common ones are GA$_1$ and GA$_1$. GA$_3$ and GA$_4$, which are synthesized from GA12 through GA20ox and GA3ox catalytic reactions (Hedden and Thomas, 2012). Numerous studies on GA biosynthesis-deficient mutants have also proved that GA is essential for seed germination. DELLA protein is an inhibitor of GA response and a class of growth inhibitors. It exists in many plants and belongs to the Gras (GAI, RGA and SCARECROW) transcription factor family. Different DELLA proteins play different roles in seed germination. For example, *AtEXPA2* is a kind of expansin gene specifically expressed in Arabidopsis seed germination. The mutant of this gene delayed germination. DELLA mutant showed that RGL1, RGL2, RGA and DELLA were involved in inhibiting the expression of *AtEXP2*, and RGL1 played a leading role in controlling the expression of *AtEXP2* (Yan et al., 2014). GA utilizes the formation of the GID1 (GA-INSENSITIVE DWARF1)-GA-DELLA complex to decompose the DELLA protein to alleviate the inhibition of GA response by DELLA and promote plant growth (Figure 2) (Nelson and Steber, 2016).

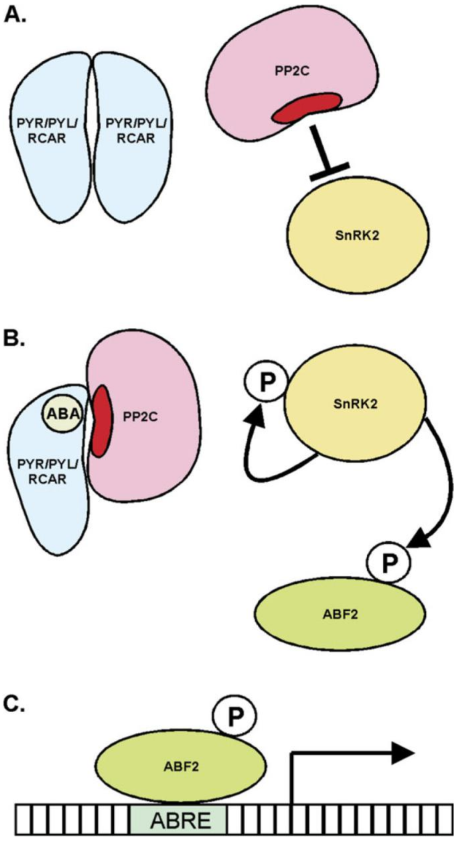

Figure 1 Schematic diagram of the ABA signal-receptor complex

Note: A: In the absence of ABA, the receptor forms a homodimer, while the PP2C inhibits both autophosphorylation of the SnRK2 and phosphorylation of ABF2; B: In the presence of ABA, a receptor protomer engulfs the hormone within a pocket, allowing the receptor to bind the PP2C and cover the phosphatase active site. This permits the autophosphorylation of the SnRK2 and phosphorylation of its ABF2 substrate; C: ABF2 binds to an ABRE in the promoter of ABA-responsive genes, activating transcription

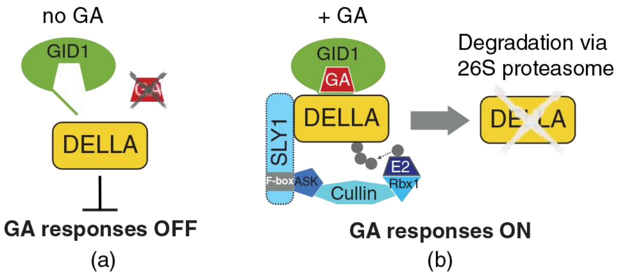

Figure 2 Schematic diagram of GA signaling

Note: (a) In the absence of GA, DELLA proteins are stable and repress GA responses; (b) GID1 binding to GA allows formation of the GID1-GA-DELLA complex, which in turn allows the SLY1/GID2 F-box protein to bind and polyubiquitinate DELLA, thereby targeting DELLA for destruction by the 26S proteasome; This lifts DELLA repression of GA responses

3 Interaction of ABA/GA in Seed Germination

3.1 The interaction of ABA and GA in metabolism

A large number of genetic studies on ABA and GA biosynthesis and signal mutations have shown that these two hormones have important antagonistic effects in dormancy and germination. GA promotes the release of seed dormancy and counteracts the effect of ABA. The ratio of ABA and GA is the main regulator of plant seed dormancy. Under suitable growth conditions, the GA biosynthetic pathway is activated, prompting the release of the inhibitory effect of ABA. For example, in cotton seeds, the level of ABA decreased continuously from after-ripening, and when the content of ABA decreased to a lower level, GA began to play a role, which changed significantly during seed germination (Wang et al., 2019). The expression of *GA3ox1* and *GA3ox2* in ABA deficient mutant *ba2-2* is higher than that in wild type, and GA biosynthesis of *aba2-2* mutant is also activated during seed germination indicating that ABA is involved in the inhibition of GA biosynthesis (Seo et al., 2006; Toh et al., 2008). *aba2-2* also showed a decrease in the expression of *SPY* (*SPINDLY*) during seed imbibition under high temperature, indicating that ABA can promote the expression of the negatively regulated gene *SPY* of GA signaling(Toh et al., 2008). ABA and GA also have tissue-specific and spatio-temporal differences in the regulation of seed dormancy and germination. *GA20ox3*, *GA3ox1* and *GA2ox5* in the endosperm of imbibing barley grains had relatively high expression, while *GA3ox2* is highly expressed in embryos; the ABA biosynthesis genes *NCED1* and *NCED2* were transcribed in the endosperm tissue, while in the late stage of seed maturation, both the ABA catabolism gene *CYP707A1* is transcribed (Park, 2015). *NCED9* has a negative effect on GA biosynthesis. The germination rate of *nced9* mutant treated with paclobutrazol and GA biosynthesis inhibitor is higher than that of wild type, indicating that ABA biosynthesis regulated the GA synthesis pathway of seeds (Seo et al., 2016). ABA and GA interact not only in metabolism, but also in many transcription factors and dormant genes.

3.2 Interaction between ABA and GA in signal transduction

DELLA can inhibit the growth of plants by promoting the accumulation of ABA. The ABA content of DELLA-Q mutant is significantly lower than that of wild type (Guo et al., 2014). Both RGL2 and RGL3 can inhibit seed coat rupture, and ABA can promote the transcription of *rgl2* and *rgl3*, *rgl3* is greatly affected by ABA, RGL2 plays a leading role in inhibiting the process of seed coat rupture (Piskurewicz and Lopez-Molina, 2009). ABI3 (ABA-INSENSITIVE3), ABI4 and ABI5 are transcription factors in ABA signal transduction, and the expression in dormant seeds is higher than seeds with lower dormant levels, which can inhibit GA biosynthesis (Shu et al., 2013; Zhao et al., 2018). RGL2 and ABI5 can work together to inhibit seed germination, RGL2 promotes ABA biosynthesis in the endosperm, and then ABA is released into the embryo to ensure the expression of ABI5, thereby inhibiting seed germination (Lee et al., 2010).

3.3 The role of dormant genes in the interaction between ABA and GA

The expression of *DOG1* (*DELAY OF GERMINATION1*) gene determines the depth of dormancy of seeds. The newly harvested seeds have higher expression of *DOG1*, and as the after-ripening progresses, dormancy is gradually released and the transcription level of *DOG1* decreases (Nakabayashi et al., 2012). Low temperature can promote the expression of *DOG1* gene, *DOG1* promotes the expression of *GA2ox6*, a gibberellin catabolism gene, affects the ABA/GA value in the seeds, and the absence of DELLAs and ABA will lead to the decrease of dog1 expression (Kendall et al., 2011). High temperature can induce *SOM* (*SOMNUS*) transcription, which encodes a CCCH type zinc finger protein. The protein can regulate the metabolism of ABA and GA at the same time, resulting in the accumulation of ABA and the decrease of GA, then the ABA/GA ratio increases and inhibits the germination of *Arabidopsis* seeds (Lim et al., 2013). *MFT* (*MOTHER-OF-FT-AND-TFL1*) is a strong promoter of seed dormancy. During seed germination of wheat (Triticum aestivum L.), low temperature or promoter mutation lead to up regulation of MFT expression and enhancement of seed dormancy (Chono et al., 2015). ABA regulates the expression of MFT through ABI3 and ABI5. The former acts as an inhibitory factor and the latter acts as a promoter. MFT directly inhibits ABI5 and negatively regulates ABA signaling pathway; on the other hand, GA down regulates MFT expression through DELLA protein and inhibits ABA synthesis (Xi et al., 2010).

3.4 The role of transcription factors in the interaction between ABA and GA

PIL5 (PHYTOCHROME-INTERACTING FACTOR3-LIKE5), also known as PIF1, is an important transcription factor regulating GA and ABA signaling. PIF1 inhibited the active GA biosynthesis genes *GA3ox1* and *GA3ox2*, and indirectly activated GA catabolism genes *GA2ox2*; Meanwhile, PIF1 had the opposite effect on ABA biosynthesis genes, including ABA biosynthesis genes *ABA1*, *NCED6* and *NCED9*, and ABA catabolic genes *CYP707A2*; PIF1 also promoted the expression of genes encoding DELLA proteins GAI and RGA (Finkelstein et al., 2008). Seed germination of many plants is triggered by sunlight, red light can promote the degradation of transcription factor PIF1, and PIF1 can promote *SOM* expression (Vaistij et al., 2018). SPT (SPATULA) is a multifunctional transcription factor, which can control the response of germination to cold and light, inhibit the expression of *GA3ox1* and *GA3ox2*, and regulate the expression of five transcription factor coding genes: *ABI4*, *ABI5*, *RGA*, *RGL3* and *MFT*, in which *ABI4*, *RGA* and *MFT* are inhibited, *ABI5* and *RGL3* are induced (Vaistij et al., 2013). SPT, SOM, PIF1, ABI5, DELLA and MFT can jointly regulate ABA and GA signal pathways to complete the response to seed germination under red light (Vaistij et al., 2018).

4 The Role of Other Hormones in the Interaction between ABA and GA

Many hormones interact with ABA and GA, and control the germination of seeds through these interactions. Exogenous auxin can enhance the inhibitory effect of ABA on seed germination, auxin response factor ARF10 enhances the sensitivity of ABA, *MIR160* can down-regulate the expression of three transcription factors ARF10, ARF16 and ARF17 in auxin signal; ARF10 and ARF16 enhance the promoting effect of ABA on seed dormancy by maintaining the expression of *ABI3* (Liu et al., 2013). Br can antagonize the inhibition of ABA on seed germination and promote seed germination by regulating plant reproductive development; MFT played a role in the regulation of seed germination by ABA and Br (Xi and Yu, 2010). BIN2 (BRASSINOSTEROID INSENSITIVE2) is a key inhibitor of BR signal. During seed germination and postgerminative growth, BIN2 can phosphorylate and stabilize ABI5 in the presence of ABA, while active BRs inhibit the regulation of ABI5 by BIN2 (Hu and Yu, 2014). Ethylene can regulate the weakening and rupture of the endosperm cap, thereby counteracting the role of ABA (Linkies et al., 2009). SNL1 (SIN3-LIKE1) and SNL2 are two members of the histone deacetylation complex in *Arabidopsis thaliana*, which promote seed dormancy by regulating ethylene and ABA content in seeds simultaneously; the double mutant *snl1 snl2* seed dormancy decreased, while the expression of ethylene biosynthesis (ACO1, ACO4) gene and ABA catabolism gene (CYP707A1, CYP707A2) increased (Wang et al., 2013). CTK promotes seed germination, and ABA can inhibit this effect by reducing CTK biosynthesis. AAR (Arabidopsis response regulator) is an important component of CTK signaling. Among them, A-type ARR4, ARR5 and ARR6 can negatively regulate the expression of *ABI5*, making CTK resist the inhibitory effect of ABA, while ABI4 can directly bind to the promoter, which negatively regulates the transcription of ARR6, ARR7 and ARR15 (Wang et al., 2011; Huang et al., 2016). In addition, some newly discovered hormones have also been found to regulate seed germination. Stipalactone can reduce ABA/GA by regulating ABA biosynthetic enzymes, thereby alleviating the thermal inhibition of seed germination; KAR (Karrikin) can promote the germination of seeds by promoting the expression of GA biosynthetic genes *GA3ox1* and *GA3ox2* (Toh et al., 2012; Meng et al., 2017).

5 Summary Points and Future Issues

Plant endogenous hormones play a multi-functional chemical regulation role in the process of seed germination. At the molecular level, their metabolic pathways and signaling pathways are regulated by various transcription factors. ABA/GA is considered to be an important factor affecting seed dormancy. GA promotes seed germination and needs to destroy DELLA protein. However, ABA has a positive regulation effect on ABI transcription factors and DELLA protein. DELLA protein in turn inhibits GA biosynthesis. Make ABA and GA form a feedback loop. ABA/GA is controlled by the stage of seed development and the environment. In this process, a variety of transcription factors are involved in the regulation of seed dormancy and germination, which affects the germination process of seeds. In the early stage of seed germination, GA sensitivity is low, ABA sensitivity is high, this situation will change with the deepening of germination process.

In addition, in the process of seed germination, other hormones will also affect the germination ability of the seed in various ways. Most of the hormones promote the germination of the seed, but auxin can synergize with ABA to jointly inhibit seed germination. At present, there are still many deficiencies in the study of the effects of other plant hormones on seed germination. Although the study of mutants can discover the relationship between related genes and phenotypes, the specific mechanism at the molecular level is not yet clear. The study of the molecular mechanism of multiple hormone signal crossings is helpful to construct a new map of hormone signal integration in plant development and environmental adaptation.

Seed dormancy and germination is a complex physiological process. Different types of plants have different mechanisms for regulating seed dormancy. Current researches on seed dormancy and germination are mostly focused on model plants, but less on other kinds of plants. A better understanding of the mechanism of plant hormones related to seed dormancy and germination is helpful to obtain new varieties with appropriate seed dormancy level.

Authors' contributions

Zuo Yue was the main executor of this paper, completing the data collection and writing the first draft of the paper; Xu Yonghua was the designer and person in charge of the thesis, who guided the writing and revision of the thesis. The two authors read and approved the final manuscript.

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