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Review

# Plant hormones and seed germination

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ABSTRACT

Seed germination is controlled by a number of mechanisms and is necessary for the growth and development of the embryo, resulting in the eventual production of a new plant. Under unfavorable conditions seeds may become dormant (secondary dormancy) to maintain their germination ability. However, when the conditions are favorable seeds can germinate. There are a number of factors controlling seed germination and dormancy, including plant hormones, which are produced by both plant and soil bacteria. Interactions between plant hormones and plant genes affect seed germination. While the activity of plant hormones is controlled by the expression of genes at different levels, there are plant genes that are activated in the presence of specific plant hormones. Hence, adjusting gene expression may be an effective way to enhance seed germination. The hormonal signaling of IAA and gibberellins has been presented as examples during plant growth and development including seed germination. Some interesting results related to the effects of seed gene distribution on regulating seed activities have also been presented. The role of soil bacteria is also of significance in the production of plant hormones during seed germination, as well as during the establishment of the seedling, by affecting the plant rhizosphere. Most recent findings regarding seed germination and dormancy are reviewed. The significance of plant hormones including abscisic acid, ethylene, gibberellins, auxin, cytokinins and brassinosteroids, with reference to proteomic and molecular biology studies on germination, is also discussed. This review article contains almost a complete set of details, which may affect seed biology during dormancy and growth.



**Contents**

1. Introduction ..... 111
2. Seed germination ..... 112
3. Seed dormancy ..... 112
4. ABA ..... 113
5. Ethylene ..... 113
6. Gibberellins ..... 114
7. IAA ..... 115
8. Cytokinins ..... 116
9. Brassinosteroids ..... 117
10. Soil microorganisms and production of plant hormones ..... 117
11. Conclusions and future perspectives ..... 117
Conflict of interest ..... 118
References ..... 118

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## 1. Introduction

Among the most important functions of plant hormones is controlling and coordinating cell division, growth and differentiation (Hooley, 1994). Plant hormones can affect different plant activities including seed dormancy and germination (Graeber et al., 2012). Plant hormones including abscisic acid (ABA), ethylene, gibberellins, auxin (IAA), cytokinins, and brassinosteroids are biochemical substances controlling many physiological and biochemical processes in the plant. These interesting products are produced by plants and also by soil microbes (Finkelstein, 2004; Jimenez, 2005; Santner et al., 2009). There are hormone receptors with high affinity in the plant, responding to the hormones. Eukaryotes and prokaryotes can utilize similar molecules, which act as hormone receptors (Urao et al., 2000; Hwang and Sheen, 2001; Mount and Chang, 2002; Santner et al., 2009).

Before a seed can germinate a set of stages must be completed, including the availability of food stores in the seed. Such food stores include starch, protein, lipid and nutrients, which become available to the seed embryo through the activity of specific enzymes and pathways (Miransari and Smith, 2009). For example, there is a group of proteins called cyctatins or phytocyctatins, which are able to inhibit the activity of cycteine proteinases as inhibitors of protein degradation and regulators during seed germination (Corre-Menguy et al., 2002; Martinez et al., 2005).

The whole-genome analyses have indicated the set of genes, which are related to development, hormonal activity and environmental conditions in Arabidopsis. Interestingly, Bassel et al. (2011) indicated the distribution of genes in different regions of a seed related to the following processes: (1) dormancy and germination, (2) ripening, (3) ABA activities, (4) gibberellins activities, and (5) stresses such as drought.

For example, in region one, seed activity is up or down regulated by different genes such as the main dormancy *QTL DOG1* and genes, which positively (*GID1A* and *GID1C*) or adversely (*ABI3*, *ABI1*, *ABI5*) affect germination. The seed dormancy or germination is determined by the interactive effects between different signals, such as the germination signals, which promote seed germination by inhibiting the activity of signals, which may result in seed dormancy. The network model presented by Bassel et al. (2011) indicates the interactions, which may result in transition from seed dormancy to germination.

Fu et al. (2005) determined the total number of proteins (1100–1300) in the dry and stratified seeds of Arabidopsis or young seedlings with respect to the time of sampling using gel electrophoresis. The properties of 437 polypeptides were indicated with the use of mass spectrometric method. Accordingly, the presence of 293 polypeptides was indicated during all stages, 95 at radicle emergence and 18 at the later stages. They also found that 226 of polypeptides may be used by different signaling pathways. One fourth of proteins were utilized for the metabolism of carbohydrate, energy and amino acids, and 3% for the metabolism of vitamins and cofactors. The production of enzymes required for the genetic processes increased quickly at the beginning of germination and was the highest at 30 h after germination.

Li et al. (2007) investigated also the trend of protein alteration during different stages of seed germination in four Arabidopsis 12S SSPs. Such kind of analyses can be important for the investigation of feeding embryos by the available proteins during germination. Using the two combined methods of 2-DE scheme and mass spectrometry the degradation and accumulation of 12S SSPs were evaluated. According to their analyses, 12 SSPs started to accumulate when the process of cell elongation completed in siliques and in seeds during their development.

According to Liu et al. (2013) the following hormonal and signaling processes are likely when a dormant seed (after-ripened) germinates. (1) The sensitivity of seed to ABA and IAA decreases. The related genes, which are affected, include *SNF1-RELATED PROTEIN KINASE2*, *PROTEIN PHOSPHATASE 2C*, *LIPID PHOSPHATE PHOSPHTASE2*, *ABA INSENSITIVES, and Auxin Response Factor of UBIQUITIN1* genes. (2) Liu et al. (2013). The inhibiting effects of ABA on seed germination are by adversely affecting the genes of chromatin assembly and modification of cell wall and positively affecting the activity of genes regulating gibberellins catabolic.

(1) The decay of seed germination is also related to the IAA and jasmonates contents of seed. The following genes are able to regulate the jasmonate levels in seed: *3-KETOACYL COENZYME A THIOLASE*, *ALLENE OXIDE SYNTHASE*, *12-OXOPHYTODIENOATE REDUCTASE and LIPOXYGENASE*. (2) The changes in the expression of *GA 20-Oxidase* and *GA* 3-*Oxidase* genes also indicate the likely role of gibberellins in the germination of dormant after-ripening seeds (Liu et al., 2013).

It has been indicated that the activity of the enzyme pectin methylesterases can affect seed germination. The homogalacturonans of the cell wall are methylestrified by the enzyme affecting the cell wall porosity and elasticity and hence cell growth and water uptake. During the process of seed germination the cell wall of the radicle and of the tissues around it must expand. Accordingly, using a wild and a transgenic type it was indicated that the enzyme can contribute to the germination of seed by affecting the properties of the cell wall (Müller et al., 2013).

The production and activity of plant hormones is controlled by the expression level of relevant genes. Accordingly, differences in the germination of different seed cultivars are related to their gene complement. The other important factor that can determine the expression level of genes in specific plant tissues is their copy number and hence their necessary concentration required for their expression. These kinds of details can be used for the determination of genes functioning at different plant growth stages, as well as under stress (Miransari, 2012; Miransari et al., 2013a).

Using microarray analyses Ransom-Hodgkins (2009) recognized four genes related to the eukaryotic elongation factor (eEF1A) family, which are expressed during the germination of *Arabidopsis thaliana* seeds. These genes are also expressed in the embryos and the meristems of plant shoots and roots. Inhibiting the expression of any one of the four genes resulted in the formation of seedlings with stunted roots and the alteration of expression in the other three genes.

The protein eEF1A is a multifunctional protein necessary for the following: (1) protein translation, (2) binding actin as well as microtubules, (3) bundling actin, and (4) interacting with ubiquitin at the time of protein degradation (Ransom-Hodgkins, 2009). There are other functions performed by eEF1A, including a role in the pathway of various signals, such as phosphatidylinositol 4-kinase (Yang and Boss, 1994), and its role as a substrate for different kinase enzymes (Izawa et al., 2000). This protein can also regulate the activities of the DNA replication/repair protein network (Toueille et al., 2007) and play a role in apoptosis (Ejiri, 2002). There is a set of 2–15 plant genes producing eEF1A proteins (Aguilar et al., 1991).

There are some photoreceptors that are necessary for plant growth and development, including seed germination. For example, phytochrome B proteins, which are stable and found in green tissues (Quail, 1997) are able to regulate the hormonal signaling pathways of auxin and cytokinin (Tian et al., 2002; Fankhauser, 2002; Choi et al., 2005). Phytochromes in the seeds are necessary for controlling seed germination, especially when the seeds are subjected to light. Light activates phytochromes, as well as hormonal activities in plants (Seo et al., 2009).

Different methods have been used for the extraction of bio-chemicals, including plant and bacterial products affecting morphological and physiological processes related to seed development. Such discoveries in combination with the use of exogenously