

ROLE OF ABSCISIC ACID AND GIBBERELLINS WITH ENVIRONMENTAL CUES IN SEED DORMANCY AND GERMINATION

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Abstract

Seed dormancy and germination are two physiological characteristics that are intricately linked and have a significant impact on seed plant survival and adaptation. They are influenced by internal and external environmental factors. The amount of water, light, temperature and nitrogen all have an impact on seed dormancy and germination. The present state of knowledge on signal transduction pathways regulating seed dormancy and germination is summarized in this article.

1. INTRODUCTION

Orthodox seeds are tolerant to desiccation and remain in a dehydrated state for a certain time before the atmosphere favours the growth of the new generation ("Finkelstein, 2010"). The arrested state of viable seeds that are unable to germinate under adverse conditions called dormancy of seeds ("Bewley, 1997; Bentsink and Koornneef, 2008"). By monitoring and combining environmental cues, seeds may determine the timing of germination. ("Donohue et al., 2005"). Temperature is the most important environmental indicator that influences seed dormancy. "Seed germination is the most crucial developmental phase in a plant's life cycle since it determines subsequent plant survival." (Finch-Savage and Leubner-Metzger, 2006). To accurately predict the germination cycle, seeds need to sense and incorporate different environmental signals (Bewley, 1997). The most important environmental factors translated into internal signals are light, temperature and nitrate, which further trigger signal interaction between endogenous phytohormones, which in turn control seed dormancy and germination (Seo et al., 2009).

This article summarizes the mechanisms through which Abscisic acid and gibberellin signaling pathways regulate seed dormancy and germination via temperature, light, and nitrate/nitric oxide..

2. THE ROLE OF PHYTOHORMONES IN SEED DORMANCY AND GERMINATION REGULATION

Abscisic acid is progressively accumulated in the seed during seed growth, contributing to the formation as well as preservation of seed dormancy (Finkelstein, 2010). Abscisic acid-deficient mutants are generally non-dormant or less dormant, even viviparous, despite the fact that overexpression of abscisic acid biosynthetic enzyme producing genes increased seed dormancy. ("Lefebvre et al., 2006) (Kushiro et al., 2004; Okamoto et al., 2006 and Lin et al., 2007)". "ABSCISIC ACID INSENSITIVE 3 (ABI3)" loss of function, a positive abscisic acid signalling regulator, induces premature germination in Arabidopsis ("Raz et al., 2001"). "HONSU is one of the key negative regulators of abscisic acid signalling, with deep seed dormancy revealing its mutant, whereas overexpression results in shallow seed dormancy (Kim et al., 2013). Abscisic acid levels steadily decrease as a requirement for seed germination initiation during dry storage of the seeds (Weitbrecht et al., 2011). Abscisic acid levels in seeds rapidly fall after a few hours of imbibition under favorable conditions (Piskurewicz et al., 2008; Preston et al., 2009), whereas adverse conditions promote de novo endogenous abscisic acid formation (Piskurewicz et al., 2008 and Preston et al., 2009). 2012 (Chiu et al.)."Gibberellins are another important phytohormone that promotes seed germination. When seeds are ingested, the primary gibberellin biosynthetic genes, "GIBBERELLIN 3-OXIDASE 1 (GA3ox1) and GA3ox2", are significantly stimulated in the cortex and endodermis of the germinating seed embryo axis, resulting in de novo gibberellin synthesis in the embryo axis ("Mitchum et al., 2006 and Holdsworth et al., 2008"). Gibberellins-deficient mutants do not germinate without exogenous application of gibberellins ("Shu et al., 2013").

A mutation in the GA2ox2 catabolic genes of gibberellins results in greater amounts of GA4 and improved seed germination potential ("Yamauchi et al., 2007"). The timing of seed germination has been shown to be determined not by abscisic acid or gibberellin alone, but by the complex balance of the levels of endogenous abscisic acid and gibberellin in the seed ("Seo et al., 2009"). As a direct application of exogenous gibberellins, transcription of abscisic acid biosynthetic genes could be repressed and catabolic gene abscisic acid triggered ("Song et al., 2019"). Gibberellin treatment could potentially decrease abscisic acid levels by downregulation of LsNCED4 during germination induction in lettuce seeds (Sawada et al., 2008).

Abscisic acid suppresses endosperm rupture during seed germination initiation, while gibberellins encourage testa rupture and decrease abscisic acid levels. Stabilized DELLA proteins (“GAI, RGA, and RGL2”) overaccumulate in the seed at low gibberellin levels, thereby blocking testa rupture and encouraging biosynthesis of abscisic acid. (Piskurewicz et al., 2008 and 2009). DELLA proteins can induce XERICO transcription, thus promoting accumulation of abscisic acid (Zentella et al., 2007). By mediating the biosynthesis of abscisic acid and gibberellins, ABI4, the main component of the abscisic acid signalling route, positively regulates primary seed dormancy.

3. REGULATION OF SEED DORMANCY BY ENVIRONMENTAL CUES VIA ABSICISIC ACID AND GIBBERELLINS

Temperature:- Seasonal temperature variance during seed growth greatly influences seed dormancy depth at seed maturity (“Footitt et al., 2011”). Low seed growth temperature will increase the content of abscisic acid while decreasing the amount of gibberellins in Arabidopsis (Kendall et al., 2011 and He et al., 2014). Expression of abscisic acid synthesis (NCED6) and gibberellin catabolism (GA3ox2) genes is increased in winter when soil temperature decreases, resulting in increased levels of endogenous abscisic acid and decreased levels of gibberellin associated with enhanced seed dormancy (Finch-Savage and Footitt, 2017). DOG1, a significant quantitative trait locus, is only expressed in seeds. Its mutant lack of function reveals a phenotype that is largely non-dormant. (“Bentsink et al., 2006, 2010 and Graeber et al., 2014”). “As its transcript and protein levels display a strong association with temperature during seed maturation, DOG1 is a good predictor of the depth of seed dormancy, with lower temperature leading to greater DOG1 accumulation, which is correlated with increased dormancy of those seeds (Nakabayashi et al., 2012). Low temperature during seed maturation increases seed dormancy depth in Arabidopsis, while low temperature during seed imbibition promotes germination (Footitt et al., 2011 and He et al., 2014). Incubation of imbibed seeds, called cold stratification, at low temperatures (about 4 ° C) for a few days is therefore commonly used to break seed dormancy and encourage germination. Yamauchi et al. (2004) showed that cold stratification upregulates a subset of gibberellin biosynthesis genes (Kim et al., 2019), especially GA3ox1, a rate-limiting gene for gibberellin biosynthesis (Ogawa et al., 2003). Many alpha-expansin genes are gibberellin-inducible and involved in seed germination, localised in the micropylar endosperm (Yan et al., 2014). Cold stratification also releases seed dormancy through the impact on the metabolism and signalling of abscisic acid. On cold imbibition, abscisic acid content is decreased, gene expression levels of many components of abscisic acid signalling are also changed (Weitbrecht et al., 2011).” Germination potential is often hindered when seeds are soaked at temperatures above optimum. Thermoinhibition is called the suppression of germination at supraoptimal temperature (Gallardo et al., 1991). “High temperatures raise the susceptibility of lettuce seeds to abscisic acid because the application of fluridone is no longer effective in preventing thermoinhibition at 33 ° C”. (“Gonai et al., 2004”). Abscisic acid content in imbibed seeds is increased at high temperatures, resulting from upregulation of biosynthetic genes of abscisic acid and downregulation of catabolic genes of abscisic acid (Liu et al., 2019). The metabolism and signaling of abscisic acid and gibberellins, when combined, serve a critical function in suppressing seed germination at unfavorable supra-optimal temperatures (Matilla, 2000 and Toh et al., 2012).

Light: -Seeds can determine whether they are near the ground's surface by analyzing the quality and strength of the light signal. If seeds are buried too deeply, seedlings will be unable to commence photosynthesis before the energy molecules contained in the seeds are depleted. (“Ballaré et al., 1992 and Batlla and Benech-Arnold, 2014”). “Photoreceptors are used by plants to detect light. Arabidopsis has four distinct photoreceptor types, including phytochromes, cryptochromes, phototropins and zeitlupes (Bae and Choi, 2008). In darkness, phytochromes are synthesised in the Pr form. The Pr shape of phytochrome changes isomeric conformation into the Pfr form, which is the bioactive form, when exposed to red light (Quail, 2002).” Lee et al. (2012) showed that early upon imbibition, a pulse of far red light inactivates phytochrome-B in the endosperm and contributes to high levels of abscisic acid accumulation in the endosperm. “In seed germination, other phytochromes-A, C, D and E also play roles in (Hennig et al., 2002; Dechaine et al., 2009 and Arana et al., 2014). Red light decreases the endogenous abscisic acid content during imbibition in lettuce and Arabidopsis seeds (Sawada et al., 2008). The decreased content of abscisic acid is associated with down-regulation of genes for abscisic acid biosynthesis and up-regulation of the catabolic gene for abscisic acid in Arabidopsis (Kim et al., 2008).” Signalling light and abscisic acid converge during seed germination at “FAR-RED ELONGATED HYPOCOTYL3 (FH3) and FAR-RED IMPAIRED RESPONSE1 (FAR1)”, two primary components of the phytochrome-A pathway in Arabidopsis (Tang et al., 2013). By increasing endogenous gibberellin levels and gibberellin reactivity, red light partially encourages phytochrome-B-dependent seed germination. The expression of anabolic genes of gibberellins is enhanced by red light in conjunction with the increased levels of gibberellins, whereas the catabolic gene of gibberellins is repressed (Oh et al., 2006 and Yamauchi et al., 2007). “In order to inhibit its transcription, RVE1 can bind directly to the promoter of GA3ox2, and subsequently suppress bioactive gibberellin biosynthesis. Phytochrome-B down-regulates the expression of RVE1 and RVE2,

indicating that RVE1 and RVE2 function downstream of phytochrome-B" ("Jiang et al., 2016"). In the dark, the stabilised PIF1, an INTERACTING FACTOR1 that interacts with phytochromes, inhibits the germination of imbibed seeds when phytochromes are inactive. "Whereas Pfr types of phytochromes-A and phytochromes-B are translocated into the nucleus and interact with PIF1 in the sun, PIF1 protein is degraded via the ubiquitin-proteasome system and seed germination is encouraged (Oh et al., 2006). PIF1 mutant loss of function can germinate in the dark, while PIF1 overexpression lines require high light fluence for germination of seeds, suggesting that phytochromes encourage germination of seeds by deactivating PIF1 (Oh et al., 2006 and Shen et al., 2005)." In the meantime, by activating the expression of ABI3 and ABI5, the positive components of the abscisic acid signalling pathway, PIF1 can increase abscisic acid responsiveness (Kim et al., 2016).

Furthermore, two articles published in 2016 indicated that the phytochromes-B light sensor also functions as a thermosensor (or temperature sensor) in Arabidopsis organ elongation growth. "Warm temperatures, according to Legris et al. (2016), reduced the quantity of phytochromes-bioologically B's active Pfr-Pfr dimer pool. Faster thermal reversion of Pfr back to inactive Pr during warm nights resulted in the loss of phytochrome-B occupancy at these target gene promoters, alleviating the repression of PIF-dependent elongation growth and boosting elongation growth to protect plants from severe temperatures.(Jung et al., 2016). Arana et al. (2017) discovered that incubating dormant Arabidopsis seeds at 15 °C/23 °C in alternate temperature cycles improves germination in response to light." (Martel et al., 2018). Nitrate and Nitric Oxide: -Nitrate is a necessary nitrogen supply for plants, but it also acts as a signal molecule in many plant species.("Alboresi et al., 2005"). Nitrate probably regulates seed dormancy by impacting the metabolism of abscisic acid. During Arabidopsis seed imbibition, exogenous nitrate application contributes to lower abscisic acid levels in imbibed seeds (Matakiadis et al., 2009). It can also decrease the abscisic acid content in dry mature seeds when nitrate is given to the mother plants during seed growth (Matakiadis et al., 2009). Nitric oxide is created in Arabidopsis in the early hours of seed imbibition at the endosperm layer, leading in a rapid rise in the catabolism of abscisic acid, which is required for dormancy breaking("Liu et al., 2009").

Nitric oxide signaling may be primarily dependent on post-translational protein modifications such as cysteine "S-nitrosylation and tyrosine nitration". ("Delledonne, 2005 and Moreau et al., 2010"). It has been documented that key components of the abscisic acid signalling pathway are targeted for post-translational nitric oxide-dependent modification during nitric oxide action over seed dormancy, indicating a crosstalk between abscisic acid signalling and the nitric oxide pathway in this process ("Albertos et al., 2015; Castillo et al., 2015 and Wang et al., 2015a, b"). In Arabidopsis, the use of S-nitroso-N-acetyl-DL-penicillamine donor nitric oxide rapidly decreases the expression of ABI5 in the seeds (Albertos et al., 2015). (Gibbs et al., 2014).

Tyrosine nitration is a post-translational covalent alteration caused by protein-to-peroxynitrite (ONOO-) interactions or other nitrating agents that results in protein deactivation. (Monteiro et al., 2008). "PYR/PYL/RCAR abscisic acid receptors are nitrated in tyrosine residues under circumstances that produce both nitric oxide and reactive oxygen species. These receptors are then polyubiquitylated with nitrated tyrosines and degraded by the proteasome."(Castillo et al., 2015). Thus, by interacting with abscisic acid receptors and decreasing receptor activity by tyrosine nitration, nitric oxide adversely regulates abscisic acid signalling.

4. CONCLUSIONS

Dormancy of seeds is an ecological feature with far-reaching implications for the evolution of whole organisms. It is a preventive measure to prevent germination during adverse environmental circumstances. Long seed dormancy is bad for business, since it tends to prevent uniform germination and delay agricultural development, both of which are bad for crop output. Crop dormancy loss may lead to sprouting and decreased seed quality. As a result, seed dormancy control is critical to the success of seed farming and the industry. It is critical that we expand our understanding of the inherent processes underpinning seed dormancy.

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