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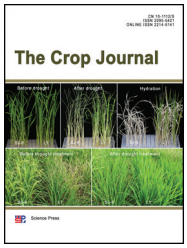


# Cell signaling mechanisms and metabolic regulation of germination and dormancy in barley seeds☆

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ABSTRACT

During germination of barley (*Hordeum vulgare* L.) seeds, important morphological and physiological changes take place, including development of organs and tissues and activation of metabolic pathways. Germination and dormancy of seeds are regulated by abscisic acid, gibberellins, reactive oxygen species (ROS), reactive nitrogen species (RNS) and several other factors. Activities of ascorbate–glutathione cycle enzymes, responsible for scavenging ROS, strongly increase. Catalase and superoxide dismutase activities, also scavenging ROS, decrease at the onset of seed germination and then increase. With the increase in aerobic metabolism after radicle protrusion, the activities of the fermentation enzymes lactate and alcohol dehydrogenase decline rapidly. The RNS-scavenging activity of S-nitrosoglutathione reductase decreases in the course of seed germination, in concert with elevation of nitric oxide production and protein nitrosylation. This activity supports the role of RNS in regulating seed germination. Transcription of various genes at different phases of seed germination exhibits phase-specific changes. During imbibition, genes involved in cell wall metabolism are highly expressed; in the middle phase of seed germination before radicle protrusion, genes involved in amino acid synthesis, protein synthesis, and transport and nucleic acid synthesis are upregulated significantly, and after radicle protrusion, genes involved in photosynthetic metabolism are induced. In summary, signal transduction and

*Abbreviations:* ABA, abscisic acid; ABI1, ABA-Insensitive 1; ABI5, ABA-Insensitive 5; ADH, alcohol dehydrogenase; APX, ascorbate peroxidase; CAT, catalase; cPTIO, 2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide; DHA, dehydroascorbate; DHAR, dehydroascorbate reductase; ELIPs, early light-inducible proteins; ETC, electron transport chain; FW, fresh weight; GA, gibberellic acid; GAMYB, GA-induced Myb (myeloblastosis)-like protein; GID1, GIBBERELLIN INSENSITIVE DWARF1; GID2, GA-insensitive dwarf2; GPCRs/GCRs, G protein-coupled receptors; GR, glutathione reductase; GSH, glutathione; GSNO, S-nitrosoglutathione; GSNOR, S-nitrosoglutathione reductase; GSSG, glutathione disulfide; *HvGA2ox*, barley *Gibberellin 2-oxidase1*; *HvHY5*, barley *Elongated Hypocotyl5*; *HvKAO1*, *Kaurenoic acid oxidase1*; HvPTR, barley scutellar peptide transporter; ICL, isocitrate lyase; LDH, lactate dehydrogenase; MDHA, monodehydroascorbate; LOV1, light, oxygen, or voltage-sensing domain 1; LOV2, light, oxygen, or voltage-sensing domain 2; MDHAR, monodehydroascorbate reductase; MS, malate synthase; NO, nitric oxide; PEP, phosphoenolpyruvate; PEPCK, phosphoenolpyruvate carboxykinase; *PHOT1*, *Phototropin 1*; PKABA, ABA-responsive protein kinase; PPDK, pyruvate phosphate dikinase; PSSG, S-glutathionylated proteins; PYR1, Pyrabactin Resistance 1; PYLs, PYR1-Like regulatory components; *PYR1*, *PYRABACTIN RESISTANCE 1*; RCAR, regulatory components of ABA receptor; RNS, reactive nitrogen species; ROS, reactive oxygen species; $SCF^{SLY/GID2}$, Skp1 (S-phase kinase-associated protein 1), Cullin, F-box; SDH, succinate dehydrogenase; SLR1, SLENDER RICE1; *SLY1*, *SLEEPY1*; SNP, sodium nitroprusside; SnRK2, subfamily 2 SNF1 (Sucrose-Nonfermenting Kinase 1)-related kinases; SOD, superoxide dismutase; SPS, sucrose-phosphate synthase; SUT, sucrose transporter; TCA, tricarboxylic acid

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metabolic regulation of seed germination involve diverse reactions and complex regulation at different levels of metabolic organization.



## Contents



## 1. Introduction

Germination and dormancy are vital elements in the plant life cycle. Bewley [1] defined seed dormancy as the incapacity of intact viable seeds to complete germination under favorable conditions. A more detailed definition of dormancy has been developed by Baskin and Baskin [2], who claimed that dormant seeds lack a capacity to germinate in a specified period of time under any combination of normal physical environmental factors that favor germination. Seed germination is a complex process influenced by many physical factors such as water, temperature, and light and by a great number of chemical factors such as ABA, GA, ROS, and RNS that play vital roles in regulation of dormancy [3,4]. Seed germination is initiated by water imbibition at appropriate temperature. During germination, NO content and the level of protein nitrosylation increase [5], exerting a major influence on seed germination, and various *S*-nitrosylated proteins control many kinds of redox-based regulation [6] such as reactions between protein thiols and thiol/disulfide exchange [7]. Although there are morphological differences between monocotyledonous and dicotyledonous seeds, the fundamental regulation of seed germination is similar in both groups of plants. In this review, barley seeds, consisting of seed coat, endosperm and embryo and thus typical monocotyledonous seeds, are used as the main example to describe signal transduction and regulation mechanism in the process of seed germination.

## 2. Seed germination

Seed germination is a complex process, starting from water uptake of dry seeds and continuing to elongation of the embryonic axis [8]. Weitbrecht et al. [9] separate the process of seed germination into three phases. Phase I, the early phase, includes imbibition of dry seeds and the early plateau phase of water uptake. Phase II, the middle phase, includes the plateau phase of water uptake and visible radicle protrusion through seed covering layers. Phase III, the later phase, is seedling development, also called the post-germination phase (Fig. 1-A). In monocotyledonous seed germination, the coleorhiza is the first part to grow out of the seed coat, whereas in dicotyledonous seed germination, roots (radicles) grow out of the seed coat first. During these processes, many physical and chemical reactions occur, including the rupture of endosperm and testa; leakage of cellular solutes; repair of organelles, membranes and DNA; and synthesis of DNA, RNA, and proteins. With imbibition, germination signal GAs stored in the embryo, mainly $GA_3$, are transported to the aleurone layer of the endosperm, which is rich in protein (Fig. 2). Hydrolytic enzymes including acid cysteine endopeptidases, serine carboxypeptidases, and neutral aminopeptidases [10,11], become activated in the endosperm, which contains aleurone cells that degrade storage proteins into amino acids (Fig. 2). $GA_3$ activates the expression of DNA encoding α-amylase in the aleurone cells, given that the GA-induced transcription factor GAMYB (GA-induced Myb (myeloblastosis)-like protein) can bind

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