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**\*Corresponding author:**

Madiha Zaynab;

**Email:**

madiha.zaynab14@gmail.com

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## Proteomics Approach Reveals Seed Germination Mechanism in Model Plants

**Madiha Zaynab<sup>1\*</sup>, Ali Noman<sup>2</sup>, Mahpara Fatima<sup>2</sup>, Tahira Saleem<sup>3</sup>, Safdar Abbas<sup>4</sup>, Ammar Raza<sup>5</sup>, Muhammad Naeem Iqbal<sup>1,6</sup>**

<sup>1</sup>The School of Life Sciences, <sup>2</sup>College of Crop Science, <sup>3</sup>College of Plant Protection, Fujian Agriculture and Forestry University, Fuzhou 350002, China.

<sup>4</sup>Department of Biochemistry Quid-e-Azam University, Islamabad, Pakistan.

<sup>5</sup>Department of Horticulture Bahaudin Zakrya University, Multan, Pakistan.

<sup>6</sup>Pakistan Science Mission (PSM), Noor Kot 51770, Pakistan.

**Abstract**

Seed germination is a complex process which occurs by the successful regulation of different factors necessary to regulate germination in a coordinated and sequential way, such as phytohormones. Among three phases of seed germination, the second phase is the most important due to reactivation of metabolic pathways. DELLAs accumulation in seed resulted in the expression of gene related to F box protein. Gibberellins receptor, GIBBERELLIN INSENSITIVE DAWRF1 (GID1) protein in rice, and F box are involved in Della degradation in the nucleus. In this mini-review, we summarize the protein related to the rice seed germination, such as protein related to energy and carbohydrate metabolism. In spite of several studies conducted to understand the genomic, transcriptomic, and metabolomics data still we are unable to understand the mechanism of seed germination. To uncover the underlying mechanism of germination, current challenges and future perspectives we write this review, which might be helpful to understand the complex process of seed germination.

**Keywords:** DELLA, Energy, Metabolism, Protein, Pathway, Translation.



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## INTRODUCTION

Seeds play a necessary role in the plant's life cycle because most of the plant's progenies are generated through seeds. It provides staple food for the world population. Recalcitrant seeds contain a high content of water and therefore they cannot be stored for a longer time but on the other hand, orthodox are dry and quiescent physiologically after ripening. They can keep their storage viability over an extended period. Germination can be defined as the process commencing with the uptake of water and ending at the radicle protrusion. Germination of seed can be divided into three phases but the most important and critical phase in the germination of the seed is the phase II as all the important metabolic pathways and physiological processes are reactivated in this phase (Bewley, 1997). Seed can germinate readily under favorable conditions in some species while in others; specific treatments are required for the dormancy breaking.

Exquisite mechanism evolved by the plants to protect the seed from damage and repair and seasonal dormancy is a most frequent phenomenon among them (Footitt *et al.*, 2011). Some genes related to ABA synthesis participate pre-harvest germination of rice seed (Fang *et al.*, 2008). During the early stages of germination, the late maturation process of seeds can be triggered again (Lopez-Molina *et al.*, 2002), which might deliver vivipary preventing knowledge. Numerous genetic factors have a significant role over tobacco seeds and on the longevity of rice (Agacka-Moldoch *et al.*, 2015; Miura *et al.*, 2002).

Proteomics has turned into a principal technology for the proteins high-throughput analysis on a genome-wide scale during the last decades. Quantitative protein data and sensitivity compared with that attained at the genetic level has become feasible through proteomics technologies. This advancement has a major association in the understanding cellular organization (Anderson *et al.*, 2000; Larance and Lamond, 2015). In rice proteomics, significant improvement has been made in the well-organized, functional characterization of proteins in the various tissues and organelles of rice (Komatsu and Tanaka, 2005; Neilson *et al.*, 2014).

Proteomic studies on germination of rice seed have been increased since the last decade. Germination of seed is a complicated process, despite this how those multiple events of seed germination are regulated in a sequential and coordinated way during the period of germination is basically mysterious. This review will assist in understanding the compact process of germination occurring in model plants such rice.

## Physiology of rice seed germination

Rice has a tiny embryo and comparatively large endosperm for nutrient accumulation. A well-known system

for rice germination is the consumption of starch in endosperm through GA-induced alpha-amylase expression (Han *et al.*, 2014; Li *et al.*, 2016). Starch in endosperm hydrolyzes into metabolizable sugars and provide the energy required for root and shoots growth (Jeon *et al.*, 2010; Zanella *et al.*, 2016). Previously, biochemical and physiological studies had revealed that the expression of  $\alpha$ -amylase occurs in the layer of aleurone. First, biosynthesis of active gibberellin (GA) commences in the embryo then GAs is transported from the embryo to the layer of aleurone (Huang *et al.*, 2017). Then,  $\alpha$ -amylase is released from the layer of aleurone into the endosperm to catalyze stored starch hydrating reaction (Hundertmark *et al.*, 2011). Some plants are capable of germination under anaerobic conditions and rice is one of them that can germinate through a rapid coleoptile elongation anaerobically (He and Yang, 2013; Miro and Ismail, 2013). But the radicle cannot grow well anaerobically, it protrudes well under aerobic conditions and continues to elongate which proposed that the availability of oxygen is another determinant feature for proper germination (Howell *et al.*, 2007).

## Role of Phytohormones

Phytohormones play a vital role in seed germination. Gibberellin (GA) and abscisic acid (ABA) have the most striking effects on the seed during germination. ABA is well known for its role in seeds dormancy, while GA has the reverse effect (Carrio-Segui *et al.*, 2016; Graeber *et al.*, 2010). The ABA inhibitory effects are through delaying the expansion of the radicle and weakening of endosperm in the seed germination. The enhanced expression of transcription factors affects the process of seed germination negatively (Graeber *et al.*, 2010; Xi *et al.*, 2010). The gibberellin repressor RGL2 has the capability to obstruct seed germination by giving rise to the production of ABA as well as the related transcription factors (Ibarra *et al.*, 2016; Roselló *et al.*, 2016; Zhong *et al.*, 2015). The H subunit of chloroplast protein, Mg-chelatase can act as ABA receptor during different stages of plant growth including germination of seed (Shen *et al.*, 2006; Zhang *et al.*, 2014). It has been reported that G-PROTEIN COUPLED RECEPTOR 2 can also act as another receptor of ABA, arbitrating different ABA activities including its effects on germination of seed (Liu *et al.*, 2007). Only one  $G\alpha$  (RGA1), one  $G\beta$  (RGB1), four putative  $G\gamma$  (RGG1, RGG2, DEP1/qPE9-1, and GS3) is present in rice (Subramaniam *et al.*, 2016; Urano, 2013). The mutant d1 in rice was identified as an RGA1 mutant. RGA1 disruption leads to the altered morphology with dwarfism erect leaves, and small round seeds (Sun *et al.*, 2014; Utsunomiya *et al.*, 2011). No RGB1 mutant has been identified in rice. Putative trans membrane protein encoding by GS3 was categorized as a major quantitative trait locus for the length of grain and weight in rice (Zhang *et al.*, 2015). Currently, it

has been revealed that qPE9-1/DEP1 is also engaged in the stress reaction of cadmium and ions of cadmium are also trapped by its C-terminal region (Kunihiro *et al.*, 2013). Besides this, two-hybrid assays in cells of yeast and bimolecular fluorescence complementation assays in leaf cells of tobacco exposed that DEP1 protein interrelates with both RGA1 and RGB1, and RGA1 reduced or enhanced the activity of RGB1 impedes responses of nitrogen (Sun *et al.*, 2014).

### DELLA proteins

DELLAs collection of seeds can result in the expression of gene producing F-box proteins. GIBBERELLIN INSENSITIVE DAWRF1 (GID1) protein interacts with proteins DELLA and eventually causing their degradation in the nucleus and can bind to the biologically active gibberellins (Ariizumi *et al.*, 2008; Willige *et al.*, 2007). Three receptors, GID1a, GID2b, and GID2c act as receptors of gibberellins in *Arabidopsis thaliana*. Activation of genes responsible for gibberellins affects the cell wall modifying proteins and hence responsible for endosperm weakening (Voegelé *et al.*, 2011). Moreover, ABA can prevent the endosperm weakening (Chen *et al.*, 2016; Linkies *et al.*, 2009). The embryo can have access to the seed endosperm, through some hydrolase enzymes activities, is made of starchy seed part and the surrounding aleurone (Bosnes *et al.*, 1992; Kawakatsu and Takaiwa, 2010; Ye *et al.*, 2015). Production of hydrolases and mainly amylase is stimulated as a result of gibberellins, resulting in the seeds germination. Such genes that are compelled for amylases production including proteases, amylase, and

glucanases, are induced by gibberellins (Yamaguchi, 2008).

### Metabolic pathway related proteins in rice

Protein is related to metabolism such as carbohydrate, glycolysis, Krebs cycle, gluconeogenesis and fermentation pathway, existing as a major protein in the germination of rice. In rice, endosperm starch exists as a principal reserve. All-important enzymes participate degradation of starch to hexose phosphate were present at 24 h of germination in rice seed but only  $\alpha$ -amylase abundance increased at phase II late stage. Other enzymes were not affected during the entire process of germination (Yang *et al.*, 2007; Chen *et al.*, 2016), which proposed that phase II lead to the degradation of starch metabolism. Pyruvate is the product of glycolysis. Proteins that play role in TCA cycle were up-regulated in rice (Table 2) (Yang *et al.*, 2007). Succinyl-CoA, malate dehydrogenase and ligase were steadily accumulated during germination (Kim *et al.*, 2009). Along with glycolysis TCA cycle might deliver the leading energy at the late stage of germination. Aerobic respiration was very low because of the scarcity of functional mitochondria.

Pathway of anaerobic respiration such as fermentation can be a primary energy source at the initial stage of germination, supported by pyruvate decarboxylase, lactate dehydrogenase and alcohol dehydrogenase identified during this stage (He *et al.*, 2011; Sharma *et al.*, 2016). In the germinating seeds, many enzymes belong to Pentose phosphate pathway (PPP) identified (Job *et al.*, 2005; Yin *et al.*, 2017).

**Table 1. Proteins involved in seed germination of rice**

Protein	Function	Reference
Aldehyde dehydrogenases	Carbohydrates metabolism	Hye Shin et al 2009
ATP synthase	Respiration	Ali Al-Ani, and Alain Pradet 1985
Citrate synthase,	TCA cycle	Dongli He and Pingfang Yang 2013
Malate dehydrogenase,	TCA cycle	Dongli He and Pingfang Yang 2013
Phosphoenolpyruvate carboxykinase	Glycolysis	Dongli He and Pingfang Yang 2013
Embryogenesis abundant protein	Stress response and development	Dongli He and Pingfang Yang 2013
lactate dehydrogenase (LDH)	Fermentation	(He et al., 2011a,b; Yang et al., 2007)
Pyruvate decarboxylase	Fermentation	(He et al., 2011a,b; Yang et al., 2007)
Alcohol dehydrogenase	fermentation	(He et al., 2011a,b; Yang et al., 2007)
Citrate lyase	Fatty acid biosynthesis	Gallardo et al. (2001)

### Mitochondrial protein

Seed germination, an energy-driven process, requires fully functional mitochondria and mitochondrial biogenesis is a complex process which is accompanied by persistent and dynamic expression of a gene, synthesis of protein and post-translational modifications. Mitochondrial proteins can

be divided into six key categories metabolism, respiration, tricarboxylic acid cycle (TCA), Import/Transport, stress response and chaperones (Czarna *et al.*, 2016; Murcha *et al.*, 2014). Many enzymes involved in mitochondrial metabolism are shown in the table (2).

**Table 2. High abundance enzymes in seed mitochondria and their importance in the process of seed germination.**

Protein	Function
Aldehyde dehydrogenase, monodehydroascorbate reductase, glyceraldehyde-3-phosphate dehydrogenase	Metabolism
Rieske protein, cytochrome c, the alpha and beta subunits of ATP Synthase	Respiration
the alpha and beta subunits of pyruvate dehydrogenase	TCA and carbon metabolism
E1, citrate synthase, malate dehydrogenase, phosphoenolpyruvate carboxykinase	
Tom40, voltage-dependent anion channel (VDAC), adenine nucleotide translocator	import/transport
manganese superoxide dismutase, late embryogenesis abundant protein	stress response and development

### Protein-protein interaction

Enzymes are key factors for most cellular processes and these enzymes are linked with each other forming temporary or stable complexes of protein complexes to enhance the efficiency, speed, and specificity of metabolic pathways. The composition and structural knowledge of these protein complexes can help to understand metabolic pathway and cellular processes because identities of these proteins are unable to deliver alone (Eubel *et al.*, 2005). After genomes sequencing, 1,429 protein kinases have been identified that play a fundamental role in regulating of different cellular processes in rice. It is clear that many kinases function through their interactions with other proteins (Ding and Goldberg, 2009).

### Phosphoproteome

Proteins labeling with  $^{32}\text{P}$  to detect phosphoproteins are the highly selective and sensitive technique (Larsen *et al.*, 2001). It is paramount to know proteins population at the state of phosphorylation at cellular or organelle level. Post Translation Modification (PTM) broader knowledge in the context of a functional cellular unit provides an understanding of inside cell changes. For the identification of phosphorylated proteins using *in vitro* protein phosphorylation, a technique like 2-DE followed by MS analysis. By phosphoproteomic germination analysis on rice embryo, 109 proteins were proved to be phosphorylation (Han *et al.*, 2013). Protein phosphorylation is involved in enhancement of stress response and phosphorylation proteins signal transduction activate during the initial germination stage, while stress response and storage protein phosphorylation were enhanced at the late stage. Phosphorylation of fructokinase, pyruvate kinase, malate dehydrogenase, GDP-mannose 3,5-epimerase1, ascorbate peroxidase and glutathione S-transferase can consistently enhance their activity its proved by enzyme assays.

### CONCLUSION

Considerable progress has been made in proteomics of model plants such as rice in the last two decades which provide an inclusive insight of the rice development. However, rice proteomics is still at preliminary stage. Data on the proteome of rice is available, but this data provides a broad description of the process of germination. Few databases had been constructed compared to *Arabidopsis thaliana* and soybean on rice proteome. it is essential to organize genome, transcriptome, and metabolomics data to understand the complex germination process in detail. Quantitative proteome study such as iTRAQ and label-free proteomics can help to understand the complex process of seed germination. Different pathways of rice seed should be studied one by one, it will provide detailed information about proteins and its functions related to seed germination process. Analysis of peptide of different pathways is very difficult but it will be a great achievement to understand the complex process of germination.

### CONFLICT OF INTEREST

The authors declare that no competing interests exist.

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