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Research article

Proteomics analysis reveals distinct involvement of embryo and endosperm proteins during seed germination in dormant and non-dormant rice seeds

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ABSTRACT

Seed germination is a complex trait which is influenced by many genetic, endogenous and environmental factors, but the key event(s) associated with seed germination are still poorly understood. In present study, the non-dormant cultivated rice Yannong S and the dormant Dongxiang wild rice seeds were used as experimental materials, we comparatively investigated the water uptake, germination time course, and the differential proteome of the effect of embryo and endosperm on germination of these two types of seeds. A total of 231 and 180 protein spots in embryo and endosperm, respectively, showed a significant change in abundance during germination. We observed that the important proteins associated with seed germination included those involved in metabolism, energy production, protein synthesis and destination, storage protein, cell growth and division, signal transduction, cell defense and rescue. The contribution of embryo and endosperm to seed germination is different. In embryo, the proteins involved in amino acid activation, sucrose cleavage, glycolysis, fermentation and protein synthesis increased; in endosperm, the proteins involved in sucrose cleavage and glycolysis decreased, and those with ATP and CoQ synthesis and proteolysis increased. Our results provide some new knowledge to understand further the mechanism of seed germination.

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1. Introduction

The ultimate role of seeds is to produce offspring and maintain species. Seed germination, therefore, is a crucial process in the seed plant life cycle, which determines when plants enter natural or agricultural ecosystems and is the basis for crop production (Weitbrecht et al., 2011; Nonogaki, 2014). Based on water uptake, seed germination can be divided into three phases, a rapid initial uptake (phase I), followed by a plateau phase (phase II), and finally a further increase in water uptake (phase III). Germination for phase I is regarded as imbibition, and for phase II, and germination sensu stricto in which the first seed germination is observed. The emergence of the embryonic axis through the structures surrounding it is considered as germination completed (Weitbrecht et al., 2011; Bewley et al., 2013).

Seed germination is a complex trait which is influenced by many genetic, endogenous and environmental factors (Joosen et al., 2013), and is driven by a lot of cellular processes, including

Abbreviation: 2-DE, two-dimensional gel electrophoresis; ABA, abscisic acid; AGT, alanine glyoxylate aminotransferase; AdePS, adenosine 5′-phosphosulfate; AspAT, aspartate aminotransferase; BADH, betaine aldehyde dehydrogenase; BBTI, Bowman-Birk type bran trypsin inhibitor; DTT, dithiothreitol; GA, gibberellic acid; GABA, γ-aminobutyrate; GDPME, GDP-mannose 3,5-epimerase; Glc-1-P, glucose-1-phosphate; Glc-6-P, glucose-6-phosphate; Gly-3-PDH, glyceraldehyde-3-phosphate dehydrogenase; GST, glutathione S-transferases; HAT, histone acetyltransferase; HSP, heat shock protein; IEF, isoelectrofocusing; IPMDH, isopropylmalate dehydrogenase; LEA, late embryogenesis abundant; MDA, monodehydroascorbate; ME, micropylar region of endosperm; MFT, MOTHER OF FT AND TFL1; MP, metallopeptidase; MS, mass spectrometry; NO, nitric oxide; PEBP, phosphatidylethanolamine-binding protein; Prxs, peroxiredoxins; RRM, RNA-recognition motif; ROS, reactive oxygen species; SOD, superoxide dismutase; SorDH, sorbitol dehydrogenase; TFA, trifluoroactic acid.

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transcription, translation, cell elongation, cell cycle activation, repair mechanisms and organellar reassembly (Weitbrecht et al., 2011; Rajjou et al., 2012; Han and Yang, 2015). It is well known that increase of gibberellic acid (GA) and removal or deactivation of abscisic acid (ABA) play an important role in seed germination (Nonogaki et al., 2010; Weitbrecht et al., 2011). Rosental et al. (2014) proposed that seed germination is regulated in a concerted manner that involves generating growth potential in the embryo to overcome the mechanical resistance of the endosperm. The micropylar region of endosperm (ME) surrounds the radicle tip and provides an opposing force to it, which is reduced during germination through weakening. The mechanical resistance of ME is mainly due to the thick and rigid cell walls in this tissue. Therefore, cell wall modification is thought to play an essential role in ME weakening (Bewley et al., 2013; Nonogaki, 2014). Although there is now much information with respect to changes in gene expression during germination, no key event(s) has been identified that results in completion of germination (Nonogaki et al., 2010).

Proteomic analysis is a very important tool that can be used to examine simultaneous changes in, and to classify temporal patterns of, protein accumulation occurring in seed development and germination (Huang et al., 2012; He and Yang, 2013; Wang et al., 2014, 2015a,b). Proteomic analyses associated with seed germination have been performed, including *Arabidopsis thaliana* (Gallardo et al., 2001, 2002a), tomato (Sheoran et al., 2005), rice (Yang et al., 2007; Kim et al., 2008; He et al., 2011a,b; Han et al., 2014a,b), maize (Lu et al., 2008; Fu et al., 2011), data palm (Sghaier-Hammami et al., 2009), *Jatropha curcas* (Yang et al., 2009), mungbean (Ghosh and Pal, 2012) and pea (Wang et al., 2012). In addition, the patterns of protein oxidation in Arabidopsis seeds during germination (Job et al., 2005), the proteomic analysis of the effect of salicylic acid on Arabidopsis seed germination and establishment of early defense mechanisms (Rajjou et al., 2006), the proteome modulated by GA and ABA (Kim et al., 2008) and affected by high temperature and ABA (Liu et al., 2015) during rice seed germination, and the effect of stored and/or de novo synthesized mRNAs on proteome from germinating seeds (Rajjou et al., 2004; Sano et al., 2012) have also been investigated. It has been proposed that many proteins were associated with seed germination, including those proteins involved in metabolism, energy, protein synthesis and destination, cell growth and division, cell defense and rescue, and storage protein (References cited in this paragraph), however, these proteins cannot still explain the well-known key events that result in seed germination. Moreover, in these studies, dry or imbibed seeds (or embryos) were used as control, some key proteins associated closely with seed germination, which occurred originally seeds, were ignored. Furthermore, embryo and endosperm are two distinct but interconnected seed parts, but how they communicate with each other and execute their functions in germination is not fully understood. Also, in most of studies mentioned above, whole seed or excised embryo was used as experimental materials, some important proteins involved in seed germination in embryos might not be detected because of a big size of endosperm or the roles of endosperm were looked down upon.

Wild rice is generally considered as a progenitor of the cultivated rice (Xie et al., 2010). It has been proven that wild rice (*Oryza rufipogon* and *Oryza glumaepatula*) seeds exhibited pronounced dormancy (Veasey et al., 2004). Bewley (1997) proposed that virtually all of the cellular and metabolic events that are known to occur before the completion of germination of non-dormant seeds also occur in imbibed dormant seeds, yet for some unknown reason, the embryonic axis (i.e., the radicle) of dormant seed fails to elongate. In this study, to identify the key proteins (events) associated with seed germination, the non-dormant cultivated rice (*Oryza stava* L. 'Yannong S') seeds were used as experimental materials, and dormant Dongxiang wild rice (*O. rufipogon* Griff.) seeds, and as negative control, we investigated the water uptake, germination time course, and the differential proteome of the effect of embryo and endosperm on seed germination by two-dimensional gel electrophoresis (2-DE) in conjunction with mass spectrometry (MS) of these two kinds of seeds. Our aims are to understand further the mechanism of seed germination and in that way provide new knowledge for promoting the germination of dormant seeds or preventing pre-harvest sprouting in seed and foodstuff production.

2. Materials and methods

2.1. Plant material

Cultivated rice (*O. stava* L. 'Yannong S', CRYS) and Dongxiang wild rice (*O. rufipogon* Griff., DXWR) seeds were planted in Liantang (28°54′ N, 115°93′ E; altitude, 28 m), Nanchang, Jiangxi, China, on April 10, 2013. The mature seeds at 30 d after flowering were collected and then dried at 25 °C and 50 ± 8% relative humidity (RH) for 5 d. When water content of CRYS and DXWR seeds was diminished respectively, to 11.7 ± 0.01% and 8.20 ± 0.01% (fresh weight basis), both kinds of seeds were sampled as experimental materials.

2.2. Water content determination

The water content of seeds was determined gravimetrically (80 °C for 48 h). Three replicates of 50 seeds each were sampled for water content determination, and water content of seeds is expressed in the percentage of fresh weight.

2.3. Water uptake by dry seeds

Three replicates of 50 seeds each were imbibed at 28 °C for different periods of time on two layers of filter paper moistened with 4 ml of distilled water in 90-mm diameter Petri dishes, and water contents of seeds were then determined and expressed on a basis of fresh weight.

2.4. Germination testing

Three replicates of 50 seeds each were incubated at 28 °C in darkness for 14 d on two layers of filter paper moistened with 4 ml of distilled water in closed 90-mm diameter Petri dishes. Germinated seeds were counted every 2–12 h, and radicle protrusion of 2 mm was used as the criterion for completion of germination.

2.5. Preparation of protein samples

The dry seeds and the 12 h-imbibed seeds were manually dehulled, and the embryos and endosperms were then carefully separated and frozen in liquid nitrogen, respectively. After that, 120 embryos (about 0.12 g of fresh weight) or endosperms (about 1.93 g of fresh weight) were ground in liquid nitrogen with mortar and pestle to a fine powder, and the powder was kept at −70 °C until used.

Three replicates of about 0.1 g embryo or 0.75 g endosperm powder each were homogenized in 1.5 ml precooled extraction buffer which contained 50 mM Tris–HCl (pH 7.5), 30% (w/v) sucrose, 10 mM ethylene glycol-bis (β-aminoethylether)-N,N,N′,N′-tetraacetic acid, 1 mM phenylmethylsulfonyl fluoride, 1 mM dithiothreitol (DTT) and 1% (v/v) Triton X-100. After washing the mortar with 0.5 ml extraction buffer, the total of 2 ml homogenate was centrifuged twice (at 16 000*g* at 4 °C for 10 min and at 32 000*g*

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