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Review

Proteomics of seed development, desiccation tolerance, germination and vigor

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ABSTRACT

Proteomics, the large-scale study of the total complement of proteins in a given sample, has been applied to all aspects of seed biology mainly using model species such as Arabidopsis or important agricultural crops such as corn and rice. Proteins extracted from the sample have typically been separated and quantified by 2-dimensional polyacrylamide gel electrophoresis followed by liquid chromatography and mass spectrometry to identify the proteins in the gel spots. In this way, qualitative and quantitative changes in the proteome during seed development, desiccation tolerance, germination, dormancy release, vigor alteration and responses to environmental factors have all been studied. Many proteins or biological processes potentially important for each seed process have been highlighted by these studies, which greatly expands our knowledge of seed biology. Proteins that have been identified to be particularly important for at least two of the seed processes are involved in detoxification of reactive oxygen species, the cytoskeleton, glycolysis, protein biosynthesis, post-translational modifications, methionine metabolism, and late embryogenesis-abundant (LEA) proteins. It will be useful for molecular biologists and molecular plant breeders to identify and study genes encoding particularly interesting target proteins with the aim to improve the yield, stress tolerance or other critical properties of our crop species.
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1. Introduction

Almost all plant cultivation in agriculture and horticulture is based on seeds. The vast majority of our domesticated plants are propagated via seeds and seeds provide most of our caloric intake either directly as food or indirectly as feed for our domestic animals. To feed the ever-growing human population we need to increase the productivity of our crop species by exploiting their full genetic potential in plant breeding. This requires that we understand the fundamental processes taking place in the seeds during their development, storage, germination and growth. An excellent overview of all aspects of seed biology is found in Bewley et al. (2013).

Seed development. The seed develops from a single fertilized zygote into an embryo and endosperm in association with the surrounding maternal tissues. Most seeds contain large quantities of nutrient reserves, mainly carbohydrates, oils, and/or proteins, which are biosynthesized and deposited during seed development. These reserves are not only important for seed germination and seedling growth, but are also vital components of human and animal diets. Their production in crops is the basis of agriculture. Before reaching maturity, the seed develops other important properties, including desiccation tolerance, germination/dormancy and vigor (Bewley et al., 2013).

Seed desiccation tolerance. Considered only in terms of tolerance of, or sensitivity to, desiccation, seeds can be categorized as orthodox or recalcitrant (Berjak and Pammenter, 2008). The orthodox seed acquires desiccation tolerance during seed development approximately halfway through development. This trait ensures that the seeds passes unharmed through maturation drying and

Abbreviations: ABA, abscisic acid; ADH, aldehyde dehydrogenase; APX, ascorbate peroxidase; CAT, catalases; Cys, cysteine; DAF, days after flowering; DAP, days after pollination; GA, gibberellic acid; GC, green carbohydrate abundant; GO, green oil abundant; GPX, glutathione peroxidase; HSP, heat shock proteins; LEA, late embryogenesis abundant; LHC, light harvesting complex; MDHR, monodehydroascorbate reductase; Met, methionine; MV, methylviologen; NGO, nongreen oil abundant; PDC, pyruvate dehydrogenase complex; PEG, polyethylene glycol; Prx, peroxiredoxin; PSII, photosystem II; PTM, post-translational modification; ROS, reactive oxygen species; Rubisco, ribulose bisphosphate carboxylase/oxygenase; SAM, S-adenosylmethionine; Ser, serine; SOD, superoxide dismutase; TCA, tricarboxylic acid; TPX, thioredoxin peroxidase; Tyr, tyrosine.

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retains viability in the dry state for long periods of time (up to hundreds of years in some case) under natural or artificial conditions (Kermode and Finch-Savage, 2002). In contrast, the recalcitrant seed is desiccation sensitive and can not survive drying during ex situ conservation (Berjak and Pammenter, 2008). This creates a serious problem in the conservation of recalcitrant species. Many species with recalcitrant seeds are economically important, such as avocado, mango, lychee, cocoa, coffee, citrus, and rubber.

Seed germination. Seed germination is the most critical phase in the seed plant life cycle. It determines when the plant enters natural or agricultural ecosystems. Cultivation of most crop species is dependent on seed germination. Seeds of most species acquire the ability to germinate during development. This is important for crop production, because it ensures that the untreated seed quickly germinates after sowing. However, in a few species, such as maize, wheat and rice, it can result in precocious germination, which typically occurs when developing seeds with a low degree of dormancy experience rainfall or humid conditions (Bewley et al., 2013). Precocious germination can decrease the grain quality and cause great economic losses. In some species, seeds are dormant at the end of development. Seed dormancy is defined as the failure of an intact viable seed to complete germination under favorable conditions (Bewley, 1997). It is an adaptive strategy for seed to survive under adverse natural conditions, but it also creates an obstacle for agricultural production, where rapid germination and growth are required.

Seed vigor. Seed deterioration occurs always during storage of orthodox seeds, resulting in the gradually loss of vigor and even death. For crop species, preventing or minimizing the loss of vigor during storage is critical for the production in the subsequent seasons. Seed longevity is dependent on storage temperature and moisture (Walters et al., 2005). Seed priming, imbibing seeds in water or chemicals, such as PEG, for a period of times followed by dehydration, is utilized commercially to increase seed vigor (Heydecker et al. 1973; McDonald, 2000).

Seed proteomics. The great biological and economic importance of seeds has led to a vast number of studies of all the above aspects of seed biology. One type of study is proteomics, the study of all the expressed proteins. Since proteins are responsible for most metabolic processes in the seed, in addition to being important structural components in the cytoskeleton, membranes, the cell wall, etc., it makes excellent sense to describe the proteome of a seed, a seed tissue, a specific cell type or a subcellular compartment. However, proteomics are also a powerful tool for detecting changes in the protein composition in response to developmental or environmental stimuli, so-called differential proteomics. In other words, proteomics can be used analytically rather than descriptively to identify proteins associated with, and therefore probably important for, specific processes and specific responses. This will be the focus in the present review – qualitative and quantitative changes in the seed proteome during the life cycle of the seed.

We will start by giving a very brief overview of the methods used to study seed proteomics. We will then review the proteomics of seed development, desiccation tolerance, germination and dormancy release and vigor. Finally, we will attempt to give some perspectives.

1.1. Proteomic methods

The seed proteome can be analyzed like any other proteome using the standard general procedure of protein extraction, separation and identification. The sampling is, as always, the basis for obtaining meaningful results. As discussed by Miernyk (2014) this is not a trivial point: The seed part to be analyzed needs to be considered carefully in relation to the question asked. It is also essential to ensure the physiological (developmental stage) and genetic uniformity of the seeds sampled.

The dynamic range for protein amount may be as high as 10^{10}–10^{12} whereas the dynamic range for the analytical methods are much lower perhaps only 10^3–10^4 (Hortin and Sviridov, 2010; Miernyk, 2014). It can therefore be an advantage to remove the superabundant storage proteins during protein extraction or during the early stages of separation in order to improve the chances of detecting lower-abundance proteins (Miernyk and Hajduch, 2011).

Gel-based methods for separation – particularly two-dimensional polyacrylamide gel electrophoresis (2D-PAGE) – have dominated and will probably continue to dominate because, in addition to being reasonably quantitative, they provide a lot of information about the proteins not provided by the gel-free shotgun methods, such as changes in protein size, *pI*, and post-translational modifications (PTMs) (Rogowska-Wrzesinska et al., 2013). This is always useful information, and particularly so for species where the genome has not yet been fully sequenced.

Mass spectrometer-based methods for protein identification have dominated completely in recent years also in seed proteomics, but the methods have been extensively reviewed recently (e.g. Pan et al., 2009; Walther and Mann, 2010; Bantscheff et al., 2012; Rogers and Overall, 2013) and since they are essentially independent of species (except for the question of access to a full genome sequence), they will not be reviewed here.

1.2. Pitfalls in the use of 2D-PAGE and other quantitative proteomic methods

Although 2D-PAGE is reasonably quantitative, a note of caution is in order concerning the way it is routinely used. The standard procedure is to extract all proteins from a series of samples, for instance a time series during seed development. The same fixed amount of protein (typically 100–500 μg protein) from each sample is then separated by 2D-PAGE and, when the gels are stained typically using Coomassie Brilliant Blue or silver nitrate, the total staining on all the gels is very similar. A total of 500–1000 discrete spots are typically discernable, where each spots normally represents one dominant unique protein. When a change in the number of pixels in a given spot is observed between different samples, it is then concluded that the amount of that protein has changed. Contrariwise, if no significant change in the number of pixels in a given spot is observed between different samples, it is concluded that the amount of that protein has not changed. Both of these conclusions can actually be wrong!

The problem is that the standard procedure for sampling and loading outlined above ensures that the number of pixels in a spot represents not the absolute amount of protein in the sample, but the fraction of the sample protein contributed by that protein.

To appreciate this point, let us consider two extreme cases in seed biology:

(1) The composition of the proteome changes strongly, e.g. due to biosynthesis of storage proteins. This happens during the reserve deposition stage. Let us assume that the storage proteins go from constituting 10% of the total protein in the seed to 40% between two samples, while all the rest of the proteins in the seed are present in unchanged amounts. This means that the non-storage proteins will make up 90% in the first sample, but only 60% in the second. As a result all their spots will therefore decrease in size to 60%/90% = 0.67 of their original size (a decrease by a factor 1.5). The relative amounts of the non-storage proteins have changed, in spite of the fact that there was no change in the absolute amounts of those proteins!

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