Seed Biology in the 21st Century: Perspectives and New Directions

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Background
Seeds are a fundamental component of the plant life cycle, as they store the genetic information necessary for the next generation of plants to disperse, establish, develop and eventually reproduce to maintain the species. However, these mysterious genetic capsules contain many secrets that have yet to be revealed. For instance, the mechanism(s) by which certain seeds undergo extreme desiccation without losing viability remain unclear. Further, the molecular network of genes conferring on seeds the ability to remain dormant for the required periods of time has yet to be fully elucidated. This special focus issue is dedicated to the latest research on seed biology aimed at tackling some of these unanswered questions.

The need for basic and translational seed research
Seeds are consumed directly as food and animal feed, providing >70% of world’s caloric intake. As the global population exceeds 7 billion, efficient production of seeds as a reliable food source is becoming ever more important; continuous modification of seed crops to enhance the yield and nutritive values of seeds is essential to tackle existing world hunger and poverty, and to relieve the pressure of even higher worldwide demands for food foreseen in the future. This theme is explored in the review by Martı́nez-Andújar et al. (pp. 5–15), where they argue the need for determining the genetics of seed de-velopment and the chemistry of seed reserves as an essential step in developing new technologies to accelerate crop improvement and ensure food security. For instance, seed companies have been ‘stacking’ elite genetic seed traits, such as insect resistance and high yields, through breeding programs. More recently, the utilization of seeds as a source of bioenergy is another important focus, which is not only limited to the replacement of fossil fuel in developed countries but also plays a significant role in aiding the local economy and improving quality of life in developing countries. For example, in the southern Malian town of Garalo, Africa, farmers cultivate 600 ha of land with jatropha (Jatropha curcas) seeds whose oil provides electricity to 350 homes—roughly half of Garalo’s population—and also powers street street light (Gilbert 2011). Modification of seeds particularly for small farmers and local production is another area of study that is yet to be fully explored; however, this is now only possible with the emerging new technology and resources available for genomic and genetic studies in plants.

Seed research in the post-genomic era
As new plant genome sequences are released almost every year, functional genomics has contributed significantly to the remarkable progress of seed biology research. Seeds sense fluxes in many different environmental factors, thereby using this information to determine whether they germinate or not. Seed germination can thus be considered a response with a simple output (i.e. embryo emergence) requiring multiple inputs (e.g. developmental programs or environmental factors.). Post-genome methodologies, such as analyses of transcriptomes, proteomes and metabolomes (Mochida and Shinozaki, 2011), have advanced our knowledge and holistic understanding of seed germination. As such, the conventional simple output system has been changed to a modern, multiple-output system to permit identification of differences in cellular status among imbibed seeds under various environmental conditions. Arabidopsis was the first genome-sequenced plant, and continues to play a key role in addressing fundamental questions on basic biology. Transcriptome analysis of Arabidopsis seeds has fueled remarkable progress in seed biology, and equipped researchers with reference gene expression data regarding temporal (Nakabayashi et al. 2005, Spencer et al. 2007, Preston et al. 2009, Le et al. 2010) and spatial (Penfield et al. 2006, Day et al. 2008, Linkies et al. 2009, Le et al. 2010) expression patterns, and phenotyping of seed mutants (Ogawa et al. 2003, Carrera et al. 2007, Okamoto et al. 2010, Yamamoto et al. 2010). In this issue, Endo et al. (pp. 16–27) report the tissue-specific transcriptome analysis of dissected embryo and endosperm from imbibed Arabidopsis seeds. While the morphology of endosperm has diversified in seeds of different plant
species, the degree of functional conservation remains elusive. The development of new methodologies to facilitate interspecies comparative analyses would, for example, be useful to determine whether the genes required for endosperm weakening, which is an important mechanism of germination in seeds containing hard and thickened endosperms (e.g. in tomato), play orthologous roles in other less persistent seed endosperms. On pp. 28–37 of this issue, Dekkers et al. (2012) report evaluation of control genes for quantitative real-time PCR analysis on Arabidopsis and tomato seeds through data mining of public microarray database and experimental validation.

The analysis of proteins at different stages of seed development, dormancy and germination has provided invaluable information about the biochemistry of such processes. For instance, proteome analyses uncovered the importance of protein synthesis during seed germination (Rajjou et al. 2004), as well as factors involved in seed viability and longevity (Rajjou et al. 2008), while metabolome profiling has shown that a metabolic switch is an important aspect of seed maturation and germination (Fait et al. 2006). Targeted metabolite analyses of Arabidopsis seeds have thus far elucidated molecular mechanisms of biosynthesis and accumulation of secondary metabolites, such as mucilage, glucosinolates and flavonoids (Kliebenstein et al. 2001, Lepiniec et al. 2006, Macquet et al. 2007). In this issue, Bai et al. (pp. 38–52) utilized targeted and non-targeted metabolome analysis to compare metabolite changes in seeds of four Arabidopsis accessions after repetitive hydration–dehydration cycles. This treatment mimics natural seed imbibition in soil where precipitation, dew formation and dehydration occur with an unpredictable regime. They found a set of metabolic changes associated with certain germination properties in response to hydration–dehydration cycles. This work demonstrates how powerful metabolomics can be for answering outstanding questions related to whole-seed germination physiology.

A major goal for modern seed biology is to unravel the complex interplay of plant hormones and novel signaling molecules to regulate germination and to determine signal transduction mechanisms in seeds. In recent years, targeted analysis of plant hormones has revealed novel aspects of seed physiology and the complex metabolic balance between multiple plant hormones during development and germination (Chiwocha et al. 2005, Preston et al. 2009, Kanno et al. 2010). An important finding is that various environmental factors alter metabolism and signaling of ABA and gibberellins (GAs; Seo et al. 2009, Nabara et al. 2010). This suggests that these hormones trigger the simple output of seed germination. In this issue, articles by Fernández-Arbaizar et al. (pp. 53–63) and Rodriguez et al. (64–80) uncover further information about the roles played by these hormones in Arabidopsis and sorghum seeds, respectively. Fernández-Arbaizar et al. (2012) report a study on ABA–jasmonate (JA) cross-talk. They developed a novel genetic screen to obtain suppressor mutants of the ABA-hypersensitive phenotype of coi1-16 mutants. This screening identified four novel CRA (coi1-16 resistant to ABA) loci distinct from known ABA-INSENSITIVE (ABI) loci, some of which were also identified as expected targets in their screen. Further characterization of the CRA genes promises to fill a gap in our understanding of ABA–JA cross-talk.

On pp. 64–80, Rodríguez et al. (2012) investigate GA metabolism in pre-harvest sprouting-resistant and -sensitive varieties of sorghum. This group previously reported hormonal regulation of seed germination in various cereal seeds. Greater knowledge of germination mechanisms in different plant species will be useful for genome-wide comparative studies in the future. The effects of chemical substances on GA action and signaling events in seeds is reported on pp. 81–95 by Oracz et al. (2012), who show that myrigalone A, a C-methylated dihydrochalcone, inhibits seed germination of garden cress through blocking both metabolism and signaling of GA as well as reactive oxygen species (ROS) accumulation. Myrigalone A is a natural compound found in the leachate of Myrica gale L. fruits, where it probably acts as a putative allelochemical or natural herbicide that impedes cell extension, thus preventing germination and seedling establishment.

The production of ROS is the focus of a study by Leymarie et al. (pp. 96–106), who utilized pharmacological, genetic and cell biology to identify it as a key process in Arabidopsis seed germination. Specifically, ROS were found to accumulate in two different subcellular compartments: the cytosol and the nucleus. Intriguingly, ROS accumulation within both sites differs with time, which may be indicative of multiple and distinct functions played by this signaling molecule during seed germination. Finally, Toh et al. (pp. 107–117) report that strigolactone auxotroph and signaling mutants of Arabidopsis show thermaninhibition-tolerant seed germination. Comprehensive hormone measurements were performed in germinating Striga seeds and compared with hormonal profiles during Arabidopsis seed germination to reveal the interaction of strigolactone with other plant hormones.

**Perspective**

Despite the current progress in seed biology, many important questions still need to be answered, including what are the cellular processes by which seed reserves important for vigor and longevity accumulate? What are the factors affecting seed dormancy and after-ripening? Moreover, as discussed in Martínez-Andújar et al. (2012), it is important to translate existing knowledge into agricultural outputs. This can only be achieved through the development of highly sensitive modern technologies, some of which are already in progress and can be applied to study more complex seed responses, such as how cereal grain filling is influenced by environmental and maternal factors. Indeed, the emergence of post-genome methodologies has already circumvented some barriers that had previously blocked the translation of knowledge from model plants to other plant species, and it is anticipated that this trend will continue into the next decade especially in light of current...
progress in generating crop functional genomic resources (Gallardo et al. 2007, Catusse et al. 2008, Barrero et al. 2009, Okabe et al. 2011). In particular, meta-genome analysis allows comparative studies that address the origin and cause of diversity in seed morphology and physiology. The integration of such methodologies and technologies is anticipated to result in novel concepts and dynamic models in seed biology. This special focus issue is designed to provide PCP readers with a snapshot of the exciting new era in seed biology research. PCP has published many excellent works in this field over the years, and it is true to say that the best is yet to come.

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**References**


