

# Systems biology of seeds: deciphering the molecular mechanisms of seed storage, dormancy and onset of germination

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**Abstract** Seeds are heterogeneous storage reserves with wide array of storage compounds that include various soluble carbohydrates, starch polymer, storage proteins and lipids. These stored reserves comprise 70% of the world's caloric intake in the form of food and animal feed produced through sustainable agriculture, which contributes to food and nutritional security. Seed systems biology remains an enigmatic subject in understanding seed storage processes, maturation and pre-germinative metabolism. The reviews and research articles covered in this special issue of Plant Cell Reports highlight recent advances made in the area of seed biology that cover various systems biology applications such as gene regulatory networks, metabolomics, epigenetics and the role of micro-RNA in seed development.

A developing seed consists of triploid endosperm and diploid embryo, which are enclosed by the maternal seed coat. In dicots, the embryo encompasses most of the space in the seed along with major lipid and protein reserves (Borisjuk et al. 2013). In cereals, the endosperm is the major storage sink where starch and storage proteins are accumulated (Olsen 2001). Vast seed genomics resources have been created from various model organisms (North et al. 2010; Olsen 2001; Sreenivasulu and Wobus 2013). The systems biology strategies provide an opportunity to discover complex developmental processes of seeds and decipher holistic molecular mechanisms using large-scale genomics data,

transcriptome, metabolome, proteome, non-coding RNAs and epigenetics (Chen et al. 2014; Francki et al. 2016; Le et al. 2010; Li et al. 2016; Wan et al. 2016; Yang et al. 2016). Such top-down systems biology is concerned with the identification of the structure of the molecular network that underlies system behavior. Integration of multiple '-omics' data is required to reconstruct complex networks that characterize the phenotypes in the cell. This leads to the identification of central hub regulatory genes that influence seed storage, maturation, dormancy and transition to seed germination. Exploring central hubs of regulatory networks involved in key transcriptional reprogramming events that assure phase transitions during seed storage is a central component to identify key hub genes that could potentially be used to manipulate seed metabolism (Belmonte et al. 2013; Sreenivasulu et al. 2006). Systems biology approaches combined with flux and spatial data using nuclear magnetic resonance can be used to systematically reveal the molecular mechanisms of seed biology and to decipher the metabolic rate limiting steps influencing seed storage metabolism (Borisjuk et al. 2013; Gupta et al. 2017; Sreenivasulu et al. 2010). Latest advances in seed oil and protein synthesis in dicots pointed out that the efficient conversion of sucrose to glycolysis intermediates in conjunction with higher copies of fatty acid synthesis genes in canola compared to that in soybean might be the causal factor of higher accumulation of oil in canola over soybean (Gupta et al. 2017).

Methionine a sulfur-containing essential amino acid is elevated in Arabidopsis seeds by suppressing *Cystathione  $\gamma$ -synthase (CGS)* gene, where the RNAi::AtCGS transgenic seeds showed reduced expression (Cohen and Amir 2017). The elevated methionine level in RNAi::AtCGS seeds supports the hypothesis that methionine is synthesized de novo in seeds by decreasing carbon/amino

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availability in the aspartate pathway using *CGS* regulatory enzyme. Alternative route to increase methionine in seeds is that a precursor of *S*-methylmethionine (SMM) that is synthesized in vegetative tissues and transported into the seeds via the phloem, is converted to methionine through homocysteine *S*-methyltransferase *AtHMT3* (Cohen et al. 2017). The data obtained by these two studies shed interesting insights into the functional role of the SMM cycle in seeds and also provided an idea on how to exploit an intrinsic property in the aspartate pathway to manipulate the methionine level in developing seeds.

Small non-coding RNAs are important regulators that control distinct phase transitions such as cellularization (miR165, miR394), seed storage (miR156, miR160) and dormancy (miR159, miR172) during seed development (Rodriguez and Miguel 2017). Liu and El-Kassaby (2017) used small RNA sequencing to identify 14 candidate microRNAs that included a novel miR8172 family that was characterized to be involved in seed storage and dormancy. They highlighted the roles of miR159 and miR319 in regulating the *GAMYB* transcription factor under the cascade of gibberellic acid responses during the breaking of seed dormancy. The importance of abscisic acid/gibberellic acid signaling network in controlling seed maturation and seed germination processes, respectively, has been reviewed through systems biology implications (Yan and Chen 2017). The current state of the field of pre-germinative seed biology through genomics and reverse genetic approaches has been captured (Macovei et al. 2017). The review highlighted the implications of reactive oxygen species and interconnections to hormones in transitioning from mature to pre-germination events. In addition, basic scientific findings were put into the context of agricultural application by creating links to current trends in seed technology such as seed priming. Results of comparative proteomics studies for instance showed that the accumulation of vicilin during the pre-treatment of two defense elicitors  $\beta$ -amino butyric acid and  $\gamma$ -amino butyric acid in citrus seed germination under salt stress conditions reversed salt stress impediment and improved germination vigor (Ziogas et al. 2017). Two additional studies unraveled the salt tolerance mechanisms through epigenetics (Pandey et al. 2016) and proteomics (Parveda et al. 2017).

The key target genes identified through systems biology approaches need to be subjected to functional validation. CRISPR/Cas9 and CRISPR-Cpf genome editing tools may be used to create mutants where target genes are silenced. Yin et al. (2017) used this technology to knockout *EPFL9*, a positive regulator of stomatal development. The future scope of seed biology will be to validate the rate limiting enzymes and key regulatory targets influencing seed storage components by characterizing the functional mutants through systems approaches and revalidate the models to

engineer seed sink for translational health benefits of consumers. It would not have been possible to bring this special issue without the due help of Editor-in Chief (Dr. G. Hahne and Dr. J. R. Liu) and managing editor Dr. B. Hahne and support team. Their support is greatly appreciated.

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