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Review

Genomics of seed development: Challenges and opportunities for genetic improvement of seed traits in crop plants

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ABSTRACT

Seed development represents an important phase in the life cycle of flowering plants including the majority of the crop plants. During this phase, developmental and metabolic programs are coordinated to produce the seed that contains the germline information and storage reserves. Although seed developmental patterns vary significantly between the monocots and dicots, they share several conserved developmental programs. The embryo is the major component of the seed in dicots whereas the endosperm is predominant in monocot seeds. The formation of the dormant seed that protects the embryo and provides nutrition during germination is a key characteristic adaptive feature in the evolution of the angiosperms and a determining factor of yield in crop plants. From a crop perspective, the metabolites and especially the storage products deposited in the seed defines the value of the seed. Despite progress in fundamental understanding of seed development, the global genetic and metabolic programs involved in the making of the seed and their implications to genetic improvement of the seed is yet to be fully exploited in crop plants. So, the major goal of several recent studies is to develop comprehensive systems-level insights into molecular and biochemical programs associated with gene expression, protein and metabolite profiles during seed development in model and crop plants. These integrated systems approaches and studies are producing foundational and comprehensive datasets. In this review, we will present an overview of advances in the developmental, genetic and genomic studies of seed biology and their implications to improve seed characteristics in crop plants.

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1. Introduction

The demand for food production is predicted to increase by 70% between now and 2050 based on the projected worldwide population growth (FAO, 2009; Van der Mensbrugghe et al., 2009). To meet this challenging goal, major advances are required in global food production and security along with addressing difficulties posed by climate change and other adversities (Beddington, 2010). Human nutrition is heavily reliant on seeds in the form of cereal grains, oilseeds and legumes as a source of carbohydrates, lipids and proteins. An estimated 50% of global human dietary calories are provided by the cereal grains (FAO Yearbook 2012; http://www.fao.org/).

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Dietary intake of livestock products is also partly dependent on seed-based feeds. Thus, increased seed production is the major activity in agriculture to ensure required food supply. To achieve this, a deeper understanding of seed biology is essential to enable further improvements in seed related quantitative and qualitative traits in crop species.

A typical seed is a complex organ system comprising of the embryo that contributes to germline continuity, the endosperm for nourishment and the seed coat for providing protection. The embryo and the endosperm are products of double fertilization whereas the seed coat that develops from the maternal integuments protects the filial tissues during development and dormancy phase of the mature seed. The first phase of seed development is morphogenetic during which genetic programs regulate the zygote to undergo well-ordered series of divisions to establish the embryonic body plan, whereas the endosperm initial cell undergoes repeated divisions to form the nutritive tissue (Fig. 1). This is followed by the maturation phase, during which the seed accumulates storage products such as carbohydrates, lipids, proteins and several important nutrients including vitamins and minerals; and undergo desiccation to initiate the dormancy phase (Jenik et al., 2007; Sreenivasulu and Wobus, 2013) (Fig. 1). Seed formation is therefore an intrusive phase selected during evolution to enable preservation of the embryo and the nutritive endosperm until the right environmental conditions are available for seed germination (Vicente-Carbajosa and Carbonero, 2005). In dicots, the embryo is the major storage organ, for example in the case of legumes and oil seeds, whereas in the monocots that includes cereals, the persistent endosperm functions as a reservoir for storage compounds.

Although the development and metabolic pathways of seeds have been studied in many species, fundamental advances have been made possible because of concerted efforts focused on model plant species, such as *Arabidopsis* in dicots and maize and rice in monocots (Bevan et al., 2010; Jung et al., 2008; North et al., 2010; Xing and Zhang, 2010). These species served as ideal experimental model plants because of the availability of extensive developmental, genetic, molecular and genomic knowledge and resources. Their diploid status further allowed large-scale mutant screens (forward genetics); synteny of their genome sequence with other related crop species facilitated assigning gene functions (reverse genetics). Together these paved the way for more recent studies of functional genomics and assignment of biological roles to a large number of identified genes (Flavell, 2009). A comprehensive understanding of the regulation of gene expression and metabolism during seed development in *Arabidopsis* has also laid an important foundation on which relevant functional genomics approaches are beginning to capture more applied insights especially by exploiting recent progress coming from the sequenced genomes of several crop species (Bevan and Uauy, 2013; Edwards et al., 2013; Hirsch and Robin Buell, 2013).

Our dependence on seed crops, which is the foundation of agriculture, has guided the progressive improvements in seed related traits via breeding and by exploitation of crop germplasm resources (Olsen and Wendel, 2013). Among the seed phenotypes and characteristics that contribute to crop productivity and performance, seed size, number, and nutritional quality are very important. Other seed related traits include reduced pod shattering to prevent seed dispersal, reduced seed dormancy, and uniform seed maturation and germination are also important for overall crop performance (Martínez-Andújar et al., 2012; Sreenivasulu and Wobus, 2013). Although significant advances have been made addressing these critical aspects during the green revolution, human population growth and demand for fuel coupled with climate change has placed an increasing pressure on agriculture to accelerate productivity to meet food, feed and biofuel needs (Fedoroff, 2010). This will require application of new emerging technologies and approaches in addition to the conventional plant breeding practices. The emergence of genomic technologies that explores biological systems and processes at a larger scale and in greater depth, are beginning to advance critical knowledge base and new insights into the biology of seed development and metabolism. Concerted efforts of integrating these new genomic tools with breeding are also leading to the development of new strategies for improvement of seed traits (Sreenivasulu and Wobus, 2013; Tester and Langridge, 2010). Since

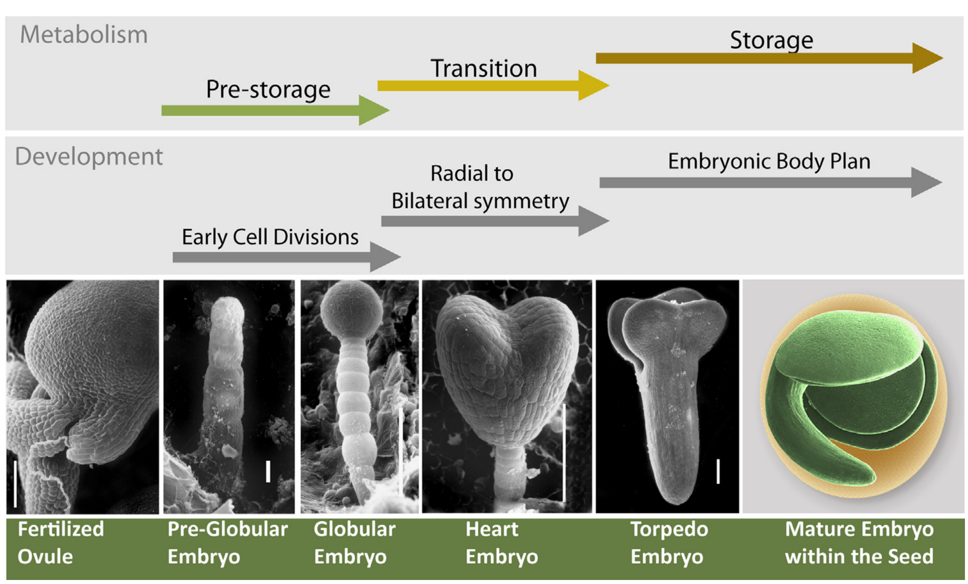

Fig. 1. Developmental and metabolic stages of seed. Seed development, shown here in a representative dicot species *Brassica napus*, commences with fertilization of the ovule when the pollen tube delivers the sperm cells to the mature embryo sac. The fertilized egg cell or zygote undergoes divisions to form the embryo proper and the suspensor. The suspensor initial undergoes a series of transverse divisions to form the suspensor. The embryo is housed inside the seed coat which develops from the integuments of the ovule. The endosperm initial that results from the fusion of the sperm cell with central cell divides to form the endosperm that is consumed to nourish the developing embryo by the heart stage. The embryo proper undergoes well-coordinated series of divisions to form the globular embryo which then undergoes patterning to establish the embryonic body plan. Activation of storage associated metabolic programs during seed development can be divided into three key phases of pre-storage, transition and storage. The developing cotyledons of the embryo serve as a major target tissue for synthesis and deposition of storage products in dicot seeds where as in monocots the persistent endosperm provides additional target for storage reserves. Bar = 10 μm for pre-globular embryo; 100 μm for the other embryo stages.