International Journal of Biotechnology and Biomedical Sciences
p-ISSN 2454-4582, e-ISSN 2454-7808, Volume 4, Issue 2; July-December, 2018 pp. 63-66

http://www.krishisanskriti.org/Publication.html

Seed Size Regulation: An Evolutionary Approach from Physiological & Molecular Perspective

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Abstract—*Concern on Production of crops has always remained the "prima-facie" priority of Agricultural sector throughout the world. But for the past few decades increasing seed production has been playing a key goal in order to meet world demand and consumption of agricultural crops because only a healthy seed set can turn into a incident of phenomenal crop reproductive success. A substantial reservoir within the seed embryo to nourish germinated seedling is a favourable criteria towards viability but large seed size are not desirable at all due to several constraints like dispersal inefficiency and so on. In this context study of physiological and molecular mechanisms controlling seed formation becomes essential as seed size is a major component of seed yield. It is also crucial for evolutionary fitness, domestication process as well as stress response. Mainly the Growth of the seed is associated with the initial growth of the endosperm, and not with the later growth of embryo. Size of a seed is the result of three different growth programs viz. diploid embryo, triploid endosperm and diploid ovule. Now control and co ordination of these programs under Genetic regulation is needed. Seed size regulation includes mechanisms underlying the developmental processes of (i) the endosperm, including genomic imprinting and parent-of-origin effects, and (ii) the seed coat/integuments (Arroyo et al., 2015). Other key regulators of seed size are- the cross talk between endosperm and seed coat, hormone synthesis and perception, transcription factors, Ubiquitin mediated pathways, G-protein signaling. Simultaneous study of molecular basis of this factors revealed that these are mostly regulated by maternal parent (Li, N. and Li, Y., 2015). Remarkable progress has been made in the field of seed size control in recent years. However, it is still unclear how maternal tissues and zygotic tissues co-coordinately control seed size in plants. Extensive datasets developed by modern technologies as well as mathematical modeling can be a promising approach to address the question of seed size control in plants.*

Keywords*: Seed production, viability, seed size, embryo. Endosperm, genetic regulation.*

1. INTRODUCTION

Increasing seed production is a key goal to meet world demand and consumption of agricultural crops. In this context study of physiological and molecular mechanisms controlling seed formation becomes essential as seed size is a major component of seed yield. Seed size is crucial for evolutionary fitness in plants, and is an important agronomic trait in crop domestication. Large seeds accumulate sufficient nourishing substances for germination and have better tolerance to abiotic stresses, whereas small seeds are efficient at dispersing and colonizing. Since the beginning of agriculture, crop plants have undergone selection for larger seed size during domestication. In various species, seed size variation is remarkably large. However, how plants know and determine their seed size is almost unknown. Seed development is a pivotal process in the plant life cycle.

2. RATIONALE OF THE STUDY

A substantial reservoir within the seed embryo to nourish germinated seedling is a favourable criteria towards viability but large seed size are not desirable at all due to several constraints like dispersal inefficiency and so on. In this context study of physiological and molecular mechanisms controlling seed formation becomes essential as seed size is a major component of seed yield. It is also crucial for evolutionary fitness, domestication process as well as stress response. Mainly the Growth of the seed is associated with the initial growth of the endosperm, and not with the later growth of embryo. Size of a seed is the result of three different growth programs viz. diploid embryo, triploid endosperm and diploid ovule. Now control and co ordination of these programs under Genetic regulation is needed.

3. THE METHODOLOGY

Concept Building

A concept is an abstraction or generalization from experience or the result of a transformation of existing ideas. The concept is instantiated (reified) by all of its actual or potential instances, whether these are things in the real world or other ideas. Concepts are treated in many if not most disciplines both explicitly, such and implicitly. In informal use the word concept often just means any idea, but formally it involves the abstraction component. In this paper the authors have tried to build a multifarious and multidimensional frame consisting of some emerging concepts related to the topic. for this, It has followed the process of axiomatic discoursement.

4. REVIEW OF LITERATURE

Various sources about seed size regulation have been intensively studied and related information were gathered

Concept Refinement

Having collected the data from various sources, the concepts was refined with consultations with different experts. In this aspect we also have taken help of different portals related to this issue. We tried to match the copybook concept with the field reality to explore the deviation.

Opinion and View Integration

Having opined the ancillary views we have taken the responses of many agricultural officers . experts of SAU, and scientists to review that of our opinion and to integrate something innovative.

Seed Development Process-

Seed development which begins with double fertilization, leads to the development of the embryo and the endosperm. One of the two sperm cells fuses with the egg cell to form the diploid zygote. The zygote undergoes elongation and a progressive transition to establish the basic embryo pattern. The embryo possesses a shoot meristem, cotyledon(s), hypocotyl, root, and root meristem. The other sperm cell fertilizes the diploid central cell to generate the triploid endosperm. Endosperm development in flowering plants progresses through four phases: syncytial, cellularization, differentiation, and death. In monocots such as rice (*Oryza sativa*) and wheat (*Triticum aestivum*), the endosperm constitutes the major part of the mature seed. In most dicots such as *Arabidopsis thaliana* and *Brassica napus*, the endosperm grows rapidly initially and is eventually consumed in later stages. Thus, the embryo occupies most of the mature seed.

The maternal integuments surrounding the developing embryo and endosperm form the seed coat after fertilization. Integument primordia initiate from the flanks of the chalaza during the early stage of megasporegenesis. These two primordia grow and enclose the functional megagametophyte and become the inner and outer integuments, respectively. After fertilization, the integuments undergo cell differentiation, accumulate pigments, mucilage, and starch granules, and eventually form mature seed coat. Seed development is influenced by the co-ordinated growth of the diploid embryo, the triploid endosperm, and the maternal integuments. Furthermore, the seed coat plays a major role in controlling communication between the two generations.

Networks Controlling Seed Size-

Seed size regulation includes mechanisms underlying the developmental processes of (i) the endosperm, including genomic imprinting and parent-of-origin effects, and (ii) the seed coat/integuments (Arroyo *et al.,* 2015). Other key regulators of seed size are- the cross talk between endosperm and seed coat, hormone synthesis and perception, transcription factors, ubiquitin mediated pathways, G-protein signaling. Simultaneous study of molecular basis of this factors revealed that these are mostly regulated by maternal parent (Li, N. and Li, Y., 2015). Endosperm proliferation is regulated by a few newly identified pathways involving transcriptional, epigenetic, and imprinting regulators, integument or seed coat development by a few transcription factors, and embryo proliferation regulated by AP2-like and bHLH proteins and phyto hormones (Xiaodong *et al* 2010). An ovule identity factor SEEDSTICK (STK) is involved in the regulation of several metabolic processes of seed coat, providing a strong basis for a connection between cell fate determination, development and metabolism (Mizzitti *et al.*, 2014). Zhang *et al* revealed a regulatory role of an R2R3 MYB transcription factor MYB56 in controlling seed size specifically in *Arabidopsis thaliana L*. Loss of function or knock down of MYB56 yielded smaller seeds as compared with the wild type. Conversely, over expression of MYB56 produced larger seeds. Further observation using semi thin sections showed that *myb56* developed smaller contracted endothelial cells and reduced cell number in the outer integument layer of the seed coat during the seed development.

Regulation Of Seed Coat Development-

The seed coat deeply influences seed size, highlighting a fundamental role for seed maternal tissues in the control of this aspect of seed yield. The seed cavity (the space enclosed by the seed coat) increases in volume after fertilization, partly due to the independent developmental plan of the seed coat and partly as the result of the interplay between the seed coat and the endosperm. After fertilization, the cells belonging to the different seed coat layers predominantly experiment intense expansion activity but still undergo division activity. Before fertilization, the female gametophyte (embryo sac) seems to have only a moderate importance in generating the signals to stimulate the integuments' proliferation. Numerous studies have identified genes involved in Arabidopsis ovule integuments and seed coat development, and some of them have provided a functional characterization of seed size contribution.

In particular, seed size mutant phenotypes showing a clear maternal inheritance are mainly due to an alteration of cell proliferation or elongation in the seed coat. A key player in the control of cell cycle and expansion in Arabidopsis is AUXIN RESPONSE FACTOR 2 (ARF2), which encodes a B3-type transcription factor of the ARF family. Among the different ARF proteins, ARF2 is thought to act as a transcriptional repressor, exercising a negative control over cell proliferation and expansion.

Pathways Involved In Endosperm Development-

Endosperm development has four phases: syncytial, cellularization, differentiation, and death. The syncytial phase is characterized by a series of divisions of the triploid nuclei without cytokinesis and parallels the maximal phase of seed growth. After eight rounds of syncytial mitoses, the cellularization process starts, initially from regions surrounding the embryo and proceeding toward the chalazal region. Cellularization is followed by a differentiation of functional tissues, and eventually most endosperm cells die during seed maturation. The timing of endosperm cellularization correlates with the end of the main stage of seed growing; therefore, the size attained by the endosperm syncytium appears to be a major determinant of seed size. Consequently, precocious endosperm cellularization results in small seeds, while delayed endosperm cellularization causes the formation of enlarged seeds The existence of three redundant pathways that control endosperm cellularization has been recently proposed.

The first pathway regulates endosperm cellularization through the action of APETALA 2 (AP2) and the MADS-box transcription factor AGL62. The second endosperm cellularization pathway includes members of the Polycomb group (PcG) proteins and their targets. The third pathway is the IKU pathway. The genes HAIKU1 (IKU1) and IKU2 have been shown to be key regulators of seed size in Arabidopsis via control of the transition from syncytial phase to the cellularization phase of the endosperm.

Cross Talk between Endosperm And Integument-

Endosperm and integument growth and development go side by side. Two models have been proposed to explain the cross talk between endosperm and the seed coat and its role in controlling seed size. The 'integument size-restriction model' suggests that the expansion of the integument cells represents a physical constraint to the size of the seed cavity, restricting the size of the embryo. As a result, this volume reduction increases the concentration of the factors triggering the cellularization process. In the second model, identified as the 'cellularization signaling model', the interaction between seed coat and endosperm is mediated by a signal that moves between integuments and endosperm. Flavonoids (proanthocyanidins [PAs]), synthesized in the endothelium, play pivotal role for the signal that triggers the endosperm cellularization process.

Hormonal Regulation Of Seed Size Regulation-

Several hormonal pathways such as brassinosteroids, cytokinins, auxins and abscisic acid have been already proposed to play a crucial role in seed development. At the cellular level, low endogenous concentrations of BR have been shown to exert a positive effect on cell elongation; while, saturating levels of BR lead to reduced cell elongation . An Arabidopsis dwarf mutant overexpressing the P450 monooxygenase gene CYP72C1 (shk1-D) showed a reduction in endogenous BR levels and produced smaller seeds than the wild type, probably due to an effect on cell elongation. Auxins exert a key role during the first steps of seed development including seed feeling and starch accumulation in pea (McAdam et al., 2017). High levels of CK are present during early seed development in many species. Studies performed on the genetics of CK production have shown that during early stages of seed development transcriptional changes are mostly associated with effects of the hormone on the development of endosperm and seed coat. Recently, it was concluded that the control of endosperm size by the IKU pathway is regulated by the cytokinin catabolic pathway through the activation of CKX2 (cytokinin oxidase 2) by MINI3 (Li et al. 2013). The predominant role of abscisic acid (ABA) regulation involves key processes occurring during the maturation stages of seed development. Key aspects of this development are accumulation of storage compounds in the embryo, seed dormancy, and the inhibition of precocious germination.

Transcription Factors Involved-

Other than the above discussed pathways, there are various transcription factors identified which are involved in control of seed size and development in different stages. APETALA2 (AP2) is a member of the AP2/EREBP (Ethylene Responsive Element Binding Protein) family of transcription factors. AP2 plays an important role in the specification of floral organ identity in *Arabidopsis*. Several studies showed that AP2 is also involved in seed size control. The mutant *transparent testa glabra2* (*ttg2*) produced yellow seeds because of defects in proanthocyanidin synthesis and mucilage deposition in the seed coat. The seeds of *ttg2* were small and round compared with wildtype seeds, due to the reduced length of cells in the integument. Apart from these various WRKY family transcription factors and MYB transcription factors are also involved in seed size regulation processes (Xiang J et al., 2017). In rice, OsWRKY78 plays important role in seed development along with stem elongation. *Loose Panicle 1*encoding a novel WRKY transcription factor contributes toward seed size control in foxtail millet (Xiang J et al., 2017).

5. CONCLUSION

Variation in seed size is common within and among plant species. Underlying this variation, and thus regulation of seed size, is a complex array of interactions involving genetic factors, developmental signals, and environmental cues. Although maternal effects in plants have long been recognized, the mechanisms whereby maternal effects affect seed size remain largely unknown, which is especially true for maize. DNA methylation is a major epigenetic mark underlying gene imprinting which has been hypothesized to regulate seed size by affecting nutrient uptake and allocation during endosperm development. Remarkable progress has been made in the field of seed size control in recent years. However, it is still unclear how maternal tissues and zygotic tissues co-ordinately control seed size in plants. Extensive datasets developed by modern technologies as well as mathematical modeling can be a promising approach to address the question of seed size control in plants.

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