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Molecular and Transcriptional Regulation of Seed Development in Cereals: Present Status and Future Prospects

Anuradha Singh, Jyotirmaya Mathan, Amit Yadav, Aakash K. Goyal and Ashok Chaudhury

Abstract

Cereals are a rich source of vitamins, minerals, carbohydrates, fats, oils and protein, making them the world's most important source of nutrition. The influence of rising global population, as well as the emergence and spread of disease, has the major impact on cereal production. To meet the demand, there is a pressing need to increase cereal production. Optimal seed development is a key agronomical trait that contributes to crop yield. The seed development and maturation is a complex process that includes not only embryo and endosperm development, but also accompanied by huge physiological, biochemical, metabolic, molecular and transcriptional changes. This chapter discusses the growth of cereal seed and highlights the novel biological insights, with a focus on transgenic and new molecular breeding, as well as biotechnological intervention strategies that have improved crop yield in two major cereal crops, primarily wheat and rice, over the last 21 years (2000–2021).

Keywords: Seed development, yield related agronomic trait, genetic, molecular and transcriptome studies

1. Introduction

Cereal seeds are the major source of starch and proteins in staple foods, animal feed, and raw materials for food and fiber-based industries all over the world [1]. Considerable efforts have been made to elucidate the molecular mechanism regulating important agronomic traits in order to improve the cereal seed production. Several agronomic traits, including grain number per spike, spike length, thousand seed weight, seed size and many others, have contributed to grain yield improvement in many cereals plants, with the development of embryo, endosperm and integuments being the most important [2]. As a result, better understanding of the genetic and molecular processes governing seed development is crucial. Here in this book chapter, we provide a comprehensive review on the ontogeny of seed development, followed by genetics, molecular and transcriptional regulation of seed development for improved crop yield.

2. Developmental process and final structure of cereals seed

Biologically, seed is a mature fertilized ovule that consists primarily three parts: the embryo, endosperm, and seed coat (integuments) [3, 4]. The development of seed begins with double fertilization, in which one of the male gamete fertilizes with haploid egg cell to form an embryo and the other male gamete fertilizes the megagametophyte's diploid central cell to form the triploid nuclear endosperm [5]. The event of seed development, which described below can be divided into three phases: a morphogenesis and cell divisions for endosperm development (0–7 Day post anthesis, DPA), embryo development (7–15 DPA), and maturation (14 to 28 DPA), which includes embryo growth at the expense of endosperm, seed desiccation and storage materials accumulation [6].

2.1 Endosperm development

The nuclear type of endosperm development is the most common in monocot plants, particularly cereals, where initial endosperm nucleus divides repeatedly without cell wall formation, resulting in a characteristic coenocyte-stage endosperm [7, 8]. The morphogenetic event of the early stages of endosperm development was observed in wheat [9] and rice [10, 11]. The first division of the triploid endosperm nucleus, in which the daughter nuclei are separated in the central cell, without cell wall formation in subsequent mitotic divisions, results in a 256 to 512 multinucleate cell (the endosperm coenocyte) [8, 12]. The nuclei enter a 2-day mitotic hiatus, lead to the formation of interzonal phragmoplast, occurs 3 days after pollination. While much information about the regulation of phragmoplast formation and expansion remain unknown, recent evidence suggests that the mitogen-activated protein kinase cascade plays a key role in this process [13]. The development of cellularization in the coenocytic endosperm then begins with the formation of radial microtubule on all nuclear surfaces. Soon after, the microtubules from the adjacent nuclei meet, creating interzones where callose-based wall material is deposited. Further, radial microtubules that encase each nucleus undergo reorganization, anchoring the nuclei to the central cell wall while extending toward the central vacuole in a canopy of microtubules. In cereals, the endosperms become fully cellular during 6 to 8 days after pollination if this process is repeated four to five times [14, 15].

The fully developed cereal endosperm consists of four main cell types: the aleurone layer, transfer cells, starchy endosperm, and cells of the embryo-surrounding region [16]. The former two cells, i.e. Aleurone layer, transfer cells remain alive at the end of cereal seed development, while later two including starchy endosperm, and cells of the embryo-surrounding have undergone programmed cell death (PCD) with characteristic DNA laddering and organelle degradation [17].

The cereal endosperm has attracted attention from researchers because of its economic importance, and much insight has accumulated about the genes underlying the accumulation of storage products such as proteins and starch. Additionally, the endosperm protects the embryo from atmospheric oxygen that eventually leads to the formation of hydroperoxides and cell death [18] and critical cross-talk between abscisic acid (ABA) and gibberellin (GA) regulating seed development, size, dormancy or storage breakdown during germination are also the results of endosperm—embryo interactions [19, 20]. Considerably less is known about the genes that regulate the developmental biology of these cell types, which is the topic of this section. Cell fate specification in cereal endosperm is believed to occur by positional signaling at an early developmental stage [12]. For simplicity, each cell type is described separately below, although cell fate specification occurs

simultaneously with the cellularization process described above. How this integration occurs is unknown, but elucidation of the molecular controls for each of the four cell types should lay the foundation for understanding the genetic specification of the entire endosperm body plan.

2.2 Starchy endosperm

Starchy endosperms, which accumulate starch and storage proteins, encoded by transcripts that are expressed differentially in these cells, make up the largest body of cell in the endosperm [21]. There are two types of starchy endosperm present in the cereal crop. The first, and most important, is the inner cells of cell files that remain after endosperm cellularization is complete. The second source of starchy endosperm cells is the inner daughter cells of aleurone cells that divide periclinally. These cells redifferentiate to become starchy endosperm cells and likely are the source of the so-called subaleurone cells found adjacent to the aleurone layer in the starchy endosperm in all cereals. Several collections of mutants such as *dek* (defective kernel) [22], and *Dee-D1* (DEFECTIVE ENDOSPERM-D1) [23], physically located on the long arm of chromosome 1D involved in the genetic control of endosperm development in wheat. The absence of *Dee-D1* in the genome of hexaploid wheat leads to a decrease in the number of grains and thousand grain weights. Similarly, DWARF AND RUNTISH SPIKELET1 (DRUS1) and DRUS2 [24] and EMBRYONIC FLOWER2a (OsEMF2a), a zinc-finger containing component of polycomb repressive complex 2 impaired endosperm development in rice [25].

2.3 Aleurone

The aleurone layer covers the perimeter of the endosperm with the exception of the transfer cell region. Wheat have one layer of aleurone cells, while rice has one to several layers, functions in seed germination by mobilizing starch and storage protein reserves in the starchy endosperm through the production of hydrolases (α -amylase), glucanases, and proteinases after hormone (gibberellic acid) stimulation from the embryo [26]. In the mature grain of cereals, the aleurone layer consists of an estimated 250,000 aleurone cells derived by an estimated 17 rounds of anticlinal divisions. Toward the end of seed maturation, a specialized developmental program confers desiccation tolerance to the aleurone cells, allowing them to survive the maturation process. *Several mutants such as, Crinkly4 (Cr4)*, a receptor like kinase protein [27], *Supernumerary aleurone layer1 (Sal1)*, homolog of the human *Charged vesicular body protein/Chromatin modulating protein1* gene [28], *Defective seed5 (des5)*, bZIP zinc finger transcription factor RISBZ1 and the DOF zinc finger transcription factor RPBF regulate both storage protein biosynthesis and the differentiation of the aleurone [29].

2.4 Transfer cells

Transfer cells develop in the basal endosperm over the main vascular tissue of the maternal plant, where they facilitate solute (mainly of amino acids, sucrose, and monosaccharides), transfer across the plasmalemma between the symplastic (maternal plant) and apoplastic (endosperm) compartments [30]. However, sucrose is not delivered in this form to transfer cell; instead, it is converted into monosaccharide glucose and fructose through the major activity of cell-wall invertase, offering a mechanism for controlling cell division and even cell differentiation in developing kernels [31].

In cereals, the *miniature1* (*mn1*) mutant and *GRAIN INCOMPLETE FILLING1* (*GIF1*) which encodes a cell-wall invertase, exclusively expressed in transfer cells, have significant smaller grains, implying that invertase contributes to create a sucrose concentration gradient in the apoplastic gap between the pedicel and the endosperm by hydrolyzing sucrose to glucose and fructose [32, 33]. Furthermore, in developing *mn1* kernels, the abundance of auxin and transcript of *YUCCA* genes was drastically reduced, implying that sugar level influence auxin level in seed, which in turn regulates specific aspects of seed developments [34].

Several groups of transcripts, for instance, *OsPR602* and *OsPR9a* in rice and Endosperm 1 (*END1*) in barley have been shown to be expressed preferentially in endosperm transfer cells during the early stages of grain filling [35]. Further, an orthologues gene from *Triticum durum* (*TdPR60*) and *Triticum aestivum* (*TaPR60*), a small cysteine-rich protein with a hydrophobic signal peptide, predicted to interact with several protein, which are involved in the regulation of regulation of secretion and degradation of signal peptides in other organisms [36].

2.5 The embryo-surrounding region

The embryo-surrounding region (ESR) lines the cavity of the endosperm in which the embryo develops and has been studied most extensively in maize. The exact role of the ESR is unknown, but possible functions include a role in embryo nutrition, the establishment of a physical barrier between the embryo and the endosperm during seed development, and providing a zone for communication between the embryo and the endosperm. The ESR development is under the control of *CLAVATA3*, a peptide hormone with the conserved domain composed on 12 to 14 amino acids, regulates embryo and endosperm development, cotyledon establishment, and pollen wall formation in Arabidopsis [37], while root and stem development in wheat plants [38].

2.6 Seed coat development

The seed coat (also known as testa) is made up of two structures covering the nucellus [39], while the single integuments ovules can be found in members of certain families. The seed coat provides a mechanical shield protecting the embryo and the endosperm from the environment, but it also regulates phloem unloading of assimilates in growing seeds [40], fluid and gas exchanges with the environment, and seed dormancy and germination [41]. Generally, seed coat development and maturation precede that of filial tissues. In cereals, after an initial phase of cell division during the first two days after flowering (DAF), pericarp differentiation involves cell elongation along the longitudinal axis between 3 and 10 DAF coupled to PCD, and it coincides with the cellularization of the endosperm [42]. PCD in the pericarp may contribute to redistribution of nutrients, relaxation of physical constraints of the maternal tissue to allow inner growth of the filial tissue, and the re-activation, together with PCD in the nucellus and the nucellar projections, of post-phloem transport functions to allow passage of solutes [42]. Crosstalk among embryo, endosperm, and seed coat appears to be complex, but gene networks that coordinate development of these three seed compartments are being elucidated [41, 43].

3. Genetic regulation of seed development for improved yield

Seed yield is a quantitative trait that is influenced by the genetics and environment. It is usually determined by plant height, number of primary and secondary

branches, plant density, date of flowering, number of panicle per plant, number of seed per panicle, seed size including seed length and seed width, and finally seed weight [44, 45]. The last two traits, i.e. seed number and weight, were found to be trade-off [46], but recent evidence from studies in wheat suggests that increasing one yield component without reducing the other is possible [47]. The grain number has maintained higher phenotypic plasticity throughout domestication events when compared with grain weight, which enables crop to effectively respond to resource availability during early reproductive stages [46]. The critical periods for determination of grain number and weight are also generally considered separated by the developmental stage of anthesis (flowering), although Ugarte et al. [48] found that grain weight was affected by pre-anthesis environmental conditions in other cereals including wheat. The genotype \times environment interaction for grain yield is likely strong in winter wheat [49] and rice [50].

To explore candidate genes underlying yield related traits, GWAS were conducted to identify underlying loci for each phenotype. Association mapping has been used to successfully discover significant marker–trait associations in cereal crops including rice [51–54] and wheat [55–58]. A large number of well-characterized QTLs such as GW2, GIF1, qSW5, GS3 and qGL7 in rice [59–63] and more than 40 QTL including TaGW2 [64–66] associated with kernel morphological traits such as kernel length, kernel width, kernel thickness, kernel length/width ratio, kernel length/thickness ratio, kernel width/thickness ratio, flag leaf width, length and area have been recently identified and mapped in wheat [67–70]. A variety of QTLs regulating seed size have been identified in other crop species, but they have yet to be functionally characterized [47, 71]. The additional genetic approaches on key agronomic traits for improved yield are presented in **Table 1**.

Cereal Crop	Traits	Gene/QTL/Markers	References
Wheat	1000-grain weight	qTgw.nwipb-4DS; qTgw.nwipb-6AL	[72]
		w SNP_Ex_c32624_41252144, BS00021705_51	[73]
	Grain yield, TKW, spike weight, spike length	rs36032, rs4772, rs736, rs50187, rs59282	[74]
	Heading and flowering dates	RAC875_c41145_189, Excalibur_c60164_137, RAC875_c50422_299, Ppd-D1, Vrn-B1, Vrn-D1	[75]
	Grain weight and grain number	TaGW2-6A, Rht-B1, Vrn-D1a	[56]
Rice	Yield associated loci	qSN8 and qSPB1	[76]
	Heading date	Ghd8/OsHAP3H	[77, 78]
	Panicle trait	DENSE AND ERECT PANICLE 1 (DEP1)	[79, 80]
	Grain length and yield	OsLG3	[81]
	Heading date and yield potential	Hd1, Ghd7, and DTH7	[82]
	Grain yield and quality traits	qPH1/OsGA20ox2, qDF3/OsMADS50, PL, QDg1, qGW-5b, grb7-2, qGL3/GS3, Amy6/Wx gene and OsNAS3	[83]

Table 1.
Genetic approaches for improved seed yield in cereal crops.

4. Molecular regulation of seed development for improved yield

Overexpression, targeted mutagenesis and mutation breeding are examples of recent biotechnological strategies that have been used to manage seed development for increased yield. The activity of ADP-glucose pyrophosphorylase (AGPase), starch synthase (SS) includes granule bound starch synthase (GBSS) and soluble starch synthase (SSS), starch branching enzyme (SBE), debranching enzyme (DBE), and amylase catalyzes the synthesis and accumulation of endosperm storage components, primarily starch, in cereal crops [84–87]. AGPase catalyzes the first committed step of starch biosynthesis, namely the conversion of Glc-1-P and ATP to ADP-glucose and pyrophosphate (PPi). Through a new α -1,4-linkage, the glucose moiety from ADP-glucose is transferred to the non-reducing end of the α -glucan receptor of existing chains of amylose and amylopectin [86]. In addition few transporters and transcription factors also play an important role in the regulation of the biosynthesis of starch [88, 89]. Modification of these enzymes has the drastic effect on different aspects of starch such as composition, and finally grain yield and summarized in **Table 2**.

Gene	Crop	Mechanism	Function/phenotypes	References
AGPase	Wheat/Rice	Over expression +Chemical mutagens	Enhanced ADP-glucose pyrophosphorylase activity in endosperm and seed yield	[90–93]
GBSS	Wheat	Combining null alleles	Low amylose and lower yield	[94]
SSI,SSII/SSIII	Wheat/Rice	RNAi silencing	Reduced SSI enzyme activity with novel starch structure	[95]
SSSIIIa	Rice	Chemical mutagen	High amylose	[96]
BEIIa	Wheat/ Durum wheat	RNAi silencing TILLING	High amylose and resistant starch	[97–99]
ISA	Rice	RNAi silencing	Alters the physicochemical properties of starch	[100]
AMY	Wheat	Overexpression	Increased the soluble carbohydrate (mainly sucrose) in dry seed	[101]
<i>OsbZIP58</i>	Rice	Overexpression	Regulates the expression of starch biosynthetic genes in rice endosperm	[102]

Table 2.
Molecular approaches for improved seed yield in cereal crops.

5. Transcriptional regulation of seed development for improved yield

In the context of seed development, genotype-specific and stage-dependent temporal shifts in gene expression profile have been reported in the aleurone, embryo and endosperm, and other cell-type of maturing seeds, potentially leading to seed phenotypic differences [103, 104]. Transcriptomic studies in several plant systems has led to the identification of transcriptional programs and regulatory networks underlying molecular functions associated with cellular activities

in endosperm [105, 106], starch metabolism [107], seed storage substances and high molecular weight glutenin genes [108–110], grain quality (glycemic index) [111], post-transcriptional regulations occurs at the end of seed development [17] and programming of seed developmental and maturation processes, and elucidation of the underlying functional transitions (**Table 3**) [103].

Cereal Crop	Traits	Transcription factor/gene	References
Wheat	Grain number per spike	<i>TaTEF-7A</i>	[112]
	Endosperm specific transcription factor	bHLH (seven tissue-specific bHLH TF clusters were identified according to their expression patterns in endosperm, aleurone, seedlings, heading-stage spikes, flag leaves, shoots and roots).	[113]
	Starch biosynthesis	bZIP (TabZIP 151, TabZIP121, TabZIP69.1, howing moderate negative to moderate positive correlation with GBSSI and SBEIIb, respectively	[89]
	Embryo and endosperm specific transcriptome	Identification of genes underlying macromolecules biosynthesis (starch, protein, lipid, protein translation)	[17]
		ABA mediated transcriptional mechanisms controlling seed maturation	[103]
		Identification of key genes for processing quality	[105]
Rice	Seed germination, grain size and yield	<i>OsSPMS1</i> (Spermine Synthase)	[114]
	Fatty acid metabolism	<i>OsACOT Acyl- CoA thioesterase</i>	[115]
	Panicle branching	miR156 targeting <i>OsSPL13</i> , <i>OsSPL14</i> and <i>OsSPL16</i>	[116]
		[117]	
	Seed setting	<i>LOW SEED SETTING RATE1 (LSSR1)</i> , regulates the seed setting rate by facilitating rice fertilization.	[118]
	Metabolism of sugars, fatty acids, amino acids, and phytosterols	Mutation on <i>OsSBEIIb</i>	[119]
	Transcriptome analysis of colored rice	Flavonoid biosynthetic pathway	[120]
	Accumulation of seed storage substance	NF-YC12	[121]
	Regulation of grain size	<i>OsPIL15</i> , targeting purine permease gene <i>OsPUP7</i>	[122]
	Early seed development	<i>MADS78</i> and <i>MADS79</i>	[123]
	Plant architecture, longer panicles, more grain number and yield	<i>OsNAC2</i>	[124]
	Leaf angle, grain size and seed quality	<i>OsmiR1848</i> regulating <i>OsCYP51C</i> expression and mediates BR biosynthesis	[125]

Table 3.
 Transcriptional approaches for improved seed yield in cereal crops.

In rice, Nie et al. [15], identified 12 classes of endosperm-specific genes, including transcription factor, stress/defense, seed storage protein (SSP), carbohydrate and energy metabolism, seed maturation, protein metabolism, lipid metabolism, transport, cell wall related, hormone related, signal transduction, and one unclassified category. In addition, several cis-regulator elements were found in the promoter region of endosperm-specific expressed genes including, AACA box, ACGT box, GCN4 motif (TGA (G/C) TCA), the prolamin box (P box: AAAG), SKN-1 cis-element, RY repeat (CATGCATG) [29], ABA responsive element (ABRE) motif, and transfer cell-specific motif TATCTCTATCT (C/A) from aleurone cell [126]. These elements may play an important role in regulating the temporal and spatial expression genes in endosperm development.

Based on the cis-element, the corresponding transcription factor were also determined. For example, the MYB protein specifically binds to the AACA box, and the GNC4 motif is bounded by transcription factors of the Opaque2-like basic leucine zipper (bZIP) activators (rice RISBZ1), ABRE motif by bZIP transcription factors, the P box by plant-specific DNA binding with one finger (DOF) zinc-finger transcription factors (rice RPBF), and FUSCA3 (FUS3) recognizes the RY repeats [29, 127, 128]. In addition, synergy between RPBF and RISBZ1 has been implicated in mediating the regulatory networks essential for seed development by binding to the GCN4 motif to trans-activate the expression of seed storage proteins in rice [29, 129]. Recently, Grimberg et al. [130] identified an oat endosperm homolog of WRINKLED1 transcription factor (*AsWRI1*), which when expressed under the control of endosperm-specific HMW1Dx5 promoter, causes substantial alterations in carbon allocation in wheat grains, including lower seed weight and a wrinkled seed phenotype.

Polyamines such as putresceine, Spermidine (Spd), and Spermine (Spm) have been implicated in regulation of spikelets postanthesis development [131]. Exogenous Spd and Spm are applied to rice panicles to improve grain filling and grain weight in inferior spikelets [132]. Furthermore, the concentrations of Spd and Spm are related to rice grain size. The *OsSPMS1* gene is involved in the conversion of Spd to Spm, as well as the production of 1-aminocyclopropane-1-carboxylic acid (ACC) and ethylene. Manipulation of the *OsSPMS1* gene has a significant impact on a variety of traits, including plant height, grain size, seed germination, and yield production [133]. More importantly, knockout of *OsSPMS1* increases grain production in a high-yield variety, implying that *OsSPMS1* is a key target gene for rice yield improvement [114].

During plant reproductive growth, cell-to-cell communication via receptor-like kinases (RLKs) regulates a wide range of biological processes. FLORALORGANNUMBER1 (FON1), a potential ortholog of CLAVATA1 (CLV1), interacts with the putative ligand FON2/FON4, a CLV3-related protein, to maintain the inflorescence meristem [134]. The orthologous *Catharanthus roseus* RLK1-like (CrRLK1L) subfamily has a putative carbohydrate binding malectin-like domain and is involved in a variety of biological processes [135], including male–female interactions mediated by the synergid-expressed genes FERONIA (FER), DWARF AND RUNTISH SPIKELET1 (DRUS1), and DRUS2. These two proteins, which operate as essential regulators, control reproductive growth in rice in a redundant manner by suppressing cell death and influencing sugar use [24]. Evidence has been presented in my laboratory which demonstrates that endogenous repression of *CCA1* gene under the control of *TOC1* promoter resulted in improved morphological traits: increased number of tillers/panicle, thousand seed weight, seed size; whereas, over-expression leads to diminution in morphological traits: decreased number of tillers/panicle, thousand seed weight, seed size as compared to the wild

type in *Agrobacterium*-mediated genetically transformed T1 and T2 transgenic progeny plants of rice variety Taipei 309 [136].

6. Conclusions and future prospects

Seed development is a multi-step process that includes the production of an embryo and endosperm. The synthesis and accumulation of storage product in the seed is controlled by genetics, molecular and transcriptional regulation, which is critical for maximum yield. For instance, seed yield improvement can be achieved directly under genetic control by selecting and applying markers, QTL linked to agronomic and physiological traits, and improved grain yield potential. Intensive use of molecular tools such as Genetic engineering, Gene silencing and Genome editing together with increase access of system biology tools would provide researchers to gain a better understanding of the pathways and genes that control seed size and number, resulting greater yield as shown in **Figure 1**. It is envisaged that a more detailed investigation is urgently required for understanding of metabolic control of seed development, storage, product partitioning, epigenetic controls, phytohormone regulation and their interplay would appear to be sufficient to solve global food security challenges faced by the world in future.

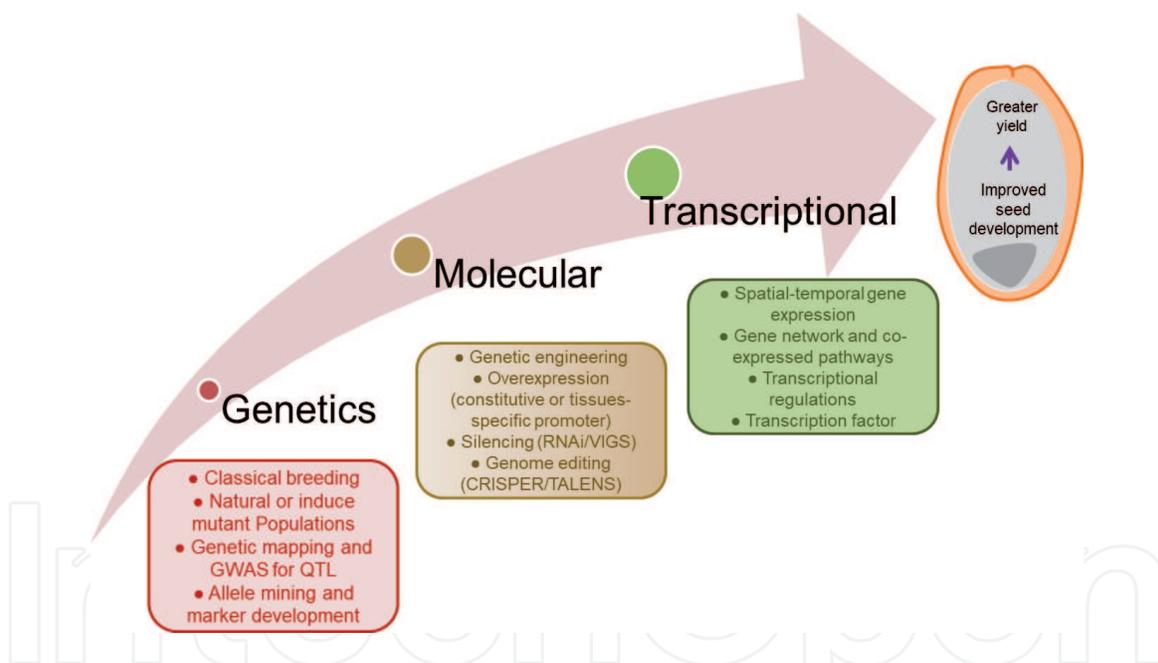


Figure 1. Summary of Molecular Approaches for Regulation of Seed Development through Plant Breeding & Genetics, Genetic Engineering & Genome Editing and at Transcriptional Levels.

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