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Combinatorial Networks Regulating Seed Development and Seed Filling

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1. Introduction

Seeds offer plants a unique opportunity to suspend their life cycles in a desiccated state. This enables them to endure adverse environmental conditions and then resume growth by using endogenous storage products when more favorable conditions develop. Seed development is pivotal to the reproductive success of flowering plants (Angiosperms). It is initiated by the process of double fertilization that gives rise to the embryo and the endosperm. The embryo develops following fertilization of the haploid egg cell by one of the sperm cells leading to the formation of a diploid zygote. In contrast, the triploid endosperm results from the fertilization of the maternal homodiploid central cell of the ovule by another sperm cell (Weterings & Russell, 2004). The diploid embryo and the triploid endosperm develop concertedly inside the maternal ovule and are protected by a seed coat constituted of maternally derived inner and outer integuments. The seed coat provides an important interface between the embryo and the external environment (Haughn & Chaudhury, 2005). Thus, different genome combinations contribute to seed ontogeny.

Seed formation is an intricate genetically programmed process that is correlated with changes in metabolite levels and is regulated by a complex signaling network mediated by sugar and hormone levels (Wobus & Weber, 1999; Lohe & Chaudhury, 2002; Weber et al., 2005; Holdsworth et al., 2008; Sun et al., 2010). Most of the basic knowledge regarding cellular differentiation, growth regulation, imprinting and signal transduction pertaining to seed development comes from studies with *Arabidopsis thaliana* (Goldberg et al., 1989; Laux & Jürgens, 1997; Harada, 1999; Smeekens, 2000; Finkelstein et al., 2002; North et al., 2010; Bauer & Fischer, 2011). There is sufficient evidence to state that the fundamental regulatory mechanisms governing seed development and maturation are similar for all plant seeds (Weber et al., 2005). Seed development can be divided into two stages, embryo morphogenesis and maturation, the latter being characterized by storage compound accumulation, acquisition of desiccation tolerance, growth arrest and entry into a dormancy period that is broken upon germination (Harada, 1999). In addition to the diversity of

shapes and sizes, a common element in plant seeds is the storage reserves that generally consist of starch, storage lipid triacylglycerols (TAGs) and specialized seed storage proteins (SSPs). Given the importance of seeds, such as those of legumes or cereals, in human and animal diets, much research has been devoted to improving qualitative and quantitative traits associated with seed components such as palatability and nutritional quality. As such, understanding the metabolism and development during seed filling has been a major focus of plant research. The recent development of a range of chemical, physiological, molecular genetics and post-genomics approaches has allowed rapid progress toward understanding the processes of early seed development, maturation, dormancy, after-ripening and germination, but has also provided opportunities to control and modify both the quality and quantity of seed products (Mazur et al., 1999; Hills, 2004 ; Baud et al., 2008; North et al., 2010). In recent years, much effort has been devoted to elucidating the intricate regulatory networks that control seed development and maturation, where hormone and sugar signaling together with a set of developmentally regulated transcription factors and chromatin remodeling proteins are involved. Here, we summarize the most recent advances in our understudying of this complex regulatory network and its role in the control of seed development and seed filling.

2. Genomic imprinting and early seed development

Genomic imprinting is a genetic phenomenon that occurs in the placenta of mammals and in the endosperm of angiosperms, in which a set of alleles that reside in the same nucleus and share the same DNA sequence is expressed in a parent-of-origin manner. Imprinting is an epigenetic process that is independent of classical Mendelian inheritance. According to the parental conflict theory (Haig & Wilczek, 2006), imprinting is described as a battle between the maternal and paternal genomes over limited maternal resources. The mother, which may carry progeny from several fathers, will attempt to distribute resources equally to all of her offspring. Conversely, the father will try to extract the maximum maternal resource for his progeny at the expense of others. Therefore, alleles that support the allocation of maternal resources for maximal growth of seeds are expressed paternally, whereas alleles that confine resource distribution from mother to seed are expressed maternally. Thus, the endosperm that is critical for embryo and seed development becomes a site where maternal and paternal genomes compete for resources via imprinting or parent-of-origin-specific gene expression.

Most imprinted genes known from flowering plants are preferentially expressed in the endosperm and some are known to be fundamental for proper early seed development (Table 1) (Gehring et al., 2004; Berger & Chaudhury, 2009; Bauer & Fischer, 2011). At least nineteen imprinted genes have been characterized in maize (*Zea mays)* (Table 2) and *Arabidopsis* (Berger & Chaudhury, 2009; Bauer & Fischer, 2011). The *R* gene was the first imprinted gene identified in maize (Kermicle, 1970) that promotes anthocyanin accumulation in the outer aleurone layer of the endosperm. All maize kernels have a fully red colored aleurone layer when a red *RR* female is crossed with a colorless *rr* male, whereas mottled aleurone pigmentation is produced by the reciprocal mating (Kermicle, 1970). Moreover, the mottled phenotype is present regardless of the number of paternal *R* alleles and maternally inherited *R* alleles are always associated with the solid red color. Other

imprinted genes that are maternally expressed in the maize endosperm include the *MO17* allele of the *dzr1* locus (Chaudhuri & Messing, 1994), one of the *a-zein* alleles (Lund et al., 1995), maize enhancer of *Zeste1* gene (*Mez1*) (Haun et al., 2009) and fertilization independent endosperm1 (*Fie1*) (Danilevskaya et al., 2003). In *Arabidopsis*, several imprinted genes involved in early seed development have been identified and include the *FIS* (*FERTILIZATION INDEPENDENT SEED*) genes *MEDEA* (*MEA*) (Grossniklaus & Schneitz, 1998; Kiyosue et al., 1999), *FERTILIZATION INDEPENDENT ENDOSPERM* (*FIE*) (Ohad et al., 1996), *FIS2* (Luo et al., 1999), and *MULTI-COPY OF IRA1* (*MSI1*) (Köhler et al., 2003; Ingouff et al., 2007), the *MEA* homologs *CURLY LEAF* (*CLF*) or *SWINGER* (*SWN*) (Makarevich et al., 2006), and other maternally imprinted genes such as *MATERNALLY EXPRESSED PAB C-TERMINAL* (*MPC*) (Tiwari et al., 2008) and *FLOWERING WAGENINGEN* (*FWA*) (Kinoshita et al., 2004; Köhler & Hennig, 2010).

Protein	Protein complex	Protein domains	Expression pattern during seed development	Loss-of-function phenotypes	References
FIS2	FIS (FERTILIZATION INDEPENDENT SEED)	C2H2 Zn finger	Endosperm, embryo, female gametophyte	Initiation of seed development in the absence of fertilization; embryo lethality; endosperm cellularization	Luo et al., 1999
MEA	FIS	SET	Endosperm, female gametophyte	Embryo lethality; cellularized endosperm without pollination	Grossniklaus & Schneitz, 1998; Kiyosue et al., 1999
MSI1	FIS, VRN, EMF?	WD 40	Embryo, female gametophyte	Parthenogenetic development including proliferation of unfertilized endosperm and embryos	Ach et al., 1997
FIE	FIS, EMF, VRN	WD 40	Endosperm, embryo, female gametophyte	Initiation of endosperm development in the absence of fertilization; flowers formed in seedlings and non-reproductive organs	Ohad et al., 1999

Table 1. PcG proteins required for early seed development in *Arabidopsis*

Gene name	Acronym	Potential function	References
R-mottled allele	*R*	Transcription factor	Kermicle, 1970
dzr1		The allele in the MO17 ecotype is maternally imprinted and zein accumulation is regulated	Chaudhuri & Messing, 1994
Fertilization independent endosperm 1	*Fie1*	PcG complex	Danilevskaya et al., 2003; Gutiérrez-Marcos et al., 2006; Hermon et al., 2007
Fertilization independent endosperm 1	*Fie2*	PcG complex	Danilevskaya et al., 2003; Gutiérrez-Marcos et al., 2006
No-apical-meristem related protein 1	*Nrp1*	Unknown	Guo et al., 2003
Maize enhancer of Zeste 1	*Mez1*	PcG complex	Haun et al., 2009
Maternally expressed gene 1	*Meg1*	Cysteine-rich peptide	Gutiérrez-Marcos et al., 2004

Table 2. Imprinted genes and their function in maize

In plants and animals, homeotic genes encoding the polycomb group (PcG) and trithorax group (trxG) proteins are key players in maintaining repressive and active state of targets, respectively, and are crucial for developmental patterning and growth control (Simon & Tamkun, 2002). PcG and trxG proteins form higher order complexes that have intrinsic histone methyltransferase (HMTase) activity for various types of lysine methylation at the amino-terminus of core histone proteins. This property is conferred by the conserved 130-residue SET (Su(var), Enhancer of Zeste, Trithorax) domain (Cao & Zhang, 2004). The FIS proteins MEA, FIE, MSI1 and FIS2 interact and form a protein complex called MEA-FIE complex that is similar to the PRC2 (Polycomb Repressive Complex 2) in animals (Simon & Tamkun, 2002; Köhler & Makarevich, 2006; Baroux et al., 2007). Mutation of any FIS component, such as MEA, leads to the formation of seeds independent of fertilization. Moreover, *fis* mutants have a prominent maternally determined phenotype after fertilization. Seed that carries a maternally inherited *fis* allele eventually aborts with an embryo that has arrested at the late heart stage and a multinucleate endosperm that fails to cellularize (Ohad et al., 1996; Grossniklaus & Schneitz, 1998; Kiyosue et al., 1999; Luo et al., 1999; Köhler et al., 2003; Ingouff et al., 2007). This phenotype is in part owing to the derepression of the type I MADS-box gene *PHERES1* (*PHE1*). *PHE1* is a direct target gene of the MEA-FIE complex in the embryo at the globular stage and in the central domain of the endosperm (Köhler et al., 2003). Mutation of *MEA* results in elevated expression of the maternal *PHE1* allele through removal of the trimethylation marks from histone 3 lysine 27 (H3K27me3), whereas this has little effect on the activity of the paternal *PHE1* allele, suggesting targeting specificity of the MEA-FIE complex to the maternal *PHE1* allele (Köhler et al., 2005; Makarevich et al., 2006). In contrast to the action of MEA that is required for PcG target repression during gametophyte and early seed development, MEA homologs CLF/SWN have been demonstrated to repress *PHE1* expression by the action of H3K27me3 at later stages of sporophyte development (Makarevich et al., 2006). In maize, genome-wide

analysis of transcriptome changes during early seed development identified transcripts of sixteen loci that were exclusively of maternal origin, suggesting a general mechanism for delayed paternal genome expression in plants (Grimanelli et al., 2005).

What are the underlying mechanisms that control genomic imprinting? DNA methylation was among the first recognized epigenetic modifications that affected early seed development (Finnegan et al., 1996). It has been demonstrated that methylation at CpG sites and plant-specific CpNpG and CpNpN was involved in embryo patterning (Xiao et al., 2006). METHYLTRANSFERASE1 (MET1) is the principal maintenance methyltransferase in *Arabidopsis* and is the homolog of mammalian Dnmt1 that maintains cytosine methylation at CG sites (Finnegan & Dennis, 1993; Kankel et al., 2003). *MET1* is expressed mainly in sperm cells (Jullien et al., 2008) and *met1* mutants display global reduction of CpG and CpNpG methylation and accompanied developmental abnormalities (Finnegan et al., 1996). Genetic and molecular studies have shown that MET1-conferred DNA methylation is involved in the imprinting of *FIS* genes (Xiao et al., 2003; Kinoshita et al., 2004; Jullien et al., 2006). The paternal MEA alleles in the endosperm are hypermethylated, whereas the maternal alleles are hypomethylated. MET1 targets methylation at CG sites in the MEA promoter and in the 3′ untranslated region (3′UTR) (Gehring et al., 2006). Recently, *MPC* and *FWA* were found to be inactivated throughout the plant life cycle until gametogenesis (Jullien et al., 2006; Tiwari et al., 2008). During male gametogenesis, these genes were repressed in sperm cells by the action of MET1 (Jullien et al., 2006; Tiwari et al., 2008). During endosperm development, the inherited paternal allele remains silenced by MET1, whereas the inherited maternal alleles are transcriptionally active (Gutiérrez-Marcos et al., 2006; Hermon et al., 2007; Tiwari et al., 2008). It was therefore suggested that the differential expression between the two parental alleles is established by the status of DNA methylation that has been epigenetically inherited from the gametes (Huh et al., 2007). This hypothesis is supported by the pattern of expression of the *PcG* genes *Fie1* and *Fie2* in maize (Danilevskaya et al., 2003). Maternally imprinted *Fie1* and *Fie2* were expressed solely during early endosperm development (Danilevskaya et al., 2003; Gutiérrez-Marcos et al., 2006). Imprinting of these two genes corresponded to the presence of differentially methylated regions at the parental alleles, which are inherited from the gametes, with high methylation in the sperm cells and none or little in the central cell, though *Fie2* did not display a DNA methylation status in the gametes as did *FIE1* (Gutiérrez-Marcos et al., 2006; Baroux et al., 2007). MET1-mediated DNA methylation is involved in the epigenetic control of seed size. During male gametogenesis, endosperm growth in *met1* mutants was inhibited and smaller seeds were produced (Luo et al., 2000; Garcia et al., 2005; Xiao et al., 2006; FitzGerald et al., 2008). This is probably due to the ectopic expression of imprinted paternal alleles of loci such as *FIS2* and *FWA*. Seeds derived from crosses between wild-type pollen and ovules from *MET1* antisense plants (*MET1a/s*) display increased seed size (Adams et al., 2000; Luo et al., 2000), owing to the loss of MET1 activity in the female gametes, the integuments, or both (Berger & Chaudhury, 2009). Similar results were obtained from crosses between wild-type pollen and homozygous *met1/met1* ovules, resulting in the formation of larger seeds, which is due to ovules with more cells and autonomous elongation (FitzGerald et al., 2008). Therefore, MET1 was proposed to play a role in inhibiting ovule proliferation and elongation and the effect of MET1 on seed size results mainly from the maternal controls (Berger & Chaudhury, 2009).

What are the mechanisms leading to the removal of DNA methylation marks from *FIS* genes in the central cell? DEMETER (DME) has been identified as a transcriptional activator that regulates *MEA*, *FIS2*, *FWA* and *MPC* expression in the central cells (Choi et al., 2002; Kinoshita et al., 2004; Gehring et al., 2006; Jullien et al., 2006; Morales-Ruiz et al., 2006; Tiwari et al., 2008; Bauer & Fischer, 2011). *DME* encodes a DNA glycosylase that removes methylated cytosine through its 5-methylcytosine DNA glycosylase activity at target loci (Choi et al., 2002; Kinoshita et al., 2004; Gehring et al., 2006; Jullien et al., 2006; Morales-Ruiz et al., 2006; Tiwari et al., 2008). *DME* is expressed predominantly in the central cell before fertilization where it activates target genes such as *MEA* (Choi et al., 2002). In *dem* mutant endosperm, the maternal *MEA* allele is not expressed due to hypermethylation and *dem* seeds eventually abort (Gehring et al., 2006). This finding suggests that DME removes DNA methylation marks at the maternal *MEA* allele in the central cell, resulting in hypomethylation and activation of *MEA* in the early endosperm, whereas the paternal imprinted *MEA* is methylated and transcriptionally silenced in the endosperm (Baroux et al., 2007; Huh et al., 2007). However, DME is not sufficient to remove all DNA methylation marks from targets such as *FIS2* as evidenced by the continued expression of *FIS2* and *MPC* in the *dme* mutant during female gametogenesis (Choi et al., 2002; Jullien et al., 2006). Recently, an additional mechanism was identified in which the Retinoblastoma pathway is involved in the regulation of maternal imprinting (Jullien et al., 2008). The *Arabidopsis* homolog RETINOBLASTOMA RELATED (RBR) directly silences *MET1* expression via interaction with MSI1 during the late stage of female gametogenesis. When the Retinoblastoma pathway is inactive, expression of *FIS2* and *FWA* in the central cell is completely repressed (Jullien et al., 2008; Berger & Chaudhury, 2009). Partial repression of *MET1* by the Retinoblastoma pathway results in DNA hemi-methylation, the preferred substrate for the 5-methylcytosine glycosylase DME (Jullien et al., 2008), and complete demethylation by DME at the promoter regions of target alleles such as *FIS2* and *FWA* leads to activation of these genes in the central cell. After fertilization, the active maternal allele inherits the demethylation marks, whereas the inactive paternal allele inherits the methylation marks (Berger & Chaudhury, 2009; Gehring et al., 2009) (Fig. 1). Deep sequencing of endosperm or embryo DNA immunoprecipited with antisera against methylcytosine demonstrated a global reduction in DNA methylation on CG sites in the endosperm. The global CG methylation level is reduced by 15-20% in the endosperm in comparison to the levels in vegetative tissues or embryos (Gehring et al., 2009; Hsieh et al., 2009). In maize, a reduction of maternal DNA methylation might also occur in the endosperm (Lauria et al., 2004). Additionally, large amounts of maternally inherited non-coding small RNAs might also affect the genome-wide DNA methylation in the endosperm and the embryos via their links to *de novo* DNA methyltransferases (Mosher et al., 2009). Recent genome-wide deep sequencing of cDNA libraries (Hsieh et al., 2011) or RNA derived from seeds of reciprocal intraspecific crosses (Gehring et al., 2011) has identified many genes that show imprinted gene expression in *Arabidopsis* endosperm. These genes include transcription factors, proteins involved in hormone signaling and regulators for histone modifications and chromatin remodeling (Gehring et al., 2011; Hsieh et al., 2011). These studies demonstrate that parent-of-origin effect on gene expression is a complex phenomenon and may affect multiple aspects of early seed development.

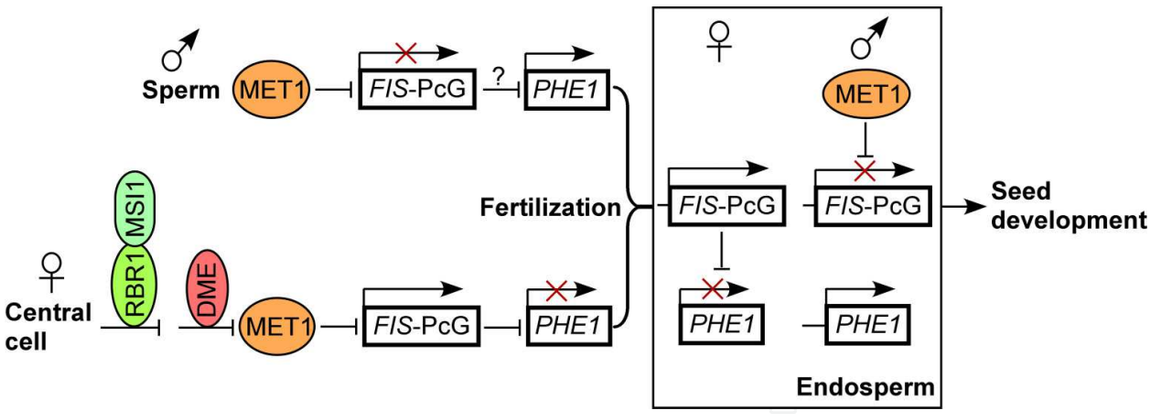


Fig. 1. A proposed model for the epigenetic control of early seed development. The FIS-PcG complex includes proteins encoded by *FIS* class genes such as *MEA* and *FIS2* (Simon & Tamkun, 2002; Köhler & Makarevich, 2006; Baroux et al., 2007). Both maternal and paternal alleles of these imprinted genes are repressed via DNA methylation from the activity of the DNA methyltransferase MET1 in the central cell and sperm (Gehring et al., 2006; Jullien et al., 2006; Huh et al., 2007). During female gametogenesis, MET1 activity is partially repressed by the Retinoblastoma pathway involving RBR1 and its interacting partner MSI1 through DNA hemi-methylation, the preferred substrate for the 5-methylcytosine glycosylase DME (Jullien et al., 2008). The complete demethylation on *MET1* in the mature central cell is mediated by DME, resulting in imprinted expression of the *FIS-PcG* genes (Jullien et al., 2008). During early endosperm development, the inherited paternal *FIS-PcG* alleles remain silenced by MET1, whereas the imprinted maternal alleles are active leading to the repression of target genes such as the maternal *PHE1* through lysine27 on histone H3 (H3K27) methylation. The mechanism underlying *PHE1* activation in sperm cell remains unknown. In contrast to the *FIS* genes *MEA* and *FIS2* that are proposed to play a role for the repression of endosperm proliferation (Kiyosue et al., 1999; Ingouff et al., 2007), paternal-specific expression of *PHE1* in the chalazal domain of the endosperm promotes endosperm development (Köhler et al., 2005).

In conjunction with DNA methylation, histone methylation also modulates genomic imprinting. Histone methylation mediated by the SET domain-containing PcG complex represses target genes by modifying the chromatin at or near target gene loci. This suppressive mechanism was proposed to regulate endosperm cell proliferation, as mutation of the target *FIS* class genes *MEA*, *FIS2* or *FIE* results in the autonomous central cell divisions (Ohad et al., 1996; Chaudhury et al., 1997; Grossniklaus & Schneitz, 1998; Kiyosue et al., 1999). As described above, the endosperm is the only site where imprinting is known to take place; however, seeds may also form when genomic imprinting mechanisms are bypassed (Nowack et al., 2007). When *CDKA;1* mutant pollen was crossed with the *FIS* gene mutants, *mea*, *fis2* and *fie*, viable single-fertilized seeds with homodiploid endosperm were produced despite smaller seed size than wild type (Nowack et al., 2007). *CDKA;1* encodes a cdc2/cdc28 homolog. Mutation of *CDKA;1* leads to the generation of pollen with only one sperm (Iwakawa et al., 2006; Nowack et al., 2006) that preferentially fertilizes the egg cell while the diploid central cell remains unfertilized. Embryos from egg cells pollinated with *cdka;1* mutant pollen abort at about 3 days after pollination and only a few divisions of the unfertilized central cell occur (Nowack et al., 2006). Furthermore, when repression exerted

by the *FIS* genes such as *MEA* in the female gametophyte is disrupted, single-fertilized seeds form (Nowack et al., 2007). This suggests that functional endosperm can arise from the central cell in the female gametophyte without a paternal contribution and that genomic imprinting in the endosperm is not always essential for seed development. This hypothesis is supported by the demonstration that fertilization of the diploid central cell acts as a trigger that initiates proliferation of the multicellular endosperm (Nowack et al., 2007).

3. Seed maturation and seed filling

According to several models, seed development can be divided into two stages; morphogenesis and maturation. The maturation phase is initiated once the embryo and endosperm have completed the morphogenesis and patterning stages (Wobus & Weber, 1999). While early embryo morphogenesis is mainly maternally controlled, transition to the maturation phase requires a switch from maternal to filial control (Weber et al., 2005). After the switch is initiated, the embryo continues to grow for a short period of time until it matures; the seed then accumulates storage products, develops desiccation tolerance and produces a protective seed coat. Maturation ends with the completion of a desiccation phase after which seed growth arrests and it enters into dormancy, thus, the embryo enters into a quiescent state but retains the capacity to regenerate after imbibition (Harada, 1999). The spatial and temporal regulation of the maturation processes requires the concerted action of several signaling pathways that integrate information from genetic and epigenetic programs, and from both hormonal and metabolic signals (Wobus & Weber, 1999; Weber et al., 2005). Moreover, recent discoveries have led to a better understanding of ABA signaling and metabolic regulation in the maternal to filial switch leading to the maturation phase (Gutierrez et al., 2007; Cutler et al., 2010).

3.1 A regulatory network for seed maturation

Precise spatial and temporal regulation of gene expression is required for proper seed maturation. The expression of genes involved in the regulation of metabolism occurring during seed maturation is highly coordinated (Vicente-Carbajosa et al., 1998; Santos-Mendoza et al., 2005; Gutierrez et al., 2007; Holdsworth et al., 2008; Sun et al., 2010). The maize *Opaque2* (*O2*) was one of the first genes encoding a plant transcription factor to be characterized (Hartings et al., 1989; Schmidt et al., 1990). The *O2* orthologs, *SPA* from wheat (*Triticum aestivum*) and *BLZ2* from barley (*Hordeum vulgare)*, were reported to have the same functions as *O2* in their corresponding species (Albani et al., 1997; Oñate et al., 1999). In *Arabidopsis*, three members of the B3 family of transcription factors, LEAFY COTYLEDON (LEC) 2, ABSCISIC ACID-INSENTITIVE 3 (ABI3) and FUSCA 3 (FUS3) and a fourth regulator, a HAP3 subunit of the CCAAT-box binding transcription factor (CBF) LEC1, are key regulators of seed maturation processes (Fig. 2). A redundant gene regulatory network linking these master regulators was elucidated by examining the expression of *ABI3*, *FUS3* and *LEC2* in *abi3*, *fus3*, *lec1* and *lec2* single, double and triple mutants (To et al., 2006). Using Affymetrix GeneChips to profile *Arabidopsis* genes active in seeds from fertilization to maturation, 289 seed-specific genes have been identified, including 48 transcription factors such as *LEC1*, *LEC2* and *FUS3* (Le et al., 2010). In combination with ABA, GA, auxin and sugar signaling, this regulatory network governs most seed-specific traits, such as accumulation of storage compounds, acquisition of desiccation tolerance and entry into

quiescence, in a partially redundant manner (Harada, 1999; Brocard-Gifford et al., 2003; Gazzarrini et al., 2004; Kagaya et al., 2005b; To et al., 2006; Stone et al., 2008). *LEC1* and *LEC2* are expressed early in embryogenesis and ectopic expression of these two regulators is sufficient to confer embryonic traits to vegetative organs (Lotan et al., 1998; Stone et al., 2001; Santos-Mendoza et al., 2005). *ABI3* and *FUS3* expression occurs later in embryogenesis and their overexpression results in ectopic expression of some seed maturation genes, such as *At2S3* and *CRC*, in vegetative tissues in an ABA-dependent manner, demonstrating that the SSP gene expression is controlled by LEC1 through the regulation of *ABI3* and *FUS3* (Parcy et al., 1994; Kagaya et al., 2005b). Genetic and molecular studies have shown that ABI3, FUS3 and LEC2 regulate oleosin gene expression and lipid accumulation (Crowe et al., 2000; Santos-Mendoza et al., 2005; Baud et al., 2007). Loss of *ABI3* function alters accumulation of seed storage reserves and leads to loss of desiccation tolerance, dormancy, ABA sensitivity upon germination and chlorophyll degradation (Vicente-Carbajosa & Carbonero, 2005). In addition, the APETALA2 (AP2) protein, ABI4, and the bZIP domain factor, ABI5, are involved in many aspects of seed maturation through their interaction with the major regulators LEC2, ABI3 and FUS3 (Carles et al., 2002; Brocard-Gifford et al., 2003; Lara et al., 2003; Acevedo-Hernández et al., 2005). In addition to these complex genetic interactions, *ABI3* expression was found to be regulated by both post-transcriptional and post-translational mechanisms. After excision of the long 5'-untranslated region (UTR) of the *ABI3* transcript, *ABI3-GUS* expression level was markedly increased, suggesting that *ABI3* expression is negatively regulated by its own 5'-UTR (Ng et al., 2006). Moreover, *ABI3* levels are regulated by an ABI3-interacting protein, AIP2 an E3 ligase that targets ABI3 to the 26S proteasome for degradation (Zhang et al., 2005). The ectopic expression of the *ABI3* maize ortholog, Viviparous (*VP1*), in *Arabidopsis* leads to the expression of a subset of seed-specific genes in vegetative tissues, indicating that *VP1* is a key determinant for embryonic traits (Suzuki et al., 2003). This also suggests that ABI3-dependent regulatory mechanisms are conserved in both dicots and cereals.

Seed maturation-related genes, such as those governing SSP and lipid accumulation, are controlled by the interaction of transcriptional regulators with *cis*-acting elements in their promoters. The best characterized *cis*-elements include the RY repeat (CATGCA), ACGT-box (CACGTG) and AACA motif, that are recognized by B3, bZIP and MYB domain transcription factors, respectively. Functional analysis and *in vitro* protein-DNA interaction assays demonstrated binding of the B3 factors (LEC2, ABI3 and FUS3) to RY repeats (Reidt et al., 2000; Kroj et al., 2003; Mönke et al., 2004; Braybrook et al., 2006), and bZIP factors (ABI5, AtbZIP10, AtbZIP25 and bZIP53) to ACGT-boxes (Bensmihen et al., 2002; Lara et al., 2003; Alonso et al., 2009; Reeves et al., 2011). Moreover, ABI5 and its homolog EEL play antagonistic roles to influence the expression of the late embryogenesis abundant (LEA) gene, *AtEm1*, through competition for the same DNA binding site (Bensmihen et al., 2002). In addition to direct binding to DNA elements, the major regulators indirectly regulate the expression of seed maturation genes. Genetic and molecular studies have shown that LEC1 and LEC2 act upstream of ABI3 and FUS3 and control SSP gene expression through the regulation of *ABI3* and *FUS3* expression (Kagaya et al., 2005b; To et al., 2006). ABI3 functions as a seed-specific transcriptional co-activator that physically interacts with ABI5, AtZIP10 and AtZIP25 (Nakamura et al., 2001; Lara et al., 2003). Recently, another G-box binding group C bZIP factor, bZIP53, was shown to be a key regulator of seed maturation gene expression and enhanced expression by heterodimerization with bZIP10 or bZIP25 (Alonso et al., 2009). *FUS3* expression

in the protoderm and its negative regulation of TRANSPARENT TESTA GLABRA1 (TTG1) are critical for embryogenesis (Tsuchiya et al., 2004). Moreover, *FUS3* was induced by auxin and indirectly influences the seed maturation process by positive and negative regulation of ABA and GA synthesis, respectively (Gazzarrini et al., 2004).

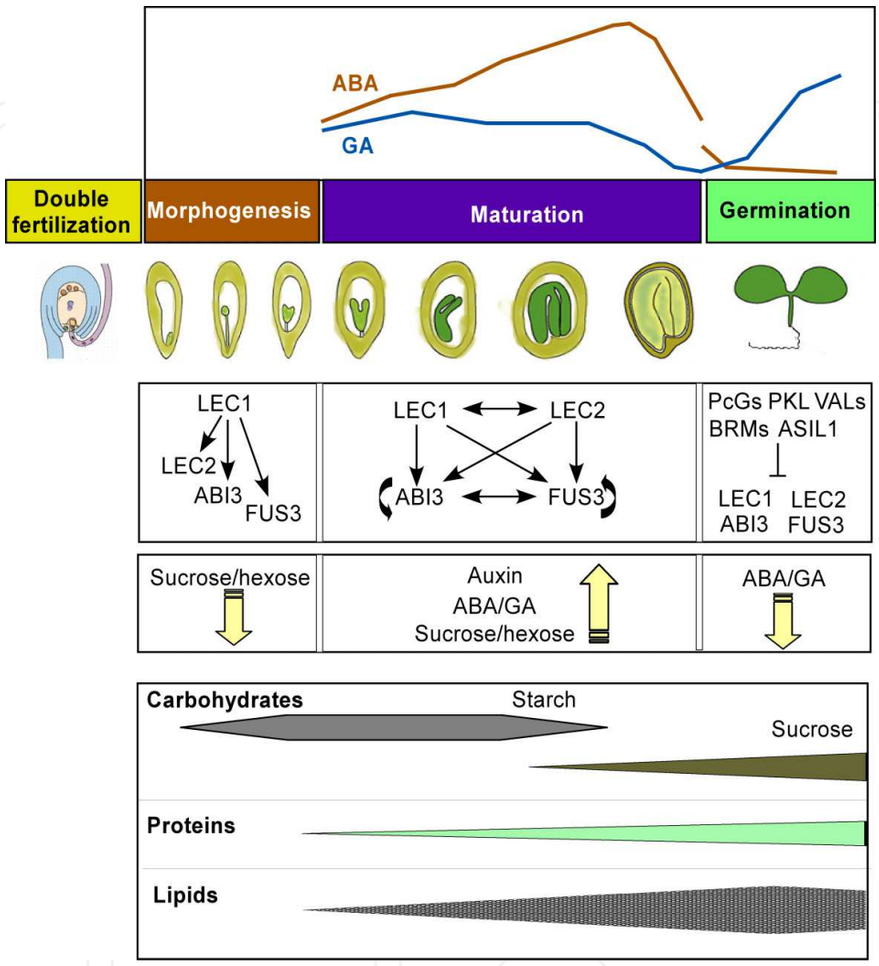


Fig. 2. Schematic representation of seed development in *Arabidopsis*. Embryogenesis after double fertilization in angiosperms involves two phases, morphogenesis and maturation. During the morphogenesis phase (approximately the first one third of the time of embryogenesis), the basic body plan is established and generates the different morphological domains of the embryo, the embryonic tissue and organ systems. After transition to the maturation phase, the embryo undergoes typical seed filling, growth arrest, acquisition of desiccation tolerance and entry into quiescence. Major reserves synthesized and accumulated during maturation phase include starch, storage proteins and lipids. Transition into the maturation phase is coordinated by the interactions of stage-specific developmental regulators such as the LEC regulators and the competing effects of sugars (sucrose-hexose ratio), hormones (ABA-GAs balance) and their synchronized interactions. The germination potential of seeds and seedling establishment are determined by the after-ripening process, hormones (GAs) and multiple embryonic repressors. Adapted from Refs. (Baud et al., 2002; Weber et al., 2005; Braybrook & Harada, 2008).

In monocots, the starchy endosperm is the prevalent storage domain, where carbohydrates and SSPs accumulate during maturation. Cereal SSP genes were among the first plant genes to be characterized. The AACA motif and the bipartite endosperm box (EB) encompassing the GCN4-like motif (GLM, ATGAGTCAT) and the prolamin box (PB, TGTAAAG) are the best characterized *cis*-elements affecting SSP gene expression (Forde et al., 1985; Wu et al., 2000). *In vitro* and *in vivo* protein-DNA interaction assays have identified direct targeting of the barley R2R3MYB factor HvGAMYB, wheat GAMYB and rice (*Oryza sativa)* OsMYB5 to the AACA motif. The Dof (DNA binding with one finger) proteins BPBF (prolamin box binding factor) and SAD (scutellum and aleurone-expressed DOF) bind to the PB box, while OPAQUE2 (O2)-like bZIP proteins, SPA (in wheat), BLZ1 and BLZ2 (in barley), bind to the GLM motif (Albani et al., 1997; Mena et al., 1998; Vicente-Carbajosa et al., 1998; Wu et al., 1998; Oñate et al., 1999; Díaz et al., 2002; Yanagisawa, 2002; Diaz et al., 2005). GAMYB was reported to activate expression of the endosperm-specific genes, such as *Itr1* which encodes the trypsin inhibitor BTI-CMe (Díaz et al., 2002). Dof proteins, BPBF and SAD, and the O2-like bZIP proteins, BLZ1 and BLZ2, activated expression of the B-hordein storage protein gene *Hor2* in barley (Mena et al., 1998; Vicente-Carbajosa et al., 1998; Oñate et al., 1999; Diaz et al., 2005). The maize Dof protein PBF was demonstrated to trans-activate the *γ-zein* gene (*γZ*) through the PB box (Marzábal et al., 2008). In addition, the R1MYB-SHA-QYF family proteins, HvMCB1 and HvMYBS3, were shown to regulate endosperm-specific gene expression through binding to the GATA motif (Rubio-Somoza et al., 2006a; 2006b). Recently, the barley FUSCA3 (HvFUS3) was demonstrated to bind to the RY-box present in the promoters of many endosperm genes (Moreno-Risueno et al., 2008). *HvFUS3* encodes a B3 domain protein that is expressed in the endosperm and embryo of developing seeds. *HvFUS3* expression peaks during the mid maturation phase and it participates in the transcriptional activation of the endosperm-specific genes *Hor2* and *Itr1* (Moreno-Risueno et al., 2008). Moreover, HvFUS3 was determined to trans-activate seed-specific genes *in planta* through interaction with the O2-like bZIP factor BLZ2 (Moreno-Risueno et al., 2008), indicating the involvement of both a B3 domain protein and a bZIP factor in the combinatorial regulation of endosperm-specific gene expression. In maize, O2 affects grain size and composition and is important in carbon allocation and amino acid biosynthesis during seed development (Hunter et al., 2002; Manicacci et al., 2009). In addition, two R1MYB transcription factor family proteins from wheat, MCB1 (MYB-related CAB promoter-binding protein) and MYBS3, were shown to interact with GARC (GA response complex) and to be involved in the regulation of SSP gene expression (Rubio-Somoza et al., 2006a; 2006b). Recent deep sequencing analysis of the transcriptome in developing rice seeds identified many differentially expressed novel transcripts and genes that are involved in the biosynthesis of starch and storage proteins. Hundreds of novel conserved patterns of *cis*-elements were found in the upregulated genes in the rice cultivars with high milling yield and good eating quality (Venu et al., 2011). Similar to the studies in *Arabidopsis* as described above, these discoveries indicate that complex combinatorial interactions of different transcription factors are pivotal for the regulation of the seed maturation program in cereals.

With the exception of those directly targeting SSP genes for which the regulatory elements in their promoters are well defined, little progress has been made in understanding the interactions between the master regulators and other target proteins, called secondary transcription factors (STF), that are also essential for the regulation of seed maturation

processes. Nonetheless, part of the seed maturation program is regulated by indirect means mediated by STF. In rice, mutual interactions have been demonstrated between two transcriptional activators, a DOF–related rice prolamin box binding protein (RPBF) and a RISBZ1 bZIP factor (Yamamoto et al., 2006). In barley, the formation of binary or ternary complexes with PBF and DOF regulatory proteins are important for controlling SSP gene expression (Rubio-Somoza et al., 2006a; 2006b; Yamamoto et al., 2006). In *Arabidopsis*, mutation of LEC-type regulators (LEC1, LEC2 and FUS3) led to reduced accumulation of SSPs and major seed lipid TAGs, while ectopic expression in seedlings caused SSPs and TAGs to accumulate in vegetative tissues (Kagaya et al., 2005b; Santos-Mendoza et al., 2005; Braybrook et al., 2006; Wang et al., 2007). The master regulator LEC2 was also shown to control seed oil accumulation through regulation of WRINKLED1 (WRI1) (Baud et al., 2007) that directly targets fatty acid synthetic genes (Baud et al., 2009; Maeo et al., 2009). WRI1 is an AP2-type transcription factor with two AP2-binding domains (Cernac & Benning, 2004) and functions downstream of LEC1 ad LEC2. Ectopic expression of *WRI1* leads to the upregulation of fatty acid synthetic and glycolytic genes in seedlings (Baud et al., 2007; Mu et al., 2008). *In vitro* and *in vivo* analyses demonstrated that WRI1 was able to bind to the AW-box [CnTnG](n)$_7$[CG] of *BCCP2* (acetyl-CoA carboxylase) and *PI-PKβ1* (a subunit of pyruvate kinase) (Baud et al., 2009; Maeo et al., 2009). These studies provide insight into the understanding of the role of WRI1 in the regulation of oil synthesis during seed maturation. Some other downstream regulatory complexes have also been identified. For instance, biosynthesis of flavonoids, which are found in most seeds and grains and are major metabolites in the embryo and seed coat (Lepiniec et al., 2006), is regulated by a complex with six components including TRANSPARENT TESTA GLABRA1 (TTG1), the expression of which is repressed by FUS3 in the protoderm (Tsuchiya et al., 2004). Discovery of additional STFs and their interactions with the upstream master regulators will allow better exploration of the molecular mechanisms that control seed filling.

3.2 Hormonal signaling during seed maturation

The phytohormone ABA, an endogenous messenger derived from epoxycarotenoid, has a wide rage of functions in plant development, and in responses to biotic and abiotic stresses through its interaction with the Mg-chelatase H subunit (CHLH) and PYR1/RCAR1 (Shen et al., 2006; Ma et al., 2009; Park et al., 2009; Cutler et al., 2010). Many factors involved in ABA signaling have been characterized (Finkelstein, 2006; Razem et al., 2006; Adie et al., 2007; Hirayama & Shinozaki, 2007). ABA is the key hormone regulating several seed maturation processes including the initiation of the maturation phase, filling of seed reserves and entrance into dormancy (Nambara & Marion-Poll, 2003; Finch-Savage & Leubner-Metzger, 2006). ABA is initially synthesized in the maternal tissues and subsequently in the embryo (Nambara & Marion-Poll, 2003; Frey et al., 2004). Many genes for seed ABA biosynthesis have been identified including *ABA1* (*ABA DEFICIENT1*) encoding a zeaxanthin epoxidase that functions in first step of the ABA biosynthesis, NCED*s* encoding 9-cis-epoxycarotenoid dioxygenases and *ABA2*/*GIN1* (*GLUCOSE INSENSITIVE1*)/*SDR1* (*SHORT-CHAIN DEHYDROGENASE REDUCTASE1*)/*SIS4* (*SUGAR-INSENSITIVE4*) encoding a cytosolic short-chain dehydrogenase/reductase involved in the conversion of xanthoxin to ABA-aldehyde during ABA biosynthesis (Nambara & Marion-Poll, 2003). A subset of ABA response mutants have been isolated and served as tools for dissecting the ABA singaling

pathway (Kucera et al., 2005). For example, mutant analyses reveal that the ABA-activated protein kinases, PP2Cs (serine-threonine phosphatase type 2C) ABI1 and ABI2, and the transcriptional regulators ABI3, ABI4 and ABI5, are involved in the ABA signaling pathway and associated with seed dormancy (Finkelstein et al., 2002; Himmelbach et al., 2003). In *Arabidopsis*, ABA level is dynamically modulated and increases concurrent with the initiation of seed maturation phase, remains high throughout the maturation phase, declines at late maturation and is very low during germination and seedling establishment (Fig. 2) (Nambara & Marion-Poll, 2003; Seo et al., 2009). During seed maturation, ABA signaling is intimately associated with the actions of the master regulators LEC1, LEC2, ABI3 and FUS3 (Finkelstein et al., 2002; Gutierrez et al., 2007; Braybrook & Harada, 2008). For instance, *FUS3* expression leads to the elevation of ABA levels (Gazzarrini et al., 2004) and exogenous application of ABA enhances *FUS3* expression (Kagaya et al., 2005a; 2005b). As well, activation of embryonic gene (e.g. storage protein, LEA and oleosin genes) expression by LEC1, FUS3 and ABI3 is enhanced by ABA application (Parcy et al., 1994; Kagaya et al., 2005a; 2005b). A number of genes have been characterized that regulate ABA homeostasis. In *Arabidopsis*, CYP707A1 and CYP707A2 are major regulators for ABA degradation in the embryo at mid maturation and in both the embryo and the endosperm during late maturation (Okamoto et al., 2006). In barley and bean (*Phaseolus vulgaris*), the expression of *CYP707A* genes is the major mechanism controlling ABA catabolism in seeds (Millar et al., 2006; Yang et al., 2006). Moreover, *HvNCED2* was shown to upregulate ABA biosynthesis during grain development, whereas *HvCYP707A1* downregulated ABA levels during the subsequent seed maturation phase (Chono et al., 2006).

GA is also important in controlling seed maturation, germination and seedling growth (Seo et al., 2009). As shown in Fig. 2, GA levels are suppressed throughout the seed maturation phase until germination at which time GA levels elevate significantly. It was demonstrated that ABA interacts with GA during the maturation process (Seo et al., 2006). GA biosynthesis is suppressed by ABA in developing seeds through activation of *AtGA2ox6*. Seed maturation and germination are not determined by ABA alone, but instead by the ABA/GA ratio (Karssen et al., 1983; Giraudat et al., 1994; Dubreucq et al., 1996; Debeaujon & Koornneef, 2000; Finkelstein et al., 2002; Koornneef et al., 2002; Ogawa et al., 2003). At the beginning of the maturation phase, ABA levels increases in seeds and the resulting elevated ABA/GA ratio promotes maturation, induces dormancy and inhibits germination. Consistent with the lower ABA/GA ratio in the seeds of *lec2* and *fus3* mutants, and with the precocious cell differentiation and growth of mutant embryos, FUS3 and LEC2 were found to inhibit GA biosynthesis through the repression of GA biosynthetic genes (Curaba et al., 2004; Gazzarrini et al., 2004). However, reduced GA levels alone are not sufficient to confer desiccation tolerance during late maturation phase and SSP accumulation was defective in the *fus3* mutant in spite of the GA status (Gazzarrini et al., 2004). Additionally, *ABI3* and *FUS3* were shown to be regulated by ABA and/or GA at the post-translational level. AIP2 (ABI3-interacting protein 2), an E3 ligase controlled by ABA, can trigger the degradation of ABI3 (Zhang et al., 2005). Besides the importance of ABA/GA ratio for the regulation of seed maturation, the balance between ABA and other hormones is also important. For example, grain-filling rate in wheat was correlated with increases in the ABA/ethylene ratio (Yang et al., 2006).

Genetic and molecular studies have shown that auxin plays an essential role in embryogenesis and post-embryonic organ formation through its dynamic directional distribution (Tanaka et al., 2006). During embryogenesis, auxin accumulation is directed by PIN-FORMED (PIN)-mediated polar transportation from the apical cells to the hypophysis, the founder cell of the root stem-cell system (Tanaka et al., 2006). It has been suggested that auxin is required for the embryonic regulators FUS3, LEC1 and LEC2 to potentiate embryogenesis and seed maturation processes (Gazzarrini et al., 2004; Casson & Lindsey, 2006; Stone et al., 2008). ABI3 has been shown to be involved auxin signaling and lateral root development (Brady & McCourt, 2003). Auxin-responsive genes can be activated by the ectopic expression of *LEC2* (Braybrook & Harada, 2008) and *FUS3* expression was induced by auxin (Gazzarrini et al., 2004). ASIL1 (for *Arabidopsis* 6b-interacting protein 1-like 1), a trihelix transcriptional repressor of seed maturation genes in *Arabidopsis*, is not responsive to ABA, but is moderately induced by auxin (Gao et al., 2009). In dry or imbibed wild-type seeds, *LEC1* and *LEC2* transcripts were not observed, whereas expression was elevated in *asil1* mutants at 1 h after imbibition with this increase being enhanced by the application of auxin (Gao et al., 2009). Given the fact that somatic embryogenesis is induced by the synthetic auxin 2,4-D (2,4-dichlorophenoxyacetic acid) (Mordhorst et al., 1998) and that derepression of *LEC1* and *LEC2* in imbibed *asil1* mutant seeds was enhanced by auxin, similar to ABA, it was suggested to function as a signal for the activation of embryonic genes. Auxin accumulation is also dynamically changed during germination and vegetative growth. For example, auxin activity was highly localized in the radical tips of germinating and germinated seeds (Liu et al., 2007) and the initiation sites of organ primordia in roots and shoots correspond to regions with increased auxin levels (Tanaka et al., 2006). *ASIL1* expression also exhibited a modest response to auxin and the level of *ASIL1* transcript is elevated at 1h post-imbibition, therefore the rise in *ASIL1* transcript levels may correspond to the distribution of auxin in cells of germinating seeds (Gao et al., 2009). LEC1 and LEC2 function upstream of other embryonic and seed maturation genes (To et al., 2006) and their ectopic expression is sufficient to provoke the embryonic program in vegetative tissues (Lotan et al., 1998; Stone et al., 2001; Santos-Mendoza et al., 2005). Therefore, expression of these two major regulators of embryonic programming should be strictly prevented during germination and seedling development. Given the up-regulation of *ASIL1* by auxin and the derepression of embryonic genes in germinating *asil1* seeds as well as in 2-week-old *asil1* seedlings, ASIL1 may prevent ectopic expression of *LEC1* and *LEC2* in cells that encounter elevated auxin levels during germination and vegetative growth (Gao et al., 2009). Although significant progress has been made in understanding the connection between seed maturation and auxin signaling, the precise roles that auxin plays and its mode of action during the maturation phase remain to be established. Only minor auxin-related traits have been detected in *lec* mutants during early embryogenesis (Lotan et al., 1998; Stone et al., 2001). The *lec1* and *lec2* mutants have strongly reduced ability to generate somatic embryos (Gaj et al., 2005), whereas ectopic expression of *LEC1* and *LEC2* in seedlings induced the formation of embryonic traits (Lotan et al., 1998; Stone et al., 2001). Therefore, it has been proposed that LEC transcription factors seem to build an environment in somatic cells that prime them to respond to auxin and undergo somatic embryogenesis; this competence might be affected by the repression of GA synthesis by LEC regulators or influenced by ABA signaling alone or by the ABA/GA balance (Braybrook & Harada, 2008).

3.3 Sugar signaling and metabolic regulation

Sugars generated by photosynthesis play a key role in plant development as structural components, storage molecules, energy sources and as intermediates for the synthesis of other organic molecules. In addition, sugars may act as signaling molecules that regulate the expression of genes involved in photosynthesis and metabolism. High sugar levels lead to a negative feedback on photosynthesis while promoting starch biosynthesis. Conversely, low sugar levels increase photosynthetic gene expression and promote storage reserve mobilization while limiting the use of carbohydrates to metabolic processes (Wobus & Weber, 1999; Rook et al., 2006). For instance, many plant developmental processes, such as seed germination, seedling establishment, flowering and senescence, are influenced by glucose (Gibson, 2000; Smeekens, 2000; Gibson, 2005; Rolland et al., 2006). Gene expression can be regulated by sugar-induced signal transduction through diverse mechanisms at the transcriptional, post-transcriptional, translational and post-translational levels (Rolland et al., 2006). Many studies have determined that the initiation of seed maturation processes is triggered by sugar signaling, notably the sucrose/hexose ratio in the embryos (Fig. 2) (Weber et al., 2005). During endosperm or cotyledon differentiation, gradients in metabolite concentrations emerge and provide signals for the transition into the maturation phase (Weber et al., 2005). Glucose concentration is directly correlated with cell division. This is supported by the observation of higher levels of glucose in nondifferentiated premature regions and low levels in mature starch-accumulating regions (Borisjuk et al., 2003). Conversely, young embryos contain moderately low levels of sucrose and the highest concentration of sucrose occurs in the actively elongating and starch-accumulating cells during maturation, which is consistent with the expression of genes involved in the storage compound synthesis (Borisjuk et al., 2002). This alteration in sugar balance is correlated with the establishment of an epidermis-localized sucrose uptake system via the formation of transfer cells (Offler et al., 2003). A strong and transient increase in sucrose uptake occurs while free hexose levels decrease markedly in the embryo. Sucrose signaling subsequently controls storage filling and differentiation processes in seeds through the regulation of gene expression and metabolic enzyme activities (Gibson, 2005; Rolland et al., 2006). In *Arabidopsis*, mutation of the gene encoding sugar transporter SUC5 delayed the conversion of sugar to lipids and AtSUC5 plays a major role in the progression into maturation phase (Baud et al., 2005). More interestingly, seed mass was increased in an *ap2* (*apetala2*) mutant, which is characterized by an increase in embryo cell size and number. This phenotype is the consequence of a prolonged period of cell division regulated by elevation of hexose/sucrose ratio (Ohto et al., 2005). In *tps1* (*TREHALOSE-6-PHOSPHATE SYNTHASE1*) mutant embryos, starch instead of lipids accumulated due to the downregulation of genes involved in the starch-sucrose breakdown and the upregulation of genes responsible for the lipid mobilization for gluconeogenesis, demonstrating the importance of trehalose in the sugar signaling pathway regulating the maturation phase (Gómez et al., 2006). As such, sugar signaling was suggested to be a ubiquitous regulatory system involved in seed maturation (Gutierrez et al., 2007).

Seed storage metabolism involves the movement of intermediates between several distinct subcellular compartments including mitochondria, plastids and cytosol (Fait et al., 2006). In cells of heterotrophic embryos, ATP is mainly generated in bioenergetic organelles, the mitochondria, by respiration and is imported into plastids through ATP/ADP translocators

in a rate-limiting manner (Tjaden et al., 1998; Rawsthorne, 2002). Studies in legumes, barley and maize have shown that ATP levels are associated with seed maturation processes. ATP levels are low in young cotyledons and increase toward maturation starting from the abaxial region. The active storage-accumulating regions contain high levels of ATP during maturation (Borisjuk et al., 2003; Rolletschek et al., 2004). The photoheterotrophic plastids in seed embryos are different from leaf chloroplasts with regard to morphology and physiology. These differences include elevated cyclic electron transport via photosystem II, but a low capacity for photosynthetic CO_2 fixation (Asokanthan et al., 1997). Seed photosynthesis plays a role in controlling biosynthetic fluxes through the production of ATP and O_2 by preventing hypoxic conditions inside the seed (Rolletschek et al., 2005a; Weber et al., 2005). The low O_2 levels in developing seeds affect enzymatic activity, gene expression patterns, mitochondrial ATP production, and metabolite fluxes. Hypoxia leads to energy depletion so that embryo cells are stressed and storage reserve accumulation is constrained (Borisjuk et al., 2003; Rolletschek et al., 2004; Rolletschek et al., 2005a; Weber et al., 2005; Borisjuk & Rolletschek, 2009). Therefore, photosynthesis in developing seeds is important for storage reserve synthesis and accumulation (Borisjuk et al., 2005; Rolletschek et al., 2005a; Fait et al., 2006). The energy status is also important for controlling the flux of substrates into different storage products (Rolletschek et al., 2005b). In general, energy demand is highest for lipids, followed by storage proteins, and lowest for starch (Weber et al., 2005). For instance, in *Brassica napus*, the developmental transfer from starch to lipid storage at mid maturation is accompanied by increased ATP/ADP ratios. Starch synthesis is saturated at lower ATP levels than is lipid synthesis (Vigeolas et al., 2003). Moreover, during seed maturation in oilseeds *B. napus* and soybean (*Glycine max*), the biosynthetic switch from starch to lipids is linked to the import of specific metabolites, suggesting that the relative fluxes into different storage products are not only energy dependant but also developmentally controlled (Eastmond & Rawsthorne, 2000; Weber et al., 2005).

Seed maturation is also influenced by nitrogen metabolism because storage protein accumulation depends on nitrogen uptake and availability (Golombek et al., 2001; Miranda et al., 2001; Rolletschek et al., 2005c). Asparagine is acquired from the phloem, metabolized and reconstructed in the seed coat and unloaded at later stages. In soybean, the level of asparagine in developing cotyledons plays a rate-limiting role in protein biosynthesis (Hernandez-Sebastia et al., 2005). Moreover, amino acid biosynthesis controls storage protein synthesis. For example, in soybean, pea (*Pisum sativum*), Fava bean (*Vicia faba*) and wheat, phosphoenolpyruvate carboxylase (PEPC), a ubiquitous and highly regulated enzyme, is as a determinant of SSP biosynthesis. Therefore, PEPC has become a promising target for increasing protein content of crop seeds. For example, overexpression of PEPC in bean seeds resulted in the accumulation of up to 20% more protein per gram seed dry weight due to the shift of metabolic fluxes from sugars/starch into organic acids and free amino acids during maturation; seed dry weight was higher by 20% - 30% possibly owing to elevated carbon fixation (Fait et al., 2006). A major metabolic switch has been identified that is associated with the transition from seed filling to the desiccation phase. Seed metabolism is fundamentally changed during this switch. Seed storage accumulation during maturation is associated with the reduction of most sugars, amino acids and organic acids. However, desiccation tolerance is associated with increases in the content of distinct sugars, organic acids, nitrogen-rich amino acids and shikimate-derived metabolites (Fait et al., 2006). Similarly, studies using gene profiling in *Medicago truncatula* seeds have demonstrated that

lipids, starch and oligosaccharides are mobilized, consistent with the elevation in sucrose level during the early desiccation stage (Buitink et al., 2006). Protein phosphorylation was shown to be involved in the metabolic regulation during seed maturation as the storage-associated enzyme PEPC is activated by phosphorylation (Goldberg & Fischer, 1999). In legume seeds, SPS (sucrose-phosphate synthase) activity is inhibited by phosphorylation during the switch from high hexose to high sucrose levels (Weber et al., 2005). In rice seeds, a calcium-dependent protein kinase (CDPK) isoform was found to control storage reserve accumulation by phosphorylation of sucrose synthase (Asano et al., 2002). Overexpression of *CDPK2* in rice arrests seed development at an early stage (Morello et al., 2000). A large number of functionally diverse phosphoproteins were expressed during seed filling in *B. napus* (Agrawal & Thelen, 2006). *OsCPK23* is markedly upregulated in developing seeds in comparison to mature leaves (Ray et al., 2007). The 12S globulin cruciferin was found to be the major phosphorylated storage protein in *Arabidopsis* seeds (Wan et al., 2007) and protein tyrosine kinases and protein tyrosine phosphatases were shown to be involved in the storage protein accumulation and lipid reserve mobilization processes (Ghelis et al., 2008). Recently, the leucine-rich repeat receptor kinase encoded by *IKU2* (*HAIKU2*) was shown to directly target the positive seed regulator SHB1 (Zhou et al., 2009). Mutation of *IKU2* reduced seed size and affected embryo and endosperm development (Luo et al., 2005).

3.4 Sugar and ABA signal interaction

As described above, transition of embryo morphogenesis into the maturation phase is governed by sugars and ABA signaling and their coordinated interaction (Brocard-Gifford et al., 2003; Gibson, 2004). Genetic and molecular studies demonstrated that sugar signaling in higher plants is intimately associated with hormone signaling, in particular with ABA (Leon & Sheen, 2003; Rook et al., 2006; Dekkers et al., 2008). Four independent screens have been conducted to identify sugar response mutants: *sun* (sucrose uncoupled), *isi* (impaired sucrose induction), *gin* and *sis*. All four screens identified the ABA deficient mutants (*aba2/isi4/gin1/sis4* and *aba3/gin5*) and *ABA insensitive4* (i.e. *abi4/sun6/isi3/gin6/sis5*) (Arenas-Huertero et al., 2000; Huijser et al., 2000; Laby et al., 2000; Rook et al., 2001) suggesting genetic interactions between sugar and ABA signaling pathways. Furthermore, ABA biosynthetic and signaling genes were found to be regulated by glucose. Several sugar signaling mutants, such as *gin1*, *gin5*, *isi4* and *sis4*, exhibit lower endogenous ABA levels (Arenas-Huertero et al., 2000; Laby et al., 2000; Rook et al., 2001), which is consistent with the previously identified ABA deficient mutants *aba1*, *aba2* and *aba3* that show a *gin* phenotype (Arenas-Huertero et al., 2000; Huijser et al., 2000; Laby et al., 2000). Transcripts of several ABA biosynthetic genes, such as *ABA1*, *AAO3* and *ABA3*, are increased by low concentrations of glucose (2%) (Cheng et al., 2002), as well as by ABA itself (Xiong et al., 2001; Cheng et al., 2002; Seo & Koshiba, 2002). These observations suggest that ABA biosynthetic genes and ABA accumulation are directly regulated by glucose. ABI4 and ABI5 were shown to be involved in ABA signaling and play important roles during seed development (Finkelstein, 1994; Brocard et al., 2002). As indicated above, sugar response mutants, such as *sun6*, *isi3*, *gin6* and *sis5*, are allelic to *abi4*. The *abi4* mutant was isolated based on its ability to germinate in the presence of high levels of ABA (3 μM) (Finkelstein, 1994). Expression of *ABI4* was activated by 6% glucose in an ABA-dependent fashion, but had a limited response to ABA alone (Arenas-Huertero et al., 2000; Cheng et al., 2002). These investigations indicate that ABA biosynthetic and signaling genes can be regulated by both

glucose and ABA. Besides *abi4* and *abi5*, *abi8* mutants also displayed a glucose insensitive phenotype, although this phenotype was not as obvious as that of the *abi4* mutant (Arenas-Huertero et al., 2000; Huijser et al., 2000; Laby et al., 2000; Brocard-Gifford et al., 2003). Similar to *ABI4*, *ABI5* expression is also induced by glucose in an ABA-dependent manner (Cheng et al., 2002) and overexpression of *ABI5* increased sensitivity to glucose (Brocard et al., 2002). Additionally, *ABI3* expression was also found to be induced by glucose in an ABA-dependent manner, although not as significant as *ABI4* and *ABI5* (Cheng et al., 2002). Overexpression of *ABI3* confers hypersensitivity to sugars (Finkelstein et al., 2002; Zeng & Kermode, 2004) and *abi3* mutants were insensitive to glucose in combination with ABA (Nambara & Marion-Poll, 2003). A similar sugar-ABA interaction was shown for the regulation of *ApL3* (ADP pyrophosphorylase large subunit) in starch biosynthesis in rice (Akihiro et al., 2005). These findings clearly connect sugar to ABA signaling; however, a number of genes are coregulated by sugar and ABA (Li et al., 2006). Additionally, *ABI1*, *ABI2* and *ABI3* appear not to have a major role in sugar signaling (Arenas-Huertero et al., 2000; Huijser et al., 2000; Laby et al., 2000). Taken together, genetic and molecular analyses of sugar signaling have uncovered complex and extensive interactions between sugar and ABA signaling pathways. Whether a direct molecular link exists between sugar and ABA signaling pathways remains unresolved, and more efforts might be devoted to the establishment of their connections in a more direct and specific way.

3.5 Epigenetic regulation of seed maturation

Accumulation of seed reserves is a major process during the seed maturation phase. The main storage products accumulated during seed filling are storage proteins, oil (often TAG) and carbohydrates (often starch). Recently, advances have been made toward understanding the regulatory, metabolic and developmental control of seed filling (Baud et al., 2008; Gallardo et al., 2008; Santos-Mendoza et al., 2008; North et al., 2010). The regulatory networks governing seed maturation in *Arabidopsis* are repressed prior to germination so that seed storage reserves are not accumulated during vegetative development (Fig. 2). Therefore, studies on the expression of seed maturation genes in non-seed tissues would facilitate understanding of the regulatory mechanisms underlying seed filling. Chromatin modification has been implicated in the repression of these regulatory networks. Phaseolin is the major SSP of bean. Phaseolin (*phas*) gene expression is temporally and spatially regulated and is completely inactive during the vegetative phase of plant development (Bustos et al., 1989; van Der Geest et al., 1995). Silencing of the *phas* gene in vegetative tissues was associated with the presence of a nucleosome positioned over the three phased TATA boxes present in the *phas* promoter (Kadosh & Struhl, 1998). Ectopic expression of the ABI3-like factor *ALF* potentiated the chromatin structure over the TATA region of the phas promoter and caused *phas* expression in vegetative tissues in an ABA-dependent manner (Goldberg & Fischer, 1999). In developing seeds, this repressive structure is remodeled concomitant with gene activation, leading to the disruption of condensed chromatin configuration and allowing transcription factors to access the *phas* promoter (Li & Hall, 1999). Chromatin immunoprecipitation assays demonstrated that histone acetylation and methylation-directed chromatin remodeling contributed to the regulation of *phas* expression (Ng et al., 2006). Acetylation and deacetylation of lysine residue in the amino-terminal tail were shown to be involved in the reversible modification of chromatin structure and had the opposite effect on transcriptional regulation (Berger,

2002). Acetylation is catalyzed by histone acetyltransferase (HAT) and results in transcriptional activation (Brownell & Allis, 1996; Kuo & Allis, 1998; Kuo et al., 2000). Deacetylation is catalyzed by histone decaetylase (HDAC) and is linked to transcriptional repression (Kadosh & Struhl, 1998; Rundlett et al., 1998). Inhibition of HDAC activity with trichostatin A during germination led to elevated expression of embryogenesis-related genes (Tanaka et al., 2008).

Several proteins have been identified that act as negative regulators of seed maturation gene expression (Table 3 and Fig. 2). PICKLE (PKL), a CHD3 chromatin remodeling factor belonging to the SWI/SNF class, acts in concert with GA to ensure that embryonic traits are not expressed after germination (Ogas et al., 1997; Ogas et al., 1999). *pkl* mutants expressed seed maturation genes in primary roots (Ogas et al., 1997; Ogas et al., 1999; Rider et al., 2003; Henderson et al., 2004; Li et al., 2005). The VP1/ABI3-LIKE (VAL) B3 proteins VAL1 and VAL2, also referred to as HSI2 and HSL1, respectively (Tsukagoshi et al., 2007), act together with sugar signaling to repress ectopic expression of seed maturation genes in seedlings and were necessary for the transition from seed maturation to active vegetative growth (Suzuki et al., 2007; Tsukagoshi et al., 2007). *VAL1* and *VAL2* encode B3 domain proteins with an ERF-associated amphiphilic repression (EAR) motif. Interestingly, a CW domain of unknown function and a putative plant homeodomain (PHD)-like zinc (Zn)-finger domain are frequently present in chromatin remodeling factors and were present in the VAL1 and VAL2 (Suzuki et al., 2007). It was revealed that VAL1/HSI2 functions as a repressor of a sugar-inducible reporter gene (Tsukagoshi et al., 2005). Most of the embryonic and seed maturation genes including *LEC1*, *ABI3*, *FUS3* and genes for seed storage compounds were derepressed in seedlings of a double mutant of *VAL1* and *VAL2* (Suzuki et al., 2007; Tsukagoshi et al., 2007). As noted above, PcG group proteins establish epigenetic inheritance of repressed gene expression states through histone methylation of H3K27 (Köhler & Grossniklaus, 2002). Genetic and molecular studies demonstrated that *FUS3* is regulated by the PcG proteins, for example, *FUS3* expression is derepressed in leaves of a double mutant of *CLF* and *SWN* and chromatin immunoprecipitation corroborated the direct targeting of *FUS3* by the PcG protein MEA (Makarevich et al., 2006). A member of BRAHMA (BRM)-containing SNF2 chromatin remodeling ATPase was also found to be involved in repression of some seed maturation genes in leaves. Mutation of *BRM* led to the accumulation of transcripts from *2S, FUS3* and some other embryogenesis-related genes in leaf tissues (Tang et al., 2008). Recently, a new embryonic repressor ASIL1 was isolated by its interaction with the *Arabidopsis* 2S albumin *At2S3* promoter (Gao et al., 2009). ASIL1 has domains conserved in the plant-specific trihelix family of DNA binding proteins and belongs to a subfamily of 6b-interacting protein 1-like factors. It is interesting that the trihelix domain of ASIL1 is highly similar to the SANT (Switching-defective protein 3 (Swi3), Adaptor 2 (Ada2), Nuclear receptor co-repressor (N-CoR), Transcription factor (TF)IIIB) domain that functions as a unique histone-interaction module in chromatin remodeling (Boyer et al., 2004). This structural feature suggests that ASIL1 may function as a gene-specific DNA-binding factor to regulate seed maturation genes by recruiting a chromatin remodeling complex. Identification of proteins that interact with ASIL1 will provide further insight into this possible regulatory mechanism. *asil1* seedlings exhibit a global shift in gene expression to a profile resembling late embryogenesis. *LEC1* and *LEC2* were markedly derepressed during early germination, as was a large subset of seed maturation genes, such as those encoding SSPs and oleosins, in seedlings of *asil1* mutants. Consistent with this, *asil1* seedlings

accumulated 2S albumin and oil with a fatty acid composition similar to that of seed-derived lipid. Moreover, ASIL1 specifically binds to a GT element that overlaps the G-box and is in close proximity to the RY repeats of the *At2S* promoters. It was suggested that ASIL1 targets GT-box–containing embryonic genes by competing with the binding of transcriptional activators to this promoter region. Thus, ASIL1 represents a novel component of the regulatory framework that negatively controls expression of seed maturation genes during post-embroyonic growth (Gao et al., 2009). This finding supports the notion that embryonic traits are actively repressed during and after germination and are directly or indirectly regulated by epigenetic means (Fig. 2).

Gene	Acronym	Protein category	Protein domains	DNA-binding property	Potential function in embryonic gene repression	References
VP1/ABI3-LIKE	*VILs*	B3	B3, Zn finger	Yes	Repression of master regulators of seed maturation LEC1, ABI3 and FUS3, and many seed maturation genes	Suzuki et al., 2007; Tsukagoshi et al., 2007
ASIL1	*ASIL1*	Trihelix	Trihelix	Yes	Repression of master regulators of seed maturation LEC1, LEC2, ABI3 and FUS3, and many seed maturation genes	Gao et al., 2009
PICKLE	*PKL*	SNF2	SNF2, CHD3, PHD	No	Repression of master regulators of seed maturation LEC1, LEC2 and FUS3, and many seed maturation genes	Ogas et al., 1997; Rider et al., 2003; Henderson et al., 2004; Li et al., 2005
CURLY LEAF/ SWINGER	*CLF/ SWN*	PcG	SET	No	Repression of master regulators of seed maturation LEC1, LEC2 and FUS3, and many seed maturation genes	Makarevich et al., 2006
BRAHAM	*BRM*	SNF2	SNF2	No	Many seed maturation genes	Tang et al., 2008
HDA6/19	*HDA6/19*	HDAC	HDAC	No	Repression of master regulators of seed maturation LEC1, ABI3 and FUS3, and many seed maturation genes	Tanaka et al., 2008

Table 3. Genes involved in seed repression in *Arabidopsis* seedlings

4. Conclusion

Seeds are the key link between two sporophytic generations in the life cycle of flowering plants. Seed development is an intricate genetically programmed process that is correlated with changes in metabolite levels and regulated by a complex signaling network mediated by sugars and hormones. The coordinated expression of embryo and endosperm tissues is required for proper early seed development, which is primarily maternally controlled through epigenetic mechanisms such as histone- and DNA-methylation. The transition to the maturation phase requires a switch to filial control which is denoted by a distinct hormone and metabolite profile. Genetic, physiological and cytological approaches have been employed to dissect the molecular mechanisms underlying seed development. Such studies have elucidated the elaborate regulatory and metabolic pathways governing the onset of seed maturation, seed filling, acquisition of desiccation tolerance and after-ripening phases. Considering the importance of seeds for human food, animal feed and sustainable feedstocks for biofuel production, much effort has been devoted to the genetic and metabolic control of starch, protein and lipid deposition in cereal grains and oilseeds. Molecular, physiological and genetic approaches are being used in combination to identify the individual steps in the pathways leading to storage compound synthesis and the factors that regulate these processes. Currently, these tools and knowledge are being applied to engineer crop plants with altered seed compositions and metabolite profiles to improve seed yield, quality and utility.

5. References

Acevedo-Hernández; G.J., León, P. & Herrera-Estrella, L.R. (2005). Sugar and ABA responsiveness of a minimal RBCS light-responsive unit is mediated by direct binding of ABI4. *Plant Journal*, Vol.43, No.4, (August 2005), pp. 506-519, ISSN 0960-7412

Ach, R.A.; Taranto, P. & Gruissem, W. (1997). A conserved family of WD-40 proteins binds to the retinoblastoma protein in both plants and animals. *Plant Cell*, Vol.9, No.9, (September 1997), pp. 1595-1606, ISSN 1040-4651

Adams, S.; Vinkenoog, R.; Spielman, M.; Dickinson, H.G. & Scott, R.J. (2000). Parent-of-origin effects on seed development in *Arabidopsis thaliana* require DNA methylation. *Development*, Vol.127, No.11, (June 2000), pp. 2493-2502, ISSN 0950-1991

Adie, B.A.; Pérez-Pérez, J.; Pérez-Pérez, M.M.; Godoy, M.; Sánchez-Serrano, J.J.; Schmelz, E.A. & Solano, R. (2007). ABA is an essential signal for plant resistance to pathogens affecting JA biosynthesis and the activation of defenses in *Arabidopsis*. *Plant Cell*, Vol.19, No.5, (May 2007), pp. 1665-1681, ISSN 1040-4651

Agrawal, G.K. & Thelen, J.J. (2006). Large scale identification and quantitative profiling of phosphoproteins expressed during seed filling in oilseed rape. *Molecular & Cellular Proteomics*, Vol.5, No.11, (November 2006), pp. 2044-2059, ISSN 1535-9476

Akihiro, T.; Mizuno, K. & Fujimura, T. (2005). Gene expression of ADP-glucose pyrophosphorylase and starch contents in rice cultured cells are cooperatively regulated by sucrose and ABA. *Plant Cell Physiology,* Vol.46, No.6, (June 2005), pp. 937-946, ISSN 0032-0781

Albani, D.; Hammond-Kosack, M.C.U.; Smith, C., Conlan, S.; Colot, V., Holdsworth, M.J. & Bevan, M.W. (1997). The wheat transcriptional activator SPA: a seed-specific bZIP protein that recognizes the GCN4-like motif in the bifactorial endosperm box of prolamin genes. *Plant Cell*, Vol.9, No.2, (February 1997), pp. 171-184, ISSN 1040-4651

Alonso, R.; Oñate-Sánchez, L.; Weltmeier, F.; Ehlert, A.; Diaz, I.; Dietrich, K.; Vicente-Carbajosa, J. & Dröge-Laser, W. (2009). A pivotal role of the basic leucine zipper transcription factor bZIP53 in the regulation of Arabidopsis seed maturation gene expression based on heterodimerization and protein complex formation. *Plant Cell*, Vol.21, No.6, (June 2009), pp. 1747-1461, ISSN 1040-4651

Arenas-Huertero, F.; Arroyo, A.; Zhou, L.; Sheen, J. & León, P. (2000). Analysis of *Arabidopsis* glucose insensitive mutants, *gin5* and *gin6*, reveals a central role of the plant hormone ABA in the regulation of plant vegetative development by sugar. *Genes & Development*, Vol.14, No.16, (August 2000), pp. 2085-2096, ISSN 0890-9369

Asano, T.; Kunieda, N.; Omura, Y.; Ibe, H.; Kawasaki, T.; Takano, M.; Sato, M.; Furuhashi, H.; Mujin, T.; Takaiwa, F.; Wu, C.Y.; Tada, Y.; Satozawa, T.; Sakamoto, M. & Shimada, H. (2002). Rice SPK, a calmodulin-like domain protein kinase, is required for storage product accumulation during seed development: phosphorylation of sucrose synthase is a possible factor. *Plant Cell*, Vol.14, No.3, (March 2002), pp. 619-628, ISSN 1040-4651

Asokanthan, P.; Johnson, R.W.; Griffith, M. & Krol, M. (1997). The photosynthetic potential of canola embryos. *Physiologia Plantarum*, Vol.101, No.2, (October 1997), pp. 353-360, ISSN 0031-9317

Baroux, C.; Pecinka, A.; Fuchs, J.; Schubert, I. & Grossniklaus, U. (2007). The triploid endosperm genome of *Arabidopsis* adopts a peculiar, parental-dosage-dependent chromatin organization. *Plant Cell*, Vol.19, No.6, (June 2007), pp. 1782-1794, ISSN 1040-4651

Baud, S.; Boutin, J.-P.; Miquel, M.; Lepiniec, L. & Rochat, C. (2002). An integrated overview of seed development in *Arabidopsis thaliana* ecotype WS. *Plant Physiology and Biochemistry*, Vol.40, No.2, (February 2002), pp. 151-160, ISSN 0981-9428

Baud, S.; Dubreucq, B. ; Miquel, M. ; Rochat, C. & Lepiniec, L. (2008). Storage Reserve Accumulation in Arabidopsis: Metabolic and Developmental Control of Seed Filling. *The Arabidopsis Book*, Vol.6,.No.e0113, ISSN 1543-8120

Baud, S.; Wuillème, S.; To, A.; Rochat, C. & Lepiniec, L. (2009). Role of WRINKLED1 in the transcriptional regulation of glycolytic and fatty acid biosynthetic genes in *Arabidopsis*. *Plant Journal*, Vol.60, No.6, (December 2009), pp. 933-947, ISSN 0960-7412

Baud, S.; Mendoza, M.S.; To, A.; Harscoët, E.; Lepiniec, L. & Dubreucq, B. (2007). WRINKLED1 specifies the regulatory action of LEAFY COTYLEDON2 towards fatty acid metabolism during seed maturation in *Arabidopsis*. *Plant Journal*, Vol.50, No.5, (June 2007), pp. 825-838, ISSN 0960-7412

Baud, S.; Wuillème, S.; Lemoine, R.; Kronenberger, J.; Caboche, M.; Lepiniec, L. & Rochat, C. (2005). The AtSUC5 sucrose transporter specifically expressed in the endosperm is involved in early seed development in *Arabidopsis*. *Plant Journal*, Vol.43, No.6, (September 2005), pp. 824-836, ISSN 0960-7412

Bauer, M.J. & Fischer, R.L. (2011). Genome demethylation and imprinting in the endosperm. *Current Opinion in Plant Biology*, Vol.14, No.2, (April 2011), pp. 162-167, ISSN 1369-5266

Bensmihen, S.; Rippa, S.; Lambert, G.; Jublot, D.; Pautot, V.; Granier, F.; Giraudat, J. & Parcy, F. (2002). The homologous ABI5 and EEL transcription factors function antagonistically to fine-tune gene expression during late embryogenesis *Plant Cell*, Vol.14, No.6, (June 2002), pp. 1391-1403, ISSN 1040-4651

Berger, F. & Chaudhury, A. (2009). Parental memories shape seeds. *Trends in Plant Science*, Vol.14, No.10, (October 2009), pp. 550-556, ISSN 1360-1385

Berger, S.L. (2002). Histone modifications in transcription regulation. *Current Opinion in Genetics & Development*, Vol.12, No.2, (April 2002), pp. 142-148, ISSN 0959-437X

Borisjuk, L. & Rolletschek, H. (2009). The oxygen status of the developing seed. *New Phytologist*, Vol.182, No.1, (October 2009), pp. 17-30, ISSN 0028-646X

Borisjuk, L.; Rolletschek, H.; Wobus, U. & Weber, H. (2003). Differentiation of legume cotyledons as related to metabolic gradients and assimilate transport into seeds. *Journal of Experimental Botany*, Vol.54, No.382, (January 2003), pp. 503-512, ISSN 0022-0957

Borisjuk, L.; Walenta, S.; Rolletschek, H.; Mueller-Klieser, W.; Wobus, U. & Weber, H. (2002). Spatial analysis of plant development: sucrose imaging within Vicia faba cotyledons reveals specific developmental patterns. *Plant Journal*, Vol.29, No.4, (February 2002), pp. 521-530, ISSN 0960-7412

Borisjuk, L.; Nguyen, T.H.; Neuberger, T.; Rutten, T;, Tschiersch, H.; Claus, B.; Feussner, I.; Webb, A.G.; Jakob, P.; Weber, H.; Wobus, U. & Rolletschek, H. (2005). Gradients of lipid storage, photosynthesis and plastid differentiation in developing soybean seeds. *New Phytologist*, Vol.167, No.3, (September 2005), pp. 761-776, ISSN 0028-646X

Boyer, L.A.; Latek, R.R. & Peterson, C.L. (2004). The SANT domain: a unique histone-tail-binding module? *Nature Reviews Molecular Cell Biology*, Vol.5, No.2, (February 2004), pp. 158-163, ISSN 1471-0072

Brady, S.M. & McCourt, P. (2003). Hormone cross-talk in seed dormancy. *Journal of Plant Growth Regulation*, Vol.22, No.1, (July 2003), pp. 25-31, ISSN 0721-7595

Braybrook, S.A. & Harada, J.J. (2008). LECs go crazy in embryo development. *Trends in Plant Science*, Vol.13, No.12, (December 2008), pp. 624-630, ISSN 1360-1385

Braybrook, S.A.; Stone, S.L.; Park, S.; Bui, A.Q.; Le, B.H.; Fischer, R.L.; Goldberg, R.B. & Harada, J.J. (2006). Genes directly regulated by LEAFY COTYLEDON2 provide insight into the control of embryo maturation and somatic embryogenesis. *Proceedings of the National Academy of Sciences USA*, Vol.103, No.9, (February 2006), pp. 3468-3473, ISSN 0027-8424

Brocard-Gifford, I.M.; Lynch, T.J. & Finkelstein, R.R. (2003). Regulatory networks in seeds integrating developmental, abscisic acid, sugar, and light signaling. *Plant Physiology*, Vol.131, No.1, (January 2003), pp. 78-92, ISSN 0032-0889

Brocard, I.M.; Lynch, T.J. & Finkelstein, R.R. (2002). Regulation and role of the *Arabidopsis abscisic acid-insensitive 5* gene in abscisic acid, sugar, and stress response. *Plant Physiology*, Vol.129, No.4, (August 2002), pp. 1533-1543, ISSN 0032-0889

Brownell, J.E. & Allis, C.D. (1996). Special HATs for special occasions: linking histone acetylation to chromatin assembly and gene activation. *Current Opinion in Genetics & Development*, Vol.6, No.2, (April 1996), pp. 176-184, ISSN 0959-437X

Buitink, J.; Leger, J.J. ; Guisle, I. ; Vu, B.L. ; Wuillème, S. ; Lamirault, G. ; Le Bars, A. ; Le Meur, N. ; Becker, A. ; Küster, H. & Leprince, O. (2006). Transcriptome profiling uncovers metabolic and regulatory processes occurring during the transition from desiccation-sensitive to desiccation-tolerant stages in *Medicago truncatula* seeds. *Plant Journal*, Vol.47, No.5, (September 2006), pp. 735-750, ISSN 0960-7412

Bustos, M.M.; Guiltinan, M.J.; Jordano, J.; Begum, D.; Kalkan, F.A. & Hall, T.C. (1989). Regulation of beta-glucuronidase expression in transgenic tobacco plants by an A/T-rich, cis-acting sequence found upstream of a French bean beta phaseolin gene. *Plant Cell*, Vol.1, No.9, (September 1989), pp. 839-853, ISSN 1040-4651

Cao, R. & Zhang, Y. (2004). The functions of E(Z)/EZH2-mediated methylation of lysine 27 in histone H3. *Current Opinion in Genetics & Development*, Vol.14, No.2, (April 2004), pp. 155-164, ISSN 0959-437X

Carles, C.; Bies-Etheve, N.; Aspart, L.; Léon-Kloosterziel, K.M.; Koornneef, M.; Echeverria, M. & Delseny, M. (2002). Regulation of *Arabidopsis thaliana* Em genes: Role of ABI5. *Plant Journal*, Vol.30, No.3, (May 2002), pp. 373-383, ISSN 0960-7412

Casson, S.A. & Lindsey, K. (2006). The turnip mutant of *Arabidopsis* reveals that *LEAFY COTYLEDON1* expression mediates the effects of auxin and sugars to promote embryonic cell identity. *Plant Physiology*, Vol.142, No.2, (October 2006), pp. 526-541, ISSN 0032-0889

Cernac, A. & Benning, C. (2004). WRINKLED1 encodes an AP2/EREB domain protein involved in the control of storage compound biosynthesis in *Arabidopsis*. *Plant Journal*, Vol.40, No.4, (November 2004), pp. 575-585, ISSN 0960-7412

Chaudhuri, S. & Messing, J. (1994). Allele-specific parental imprinting of dzr1, a posttranscriptional regulator of zein accumulation. *Proceedings of the National Academy of Sciences USA*, Vol.91, No.11, (May 1994), pp. 4867-4871, ISSN 0027-8424

Chaudhury, A.M.; Ming, L.; Miller, C.; Craig, S.; Dennis, E.S. & Peacock, W.J. (1997). Fertilization-independent seed development in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences USA*, Vol.94, No.8, (April 1997), pp. 4223-4228, ISSN 0027-8424

Cheng, W.H.; Endo, A.; Zhou, L.; Penney, J.; Chen, H.C.; Arroyo, A.; Leon, P.; Nambara, E.; Asami, T.; Seo, M.; Koshiba, T. & Sheen, J. (2002). A unique short-chain dehydrogenase/reductase in *Arabidopsis* glucose signaling and abscisic acid biosynthesis and functions. *Plant Cell*, Vol.14, No.11, (November 2002), pp. 2723-2743, ISSN 1040-4651

Choi, Y.; Gehring, M.; Johnson, L.; Hannon, M.; Harada, J.J.; Goldberg, R.B.; Jacobsen, S.E. & Fischer, R.L. (2002). DEMETER, a DNA glycosylase domain protein, is required for endosperm gene imprinting and seed viability in *Arabidopsis*. *Cell*, Vol.110, No.1, (July 2002), pp. 33-42, ISSN 0092-8674

Chono, M.; Honda, I.; Shinoda, S.; Kushiro, T.; Kamiya, Y.; Nambara, E.; Kawakami, N.; Kaneko, S. & Watanabe, Y. (2006). Field studies on the regulation of abscisic acid content and germinability during grain development of barley: molecular and

chemical analysis of pre-harvest sprouting. *Journal of Experimental Botany*, Vol.57, No.10, (June 2006), pp. 2421-2434, ISSN 0022-0957

Crowe, A.J.; Abenes, M.; Plant, A. & Moloney, M.M. (2000). The seed-specific transactivator, ABI3, induces oleosin gene expression. *Plant Science*, Vol.151, No.2, (February 2000), pp. 171-181, ISSN 0168-9452

Curaba, J.; Moritz, T.; Blervaque, R.; Parcy, F.; Raz, V.; Herzog, M. & Vachon, G. (2004). *AtGA3ox2*, a key gene responsible for bioactive gibberellin biosynthesis, is regulated during embryogenesis by LEAFY COTYLEDON2 and FUSCA3 in *Arabidopsis*. *Plant Physiology*, Vol.136, No.3, (November 2004), pp. 3660-3669, ISSN 0032-0889

Cutler, S.R.; Rodriguez, P.L.; Finkelstein, R.R. & Abrams, S.R. (2010). Abscisic acid: emergence of a core signaling network. *Annual Review of Plant Biology*, Vol.61, pp. 651-679, ISSN 1543-5008

Danilevskaya, O.N.; Hermon, P.; Hantke, S.; Muszynski, M.G.; Kollipara, K. & Ananiev, E.V. (2003). Duplicated fie genes in maize: expression pattern and imprinting suggest distinct functions. *Plant Cell*, Vol.15, No.2, (February 2003), pp. 425-438, ISSN 1040-4651

Debeaujon, I. & Koornneef, M. (2000). Gibberellin requirement for *Arabidopsis* seed germination is determined both by testa characteristics and embryonic abscisic acid. *Plant Physiology*, Vol.122, No.2, (February 2000), pp. 415-424, ISSN 0032-0889

Dekkers, B.J.; Schuurmans, J.A. & Smeekens, S.C. (2008). Interaction between sugar and abscisic acid signalling during early seedling development in *Arabidopsis*. *Plant Molecular Biology*, Vol.67, No.1-2, (May 2008), pp. 151-167, ISSN 0167-4412

Diaz, I.; Martinez, M.; Isabel-LaMoneda, I.; Rubio-Somoza, I. & Carbonero, P. (2005). The DOF protein, SAD, interacts with GAMYB in plant nuclei and activates transcription of endosperm-specific genes during barley seed development. *Plant Journal*, Vol.42, No.5, (June 2005), pp. 652-662, ISSN 0960-7412

Díaz, I.; Vicente-Carbajosa, J.; Abraham, Z.; Martínez, M.; Isabel-LaMoneda, I. & Carbonero, P. (2002). The GAMYB protein from barley interacts with the DOF transcription factor BPBF and activates endosperm-specific genes during seed development. *Plant Journal*, Vol.29, No.4, (February 2002), pp. 453-464, ISSN 0960-7412

Dubreucq, B.; Grappin, P. & Caboche, M. (1996). A new method for the identification and isolation of genes essential for *Arabidopsis thaliana* seed germination. *Molecular Genetics and Genomics*, Vol.252, No.1-2, (August 1996), pp. 42-50, ISSN 1617-4623

Eastmond, P.J. & Rawsthorne, S. (2000). Coordinate changes in carbon partitioning and plastidial metabolism during the development of oilseed rape embryos. *Plant Physiology*, Vol.122, No.3, (March 2000), pp. 767-774, ISSN 0032-0889

Fait, A.; Angelovici, R.; Less, H.; Ohad, I.; Urbanczyk-Wochniak, E.; Fernie, A.R. & Galili, G. (2006). *Arabidopsis* seed development and germination is associated with temporally distinct metabolic switches. *Plant Physiology*, Vol.142, No.3, (November 2006), pp. 839-854, ISSN 0032-0889

Finch-Savage, W.E. & Leubner-Metzger, G. (2006). Seed dormancy and the control of germination. *New Phytologist*, Vol.171, No.3, pp. 501-523, ISSN 0028-646X

Finkelstein, R.R. (1994). Mutations at two new *Arabidopsis* ABA response loci are similar to the *abi3* mutations. *Plant Journal*, Vol.5, No.6, pp. 765-771, ISSN 0960-7412

Finkelstein, R.R. (2006). Studies of abscisic acid perception finally flower. *Plant Cell*, Vol.18, No.4, (April 2006), pp. 786-791, ISSN 1040-4651

Finkelstein, R.R.; Gampala, S.S.L. & Rock, C.D. (2002). Abscisic acid signaling in seeds and seedlings. *Plant Cell*, Vol.14 (Suppl), pp. S15-45, ISSN 1040-4651

Finnegan, E.J. & Dennis, E.S. (1993). Isolation and identification by sequence homology of a putative cytosine methyltransferase from *Arabidopsis thaliana*. *Nucleic Acids Research*, Vol.21, No.10, (May 1993), pp. 2383-2388, ISSN 0305-1048

Finnegan, E.J.; Peacock, W.J. & Dennis, E. (1996). Reduced DNA methylation in *Arabidopsis thaliana* results in abnormal plant development. *Proceedings of the National Academy of Sciences USA*, Vol.93, No.16, (August 1996), pp. 8449-8454, ISSN 0027-8424

FitzGerald, J.; Luo, M.; Chaudhury, A. & Berger, F. (2008). DNA methylation causes predominant maternal controls of plant embryo growth. *PLoS ONE*, Vol.3, No.e2298, ISSN 1932-6203

Forde, B.G.; Heyworth, A.; Pywell, J. & Kreis, M. (1985). Nucleotide sequence of a B1 hordein gene and the identification of possible upstream regulatory elements in endosperm storage protein genes from barley, wheat and maize. *Nucleic Acids Research*, Vol.13, No.20, (October 1985), pp. 7327-7339, ISSN 0305-1048

Frey, A.; Godin, B.; Bonnet, M.; Sotta, B. & Marion-Poll, A. (2004). Maternal synthesis of abscisic acid controls seed development and yield in *N. plumbaginifolia*. *Planta*, Vol.218, No.6, (April 2004), pp. 958-964, ISSN 0032-0935

Gaj, M.D.; Zhang, S.; Harada, J.J. & Lemaux, P.G. (2005). Leafy cotyledon genes are essential for induction of somatic embryogenesis of *Arabidopsis*. *Planta*, Vol.222, No.6, (December 2005), pp. 977-988, ISSN 0032-0935

Gallardo, K.; Thompson, R. & Burstin, J. (2008). Reserve accumulation in legume seeds. *Comptes Rendus Biologies*, Vol.331, No.10, (October 2008), pp. 755-762, ISSN 1631-0691

Gao, M.-J.; Lydiate, D.J.; Li, X.; Lui, H.; Gjetvaj, B.; Hegedus, D.D. and Rozwadowski, K. (2009). Repression of seed maturation genes by a trihelix transcriptional repressor in *Arabidopsis* seedlings. *Plant Cell*, Vol.21, No.1, (January 2009), pp. 54-71, ISSN 1040-4651

Garcia, D.; Gerald, J.N.F. & Berger, F. (2005). Maternal control of integument cell elongation and zygotic control of endosperm growth are coordinated to determine seed size in *Arabidopsis*. *Plan Cell*, Vol.17, No.1, (January 2005), pp. 52-60, ISSN 1040-4651

Gazzarrini, S.; Tsuchiya, Y.; Lumba, S.; Okamoto, M. & McCourt, P. (2004). The transcription factor FUSCA3 controls developmental timing in *Arabidopsis* through the hormones gibberellin and abscisic acid. *Developmental Cell*, Vol.7, No.3, (September 2004), pp. 373-385, ISSN 1534-5807

Gehring, M.; Choi, Y. & Fischer, R.L. (2004). Imprinting and seed development. *Plant Cell*, Vol.16 (suppl), (March 2004), pp. S203-S213, ISSN 1040-4651

Gehring, M.; Bubb, K.L. & Henikoff, S. (2009). Extensive demethylation of repetitive elements during seed development underlies gene imprinting. *Science*, Vol.324, No.5933, (June 2009), pp. 1447-1451, ISSN 0036-8075

Gehring, M.; Missirian, V. & Henikoff, S. (2011). Genomic analysis of parent-of-origin allelic expression in *Arabidopsis thaliana* seeds. *PLoS One*, Vol.6, (August 2011), No.e23687, ISSN 1932-6203

Gehring, M.; Huh, J.H.; Hsieh, T.F.; Penterman, J.; Choi, Y.; Harada, J.J.; Goldberg, R.B. & Fischer, R.L. (2006). Demeter DNA glycosylase establishes MEDEA polycomb gene self-imprinting by allele-specific demethylation. *Cell*, Vol.124, No.3, (February 2006), pp. 495-506, ISSN 0092-8674

Ghelis, T.; Bolbach, G.; Clodic, G.; Habricot, Y.; Miginiac, E.; Sotta, B. & Jeannette, E. (2008). Protein tyrosine kinases and protein tyrosine phosphatases are involved in abscisic acid-dependent processes in *Arabidopsis* seeds and suspension cells. *Plant Physiology*, Vol.148, No.3, (November 2008), pp. 1668-1680, ISSN 0032-0889

Gibson, S.I. (2000). Plant sugar-response pathways. Part of a complex regulatory web. *Plant Physiology*, Vol.124, No.4, (December 2000), pp. 1532-1539, ISSN 0032-0889

Gibson, S.I. (2004). Sugar and phytohormone response pathway: navigating a signalling network. *Journal of Experimental Botany,* Vol.55, No.395, (January 2004), pp. 253-264, ISSN 0022-0957

Gibson, S.I. (2005). Control of plant development and gene expression by sugar signalling. *Current Opinion in Plant Biology*, Vol.8, No.1, (February 2005), pp. 93-102, ISSN 1369-5266

Giraudat, J.; Parcy, F. ; Bertauche, N. ; Gosti, F. ; Leung, J. ; Morris, P.C. ; Bouvier-Durand, M. & Vartanian, N. (1994). Current advances in abscisic acid action and signalling. *Plant Molecular Biology*, Vol.26, No.5, (December 1994), pp. 1557-1577, ISSN 0167-4412

Goldberg, R.B. & Fischer, R.L. (1999). Mutations in *FIE*, a WD Polycomb group gene, allow endosperm development without fertilization. *Plant Cell*, Vol.11, No.3, (March 1999), pp. 407-415, ISSN 1040-4651

Goldberg, R.B.; Barker, S.J. & Perez-Grau, L. (1989). Regulation of gene expression during plant embryogenesis. *Cell*, Vol.56, No.2, (January 1989), pp. 149-160, ISSN 0092-8674

Golombek, S.; Rolletschek, H.; Wobus, U. & Weber, H. (2001). Control of storage protein accumulation during legume seed development. *Journal of Plant Physiology*, Vol.158, No.4, pp. 457-464, ISSN 0032-0889

Gómez, L.D.; Baud, S.; Gilday, A.; Li, Y. & Graham, I.A. (2006). Delayed embryo development in the *ARABIDOPSIS TREHALOSE-6-PHOSPHATE SYNTHASE 1* mutant is associated with altered cell wall structure, decreased cell division and starch accumulation. *Plant Journal*, Vol.46, No.1, (April 2006), pp. 69-84, ISSN 0960-7412

Grimanelli, D. ; Perotti, E. ; Ramirez, J. & Leblanc, O. (2005). Timing of the maternal-to-zygotic transition during early seed development in maize. *Plant Cell*, Vol.17, No.4, (April 2005), pp. 1061-1072, ISSN 1040-4651

Grossniklaus, U. & Schneitz, K. (1998). The molecular and genetic basis of ovule and megagametophyte development. *Seminars in Cell & Developmental Biology,* Vol.9, No.2, (April 1998), pp. 227-238, ISSN 1084-9521

Guo, M.; Rupe, M.A.; Danilevskaya, O.N.; Yang, X. & Hu, Z. (2003). Genome-wide mRNA profiling reveals heterochronic allelic variation and a new imprinted gene in hybrid maize endosperm. *Plant Journal*, Vol.36, No.1, (October 2003), pp. 30-44, ISSN 0960-7412

Gutiérrez-Marcos, J.F.; Costa, L.M.; Dal Prà, M.; Scholten, S.; Kranz, E.; Perez, P. & Dickinson, H.G. (2006). Epigenetic asymmetry of imprinted genes in plant gametes. *Nature Genetics*, Vol.38, No.8, (August 2006), pp. 876-878, ISSN 1061-4036

Gutiérrez-Marcos, J.F.; Costa, L.M.; Biderre-Petit, C.; Khbaya, B.; O'Sullivan, D.M.; Wormald, M.; Perez, P. & Dickinson, H.G. (2004). *Maternally expressed gene1* Is a novel maize endosperm transfer cell-specific gene with a maternal parent-of-origin pattern of expression. *Plant Cell*, Vol.16, No.5, (May 2004), pp. 1288-1301, ISSN 1040-4651

Gutierrez, L.; Van Wuytswinkel, O.; Castelain, M. & Bellini, C. (2007). Combined networks regulating seed maturation. *Trends in Plant Science*, Vol.12, No.7, (July 2007), pp. 294-300, ISSN 1360-1385

Haig, D. & Wilczek, A. (2006). Sexual conflict and the alternation of haploid and diploid generations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, Vol.361, No.1466, (February 2006), pp. 335-343, ISSN 0962-8436

Harada, J.J. (1999). Signaling in plant embryogenesis. *Current Opinion in Plant Biology*, Vol.2, No.1, (February 1999), pp. 23-27, ISSN 1369-5266

Hartings, H.; Maddaloni, M.; Lazzaroni, N.; Di Fonzo, N.; Motto, M.; Salamini, F. & Thompson, R. (1989). The *O2* gene which regulates zein deposition in maize endosperm encodes a protein with structural homologies to transcriptional activators. *EMBO Journal*, Vol.8, No.10, (October 1989), pp. 2795-2801, ISSN 0261-4189

Haughn, G. & Chaudhury, A. (2005). Genetic analysis of seed coat development in *Arabidopsis*. *Trends in Plant Science*, Vol.10, No.10, (October 2005), pp. 472-477, ISSN 1360-1385

Haun, W.J.; Danilevskaya, O.N.; Meeley, R.B. & Springer, N.M. (2009). Disruption of imprinting by mutator transposon insertions in the 5' proximal regions of the *Zea mays Mez1* locus. *Genetics*, Vol.181, No.4, (April 2009), pp. 1229-1237, ISSN 0016-6731

Henderson, J.T.; Li, H.C.; Rider, S.D.; Mordhorst, A.P.; Romero-Severson, J.; Cheng, J.C.; Robey, J.; Sung, Z.R.; de Vries, S.C. & Ogas, J. (2004). *PICKLE* acts throughout the plant to repress expression of embryonic traits and may play a role in gibberellin-dependent responses. *Plant Physiology*, Vol.134, No.3, (March 2004), pp. 995-1005, ISSN 0032-0889

Hermon, P.; Srilunchang, K.O.; Zou, J.; Dresselhaus, T. & Danilevskaya, O.N. (2007). Activation of the imprinted Polycomb Group Fie1 gene in maize endosperm requires demethylation of the maternal allele. *Plant Molecular Biology*, Vol.64, No.4, (July 2007), pp. pp. 387-395, ISSN 0167-4412

Hernandez-Sebastia, C.; Marsolais, F., Saravitz, C.; Israel, D.; Dewey, R.E. & Huber, S.C. (2005). Free amino acid profiles suggest a possible role for asparagines in the control of storage-product accumulation in developing seeds of low- and high-protein soybean lines. *Journal of Experimental Botany*, Vol.56, No.417, (May 2005), pp. 1951-1963, ISSN 0022-0957

Hills, M.J. (2004). Control of storage-product synthesis in seeds. *Current Opinion in Plant Biology*, Vol.7, No.3, (June 2004), pp. 302-308, ISSN 1369-5266

Himmelbach, A.; Yang, Y. & Grill, E. (2003). Relay and control of abscisic acid signaling. *Current Opinion in Plant Biology*, Vol.6, No.5, (October 2003), pp. 470-479, ISSN 1369-5266

Hirayama, T. & Shinozaki, K. (2007). Perception and transduction of abscisic acid signals: keys to the function of the versatile plant hormone ABA. *Trends in Plant Science*, Vol.12, No.8, (July 2007), pp. 343-351, ISSN 1360-1385

Holdsworth, M.J.; Bentsink, L. & Soppe, W.J. (2008). Molecular networks regulating Arabidopsis seed maturation, after-ripening, dormancy and germination. *New Phytologist*, Vol.179, No.1, (April 2008), pp. 33-54, ISSN 0028-646X

Hsieh, T.F.; Ibarra, C.A.; Silva, P.; Zemach, A.; Eshed-Williams, L.; Fischer, R.L. & Zilberman, D. (2009). Genome-wide demethylation of *Arabidopsis* endosperm. *Science*, Vol.324, No.5933, (June 2009), pp. 1451-1454, ISSN 0036-8075

Hsieh, T.F.; Shin, J.; Uzawa, R.; Silva, P.; Cohen, S.; Bauer, M.J.; Hashimoto, M.; Kirkbride, R.C.; Harada, J.J.; Zilberman, D. & Fischer, R.L. (2011). Regulation of imprinted gene expression in *Arabidopsis* endosperm. *Proceedings of the National Academy of Sciences USA*, Vol.08, No.5, (February 2011), pp. 1755-1762, ISSN 0027-8424

Huh, J.H.; Bauer, M.J.; Hsieh, T.F. & Fischer, R. (2007). Endosperm gene imprinting and seed development. *Current Opinion in Genetics & Development*, Vol.17, No.6, (December 2007), pp. 480-485, ISSN 0959-437X

Huijser, C.; Kortstee, A.; Pego, J.; Weisbeek, P.; Wisman, E. & Smeekens, S. (2000). The *Arabidopsis SUCROSE UNCOUPLED-6* gene is identical to *ABSCISIC ACID INSENSITIVE-4*: involvement of abscisic acid in sugar responses. *Plant Journal*, 23, No.5, (September 2000), pp. 577-585, ISSN 0960-7412

Hunter, B.G.; Beatty, M.K.; Singletary, G.W.; Hamaker, B.R.; Dilkes, B.P.; Larkins, B.A. & Jung, R. (2002). Maize opaque endosperm mutations create extensive changes in patterns of gene expression. *Plant Cell*, 14, No.10, (October 2002), pp. 2591-2612, ISSN 1040-4651

Ingouff, M.; Hamamura, Y.; Gourgues, M.; Higashiyama, T. & Berger, F. (2007). Distinct dynamics of HISTONE3 variants between the two fertilization products in plants. *Current Biology*, Vol.17, No.12, (June 2007), pp. 1032-1037, ISSN 0960-9822

Iwakawa, H.; Shinmyo, A. & Sekine, M. (2006). *Arabidopsis* CDKA;1, a cdc2 homologue, controls proliferation of generative cells in male gametogenesis. *Plant Journal*, Vol.45, No.5, (March 2006), pp. 819-831, ISSN 0960-7412

Jullien, P.E.; Kinoshita, T.; Ohad, N. & Berger, F. (2006). Maintenance of DNA methylation during the *Arabidopsis* life cycle is essential for parental imprinting. *Plant Cell*, 18, No.6, (June 2006), pp. 1360-1372, ISSN 1040-4651

Jullien, P.E.; Mosquna, A.; Ingouff, M.; Sakata, T.; Ohad, N. & Berger, F. (2008). Retinoblastoma and its binding partner MSI1 control imprinting in *Arabidopsis*. *PLoS Biology*, Vol.6, (August 2008), No.e194, ISSN 1544-9173

Kadosh, D. & Struhl, K. (1998). Targeted recruitment of the Sin3-Rpd3 histone deacetylase complex generates a highly localized domain of repressed chromatin in vivo. *Molecular and Cellular Biology*, Vol.18, No.9, (September 1998), pp. 5121-5127, ISSN 0270-7306

Kagaya, Y.; Toyoshima, R.; Okuda, R.; Usui, H.; Yamamoto, A. & Hattori, T. (2005a). LEAFY COTYLEDON1 controls seed storage protein genes through its regulation of

FUSCA3 and *ABSCISIC ACID INSENSITIVE3*. *Plant Cell Physiology*, Vol.46, No.3, (March 2005), pp. 399-406, ISSN 0032-0781

Kagaya, Y.; Okuda, R.; Ban, A.; Toyoshima, R.; Tsutsumida, K.; Usui, H.; Yamamoto, A. & Hattori, T. (2005b). Indirect ABA-dependent regulation of seed storage protein genes by FUSCA3 transcription factor in *Arabidopsis*. *Plant Cell Physiology,* Vol.46, No.2, (February 2005), pp. 300-311, ISSN 0032-0781

Kankel, M.W.; Ramsey, D.E.; Stokes, T.L.; Flowers, S.K.; Haag, J.R.; Jeddeloh, J.A.; Riddle, N.C.; Verbsky, M.L. & Richards, E.J. (2003). *Arabidopsis* MET1 cytosine methyltransferase mutants. *Genetics*, Vol.163, No.3, (March 2003), pp. 1109-1122, ISSN 0016-6731

Karssen, C.M.; Brinkhorst Van der Swan, D.L.C.; Breekland, A.E. & Koornneef, M. (1983). Induction of dormancy during seed development by endogenous Abscisic-Acid - studies on Abscisic-Acid deficient genotypes of *Arabidopsis thaliana* (L.) Heynh. *Planta*, Vol.157, No.2, pp. 158-165, ISSN 0032-0935

Kermicle, J.L. (1970). Dependence of the R-mottled aleurone phenotype in maize on mode of sexual transmission. *Genetics*, Vol.66, No.1, (September 1970), pp. 69-85, ISSN 0016-6731

Kinoshita, T.; Miura, A.; Choi, Y.; Kinoshita, Y.; Cao, X.F.; Jacobsen, S.E.; Fischer, R.L. & Kakutani, T. (2004). One-way control of FWA imprinting in *Arabidopsis* endosperm by DNA methylation. *Science*, Vol.303, No.5657, (January 2004), pp. 521-523, ISSN 0036-8075

Kiyosue, T.; Ohad, N.; Yadegari, R.; Hannon, M.; Dinneny, J.; Wells, D.; Katz, A.; Margossian, L.; Harada, J.J.; Goldberg, R.B. & Fischer, R.L. (1999). Control of fertilization-independent endosperm development by the *MEDEA* polycomb gene in *Arabidopsis*. *Proceedings of the National Academy of Sciences USA*, 96, No.7, (March 1999), pp. 4186-4191, ISSN 0027-8424

Köhler, C. & Grossniklaus, U. (2002). Epigenetic inheritance of expression states in plant development: the role of Polycomb group proteins. *Current Opinion in Cell Biology*, Vol.14, No.6, (December 2002), pp. 773-779, ISSN 0955-0674

Köhler, C. & Makarevich, G. (2006). Epigenetic mechanisms governing seed development in plants. *EMBO Reports*, Vol.7, No.12, (December 2006), pp. 1223-1227, ISSN 1469-221X

Köhler, C. & Hennig, L. (2010). Regulation of cell identity by plant Polycomb and trithorax group proteins. *Current Opinion in Genetics & Development*, Vol.20, No.5, (October 2010), pp. 541-547, ISSN 0959-437X

Köhler, C.; Page, D.R.; Gagliardini, V. & Grossniklaus, U. (2005). The *Arabidopsis thaliana* MEDEA Polycomb group protein controls expression of PHERES1 by parental imprinting. *Nature Genetics*, 37, No.1, (January 2005), pp. 28-30, ISSN 1061-4036

Köhler, C.; Hennig, L.; Bouveret, R.; Gheyselinck, J.; Grossniklaus, U. & Gruissem, W. (2003). *Arabidopsis* MSI1 is a component of the MEA/FIE Polycomb group complex and required for seed development. *EMBO Journal*, Vol.22, No.18, (September 2003), pp. 4804-4814, ISSN 0261-4189

Koornneef, M.; Bentsink, L. & Hilhorst, H. (2002). Seed dormancy and germination. *Current Opinion in Plant Biology*, Vol.5, No.1, (February 2002), pp. 33-36, ISSN 1369-5266

Kroj, T.; Savino, G.; Valon, C.; Giraudat, J. & Parcy, F. (2003). Regulation of storage protein gene expression in *Arabidopsis*. *Development*, 130, No.24, (December 2003), pp. 6065-6073, ISSN 0950-1991

Kucera, B.; Cohn, M.A. & Leubner-Metzger, G. (2005). Plant hormone interactions during seed dormancy release and germination. *Seed Science Research*, Vol.15, No.4, pp. 281-307, ISSN 0960-2985

Kuo, M.H. & Allis, C.D. (1998). Roles of histone acetyltransferases and deacetylases in gene regulation. *Bioessays*, 20, No.8, (August 1998), pp. 615-626, ISSN 0265-9247

Kuo, M.H.; vom Baur, E.; Struhl, K. & Allis, C.D. (2000). Gcn4 activator targets Gcn5 histone acetyltransferase to specific promoters independently of transcription. *Molecular Cell*, Vol.6, No.6, (December 2000), pp. 1309-1320, ISSN 1907-2765

Laby, R.J.; Kincaid, M.S.; Kim, D. & Gibson, S.I. (2000). The *Arabidopsis* sugar-insensitive mutants *sis4* and *sis5* are defective in abscisic acid synthesis and response. *Plant Journal*, Vol.23, No.5, (September 2000), pp. 587-596, ISSN 0960-7412

Lara, P.; Onate-Sanchez, L.; Abraham, Z.; Ferrandiz, C.; Diaz, I.; Carbonero, P. & Vicente-Carbajosa, J. (2003). Synergistic activation of seed storage protein gene expression in *Arabidopsis* by ABI3 and two bZIPs related to OPAQUE2. *Journal of Biological Chemistry*, Vol.278, No.23, (June 2003), pp. 21003-21011, ISSN 0021-9258

Lauria, M.; Rupe, M.; Guo, M.; Kranz, E.; Pirona, R.; Viotti, A. & Lund, G. (2004). Extensive maternal DNA hypomethylation in the endosperm of *Zea mays*. *Plant Cell*, Vol.16, No.2, (February 2004), pp. 510-522, ISSN 1040-4651

Laux, T. & Jürgens, G. (1997). Embryogenesis: a new start in life. *Plant Cell*, Vol.9, No.7, (July 1997), pp.989-1000, ISSN 1040-4651

Le, B.H.; Cheng, C.; Bui, A.Q.; Wagmaister, J.A.; Henry, K.F.; Pelletier, J.; Kwong, L.W.; Belmonte, M.; Kirkbride, R.; Horvath, S.; Drews, G.N.; Fischer, R.L.; Okamuro, J.K.; Harada, J.J. & Goldberg, R. (2010). Global analysis of gene activity during *Arabidopsis* seed development and identification of seed-specific transcription factors. *Proceedings of the National Academy of Sciences USA*, Vol.107, No.18, (May 2010), pp. 8063-8070, ISSN 0027-8424

Leon, P. & Sheen, J. (2003). Sugar and hormone connections. *Trends in Plant Science*, Vol.8, No.3, (March 2003), pp. 110-116, ISSN 1360-1385

Lepiniec, L. ; Debeaujon, I. ; Routaboul, J.; Baudry, A. ; Pourcel, L. ; Nesi, N. & Caboche, M. (2006). Genetics and biochemistry of seed flavonoids. *Annual Review of Plant Biology*, Vol.57, pp. 405-430, ISSN 1543-5008

Li, G. & Hall, T.C. (1999). Footprinting in vivo reveals changing profiles of multiple factor interactions with the *ß-phaseolin* promoter during embryogenesis. *Plant Journal*, Vol.18, No.6, (June 1999), pp. 633-641, ISSN 0960-7412

Li, H.C.; Chuang, K.; Henderson, J.T.; Rider, S.D.J.; Bai, Y.; Zhang, H.; Fountain, M.; Gerber, J. & Ogas, J. (2005). *PICKLE* acts during germination to repress expression of embryonic traits. *Plant Journal*, Vol.44, No.6, (December 2005), pp. 1010-1022, ISSN 0960-7412

Li, Y.; Lee, K.K.; Smith, C.; Walsh, S.; Hadingham, S.A.; Sorefan, K.; Cawley, G. & Bevan, M.W. (2006). Establishing glucose- and ABA- regulated transcription networks in *Arabidopsis* by microarray analysis and promoter classification using a relevance

vector machine. *Genome Research*, Vol.16, No.3, (March 2006), pp. 414-427, ISSN 1088-9051

Liu, P.P.; Montgomery, T.A.; Fahlgren, N.; Kasschau, K.D.; Nonogaki, H. & Carrington, J.C. (2007). Repression of AUXIN RESPONSE FACTOR10 by microRNA160 is critical for seed germination and post-germination stages. *Plant Journal*, Vol.52, No.1, (Octomber 2007), pp. 133-146, ISSN 0960-7412

Lohe, A.R. & Chaudhury, A. (2002). Genetic and epigenetic processes in seed development. *Current Opinion in Plant Biology*, Vol.5, No.1, (February 2002), pp. 19-25, ISSN 1369-5266

Lotan, T.; Ohto, M.; Yee, K.M.; West, M.A.; Lo, R.; Kwong, R.W.; Yamagishi, K.; Fischer, R.L.; Goldberg, R.B. & Harada, J.J. (1998). *Arabidopsis* LEAFY COTYLEDON1 is sufficient to induce embryo development in vegetative cells. *Cell*, Vol.93, No.7, (June 1998), pp. 1195-1205, ISSN 0092-8674

Lund, G.; Ciceri, P. & Viotti, A. (1995). Maternal-specific demethylation and expression of specific alleles of zein genes in the endosperm of *Zea mays* L. *Plant Journal*, Vol.8, No.4, (October 1995), pp. 571-581, ISSN 0960-7412

Luo, M.; Bilodeau, P.; Dennis, E.; Peacock, W.J. & Chaudhury, A.M. (2000). Expression and parent-of-origin effects for FIS2, MEA and FIE in the endosperm and embryo of developing *Arabidopsis* seeds. *Proceedings of the National Academy of Sciences USA*, Vol.97, No.19, (September 2000), pp. 10637-10642, ISSN 0027-8424

Luo, M.; Dennis, E.S.; Berger, F.; Peacock, W.J. & Chaudhury, A. (2005). *MINISEED3* (*MINI3*), a WRKY family gene, and *HAIKU2* (*IKU2*), a leucine-rich repeat (LRR) kinase gene, are regulators of seed size in *Arabidopsis*. *Proceedings of the National Academy of Sciences USA*, Vol.102, No.48, (November 2005), pp. 17531-17536, ISSN 0027-8424

Luo, M.; Bilodeau, P.; Koltunow, A.; Dennis, E.S.; Peacock, W.J. & Chaudhury, A.M. (1999). Genes controlling fertilization-independent seed development in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences USA*, Vol.96, No.1, (January 1999), pp. 296-301, ISSN 0027-8424

Ma, Y.; Szostkiewicz, I.; Korte, A.; Moes, D.; Yang, Y.; Christmann, A. and Grill, E. (2009). Regulators of PP2C phosphatase activity function as abscisic acid sensors. *Science*, Vol.324, No.5930, (May 2009), pp. 1064-1068, ISSN 0036-8075

Maeo, K.; Tokuda, T.; Ayame, A.; Mitsui, N.; Kawai, T.; Tsukagoshi, H.; Ishiguro, S. & Nakamura, K. (2009). An AP2-type transcription factor, WRINKLED1, of Arabidopsis thaliana binds to the AW-box sequence conserved among proximal upstream regions of genes involved in fatty acid synthesis. *Plant Journal*, Vol.60, No.3, (July 2009), pp. 476-487, ISSN 0960-7412

Makarevich, G.; Leroy, O.; Akinci, U.; Schubert, D.; Clarenz, O.; Goodrich, J.; Grossniklaus, U. & Köhler, C. (2006). Different Polycomb group complexes regulate common target genes in *Arabidopsis*. *EMBO Reports*, Vol.7, No.9, (September 2006), pp. 947-952, ISSN 1469-221X

Manicacci, D.; Camus-Kulandaivelu, L.; Fourmann, M.; Arar, C.; Barrault, S.; Rousselet, A.; Feminias, N.; Consoli, L.; Francès, L.; Méchin, V.; Murigneux, A.; Prioul, J.L.; Charcosset, A. & Damerval, C. (2009). Epistatic interactions between Opaque2

transcriptional activator and its target gene CyPPDK1 control kernel trait variation in maize. *Plant Physiology*, Vol.150, No.1, (May 2009), pp. 506-520, ISSN 0032-0889

Marzábal, P.; Gas, E.; Fontanet, P.; Vicente-Carbajosa, J.; Torrent, M. & Ludevid, M.D. (2008). The maize Dof protein PBF activates transcription of gamma-zein during maize seed development. *Plant Molecular Biology*, Vol.67, No.5, (July 2008), pp. 441-454, ISSN 0167-4412

Mazur, B.; Krebbers, E. & Tingey, S. (1999). Gene discovery and product development for grain quality traits. *Science*, Vol.285, No.5426, (July 1999), pp. 372-375, ISSN 0036-8075

Mena, M.; Vicente-Carbajosa, J.; Schmidt, R.J. & Carbonero, P. (1998). An endosperm-specific DOF protein from barley, highly conserved in wheat, binds to and activates transcription from the prolamine-box of a native B-hordein promoter in barley endosperm. *Plant Journal*, Vol.16, No.1, (Octomber 1998), pp. 53-62, ISSN 0960-7412

Millar, A.A.; Jacobsen, J.V.; Ross, J.J.; Helliwell, C.A.; Poole, A.T.; Scofield, G.; Reid, J.B. & Gubler, F. (2006). Seed dormancy and ABA metabolism in Arabidopsis and barley: the role of ABA 8′-hydroxylase. *Plant Journal*, Vol.45, No.6, (March 2006), pp. 942-954, ISSN 0960-7412

Miranda, M.; Borisjuk, L.; Tewes, A.; Heim, U.; Sauer, N.; Wobus, U. & Weber, H. (2001). Amino acid permeases in developing seeds of *Vicia faba* L.: expression precedes storage protein synthesis and is regulated by amino acid supply. *Plant Journal,* Vol.28, No.1, (October 2001), pp. 61-72, ISSN 0960-7412

Mönke, G.; Altschmied, L.; Tewes, A.; Reidt, W.; Mock, H.P.; Bäumlein, H. & Conrad, U. (2004). Seed-specific transcription factors ABI3 and FUS3: molecular interaction with DNA. *Planta*, Vol.219, No.1, (May 2004), pp. 158-166, ISSN 0032-0935

Morales-Ruiz, T.; Ortega-Galisteo, A.P.; Ponferrada-Marín, M.I.; Martínez-Macías, M.I.; Ariza, R.R. & Roldán-Arjona, T. (2006). DEMETER and REPRESSOR OF SILENCING 1 encode 5-methylcytosine DNA glycosylases. *Proceedings of the National Academy of Sciences USA*, Vol.103, No.18, (May 2006), pp. 6853-6858, ISSN 0027-8424

Mordhorst, A.P.; Voerman, K.J.; Hartog, M.V.; Meijer, E.A.; van Went, J.; Koornneef, M. & de Vries, S.C. (1998). Somatic embryogenesis in *Arabidopsis thaliana* is facilitated by mutations in genes repressing meristematic cell divisions. *Genetics*, Vol.149, No.2, (June 1998), pp. 549-563, ISSN 0016-6731

Morello, L.; Frattini, M.; Gianì, S.; Christou, P. & Breviario, D. (2000). Overexpression of the calcium-dependent protein kinase *OsCDPK2* in transgenic rice is repressed by light in leaves and disrupts seed development. *Transgenic Research*, Vol.9, No.6, (December 2000), pp. 453-462, ISSN 0962-8819

Moreno-Risueno, M.A.; González, N.; Díaz, I.; Parcy, F.; Carbonero, P. & Vicente-Carbajosa, J. (2008). FUSCA3 from barley unveils a common transcriptional regulation of seed-specific genes between cereals and *Arabidopsis*. *Plant Journal*, Vol.53, No.6, (March 2008), pp. 882-894, ISSN 0960-7412

Mosher, R.A.; Melnyk, C.W.; Kelly, K.A.; Dunn, R.M.; Studholme, D.J. & Baulcombe, D.C. (2009). Uniparental expression of PolIV-dependent siRNAs in developing endosperm of *Arabidopsis*. *Nature*, Vol.460, No.7252, (July 2009), pp. 283-286, ISSN 0028-0836

Mu, J.; Tan, H.; Zheng, Q.; Fu, F.; Liang, Y.; Zhang, J.; Yang, X.; Wang, T.; Chong, K.; Wang, X. & Zuo, J. (2008). LEAFY COTYLEDON1 is a key regulator of fatty acid biosynthesis in *Arabidopsis*. *Plant Physiology*, Vol.148, No.2, (October 2008), pp. 1042-1054, ISSN 0032-0889

Nakamura, S.; Lynch, T.J. & Finkelstein, R.R. (2001). Physical interactions between ABA response loci of *Arabidopsis*. *Plant Journal*, Vol.26, No.6, (June 2001), pp. 627-635, ISSN 0960-7412

Nambara, E. & Marion-Poll, A. (2003). ABA action and interactions in seeds. *Trends in Plant Science*, Vol.8, No.5, (May 2003), pp. 213-217, ISSN 1360-1385

Ng, D.W.; Chandrasekharan, M.B. & Hall, T.C. (2006). Ordered histone modifications are associated with transcriptional poising and activation of the phaseolin promoter. *Plant Cell*, Vol.18, No.1, (January 2006), pp. 119-132, ISSN 1040-4651

North, H.; Baud, S.; Debeaujon, I.; Dubos, C.; Dubreucq, B.; Grappin, P.; Jullien, M.; Lepiniec, L.; Marion-Poll, A.; Miquel, M.; Rajjou, L.; Routaboul, J.M. & Caboche, M. (2010). Arabidopsis seed secrets unravelled after a decade of genetic and omics-driven research. *Plant Journal*, Vol.61, No.6, (March 2010), pp. 971-981, ISSN 0960-7412

Nowack, M.K.; Grini, P.E.; Jakoby, M.J.; Lafos, M.; Koncz, C. & Schnittger, A. (2006). A positive signal from the fertilization of the egg cell sets off endosperm proliferation in angiosperm embryogenesis. *Nature Genetics*, Vol.38, No.1, (January 2006), pp. 63-67, ISSN 1061-4036

Nowack, M.K.; Shirzadi, R.; Dissmeyer, N.; Dolf, A.; Endl, E.; Grini, P.E. & Schnittger, A. (2007). Bypassing genomic imprinting allows seed development. *Nature*, Vol.447, No.7142, (May 2007), pp. 312-315, ISSN 0028-0836

Offler, C.E.; McCurdy; D.W.; Patrick, J.W. & Talbot, M.J. (2003). Transfer cells: cells specialized for a special purpose. *Annual Review of Plant Biology*, Vol.54, pp. 431-454, ISSN 1543-5008

Ogas, J.; Cheng, J.C.; Sung, Z.R. & Somerville, C. (1997). Cellular differentiation regulated by gibberellin in the *Arabidopsis thaliana* pickle mutant. *Science*, Vol.277, No.5322, (July 1997). pp. 91-94, ISSN 0036-8075

Ogas, J.; Kaufmann, S.; Henderson, J. & Somerville, C. (1999). PICKLE is a CHD3 chromatin-remodeling factor that regulates the transition from embryonic to vegetative development in *Arabidopsis*. *Proceedings of the National Academy of Sciences USA*, Vol.96, No.24, (November 1999), pp. 13839-13844, ISSN 0027-8424

Ogawa, M.; Hanada, A.; Yamauchi, Y.; Kuwalhara, A.; Kamiya, Y. & Yamaguchi, S. (2003). Gibberellin biosynthesis and response during *Arabidopsis* seed germination. *Plant Cell*, Vol.15, No.7, (July 2003), pp. 1591-1604, ISSN 1040-4651

Ohad, N.; Margossian, L.; Hsu Yung, C.; Williams, C.; Repetti, P. & Fischer, R.L. (1996). A mutation that allows endosperm development without fertilization. *Proceedings of the National Academy of Sciences USA*, Vol.93, No.11, (May 1996), pp. 5319-5324, ISSN 0027-8424

Ohad, N.; Yadegari, R.; Margossian, L.; Hannon, M.; Michaeli, D.; Harada, J.J.; Goldberg, R.B. & Fischer, R.L. (1999). Mutations in FIE, a WD polycomb group gene, allow endosperm development without fertilization. *Plant Cell*, Vol.11, No.3, (March 1999), pp. 407-416, ISSN 1040-4651

Ohto, M.; Fischer, R.L.; Goldberg, R.B.; Nakamura, K. & Harada, J.J. (2005). Control of seed mass by APETALA2. *Proceedings of the National Academy of Sciences USA*, Vol.102, No.8, (Febryary 2005), pp. 3123-3128, ISSN 0027-8424

Okamoto, M.; Kuwahara, A.; Seo, M.; Kushiro, T.; Asami, T.; Hirai, N.; Kamiya, Y.; Koshiba, T. &Nambara, E. (2006). CYP707A1 and CYP707A2, which encode abscisic acid 8 ¢-hydroxylases, are indispensable for proper control of seed dormancy and germination in *Arabidopsis*. *Plant Physiology*, Vol.141, No.1, (May 2006), pp. 97-107, ISSN 0032-0889

Oñate, L. ; Vicente-Carbajosa, J.; Lara, P. ; Díaz, I. & Carbonero, P. (1999). Barley BLZ2, a seed-specific bZIP protein that interacts with BLZ1 in vivo and activates transcription from the GCN4-like motif of B-hordein promoters in barley endosperm. *Journal of Biological Chemistry*, Vol.274, No.14, (April 1999), pp. 9175-9182, ISSN 0021-9258

Parcy, F.; Valon, C.; Raynal, M.; Gaubier-Comella, P.; Delseny, M. & Giradaut, J. (1994). Regulation of gene expression program during *Arabidopsis* seed development: roles of the ABI3 locus and of endogenous abscisic acid. *Plant Cell*, Vol.6, No.11, pp. 1567-1582, ISSN 1040-4651

Park, S.-Y.; Fung, P.; Nishimura, N.; Jensen, D.R.; Fujii, H.; Zhao, Y.; Lumba, S.; Santiago, J.; Rodrigues, A.; Chow, T.F.; Alfred, S.E.; Bonetta, D.; Finkelstein, R.R.; Provart, N.J.; Desveaux, D.; Rodriguez, P.L.; McCourt, P.; Zhu, J.K.; Schroeder, J.I.; Volkman, B.F. & Cutler, S.R. (2009). Abscisic acid inhibits type 2C protein phosphatases via the PYR/PYL family of START proteins. *Science*, Vol.324, No.5930, (May 2009), pp. 1068-1071, ISSN 0036-8075

Rawsthorne, S. (2002). Carbon flux and fatty acid synthesis in plants. *Progress in Lipid Research*, Vol.41, No.2, (March 2002), pp. 182-196, ISSN 0163-7827

Ray, S.; Agarwal, P.; Arora, R.; Kapoor, S. & Tyagi, A.K. (2007). Expression analysis of calcium-dependent protein kinase gene family during reproductive development and abiotic stress conditions in rice (*Oryza sativa* L. ssp. indica). *Molecular Genetics and Genomics*, Vol.278, No.5, (November 2007), pp. 493-505, ISSN 1617-4623

Razem, F.A.; El-Kereamy, A.; Abrams, S.R. & Hill, R.D. (2006). The RNA-binding protein FCA is an abscisic acid receptor. *Nature*, Vol.439, No.7074, (January 2006), pp. 290-294, ISSN 0028-0836

Reeves, W.M.; Lynch, T.J.; Mobin, R. & Finkelstein, R.R. (2011). Direct targets of the transcription factors ABA-Insensitive(ABI)4 and ABI5 reveal synergistic action by ABI4 and several bZIP ABA response factors. *Plant Molecular Biology*, Vol. 75, No.4-5, (March 2011), pp. 347-363, ISSN 0167-4412

Reidt, W.; Wohlfarth, T.; Ellerstrom, M.; Czihal, A.; Tewes, A.; Ezcurra, I.; Rask, L. & Bäumlein, H. (2000). Gene regulation during late embryogenesis: the RY motif of maturation-specific gene promoters is a direct target of the *FUS3* gene product. *Plant Journal*, Vol.21, No.5, (March 2000), pp. 401-408, ISSN 0960-7412

Rider, S.D.; Henderson, J.T.; Jerome, R.E.; Edenberg, H.J.; Romero-Severson, J. & Ogas, J. (2003). Coordinate repression of regulators of embryonic identity by PICKLE during germination in *Arabidopsis*. *Plant Journal*, Vol.35, No.1, (July 2003), pp. 33-43, ISSN 0960-7412

Rolland, F.; Baena-Gonzalez, E. & Sheen, J. (2006). Sugar sensing and signaling in plants: conserved and novel mechanisms. *Annual Review of Plant Biology*, Vol.57, pp. 675-709, ISSN 1543-5008

Rolletschek, H.; Koch, K.; Wobus, U. & Borisjuk, L. (2005a). Positional cues for the starch/lipid balance in maize kernels and resource partitioning to the embryo. *Plant Journal*, Vol.42, No.1, (April 2005), pp. 69-83, ISSN 0960-7412

Rolletschek, H.; Radchuk, R.; Klukas, C.; Schreiber, F.; Wobus, U. & Borisjuk, L. (2005b). Evidence of a key role for photosynthetic oxygen release in oil storage in developing soybean seeds. *New Phytologist*, Vol.167, No.3, (September 2005), pp. 777-786, ISSN 0028-646X

Rolletschek, H.; Borisjuk, L.; Radchuk, R.; Miranda, M.; Heim, U.; Wobus, U. & Weber, H. (2004). Seed-specific expression of a bacterial phosphoenolpyruvate carboxylase in *Vicia* narbonensis increases protein content and improves carbon economy. *Plant Biotechnology Journal*, Vol.2, No.3, (May 2004), pp. 211-219, ISSN 1467-7644

Rolletschek, H.; Hosein, F.; Miranda, M.; Heim, U.; Götz, K.P.; Schlereth, A.; Borisjuk, L.; Saalbach, I.; Wobus, U. & Weber, H. (2005c). Ectopic expression of an amino acid transporter (VfAAP1) in seeds of Vicia narbonensis and pea increases storage proteins. *Plant Physiology*, Vol.137, No.4, (April 2005), pp. 1236-1249, ISSN 0032-0889

Rook, F.; Hadingham, S.A.; Li, Y. & Bevan, M.W. (2006). Sugar and ABA response pathways and the control of gene expression. *Plant, Cell & Environment*, Vol.29, No.3, (March 2006), pp. 426-434, ISSN 0140-7791

Rook, F.; Corke, F.; Card, R.; Munz, G.; Smith, C. & Bevan, M.W. (2001). Impaired sucrose-induction mutants reveal the modulation of sugar-induced starch biosynthetic gene expression by abscisic acid signalling. *Plant Journal*, Vol.26, No.4, (May 2001), pp. 421-433, ISSN 0960-7412

Rubio-Somoza, I.; Martinez, M.; Diaz, I. & Carbonero, P. (2006a). HvMCB1, a R1MYB transcription factor from barley with antagonistic regulatory functions during seed development and germination. *Plant Journal*, Vol.45, No.1, (January 2006), pp. 17-30, ISSN 0960-7412

Rubio-Somoza, I.; Martinez, M.; Abraham, Z.; Diaz, I. & Carbonero, P. (2006b). Ternary complex formation between HvMYBS3 and other factors involved in transcriptional control in barley seeds. *Plant Journal*, Vol.47, No.2, (July 2006), pp. 269-281, ISSN 0960-7412

Rundlett, S.E.; Carmen, A.A.; Suka, N.; Turner, B.M. & Grunstein, M. (1998). Transcription repression by UME6 involves deacetylation of lysine 5 of histone H4 by RPD3. *Nature*, Vol.392, No.6678, (April 1998), pp. 831-835, ISSN 0028-0836

Santos-Mendoza, M. ; Dubreucq, B. ; Miquel, M. ; Caboche, M. & Lepiniec, L. (2005). LEAFY COTYLEDON 2 activation is sufficient to trigger the accumulation of oil and seed specific mRNAs in *Arabidopsis* leaves. *FEBS Letter*, Vol.579, No.21, (August 2005), pp. 4666-4670, ISSN 0014-5793

Santos-Mendoza, M. ; Dubreucq, B. ; Baud, S. ; Parcy, F. ; Caboche, M. & Lepiniec, L. (2008). Deciphering gene regulatory networks that control seed development and maturation in Arabidopsis. *Plant Journal*, Vol.54, No.4, (May 2008), pp. 608-620, ISSN 0960-7412

Schmidt, R.J.; Burr, F.A.; Aukerman, M.J. & Burr, B. (1990). Maize regulatory gene opaque-2 encodes a protein with a "leucine-zipper" motif that binds to zein DNA. *Proceedings of the National Academy of Sciences USA*, Vol.87, No.1, (January 1990), pp. 46-50, ISSN 0027-8424

Seo, M. & Koshiba, T. (2002). The complex regulation of ABA biosynthesis in plants. *Trends in Plant Science*, Vol.7, No.1, (January 2002), pp. 41-48, ISSN 1360-1385

Seo, M. ; Nambara, E. ; Choi, G. & Yamaguchi, S. (2009). Interaction of light and hormone signals in germinating seeds. *Plant Molecular Biology*, *Vol.*69, No.4, (March 2009), pp. 463-472, ISSN 0167-4412

Seo, M.; Hanada, A.; Kuwahara, A.; Endo, A.; Okamoto, M.; Yamauchi, Y.; North, H.; Marion-Poll, A.; Sun, T.P.; Koshiba, T.; Kamiya, Y.; Yamaguchi, S. & Nambara, E. (2006). Regulation of hormone metabolism in Arabidopsis seeds: phytochrome regulation of abscisic acid metabolism and abscisic acid regulation of gibberellin metabolism. *Plant Journal*, Vol.48, No.3, (November 2006), pp. 354-366, ISSN 0960-7412

Shen, Y.Y.; Wang, X.F.; Wu, F.Q.; Du, S.Y.; Cao, Z.; Shang, Y.; Wang, X.L.; Peng, C.C.; Yu, X.C.; Zhu, S.Y.; Fan, R.C.; Xu, Y.H. & Zhang, D.P. (2006). The Mg-chelatase H subunit is an abscisic acid receptor. *Nature*, Vol.443, No.7113, (October 2006), pp. 823-826, ISSN 0028-0836

Simon, J.A. & Tamkun, J.W. (2002). Programming off and on states in chromatin: mechanisms of Polycomb and trithorax group complexes. *Current Opinion in Genetics & Development*, Vol.12, No.2, (April 2002), pp. 210-218, ISSN 0959-437X

Smeekens, S. (2000). Sugar-induced signal transduction in plants. *Annual Review of Plant Physiology and Plant Molecular Biology*, Vol.51, (June 2000), pp. 49-81, ISSN 0167-4412

Stone, S.L.; Kwong, L.W.; Yee, K.M.; Pelletier, J.; Lepiniec, L.; Fischer, R.L.; Goldberg, R.B. & Harada, J.J. (2001). LEAFY COTYLEDON2 encodes a B3 domain transcription factor that induces embryo development. *Proceedings of the National Academy of Sciences USA*, Vol.98, No.20, (September 2001), pp. 11806-11811, ISSN 0027-8424

Stone, S.L.; Braybrook, S.A.; Paula, S.L.; Kwong, L.W.; Meuser, J.; Pelletier, J.; Hsieh, T.F.; Fischer, R.L.; Goldberg, R.B. & Harada, J.J. (2008). *Arabidopsis* LEAFY COTYLEDON2 induces maturation traits and auxin activity: Implications for somatic embryogenesis. *Proceedings of the National Academy of Sciences USA*, Vol.105, No.8, (February 2008), pp. 3151-3156, ISSN 0027-8424

Sun, X.; Shantharaj, D.; Kang, X. & Ni, M. (2010). Transcriptional and hormonal signaling control of Arabidopsis seed development. *Current Opinion in Plant Biology*, Vol.13, No.5, (October 2010), pp. 611-620, ISSN 1369-5266

Suzuki, M.; Wang, H.H. & McCarty, D.R. (2007). Repression of the LEAFY COTYLEDON 1/B3 regulatory network in plant embryo development by VP1/ABSCISIC ACID INSENSITIVE 3-LIKE B3 genes. *Plant Physiology*, Vol.143, No.2, (February 2007), pp. 902-911, ISSN 0032-0889

Suzuki, M.; Ketterling, M.G.; Li, Q.B. & McCarty, D.R. (2003). Viviparous1 alters global gene expression patterns through regulation of abscisic acid signalling. *Plant Physiology*, Vol.132, No.3, (July 2003), pp. 1664-1677, ISSN 0032-0889

Tanaka, H.; Dhonukshe, P.; Brewer, P.B. & Friml, J. (2006). Spatiotemporal asymmetric auxin distribution: A means to coordinate plant development. *Cellular and Molecular Life Sciences*, Vol.63, No.23, (December 2006), pp. 2738-2754.

Tanaka, M.; Kikuchi, A. & Kamada, H. (2008). The *Arabidopsis* histone deacetylases HDA6 and HDA19 contribute to the repression of embryonic properties after germination. *Plant Physiology*, Vol.146, No.1, (January 2008), pp. 149-161, ISSN 0032-0889

Tang, X.; Hou, A.; Babu, M.; Nguyen, V.; Hurtado, L.; Lu, Q.; Reyes, J.C.; Wang, A.; Keller, W.A.; Harada, J.J.; Tsang, E.W. & Cui, Y. (2008). The *Arabidopsis* BRAHMA chromatin remodelling ATPase is involved in repression of seed maturation genes in leaves. *Plant Physiology*, Vol.147, No.3, (July 2008), pp. 1143-1157, ISSN 0032-0889

Tiwari, S.; Schulz, R.; Ikeda, Y.; Dytham, L.; Bravo, J.; Mathers, L.; Spielman, M.; Guzmán, P.; Oakey, R.J.; Kinoshita, T. & Scott, R.J. (2008). MATERNALLY EXPRESSED PAB C-TERMINAL, a novel imprinted gene in *Arabidopsis*, encodes the conserved C-terminal domain of polyadenylate binding proteins. *Plant Cell*, Vol.20, No.9, (September 2008), pp. 2387-2398, ISSN 1040-4651

Tjaden, J.; Möhlmann, T.; Kampfenkel, K.; Henrichs, G. & Neuhaus, H.E. (1998). Altered plastidic ATP/ADP-transporter activity influences potato (*Solanum tuberosum* L.) tuber morphology, yield and composition of starch. *Plant Journal*, Vol.16, No.5, pp. 531-540, ISSN 0960-7412

To, A.; Valon, C.; Savino, G.; Guilleminot, J.; Devic, M.; Giraudat, J. & Parcy, F. (2006). A network of local and redundant gene regulation governs *Arabidopsis* seed maturation. *Plant Cell*, Vol.18, No.7, (July 2006), pp. 1642-1651, ISSN 1040-4651

Tsuchiya, Y.; Nambara, E.; Naito, S. & McCourt, P. (2004). The FUS3 transcription factor functions through the epidermal regulator TTG1 during embryogenesis in *Arabidopsis*. *Plant Journal*, Vol.37, No.1, (January 2004), pp. 73-81, ISSN 0960-7412

Tsukagoshi, H.; Morikami, A. & Nakamura, K. (2007). Two B3 domain transcriptional repressors prevent sugar-inducible expression of seed maturation genes in *Arabidopsis* seedlings. *Proceedings of the National Academy of Sciences USA*, Vol.104, No.7, (February 2007), pp. 2543-2547, ISSN 0027-8424

Tsukagoshi, H.; Saijo, T.; Shibata, D.; Morikami, A. & Nakamura, K. (2005). Analysis of a sugar response mutant of *Arabidopsis* identified a novel B3 domain protein that functions as an active transcriptional repressor. *Plant Physiology*, Vol.138, No.2, (June 2005), pp. 675-685, ISSN 0032-0889

van Der Geest, A.; Frisch, D.A.; Kemp, J.D. & Hall, T.C. (1995). Cell ablation reveals that expression from the phaseolin promoter Is confined to embryogenesis and microsporogenesis. *Plant Physiology*, Vol.109, No.4, (December 1995), pp. 1151-1158, ISSN 0032-0889

Venu, R.; Sreerekha, M.; Nobuta, K.; Beló, A.; Ning, Y.; An, G.; Meyers, B.C. & Wang, G.L. (2011). Deep sequencing reveals the complex and coordinated transcriptional regulation of genes related to grain quality in rice cultivars. *BMC Genomics*, Vol.12, pp. 190, ISSN 1471-2164

Vicente-Carbajosa, J. & Carbonero, P. (2005). Seed maturation: developing an intrusive phase to accomplish a quiescent state. *International Journal of Developmental Biology*, Vol.49, No.5-6, pp. 645-651, ISSN 0214-6282

Vicente-Carbajosa, J.; Oñate, L.; Lara, P.; Diaz, I. & Carbonero, P. (1998). Barley BLZ1: a bZIP transcriptional activator that interacts with endosperm-specific gene promoters. *Plant Journal*, Vol.13, No.5, (March 1998), pp. 629-640, ISSN 0960-7412

Vigeolas, H.; van Dongen, J.T.; Waldeck, P.; Hühn, D. & Geigenberger, P. (2003). Lipid storage metabolism is limited by the prevailing low oxygen concentrations within developing seeds of oilseed rape. *Plant Physiology*, Vol.133, No.4, (December 2003), pp. 2048-2060, ISSN 0032-0889

Wan, L.; Ross, A.R.; Yang, J.; Hegedus, D.D. & Kermode, A.R. (2007). Phosphorylation of the 12 S globulin cruciferin in wild-type and abi1-1 mutant *Arabidopsis thaliana* (thale cress) seeds. *Biochemical Journal*, Vol.404, No.2, (June 2007), pp. 247-256, ISSN 0264-6021

Wang, H.; Guo, J.; Lambert, K.N. & Lin, Y. (2007). Developmental control of Arabidopsis seed oil biosynthesis. *Planta*, Vol.226, No.3, (August 2007), pp. 773-783, ISSN 0032-0935

Weber, H.; Borisjuk, L. & Wobus, U. (2005). Molecular physiology of legume seed development. *Annual Review of Plant Biology*, Vol.56, pp. 253-279, ISSN 1543-5008

Weterings, K. & Russell, S.D. (2004). Experimental analysis of the fertilization process. *Plant Cell*, Vol.16 (suppl), pp. S107-S118, ISSN 1040-4651

Wobus, U. & Weber, H. (1999). Seed maturation: genetic programmes and control signals. *Current Opinion in Plant Biology*, Vol.2, No.1, (February 1999), pp. 33-38, ISSN 1369-5266

Wu, C.Y.; Suzuki, A.; Washida, H. & Takaiwa, F. (1998). The GCN4 motif in a rice glutelin gene is essential for endosperm-specific gene expression and is activated by Opaque-2 in transgenic rice plant. *Plant Journal*, Vol.14, No.6, (June 1998), pp. 673-683, ISSN 0960-7412

Wu, C.Y.; Washida, H.; Onodera, Y.; Harada, K. & Takaiwa, F. (2000). Quantitative nature of the prolamin-box, ACGT and AACA motifs in a rice glutelin gene promoter: minimal cis-element requirements for endosperm-specific gene expression. *Plant Journal*, Vol.23, No.3, (August 2000), pp. 415-421, ISSN 0960-7412

Xiao, W.; Custard, K.D.; Brown, R.C.; Lemmon, B.E.; Harada, J.J.; Goldberg, R.B. & Fischer, R.L. (2006). DNA methylation is critical for *Arabidopsis* embryogenesis and seed viability. *Plant Cell*, Vol.18, No.4, (April 2006), pp. 805-814, ISSN 1040-4651

Xiao, W.; Gehring, M.; Choi, Y.; Margossian, L.; Pu, H.; Harada, J.J.; Goldberg, R.B.; Pennell, R.I. & Fischer, R.L. (2003). Imprinting of the MEA Polycomb gene is controlled by antagonism between MET1 methyltransferase and DME glycosylase. *Developmental Cell*, Vol.5, No.6, (December 2003), pp. 891-901, ISSN 1534-5807

Xiong, L.M.; Gong, Z.Z.; Rock, C.D.; Subramanian, S.; Guo, Y.; Xu, W.Y.; Galbraith, D. & Zhu, J.K. (2001). Modulation of abscisic acid signal transduction and biosynthesis by an Sm-like protein in *Arabidopsis*. *Developmental Cell*, Vol.1, No.6, (December 2001), pp. 771-781, ISSN 1534-5807

Yamamoto, M.P.; Onodera, Y.; Touno, S.M. & Takaiwa, F. (2006). Synergism between RPBF Dof and RISBZ1 bZIP activators in the regulation of rice seed expression genes. *Plant Physiology*, Vol.141, No.4, (June 2006), pp. 1694-1707, ISSN 0032-0889

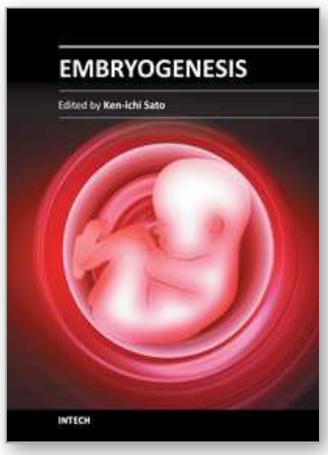
Yanagisawa, S. (2002). The Dof family of plant transcription factors. *Trends in Plant Science*, Vol.7, No.12, (December 2002), pp. 555-560, ISSN 1360-1385

Yang, J.; Zhang, J.; Liu, K.; Wang, Z. & Liu, L. (2006). Abscisic acid and ethylene interact in wheat grains in response to soil drying during grain filling. *New Phytologist*, Vol.171, No.2, pp. 293-303, ISSN 0028-646X

Zeng, Y. & Kermode, A.R. (2004). A gymnosperm *ABI3* gene functions in a severe abscisic acid-insensitive mutant of *Arabidopsis* (*abi3-6*) to restore the wild-type phenotype and demonstrates a strong synergistic effect with sugar in the inhibition of post-germinative growth. *Plant Molecular Biology*, Vol.56, No.5, (November 2004), pp. 731-746, ISSN 0167-4412

Zhang, X.R. ; Garreton, V. & Chua, N.H. (2005). The AIP2 E3 ligase acts as a novel negative regulator of ABA signaling by promoting ABI3 degradation. *Genes & Development*, Vol.19, No.13, (July 2005), pp. 1532-1543, ISSN 0890-9369

Zhou, Y.; Zhang, X.; Kang, X.; Zhao, X.; Zhang, X. & Ni, M. (2009). SHORT HYPOCOTYL UNDER BLUE1 associates with MINISEED3 and HAIKU2 promoters in vivo to regulate *Arabidopsis* seed development. *Plant Cell*, Vol.21, No.1, (January 2009), pp. 106-117, ISSN 1040-4651



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