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Post-transcriptional regulation of seed dormancy and germination: Current understanding and future directions

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ABSTRACT

Seed dormancy is a developmental checkpoint that prevents mature seeds from germinating under conditions that are otherwise favorable for germination. Temperature and light are the most relevant environmental factors that regulate seed dormancy and germination. These environmental cues can trigger molecular and physiological responses including hormone signaling, particularly that of abscisic acid and gibberellin. The balance between the content and sensitivity of these hormones is the key to the regulation of seed dormancy. Temperature and light tightly regulate the transcription of thousands of genes, as well as other aspects of gene expression such as mRNA splicing, translation, and stability. Chromatin remodeling determines specific transcriptional outputs, and alternative splicing leads to different outcomes and produces transcripts that encode proteins with altered or lost functions. Proper regulation of chromatin remodeling and alternative splicing may be highly relevant to seed germination. Moreover, microRNAs are also critical for the control of gene expression in seeds. This review aims to discuss recent updates on post-transcriptional regulation during seed maturation, dormancy, germination, and post-germination events. We propose future prospects for understanding how different post-transcriptional processes in crop seeds can contribute to the design of genotypes with better performance and higher productivity.

Key words: alternative splicing, chromatin remodeling, dormancy, germination, microRNA (miRNA), seeds

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INTRODUCTION

Seed dormancy plays a central role in the adjustment of plant populations to their environment. Environmental signals that modulate the depth and alleviation of dormancy control the germination timing of seed populations and are therefore of the utmost adaptive importance (Donohue et al., 2005). Seeds can enter dormancy during maturation in the mother plant. Seed dormancy prevents pre-harvest sprouting and optimizes seedling establishment. Seed dormancy gradually changes during post-maturation (after-ripening), principally in response to temperature changes surrounding buried seeds (seedbanks). When the level of dormancy is low, alternating temperatures and light remove the final germination constraints, and germination occurs if water potential is sufficient for the protrusion of the radicle (Batlla and Benech-Arnold, 2015). Extensive studies have shown that hormonal signals, mainly those of abscisic acid (ABA) and gibberellin (GA), act as integrators between environmental cues and molecular signals for the regulation of gene expression. The balance between ABA and GA content and sensitivity is a key factor in the regulation of seed dormancy and germination status.

Temperature and light induce massive reprogramming of gene expression and shape the seed transcriptome by affecting every possible level of gene expression regulation. Environmental signals regulate the transcription of thousands of genes and also affect many other layers of gene expression such as mRNA splicing, translation, and stability. Gene expression is modulated at different levels, including transcription initiation and the processing, splicing, export, translation, and degradation of mRNA. Post-transcriptional regulation, which involves both

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epigenetic and splicing process, is an area of increasing interest in seed biology. Epigenetic changes in gene function, which include DNA methylation, histone modifications, chromatin remodeling, and the activities of small RNAs, are heritable but do not follow known patterns of inheritance explained by changes in DNA sequence (Russo et al., 1996; Bräutigam et al., 2013). There is an increasing body of evidence showing that post-transcriptional processes substantially increase transcriptome complexity and play an important role in modulating gene expression in response to internal and external cues.

The aim of this review is to discuss the post-transcriptional mechanisms that regulate seed dormancy and germination and to provide insights into the latest findings on this topic, focusing not only on the model plant *Arabidopsis thaliana* but also on crop species. In the first part of the review, we briefly discuss the roles of temperature, light, and the circadian clock on seed dormancy and germination. In the second part, we focus on post-transcriptional processes in seeds and analyze recent work on seed maturation, dormancy, germination, and post-germination processes. In the last part of the work, we analyze the post-transcriptional mechanisms that promote germination in crop seeds and present some prospects for future research. For general aspects of seed dormancy and germination, we recommend some excellent recently published reviews (Chahtane et al., 2017; Finch-Savage and Footitt, 2017; Carrera-Castaño et al., 2020; Yan and Chen, 2020; Yang et al., 2020a, 2020b).

ENVIRONMENTAL FACTORS IN SEED DORMANCY AND GERMINATION

Temperature

The most common and abundant type of dormancy that occurs in almost all angiosperm seeds is known as physiological dormancy (Finch-Savage and Leubner-Metzger, 2006). During seed development on the mother plant, dormancy levels increase gradually and reach a maximum in freshly matured seeds (Bewley et al., 2013). After seeds fall to the ground, they can show cyclic changes in sensitivity to environmental signals during the time of burial (Bouwmeester et al., 1994; Derkx and Karssen, 1994). Soil temperature is the predominant environmental cue that controls the depth of dormancy during cycling in seedbanks (Finch-Savage and Leubner-Metzger, 2006; Probert, 2009).

A well-known genetic barrier to germination is DOG1 (DELAY OF GERMINATION 1). *DOG1* is specifically expressed in seeds and encodes a protein with unknown molecular functions. DOG1 protein levels in freshly harvested seeds correlate with the depth of seed dormancy under both laboratory and natural conditions (Nakabayashi et al., 2012). Reduced dormancy levels in seeds are associated with the inactivation of DOG1 protein, and its expression fluctuates during the year in buried seeds of *A. thaliana*, accompanying variations in cyclic dormancy (Footitt et al., 2013). During seed maturation, low temperatures of 16°C increase seed dormancy, and this increase is positively correlated with *DOG1* transcript levels (Chiang et al., 2011; Kendall et al., 2011; Nakabayashi et al., 2012). LEUCINE ZIPPER TRANSCRIPTION FACTOR 67 (bZIP67) acts downstream of LEAFY COTYLEDON 1 (LEC1) to transactivate DOG1 by binding G-box-like *cis* elements on the *DOG1* promoter, thereby enhancing primary dormancy (Bryant et al., 2019). The ABA and DOG1 pathways converge downstream of the ABA-HYPERSENSITIVE GERMINATION 1 (AHG1) and AHG3 protein phosphatases, which interact physically with DOG1 to promote seed germination (Née et al., 2017; Nishimura et al., 2018). *DOG1* transcription is also repressed by the ETHYLENE RESPONSE FACTOR 12 (ERF12) and TOPLESS complex downstream of the ethylene receptor RDO3/ETR1 (Li et al., 2019). Although DOG1 controls the depth of dormancy established during seed maturation, it plays an indirect role in mediating seasonal patterns of seedling emergence under field conditions. A very close QTL, *SEEDLING EMERGENCE TIME 1* (*SET1*), appears to be the main regulator of seedling emergence timing, with contrasting effects on ABA signaling (Footitt et al., 2020).

When the dormancy level is low, a fraction of the seedbank can germinate while the remaining fraction can be induced into secondary dormancy (Finch-Savage and Leubner-Metzger, 2006). Secondary dormancy is induced by a reduction in GA sensitivity of the seeds and the activation of the RGA-LIKE 2 (RGL2) and ABI5 signaling pathway (Ibarra et al., 2016). Interestingly, *REPRESSOR OF GA1-3* (*RGA*) and *RGL2* expression is kept high during the low dormancy phase, probably to be ready for the re-induction of dormancy (Footitt et al., 2013, 2017). RGL2 can also maintain primary dormancy by forming a protein complex with DNA BINDING 1 ZINC FINGER 6 (DOF6) and activating the expression of the *GATA12* zinc finger transcription factor (Ravindran et al., 2017). Alternating temperatures can remove the ultimate constraints on germination (Batlla and Benech-Arnold, 2015). In *Sorghum halepense* seeds, alternating temperatures provide information about the depth of seed burial and the presence of a plant canopy, thereby controlling the dynamics of seedling emergence in the field (Benech-Arnold et al., 1988; Ghersa et al., 1992). Alternating temperatures increase the GA/ABA ratio in *Cynara cardunculus* seeds by decreasing ABA content and sensitivity through the inhibition of *NCED* and *ABI5* expression (Huarte et al., 2014). Similarly, in *Euphorbia esula* seeds, alternating temperatures reduce the expression of ABA-related genes such as *ABI5* (Foley et al., 2010). In *A. thaliana* seeds, alternating temperatures can be a prerequisite for the phytochrome induction of germination (Arana et al., 2017). The incubation of dormant *Arabidopsis* seeds at alternating temperature cycles of 15°C/23°C for 2 days enhances germination by increasing the expression of *GA3OX1* mediated by phytochrome B (phyB; Arana et al., 2017).

Light

Light absorbed by photoreceptors is a key factor for the induction of seed germination. Phytochromes are the principal photoreceptors that mediate seed germination in *A. thaliana*. The classical red–far-red (R-FR) reversible photoresponse is mediated by photobiological stable phytochromes, principally phyB (Botto et al., 1995; Shinomura et al., 1996; Hennig et al., 2002; Arana et al., 2014). When seeds acquire very high light sensitivity, phyA becomes the main photoreceptor for FR-induced seed germination (Botto et al., 1996; Shinomura et al., 1996). The ecological relevance of the acquisition of high light sensitivity

by seedbanks lies in the opportunity for weed seeds to germinate immediately after soil tillage before crop establishment (Scopel et al., 1991; Botto et al., 1998a, 1998b, 2000). More recently, it has been demonstrated that buried *A. thaliana* seeds show strong cyclic patterns of *PHYA* transcript levels, suggesting that high light sensitivity may be correlated with the gene expression of this photoreceptor (Cadman et al., 2006; Finch-Savage et al., 2007). In germinating seeds, phyA in the embryo can act as a sensor for the removal of the last constraints on dormancy, whereas phyB promotes ABA biosynthesis in the endosperm, suggesting that the phytochromes have distinct spatial functions (Lee et al., 2012).

Phytochrome-mediated seed germination is associated with a decrease in ABA content and signaling as well as an increase in GA content and responsiveness. In darkness, the PIL5/PIF1 (PHYTOCHROME INTERACTING FACTOR 1) signaling pathway and a plethora of transcription factors repress seed germination by reducing GA content and enhancing ABA accumulation in imbibed seeds (Oh et al., 2006, 2007; Dong et al., 2008). PIF1 upregulates the expression of *SOMNUS* (*SOM*) in concert with ABI3 (Dong et al., 2008; Park et al., 2011). PIF1 directly binds the promoters of two DELLA genes (*GIBBERELLIC ACID INSENSITIVE* [*GAI*] and *RGA*) and inhibits GA biosynthetic genes (Oh et al., 2007). GAI cooperates with DOG AFFECTING GERMINATION 1 (DAG1), which represses seed germination by directly binding the promoter of *GA3ox1* (Gabriele et al., 2010; Boccaccini et al., 2014). Furthermore, the MYB transcription factor REVEILLE 1 (RVE1) represses the expression of *GA3ox2* through physical interaction with RGL2 and SLEEPY 1 (SLY1), an E3 ubiquitin ligase, consequently increasing the stability of RGL2 (Yang et al., 2020a, 2020b). Similarly, VASCULAR PLANT ONE ZINC FINGER 1 (VOZ1) and VOZ2 are transcription factors that act downstream of PIF1 by directly binding the *GA3ox1* promoter to repress its expression and, consequently, seed germination (Luo et al., 2020). Upon light irradiation, the phyB- and phyA-Pfr active forms translocate to the nucleus and degrade PIF1 protein via the ubiquitin–proteasome system (Oh et al., 2004), initiating a vast alteration in the pattern of gene expression and directly or indirectly influencing ABA and GA metabolism or sensitivity. Moreover, heterotrimeric G proteins can promote light responsiveness in seeds, mediated by phyA and phyB (Botto et al., 2009), suggesting a potential mechanism for signal amplification, as has been demonstrated in the retinal rod photoreceptors of animals (Kolesnikov et al., 2011). Although phyA and phyB can both promote seed germination, their transcriptional programs are partially independent (Ibarra et al., 2013). Furthermore, cell wall-loosening genes such as *EXPANSIN* (*EXP*) and *XYLOGLUCAN ENDO-TRANSGLYCOSYLASE/HYDROLASE* (*XTH*) are induced (Oh et al., 2009; Ibarra et al., 2013). TEOSINTE BRANCHED, CYCLOIDEA AND PCF 14 (TCP14) and TCP15, two basic helix-loop-helix (HLH) transcription factors, bind the promoter of *EXP9* to induce GA-mediated seed germination (Xu et al., 2020a).

Some pieces of evidence clearly suggest that clock genes may act as integrators of environmental input signals such as light and temperature to adjust the release of dormancy and the promotion of seed germination. At the molecular level, Kurup et al. (2000) demonstrated that ABI3, an inhibitor of seed germination, can interact *in vivo* with TOC1, TIMING OF CAB EXPRESSION 1 (Kurup et al., 2000). Penfield and Hall (2009) showed that LATE ELONGATED HYPOCOTYL (LHY), CIRCADIAN CLOCK ASSOCIATED 1 (CCA1), GIGANTEA (GI), ZEITLUPE (ZTL), and LUX ARRYTHMO (LUX) mutant seeds of *A. thaliana* have a defective germination response to chilling, alternating temperatures, and after-ripening. Interestingly, the promotion of seed germination by R-light and alternating 15°C/23°C temperatures (compared with 17.5°C constant temperature) requires the expression of *TOC1* and *PRR7*, but other circadian clock genes such as *LHY* and *CCA1* are not necessary (Arana et al., 2017). Furthermore, DOG1 represses *TOC1* expression at a constant temperature, but DOG1 levels are downregulated by alternating temperatures (Arana et al., 2017). In a laboratory-simulated cycling dormancy experiment, *cca1* and *lhy* mutant seeds had greater ABA sensitivity and consequently more rapid dormancy induction, whereas *PSEUDO RESPONSE REGULATOR* triple mutant seeds (*prr5 prr7 prr9*) had lowest ABA sensitivity and slowest dormancy induction, suggesting a critical balance between morning and evening signaling components (Footitt et al., 2017).

POST-TRANSCRIPTIONAL PROCESSES IN *A. THALIANA* SEEDS

The "life" of a seed is characterized by two major phase transitions: embryogenesis to seed maturation, and dry seed to seed germination. These different stages display specific transcriptomes and require the activation or repression of diverse sets of genes (Table 1). Post-transcriptional processes tightly regulate the expression of thousands of genes, as well as many other aspects of gene expression such as mRNA splicing, translation, and stability. Epigenetic regulation in seeds includes RNA splicing, chromatin remodeling, and the activity of microRNAs (miRNAs).

- RNA splicing, a co-transcriptional molecular event, is carried out by a macromolecular complex called a spliceosome that recognizes and removes some regions (introns) while joining others (exons). This process involves more than 200 proteins and five small RNAs, which are associated with the spliceosome (Wahl et al., 2009). Alternative splicing is the process that generates multiple transcripts from a single gene by using different combinations of available splice sites, leading to different outcomes (Figure 1A). Because splicing reactions occur mainly while transcription takes place (co-transcriptionally), the regulation of RNA polymerase II (RNAPII) transcription affects the splicing outcomes (Jabre et al., 2019; Zhu et al., 2020).
- Chromatin remodeling factors also regulate gene expression. Histone deacetylases remove acetyl groups from histones (Grandperret et al., 2014)whereas histone acetyltransferases transfer acetyl groups to lysine residues at the N-terminal regions of histones (Boycheva et al., 2014). Epigenetic regulation involves histone protein modifications and DNA methylation (Vaissière et al., 2008; Shim et al., 2017).
- miRNAs are also critical for the control of gene expression in seeds. They are a type of 20- to 24-nucleotide non-coding RNA molecule that regulates the expression of genes encoding transcription factors and key regulatory proteins with sequences complementary to those of the

	Name	Developmental stage	Species	Description	References
Alternative splicing related	*DEK42*	Seed development	Maize	DEK42 participates in the regulation of pre-messenger RNA splicing into the spliceosome	Zuo et al., 2019
	DEK2	Seed development	Maize	DEK2 is implicated in the splicing of mitochondrion-encoded mRNA	Qi et al., 2017
	RGH3	Seed development	Maize	RGH3 encodes a predicted RNA splicing factor involved in the spliceosome. RGH3 produces 19 splice variants regulated in a tissue- and developmental-specific manner	Fouquet et al., 2011; Gault et al., 2017
	OsbZIP58	Seed development	Rice	The alternative splicing of OsbZIP58 is altered by high temperature of 35°C	Xu et al., 2020a, 2020b
	Vp1	Seed development	Wheat	Vp1 transcript structure shows that each homolog produces cytoplasmic mRNAs of different sizes, being the majority incorrectly spliced, and therefore unlikely to encode functional proteins	McKibbin et al.,2002; Wilkinson et al., 2005
	SUA	Seed maturation	*Arabidopsis*	The splicing factor SUA controls the alternative splicing of ABI3	Sugliani et al., 2010
	ABI3	Seed maturation	*Arabidopsis*	ABI3 produces two transcripts: ABI3-α (encoding the full-length protein) and ABI3-β (encoding a truncated protein containing two of the four functional domains)	Sugliani et al., 2010
	ABI5	Seed maturation	Rice	ABI5 produces two transcripts, OsABI5-1 and OsABI5-2, that are simultaneously present in some rice tissues but with different expression patterns	Zou et al., 2007
	DOG1	Seed dormancy	*Arabidopsis*	The second intron is subjected to alternative splicing, and five different transcript variants are produced	Nakabayashi et al., 2015
				An antisense transcript, originating close to the DOG1 proximal (main) termination site, strongly inhibits dormancy strength and DOG1 expression	Fedak et al., 2016; Yatusevich et al., 2017
				Alternative polyadenylation produces two DOG1 transcripts: a shorter two-exon short DOG1 (shDOG1) and a longer three-exon long DOG1 (lgDOG1)	Cyrek et al., 2016; Kowalczyk et al., 2017;
				DOG1 transcription is also enhanced by transcription elongation factor TFIIS	Mortensen et al., 2011; Mortensen and Grasser, 2014
	PIF6	Seed dormancy	*Arabidopsis*	PIF6 pre-mRNA has four known AS isoforms PIF6-α encodes the full-length protein, whereas PIF6-β encodes a truncated protein that lacks the HLH binding domain	Penfield et al., 2010; Narsai et al., 2017

Table 1. List of alternative splicing-, chromatin-, and miRNA-related events that occur in seeds

(Continued on next page)

	Name	Developmental stage	Species	Description	References
	HAB1	Seed germination	*Arabidopsis*	Two splice variants: HAB1.1 promotes seed germination, and HAB1.2 inhibits germination by acting as a positive regulator of ABA	Wang et al., 2015
	DRT111	Seed germination	*Arabidopsis*	DRT111 controls the splicing of ABI3 and acts upstream of the splicing factor SUA, integrating the ABA- and light-regulated pathways	Punzo et al., 2020
	VP1	Seed germination	Rice	Post-transcriptional processing patterns in the OsVP1 gene alter pre-harvest sprouting among rice varieties	Fan et al., 2007
	RRC1	Post-germination	*Arabidopsis*	RRC1 splicing factor is involved in seedling development under red light	Shikata et al., 2012
	SFPS	Post-germination	*Arabidopsis*	SFPS splicing factor controls hypocotyl growth in response to light	Xin et al., 2017
	HSFA2	Post-germination	Tomato	The splice isoform HsfA2-II is implicated in the early stress response at the expense of HsfA2-I, which is involved in short-term thermotolerance	Hu et al., 2020
Chromatin remodeling related	*PKL*	Seed development	*Arabidopsis*	Involved in chromatin remodeling during seed development	Eshed et al., 1999; Ogas et al., 1999; Gehring et al., 2004
	OsFIE1	Seed development	Rice	OsFIE1, a member of PRC2 (polycomb repressive complex), is repressed at 42°C. OsFIE1 overexpression reduces seed size and DNA methylation of OsFIE1 at 42°C	Folsom et al., 2014
	OsROS1	Seed development	Rice	OsROS1, a DNA demethylase, restricts the number of aleurone cell layers in rice and increases grain quality	Liu et al., 2018
	PKL	Seed maturation	*Arabidopsis*	PKL contributes to maintaining the repression of LEC1 and FUS3 during seed imbibition	Ogas et al., 1999
	ASIL1, *ASIL2*, *HDA6*	Seed maturation	*Arabidopsis*	Act downstream of miRNAs to repress seed maturation during embryogenesis	Willmann et al., 2011
	SUVH4	Seed dormancy	*Arabidopsis*	SUVH4 affects ABA/GA sensitivity by decreasing the expression of dormancy- and ABA-related genes (DOG1, ABI3, and ABI4)	Zheng et al., 2012
	DOG1	Seed dormancy	*Arabidopsis*	H3K4me3 active marks on DOG1 are removed and H3K27me3 repressive marks are enhanced when seeds are exposed to light	Muller et al., 2012; Molitor et al., 2014; Footitt et al., 2015
				H2B ubiquitin transferase HUB is required for DOG1 expression	Liu et al., 2007
	PKL	Seed dormancy	*Arabidopsis*	PKL inhibits seed dormancy by binding to different chromatin regions of DOG1	Zha et al., 2020

Table 1. ***Continued***

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	Name	Developmental stage	Species	Description	References
	HUB1	Seed dormancy	*Arabidopsis*	HUB1 is necessary for histone H2B monoubiquitination and affects gene expression of dormancy-related genes such as DOG1	Liu et al., 2007
	HD2B	Seed dormancy	*Arabidopsis*	HD2B expression is upregulated by cold or after-ripening in *Arabidopsis* accessions with low dormancy	Yano et al., 2013
	HDA19	Seed germination	*Arabidopsis*	HDA19 interacts with SUVH5 and promotes seed germination by inhibiting the expression of seed dormancy genes	Zhou et al., 2020
	SUVH5	Seed germination	*Arabidopsis*	SUVH5 acts as a positive regulator of the light-mediated transcriptional regulatory network	Gu et al., 2019
	JMJ20, *JMJ22*	Seed germination	*Arabidopsis*	JMJ20/22 act downstream of SOM to positively regulate seed germination in response to light	Cho et al., 2012
	PKL	Seed germination	*Arabidopsis*	PKL promotes seed germination	Perruc et al., 2007
miRNA related	miR156, miR167, miR390, miR394, miR403, miR393	Seed maturation	*Arabidopsis*	Accumulate during the late transition phase and persist in mature green embryos	Plotnikova et al., 2019
	miR170	Seed maturation	*Arabidopsis*	Accumulates during the late transition phase and persists in mature green embryos	Chung et al., 2016
	miR171	Seed maturation	*Arabidopsis*	Accumulates during the late transition phase and persists in mature green embryos	Takanashi et al., 2018
	miR172	Seed dormancy	*Arabidopsis*	High levels of miR172 reduce seed dormancy	Huo et al., 2016
	miR156	Seed dormancy	*Arabidopsis*	High levels of miR156 enhance seed dormancy	Huo et al., 2016
	DCL1	Seed dormancy	*Arabidopsis*	DOG1 induces DCL1 transcripts for miRNA processing proteins	Huo et al., 2016
	HYL1	Seed dormancy	*Arabidopsis*	DOG1 induces HYL1 transcripts for miRNA processing proteins	Huo et al., 2016
	SERRATE	Seed dormancy	*Arabidopsis*	DOG1 inhibits SERRATE for miRNA processing proteins in dry seeds	Huo et al., 2016
	miR172	Seed dormancy	Lettuce	LsDOG1 expression inhibits miR172	Huo et al., 2016
	miR156	Seed dormancy	Lettuce	LsDOG1 expression induces miR156	Huo et al., 2016
	miR159	Seed germination	*Arabidopsis*	miR159 targets mRNAs encoding GA-MYB transcription factors that interact with GA-response elements. The expression of miR159 is repressed in the absence of GA	Achard et al., 2004; Millar and Gubler, 2005
	miR393	Seed germination	*Arabidopsis*	miR393 targets TIR1, an auxin receptor, and other three related F-box proteins	Jones-Rhoades and Bartel, 2004; Sunkar and Zhu, 2004

Table 1. ***Continued***

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	Name	Developmental stage	Species	Description	References
	miR163	Seed germination	*Arabidopsis*	miR163 is highly induced by light and promotes seed germination. miR163 inhibits PXMT1, encoding a methyltransferase that methylates 1,7-paraxanthine	Huo et al., 2016
	miR402	Seed germination	*Arabidopsis*	miR402 plays a role as a positive regulator of seed germination under stress by miRNA-guided regulation of DML3 DNA demethylation	Ortega-Galisteo et al., 2008
	miR167	Seed germination	*Arabidopsis*	mir167 targets ARF6 and ARF8	Rhoades et al., 2002; Kasschau et al., 2003; Jones-Rhoades and Bartel, 2004; Vazquez et al., 2004
	miR160	Seed germination	*Arabidopsis*	ARF10 is repressed by miR160, and it plays a key role in the interaction between auxin and ABA pathways during germination. mir160 targets ARF10, ARF16, and ARF17	Rhoades et al., 2002; Kasschau et al., 2003; Jones-Rhoades and Bartel, 2004; Vazquez et al., 2004; Liu et al., 2007
	DCL1	Seed germination	*Arabidopsis*	The dcl1-11 mutant exhibits germination sensitivity to salt and osmotic stresses	Lu et al., 2000; Zhang et al., 2008
	HYL1	Seed germination	*Arabidopsis*	HYL1 affects the ABI5- or ABI3-mediated ABA signaling pathway to control seed germination	Lu et al., 2000
	miR402	Post-germination	*Arabidopsis*	miR402 acts as a positive regulator of seedling growth under stress by miRNA-guided regulation of DML3 DNA demethylation	Ortega-Galisteo et al., 2008
	miR160	Post-germination	*Arabidopsis*	The mARF10 transgene causes defects in post-germinative seedling establishment. The release of ARF10 from repression by miR160 also affects ABA sensitivity during post-germination stages	Liu et al., 2007
	DCL1	Post-germination	*Arabidopsis*	DCL1 inhibits photomorphogenesis for hypocotyl length	Sun et al., 2018
	HYL1	Post-germination	*Arabidopsis*	HYL1 is stabilized by COP1 and interacts with PIF4. HYL1, DCL1, HEN, and HASTY maintain active hypocotyl growth of seedlings in darkness. HYL1 may affect the ABI5- or ABI3-mediated ABA signaling pathway to control seedling establishment	Lu et al., 2002; Cho et al., 2014; Sun et al., 2018
	HEN1	Post-germination	*Arabidopsis*	HEN maintains active hypocotyl growth of seedlings in darkness	Cho et al., 2014; Tsai et al., 2014; Sun et al., 2018; Sacnun et al., 2020
	HASTY	Post-germination	*Arabidopsis*	HASTY maintains active hypocotyl growth of seedlings in darkness	Cho et al., 2014; Tsai et al., 2014; Sun et al., 2018; Sacnun et al., 2020

Table 1. ***Continued***

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	Name	Developmental stage	Species	Description	References
	miR156	Grain quality	Rice	SPL genes have been shown to be regulated by Os-miR156. Os-miR156 has a role in rice grain size, suggesting post-transcriptional modifications by miRNAs	Xie et al., 2006; Schwarz et al., 2008; Wang et al., 2008, 2009, 2012, 2015; Wu et al., 2009; Jiao et al., 2010; Miura et al., 2010
	miR396	Grain quality	Rice	Os-miR396 has a role in rice grain size, suggesting post-transcriptional modifications by miRNAs	Wang et al., 2012, 2015
	miR397	Grain quality	Rice	Overexpression of Os-miR397 enlarges grain size and promotes panicle branching	Zhang et al., 2017
	miR160	Grain quality	Rice	Expression of Os-miR160-resistant Os-ARF18, a negative regulator of grain size, produces smaller seeds and reduces starch grain accumulation	Huang et al., 2016

Table 1. ***Continued***

miRNAs (Bartel, 2004; Yu et al., 2017). Plant miRNAs are transcribed by RNAPII and are regulated by *cis*- and *trans*-acting regulatory elements (Achkar et al., 2016; Chorostecki et al., 2017; Song et al., 2019). Primary *MIR* transcripts are processed into hairpin precursors, a process catalyzed by the DICER-LIKE 1 (DCL1) enzyme and the two RNA-binding proteins HYPONASTIC LEAVES 1 (HYL1) and SERRATE (SE). The pre-miRNAs undergo another DLC-mediated cleavage and form a duplex. The 3′ ends of this duplex are then methylated by HUA ENHANCER 1 (HEN1) and transported to the cytoplasm for further incorporation into an miRNA-induced silencing complex (Figure 1B). The miRNAs can then function in post-transcriptional gene silencing or repression of translation, or they can trigger the cleavage of transcripts to generate another class of miRNAs. ARGONAUTE 1 (AGO1) protein, a central component of the miRNA-induced silencing complex, guides the complex to sequences in target RNAs that are almost perfectly complementary to the miRNA (Jones-Rhoades and Bartel, 2004; Allen et al., 2005).

In recent years, our appreciation of the relevance of alternative splicing, chromatin remodeling, and miRNA regulation in seeds has increased. In this section, we discuss post-transcriptional events that occur in seed development, dormancy, germination, and post-germination.

Seed maturation

In *A. thaliana*, seed maturation is genetically controlled by at least four central regulators: *LEC1*, *LEC2*, *FUSCA3* (*FUS3*), and *ABI3* (Raz et al., 2001; Kroj et al., 2003; To et al., 2006). Seed maturation is frequently accompanied by active modification of the chromatin structure (Exner and Hennig, 2008). However, it is still not fully understood whether the reduced metabolic activity of dry seeds is associated with changes in chromatin organization. In addition, genomic imprinting is a type of epigenetic regulation in which a set of genes is expressed based on their parent of origin. Genomic imprinting it involves DNA methylation and histone modification in the endosperm tissue (Huh et al., 2013). PICKLE (PKL), an SWI/SNF class chromatin remodeling factor, is involved in chromatin remodeling in seed development (Eshed et al., 1999; Ogas et al., 1999; Gehring et al., 2004). PKL helps to maintain the repression of *LEC1* and *FUS3* during seed imbibition, as *pkl* mutant seeds abnormally express *LEC1* and *FUS3* upon imbibition (Ogas et al., 1999). *ABI3*, the main actor in the ABA signaling pathway, is also repressed by PKL (Perruc et al., 2007), and ABI3 protein is targeted for degradation by ABI3-INTERACTING PROTEIN 2 (Zhang et al., 2005). The abundance of ABI3 is finely regulated at multiple levels. At the post-transcriptional level, alternative splicing is important for controlling *ABI3* expression, and several splice variants of *ABI3* homologs in monocots and dicots have been identified (McKibbin et al., 2002; Fan et al., 2007; Gagete et al., 2009; Sugliani et al., 2010; Gao et al., 2013). In *A. thaliana*, the *ABI3* intron is alternatively spliced, giving rise to two transcripts: *ABI3*-α (encoding the full-length protein) and *ABI3*-β (encoding a truncated protein that contains two of the four functional domains). The alternative splicing of *ABI3* is developmentally regulated; only *ABI3*-β accumulates at the end of the seed maturation phase, probably contributing to a rapid downregulation of the full-length protein in ripe seeds (Sugliani et al., 2010; Figure 2A). The splicing factor *SUA* (*SUPPRESSOR OF abi3-5*), an homolog of the human splicing regulator *RBM5*, also affects seed maturation by regulating the splicing of *ABI3* (Sugliani et al., 2010; Figure 2A).

miRNAs are also involved in the regulation of gene expression during seed maturation (Figure 2C). Willmann et al. (2011) demonstrated that miRNAs can operate by repressing the master regulators *LEC2* and *FUS3*. In this study, the authors showed that two trihelix transcription factors *ARABIDOPSIS 6B-INTERACTING PROTEIN1-LIKE 1* (*ASIL1*) and *ASIL2*, together with the histone deacetylase *HDA6*, acted downstream of miRNAs to repress the maturation program during

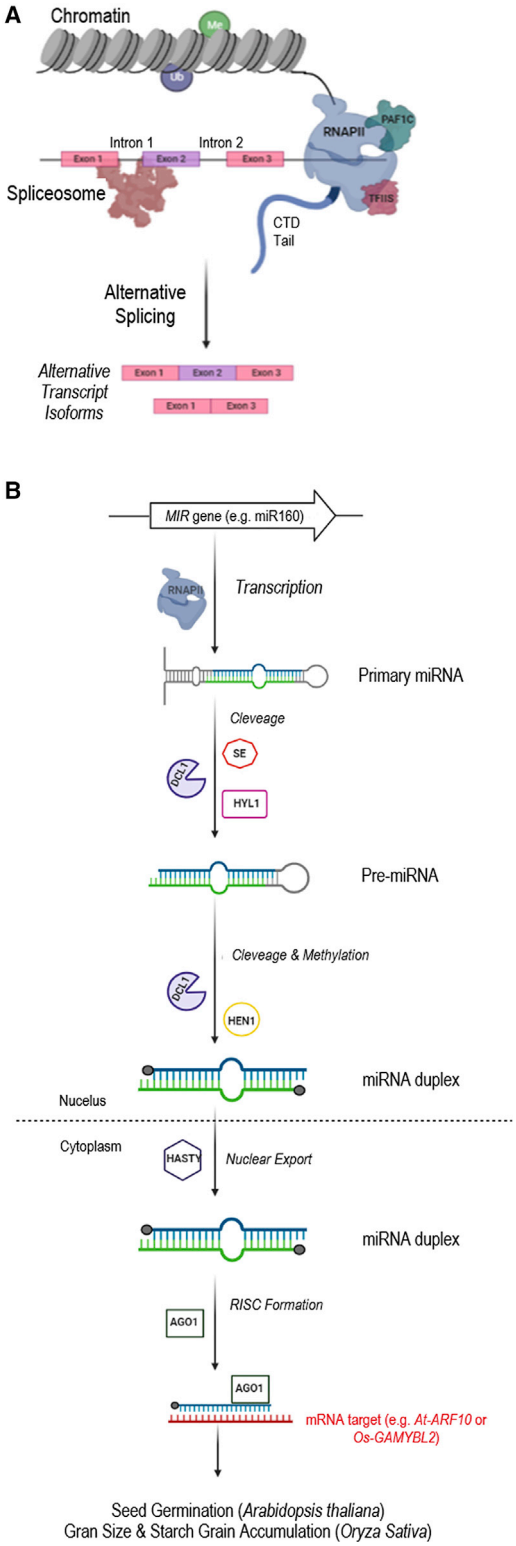

Figure 1. Alternative splicing regulation and miRNA biogenesis in seeds.

(A) RNA splicing is carried out by the spliceosome. Genes subjected to alternative splicing regulation encode proteins with regulatory functions. Chromatin compaction and modifications also affect transcription and splicing. Major transcriptional changes, together with chromatin remodeling, regulate seed maturation, dormancy, and germination. Ub, ubiquitination; Me, methylation; RNAPII, RNA polymerase II; PAF1C, polymerase II-associated factor 1 complex; CTD, carboxy-terminal domain; TFIIS, transcription factor IIS. Depicted in bold are known seed maturation, dormancy, and germination regulators. Adapted from Tognacca et al. (2020).

(B) *MIR* genes are transcribed by RNAPII. Primary miRNAs are processed into hairpin precursors, a process catalyzed by a dicing complex consisting of DCL1, HYL1, and SE. The resulting pre-miRNAs undergo another DLC-mediated cleavage and form a duplex. The 3′ ends of this duplex are then methylated by HEN1 and transported to the cytoplasm for further incorporation into a miRNA-induced silencing complex. AGO1 protein guides the complex to sequences in target mRNAs that are almost perfectly complementary to the miRNA. Shown as an example is the regulation of miR160 in *Arabidopsis thaliana* and *Oryza sativa*. DCL, DICER-LIKE 1; HYL1, HYPONASTIC LEAVES 1; SE, SERRATE; HEN1, HUA ENHANCER 1; AGO1, ARGONAUTE. Gray circles denote methylation.

early embryogenesis (Willmann et al., 2011). Using a low-input small RNA sequencing (RNA-seq) method, a recent study identified 349 miRNA-mediated cleavages and repressions of targeted transcription factors during different stages of embryogenesis in *A. thaliana* (Plotnikova et al., 2019). Twenty-two miRNA families accumulate during the late transition phase and persist in mature green embryos (Figure 2C). These families include miR394, miR403, and miR170/171, as well as miR156, miR167, and miR390 (Plotnikova et al., 2019). Elevated levels of miR156 and reduced levels of mir172 and three SQUAMOSA promoter-binding protein-like transcription factors (*SPL3*, *SPL4*, and *SPL5*) in the mature embryo downregulate the developmental transition and maintain seed dormancy (Martin et al., 2010; Huang et al., 2013; Figure 2C).

Seed desiccation is associated with a major loss of water, drying the seed in preparation for a quiescent period with an increase in dormancy and an accumulation of storage proteins (Tweddle et al., 2003; Blöchl et al., 2007; Gutierrez et al., 2007; Finkelstein et al., 2008; Angelovici et al., 2010). During the development of *A. thaliana* seeds, Srinivasan et al. (2016) found that more than a quarter of the genes undergoing alternative splicing were related to RNA processing, potentially intensifying the alternative splicing regulatory effect in preparation for seed germination after imbibition.

Seed dormancy

DOG1 is a master regulator of seed dormancy, and several *DOG1* homologs have been identified. Seeds from several species, such as *Lepidium*, originating from diverse environments across the continents present varying levels of dormancy owing to the presence of orthologs of *A. thaliana DOG1* (Graeber et al., 2010, 2014). Chiang et al. (2011) demonstrated that the plasticity of *DOG1* expression in *A. thaliana* is highly dependent on maternal effects associated with the geographic location of seed maturation. Accessions from the south expressed higher levels of DOG1 and, consequently, higher levels of dormancy. The *DOG1* gene consists of three exons and two introns. The second intron is subject to alternative splicing, leading to five different transcript variants (*DOG1*-α to *DOG1*-ε, Nakabayashi et al., 2015; Figure 2A) and three protein variants, as translation of the β, γ, and ε transcripts generates the same protein

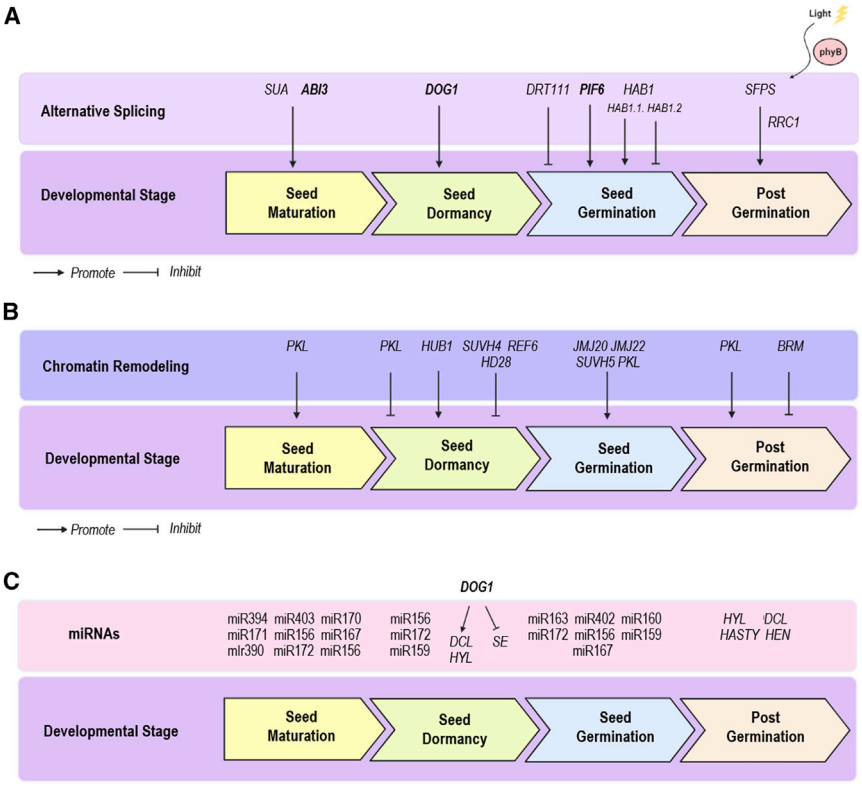

Figure 2. Alternative splicing, chromatin remodeling, and miRNA function in *Arabidopsis* seeds.
Simplified diagrams show the genes involved in **(A)** alternative splicing, **(B)** chromatin remodeling, and **(C)** miRNA function documented for gene regulation in seeds. DCL, DICER-LIKE 1; HYL1, HYPONASTIC LEAVES 1; SE, SERRATE; HEN1, HUA ENHANCER 1.

(Bentsink et al., 2006; Nakabayashi et al., 2015). Tight coupling between transcription and alternative splice site selection has been shown: mutations in the transcription elongation factor TFIIS lead to the selection of proximal splice sites on *DOG1* (and also at more genome-wide targets), suggesting the existence of a kinetic coupling between RNAPII elongation and splicing in plants (Brzyżek and Świeżewski, 2015). Dolata et al. (2015) studied the spliceosome disassembly factor NTC-related protein 1 (NTR1) and showed that it is required for the correct expression and splicing of *DOG1* (Dolata et al., 2015).

To add another level of complexity to its regulation, *DOG1* is also subjected to alternative polyadenylation (Cyrek et al., 2016; Kowalczyk et al., 2017) and antisense regulation during dormancy establishment (Fedak et al., 2016; Yatusevich et al., 2017). Alternative polyadenylation results in the production of two *DOG1* transcripts: the shorter two-exon *short DOG1* (*shDOG1*) and the longer three-exon *long DOG1* (*lgDOG1*). The *shDOG1* transcript is evolutionarily conserved at the amino acid level; it is translated and is sufficient to complement the *dog1* mutant (Cyrek et al., 2016). In addition, transcription generates an extensive array of non-protein-coding RNA (ncRNA), the functional significance of which is mostly unknown. Non-coding transcription changes in a complex manner during development and in response to environmental signals. One specific class of ncRNA is the antisense transcripts. One antisense transcript that originates close to the *DOG1* proximal (main) termination site strongly inhibits dormancy strength and *DOG1* expression. This transcript acts in *cis*, as it is unable to silence *DOG1* transcribed from a second allele (Fedak et al., 2016). DOG1 transcription is also enhanced by transcription elongation factor TFIIS (Mortensen et al., 2011; Mortensen and Grasser, 2014).

Transcriptional regulation of seed dormancy is also associated with chromatin remodeling (Née et al., 2017; Figure 2B). An interesting example of this is the interconnection between the PKL chromatin remodeling factor and DOG1. PKL inhibits primary seed dormancy (Zha et al., 2020) and promotes seed germination (Perruc et al., 2007). Downregulation of *DOG1* during seed imbibition is less inhibited in *pkl* mutant seeds, suggesting that PKL inhibits *DOG1* expression. By performing chromatin immunoprecipitation assays, Zha et al. (2020) demonstrated that PKL binds to chromatin regions of *DOG1* other than the promoter regions, indicating that PKL associates with the gene body of *DOG1*. Seeds can respond and adapt to the environment by controlling gene expression through changes in chromatin structure that are specifically associated with histone modifications. *H2B MONOUBIQUITINATION 1* (*HUB1*) is necessary for histone H2B monoubiquitination and influences gene expression of dormancy-related genes such as *DOG1* (Liu et al., 2007; Figure 2B). Chromatin remodeling contributes to the regulation of *DOG1* expression, with histone modification acting as part of the mechanism before *DOG1* gene expression is finally silenced (Footitt et al., 2017). The distribution of histone modifications on *DOG1* chromatin during dormancy cycling suggests that the regulation of *DOG1* at the chromatin level is reversible until seeds are committed to germination. Distribution and abundance of specific activating (H3K4me3) and repressing (H3K27me3) marks on *DOG1* change during dormancy cycling. In addition, when seed germination is promoted by light, the activating marks are removed from *DOG1*, and the repressing marks are enhanced (Müller et al., 2012; Molitor et al., 2014; Footitt et al., 2015). Furthermore, *KYP/SUVH4*, which encodes an H3 Lys 9 methyltransferase, reduces seed dormancy and ABA/GA sensitivity by decreasing the expression of dormancy- and ABA-related genes such as *DOG1*, *ABI3*, and *ABI4* (Zheng et al., 2012; Figure 2B). HD2B, a plant-specific HD2 histone deacetylase, is also associated with reduced seed dormancy and increased GA levels in imbibed seeds (Figure 2B). *HD2B* expression is upregulated by cold or after-ripening in *A. thaliana* seeds with low dormancy and correlates with the inhibition of *GA2ox2* and the increase of *GA3ox1* and *GA3ox2* expression. This upregulation of *HD2B* expression is significantly suppressed in *A. thaliana* accessions that show higher dormancy levels (Yano et al., 2013; Figure 2B). Very recently, additional epigenetic regulation of ABA levels in seeds through the

H3K27me3 demethylase RELATIVE OF EARLY FLOWERING 6 (REF6) has been described (Lu et al., 2011). Enhanced seed dormancy and ABA content in *ref6* mutants depend on the reduced transcript levels of *CYP707A1* and *CYP707A3*. These results suggest that an epigenetic mechanism is involved in the regulation of ABA content in seeds (Chen et al., 2020; Figure 2B).

Seed germination

Although there is abundant information about the molecular basis of light-induced germination at the gene expression/transcription level (Penfield et al., 2005; Oh et al., 2006, 2007, 2009; Park et al., 2012; Ibarra et al., 2013), the effects of light on alternative splicing have been documented only recently. Narsai et al. (2017) analyzed the dynamics of gene expression during germination induced by a white light/dark photoperiod and generated the first dynamic transcription network for seed germination. They found 620 genes undergoing alternative splicing whose expression was time- and tissue-specific (Narsai et al., 2017). Tognacca et al. (2019) showed that a pulse of R-light changes the expression of ~20% of the transcriptome and modifies the alternative splicing pattern of 226 genes, including splicing-related factors (*SR30*, *RS31a*, *RS31*, and *U2AF65A*), light-signaling components (*PIF6*), and dormancy-related genes (*DRM1*). Interestingly, phyB is responsible for the change in the *U2AF65A* and *PIF6* alternative splicing patterns, whereas the other splicing events are phyB independent (Tognacca et al., 2019).

More recently, Punzo et al. (2020) showed that the negative control of germination by the splicing factor DRT111 (DNA-DAMAGE REPAIR/TOLERATION PROTEIN 111) is caused by its effects on the ABA- and light-regulated pathways. DRT111 controls the splicing of *ABI3* and acts upstream of the splicing factor SUA. Interestingly, DRT111 can also modulate the activity of PIFs to promote photomorphogenesis (Xin et al., 2017), suggesting that DRT111 may be a major point of convergence in the transition between seed germination and post-germination events (Figure 2A). The PIF6 transcription factor is also involved in the promotion of germination by light. *PIF6* pre-mRNA expresses four alternative splicing isoforms (Narsai et al., 2017). *PIF6*-α encodes the full-length protein, whereas *PIF6*-β (originating from an exon-skipping event that creates a premature stop codon) encodes a truncated protein that lacks the HLH binding domain (Penfield et al., 2010). The *PIF6*-α isoform predominates before seed imbibition, and *PIF6*-β is the dominant isoform during dark stratification at 12 and 48 h (Narsai et al., 2017). Although the *PIF6*-α isoform has no evident function during germination, seeds that overexpress *PIF6*-β show greater germination than the wild type, implying that it has an active role in this process (Figure 2A). Seedlings that overexpress *PIF6*-α and *PIF6*-β have shorter hypocotyls than the wild type in R-light, implying that *PIF6* alternative splicing isoforms can have distinct functions with different physiological outputs (Penfield et al., 2010). In *A. thaliana*, *HAB1* (a group A protein type 2C phosphatase, PP2C) has two splice variants (*HAB1.1* and *HAB1.2*) with opposite functions in seed germination (Wang et al., 2015). PP2Cs interact with subclass III SNF1-related protein kinases (SnRK2.2, 2.3, and 2.6) to dephosphorylate and inhibit their kinase activity, thereby turning off ABA signaling. Whereas *HAB1.1* promotes seed germination, *HAB1.2* is a positive regulator of ABA signaling and prevents seed germination (Figure 2A). Interestingly, RBM25, an RNA-binding motif (RBM)-containing protein, is a key regulator of *HAB1* alternative splicing. The high ABA sensitivity of *rbm25* seedlings is caused by reduced expression of the *HAB1.1* isoform (Wang et al., 2015).

Chromatin remodeling is also involved in seed germination promoted by light. The histone arginine demethylases *JUMONJI C DOMAIN-CONTAINING PROTEIN 20* (*JMJ20*) and *JMJ22* act downstream of SOMNUS to positively regulate seed germination in response to light (Cho et al., 2012; Figure 2B). More recently, it has been demonstrated that SUVH5 acts as a positive regulator of the light-mediated transcriptional regulatory network in germinating *A. thaliana* seeds (Gu et al., 2019; Figure 2B). In addition, a global study at the chromatin level found that HDA19, a histone deacetylase, interacts with SUVH5 and promotes seed germination by inhibiting the expression of seed dormancy genes (Zhou et al., 2020). Increased activity of H4K16ac and H3K18ac in imbibed embryos of *Brachypodium distachyon* has also been described (Wolny et al., 2017). In *A. thaliana*, *PKL* is rapidly activated upon seed imbibition (Henderson et al., 2004; Li et al., 2005). Thus, PKL-mediated chromatin remodeling events probably take place during germination, repressing early-embryonic gene expression programs and enabling the developmental switch to post-germinative growth (Ogas et al., 1997; Li et al., 2005; Figure 2B). Interestingly, PKL promotes seed germination, inhibiting ABA signaling by repressing *ABI3* and *ABI5* expression. Higher gene expression of both genes in *pkl* mutant seeds correlates with lower methylation in histone markers for repressed chromatin (Perruc et al., 2007).

In *A. thaliana* seeds, miR163 is highly induced by light and promotes seed germination and radicle growth (Chung et al., 2016; Figure 2C). In addition, miR402 positively regulates seed germination and seedling growth under stress by miRNA-guided regulation of DEMETER-LIKE PROTEIN 3 (DML3), which is involved in DNA demethylation (Ortega-Galisteo et al., 2008; Figure 2C). Numerous hormonal signal transduction pathways related to the germination process are also controlled by miRNAs. For example, miR159 participates in seed germination by modulating GA and ABA hormone signaling; it targets mRNAs encoding GA-MYB transcription factors that interact with GA-response elements (Achard et al., 2004; Millar and Gubler, 2005). The expression of miR159 is controlled by both GA and ABA (Martin et al., 2010). In the absence of GA, the expression of miR159 is repressed, possibly through the action of DELLA proteins (Achard et al., 2004).

Auxin-related pathways are also under the control of miRNAs. miR393 targets the *TIR1* auxin receptor and three other related F-box proteins (Jones-Rhoades and Bartel, 2004; Sunkar and Zhu, 2004). mir160 targets *ARF10* (AUXIN RESPONSE FACTOR 10), *ARF16*, and *ARF17*, and mir167 targets *ARF6* and *ARF8* (Rhoades et al., 2002; Kasschau et al., 2003; Jones-Rhoades and Bartel, 2004; Vazquez et al., 2004). Liu et al. (2007) showed that *ARF10* is repressed by miR160, and its regulation plays a key role in the crosstalk between auxin and ABA pathways in germination and post-germination events (Figure 2C). Derepression of *ARF10* increases the sensitivity of seeds to

ABA, and overexpression of *MIR160a* reduces the sensitivity of *A. thaliana* seeds to ABA (Liu et al., 2007). These pieces of evidence suggest that miR160 acts as a convergence point for auxin- and ABA-mediated crosstalk during seed germination (Liu et al., 2007).

DOG1 can also affect miRNA production and the thermo-inhibition at 32°C of imbibed *A. thaliana* seeds (Huo et al., 2016). Interestingly, DOG1 affects the expression of genes encoding miRNA processing proteins: *DCL1* and *HYL1* transcripts are induced, whereas *SERRATE* (SE) is inhibited by *DOG1* in dry seeds, suggesting that DOG1 can control seed germination through the regulation of miRNA processing (Huo et al., 2016; Figure 2C). In addition, high levels of miR156 inhibits whereas miR172 enhances seed germination at high temperatures. Also Also, miR159 c controls the transcription factors MYB33 and MYB101 which are positive regulators of ABA signaling ng (Reyes and Chua, 2007; Martin et al., 2010; Figure 2C).

A recent topic of interest is the translational processes that occur between the dry and imbibition states of seeds during germination. Some time ago, an important role was suggested for stored mRNAs in dry seeds. Using a new technological approach in which polysome occupancy (i.e., polysome loading) is measured as a proxy for translational efficiency, it has been demonstrated that mRNAs stored in dry seeds are selectively translated during seed germination (Sano et al., 2012; Galland et al., 2014; Layat et al., 2014; Bai et al., 2017). A fraction of the monosome-specific transcripts (~50% of seed-stored mRNAs that are bound to ribosomes) is associated with polysomes during imbibition, with some enrichment in proteins that function against oxidative stress (Bai et al., 2020). In addition, some transcripts are translationally downregulated, and it has been suggested that the P-body protein VARICOSE is required for mRNA degradation during seed imbibition (Basbouss-Serhal et al., 2017). How specific mRNAs are targeted to the monosome complex is still unknown, although it has been suggested that GC content, transcript length, and upstream open reading frames are key features for ribosome association that ensure mRNA survival during the dry storage of seeds (Bai et al., 2017).

Post-germination

Seed germination and post-germination development are different and interconnected processes with distinct regulatory mechanisms. Post-germination seedling establishment denotes the developmental window after germination that involves the opening, greening, and expansion of cotyledons, marking the switch to autotrophic development (Weitbrecht et al., 2011). Seedlings growing in darkness display skotomorphogenic development, characterized by elongated hypocotyls, apical hooks, pale cotyledons, and short roots. Genome-wide effects of light on alternative splicing were analyzed by RNA-seq in etiolated *A. thaliana* seedlings (Shikata et al., 2012, 2014; Hartmann et al., 2016; Xin et al., 2017, 2019). These studies found several hundred light-regulated alternative splicing events, many of which were associated with genes encoding splicing factors and light-signaling components. Interestingly, the effects of brief light treatments on alternative splicing are modulated to a great extent, although not exclusively, by the phytochromes (Wu et al., 2013; Shikata et al., 2014). Shikata et al. (2014) showed changes in the alternative splicing patterns of over 1500 genes, with over-representation of splicing factor and transcription factor genes, in seedlings exposed to R-light for 1 h. RRC1 (REGULATOR OF CHROMOSOME CONDENSATION 1), an SR-like protein, is required for normal seedling development and undergoes alternative splicing in response to different light conditions, independent of the major photoreceptors (Hartmann et al., 2016; Figure 2A). SFPS (SPLICING FACTOR FOR PHYTOCHROME SIGNALING) is also involved in the fine-tuning of photomorphogenesis by controlling pre-mRNA splicing through interaction with RRC1 (Xin et al., 2017). The latter interacts with phyB in an R-light-dependent manner to coordinately regulate the splicing of a subset of genes involved in light-signaling and circadian-clock pathways to promote photomorphogenesis (Figure 2A).

During post-germination, the embryo is vulnerable to drought stress, as it is no longer protected by the seed coat. If seedlings are exposed to water stress during this phase, growth arrest is triggered to ensure that germinated embryos are protected from cell and tissue damage (Lopez-Molina et al., 2001). This kind of growth arrest involves signaling and response mechanisms similar to those that are active during seed development, when desiccation tolerance and dormancy are induced (Lopez-Molina et al., 2001, 2002; Bensmihen et al., 2002; Finkelstein et al., 2008). In this scenario, ABA levels are increased (Nambara and Marion-Poll, 2005), and the loss of function mutant of BRAHMA (BRM), an SWI2/SNF2 chromatin remodeling ATPase, causes ABA hypersensitivity and directly represses *ABI5* (Han et al., 2012). These results suggest an important role for chromatin-mediated regulation during water stress responses prior to seedling establishment (Figure 2B). Moreover, BRM plays a direct role in the positive regulation of GA biosynthesis by activating the *GA3ox*1 promoter, and *brm-1* and *brm-3* mutant seeds exhibit a significant decrease in active GA levels (Archacki et al., 2013). It is also known that *PKL* expression represses the embryonic state by controlling a significant number of GA-responsive genes (Zhang et al., 2008). PKL also regulates most GA-regulated developmental processes, including the promotion of vegetative growth and phase transitions (Park et al., 2017; Figure 2B).

Different components of miRNA biogenesis also contribute to the adjustment of post-germination events. HYL1, DCL1, HEN, and HASTY increase the hypocotyl growth of seedlings in darkness (Cho et al., 2014; Tsai et al., 2014; Sun et al., 2018; Sacnun et al., 2020). HYL1 is stabilized by CONSTITUTIVE PHOTOMORPHOGENESIS 1 (COP1) and interacts with PIF4 (Cho et al., 2014; Sun et al., 2018). In opposition to HYL1, DCL1 and SE promote the hook unfolding during seedling photomorphogenesis. These results suggest that the miRNA biogenesis machinery tightly regulates the fine-tuning of seedling development (Sacnun et al., 2020; Figure 2C).

POST-TRANSCRIPTIONAL PROCESSES IN CROP SEEDS

Post-transcriptional processes are relevant in monocot and dicot crops such as rice, maize, wheat, barley, and soybean.

Using RNA-seq, Zhang et al. (2016) identified between 552 and 669 alternatively spliced transcripts in germinating embryos from four barley varieties with an early dynamic pattern of expression between 24 and 48 h after seed imbibition. The pathways with the most alternatively spliced transcripts were related to post-transcriptional regulation, plant hormone signal transduction, and cell wall modification, suggesting that these processes have important roles in the regulation of seed germination (Zhang et al., 2016). Endosperm and embryo development are coordinated by epigenetic regulation and signaling between these two organs. In maize (*Zea mays*), epigenetic control of the endosperm has a strong influence on embryo viability (Lin, 1984). The *rough endosperm 3* (*rgh3*) maize mutant shows impaired embryo development and endosperm cell differentiation. *RGH3*, which encodes a predicted RNA splicing factor involved in the spliceosome, is required in the endosperm to switch from cellular proliferation to differentiation. Interestingly, the molecular cloning of *RGH3* suggests that it has 19 splice variants that are regulated in a tissue- and development-specific manner (Fouquet et al., 2011). Gault et al. (2017) demonstrated that *rgh3* mutant protein disrupts colocalization with U2AF2 and causes aberrant endosperm cell differentiation and proliferation. The RRM_RBM48-type RNA-binding protein DEK42 also participates in the regulation of pre-mRNA splicing through its interaction with other spliceosome components (Zuo et al., 2019). The *dek42* maize mutant produces small defective kernels and lethal seedlings due to alternative splicing changes (Zuo et al., 2019). In another study, the P-type PPR nuclear protein DEK2 was implicated in the splicing of mitochondrion-encoded mRNA (Qi et al., 2017). The *dek2* mutation reduces the splicing efficiency of mitochondrial *nad1* intron 1 and shows severe impairments in respiratory complex I assembly and mitochondrial function (Qi et al., 2017).

The *Viviparous1* (*Vp1*) transcription factor is an important regulator of late embryogenesis in maize, simultaneously activating genes involved in embryo maturation and repressing genes associated with germination. Wheat caryopses are characterized by relatively weak embryo dormancy and are susceptible to pre-harvest sprouting, an event that is phenotypically similar to the *vp1* maize mutation and the *abi3* mutation in *A. thaliana* seeds. McKibbin et al. (2002) demonstrated that *Vp1* transcripts produce different cytoplasmic mRNA variants, the majority being incorrectly spliced and therefore unlikely to encode functional protein during wheat grain development. Interestingly, transgenic wheat plants expressing the *Avena fatua Vp1* homolog (*AfVp1*) under the control of the constitutive ubiquitin promoter showed enhanced responsiveness to ABA, and the grains were less susceptible to pre-harvest sprouting (McKibbin et al., 2002). Pre-harvest sprouting among different rice varieties is also associated with unusual post-transcriptional processing patterns in the *OsVP1* gene (Fan et al., 2007). Alternative splicing products of *OsABI5* (*OsABI5-1* and *OsABI5-2*) are simultaneously present in some rice tissues, but with different expression patterns (Zou et al., 2007). During seed maturation, the physical interaction between *Os*ABI5-2 and *Os*ABI5-1 regulates downstream genes together with *Os*VP1, and the constitutive expression of *OsABI5-1* or *OsABI5-2* can rescue the ABA insensitivity of *abi5-1* seeds (Zou et al., 2007).

High temperature can harm rice grain quality by significantly reducing the accumulation of storage materials. Xu et al. (2020a, 2020b) found that the alternative splicing of *OsbZIP58* is altered at high temperatures. Cultivation of rice plants under a cycle of 12 h light at 35°C and 12 h dark at 28°C for several days after pollination lowered the activity of the *OsbZIP58-β* splice isoform, decreasing seed quality related to grain weight and thickness, and starch and lipid content (Xu et al., 2020b). In tomato seedlings, a splice variant of the heat-shock factor *HsfA2-I* increases during short-term acclimation to high temperature, enhancing thermotolerance, whereas the *HsfA2-II* variant, whose truncated C-terminal activation motif lacks a nuclear export signal, is rapidly degraded (Hu et al., 2020).

In a comparative RNA-seq study of 28 different soybean tissues, including seed developmental and germination stages, Shen et al. (2014) found that 63% of the genes (i.e., 27 764 genes) were alternatively spliced, and alternative splicing was more common in younger than older developmental stages of a given tissue type. Alternative splicing events were associated with genes related to RNA splicing machinery, and at least one-third of the splicing events differed in expression among tissues. The frequency of alternative splicing was positively correlated with intron length and exon number (Shen et al., 2014). Another RNA-seq analysis using developing soybean embryos showed that post-transcriptional splicing events were related to carbon and nitrogen metabolism, dormancy, and splicing machinery processes, as part of the acquisition of desiccation tolerance during seed maturation (Aghamirzaie et al., 2013). Some RNA isoforms exhibited altered domains that could contribute to changes in protein subcellular localization or activity (Aghamirzaie et al., 2013).

At the level of chromatin and DNA modifications, a screen of rice grains with a thick aleurone phenotype identified *OsROS1*, a DNA demethylase responsible for restricting the number of aleurone cell layers that also increases grain quality (Liu et al., 2018). The study demonstrated that *OsROS1* is involved in CG and CHG demethylation in the endosperm, regulating the expression of the RISBZ1 bZIP and RPBF Dof transcription factors. A study of developing rice seeds maintained at 42°C for 24 or 48 h found that heat treatment reduced seed size and promoted precocious cellularization due to impaired H3K9 methylation of *FERTILIZATION ENDOSPERM INDEPENDENT 1* (*OsFIE1*), which encodes a polycomb repressive complex 2 (PRC2) member (Folsom et al., 2014). The DNA demethylation of *PrCYP707A1* is a prerequisite for the seed germination of the parasitic weed *Phelipanche ramose* in a medium with a synthetic strigolactone analog (Lechat et al., 2015). A comparative methylome study of *Arabidopsis* and soybean seeds found an increase in CHH methylation during development and dormancy imposition, but CHH methylation then dropped precipitously in germinating seeds. By contrast, no changes in CG and CHG methylation occurred during the same developmental period. Although normal seed development was observed in the *Arabidopsis ddcc* mutant that lacks CHH and CHG methylation, 106 transposons were transcriptionally derepressed, suggesting that the increase in CHH methylation may be a failsafe mechanism to reinforce transposon silencing (Lin et al., 2017). By contrast, no significant DNA methylation changes occur around genes

known to be important for seed formation, including genes encoding storage proteins, fatty acid biosynthesis proteins, and several major transcription factors. Many of these genes are located in genomic regions devoid of DNA methylation at any stage of development (Lin et al., 2017). However, another study found that major CHH methylated regions of the soybean genome were transcriptionally downregulated and associated with DNA replication and cell division in mature seeds (An et al., 2017).

In rice, different subfamilies of *OsmiR156* contribute to different seed traits. *OsmiR156* is encoded by 12 genes that produce three *OsmiR156-5p* isoforms and four *OsmiR156-3p* isoforms (Xie et al., 2006). *OsmiR156* regulates the expression of *SPL* and *IPA1* (*Ideal Plant Architecture 1*) genes. *SPL13*, *SPL16*, and *IPA1* are positive regulators of seed size (Wang et al., 2012; Wang and Wang, 2015; Si et al., 2016), and *SPL12* and *IPA1* enhance seed dormancy through the direct regulation of multiple genes in the GA pathway (Miao et al., 2019; Qin et al., 2020). The *Os*miR396 gene family is also highly conserved and abundant in rice. It consists of eight genes encoding five mature isoforms that target 11 *GROWTH REGULATING FACTOR* (*GRF*) transcription factor genes. This family is involved in grain size regulation (Duan et al., 2015; Gao et al., 2015; Li et al., 2016). Wang et al. (2012, 2015) found that *Os*miR156 and *Os*miR396 have a role in rice grain size, suggesting that post-transcriptional modifications by miRNAs can contribute to the development of better genetic materials with improved yields. Another study demonstrated that the expression of *Os*miR160-resistant *OsARF18*, a negative regulator of grain size, produces smaller seeds with reduced starch grain accumulation, suggesting that miRNAs can act to finely adjust development (Huang et al., 2016; Figure 1B). *Os*miR397 is highly expressed in young panicles and grains, and its overexpression enlarges grain size and promotes panicle branching (Zhang et al., 2017).

CONCLUDING REMARKS AND FUTURE DIRECTIONS

The complex molecular networks that underlie the successful transitions from dormancy to germination and from germination to seedling establishment involve the integration of environmental cues and hormonal signals into regulatory mechanisms that include transcriptional, translational, and epigenetic processes. These processes are not completely understood, and more research is needed to fully elucidate the mechanisms by which they control the developmental programs of seeds.

Alternative splicing regulation is guided by the functional coupling between transcription and splicing, with chromatin structure influencing both processes. A future challenge could be to determine whether alternative splicing induced by light and/or temperature is due to changes in the chromatin landscape and, if so, which underlying molecular mechanism(s) are involved. The identification of networks and functional genes that alter splicing in seeds is another open area for further investigation. It is therefore of interest to study transcriptional and post-transcriptional changes during seed developmental stages and seed-related processes. Furthermore, it will also be very interesting to explore the putative direct link between epigenetic modifications and alternative splicing regulation in seeds. This could increase our understanding of the complex regulatory mechanisms that control post-transcriptional events under specific conditions or in specific tissues and cell types. Such studies can help us understand how different molecular events are interconnected, and that knowledge can potentially guide the development of more accurate strategies for selecting genotypes of important crops that show better performance under suboptimal and real environmental conditions.

We must not forget that the history of a seed's experiences during development affects seedling establishment and the success of the future plant. For example, DOG1 is a master regulator of seed dormancy, but it also regulates flowering time (Atwell et al., 2010; Liu et al., 2010). *DOG1* variation affects the level of dormancy that correlates with seasonal germination timing and also has pleiotropic effects on flowering time (Martínez-Berdeja et al., 2020). In mature plants, *DOG1* antisense is strongly downregulated by ABA, allowing the upregulation of *DOG1* expression in response to drought (Yatusevich et al., 2017). These results suggest a novel function of DOG1 in other life history traits, opening a new and interesting avenue of research.

Identifying the mechanisms by which some key genes may be responsible for germination under different environmental conditions will surely provide insight into other important economic parameters of crop seeds, such as germination rate and seed vigor. One of the main objectives of seed vigor testing is to identify seed batches with higher-quality behavior after harvest. Therefore, a deeper understanding of seed vigor associated with quality parameters, such as biochemical markers, variations in specific protein profiles, and changes at the DNA/RNA level, will help to identify the effects of different factors that affect seed performance (Corbineau, 2012).

miRNAs are also a new area of potential crop improvement because of their role as master regulators of gene expression at the post-transcriptional level. As previously stated by other authors, miRNAs are emerging as the next generation of key targets for crop genetic engineering. Therefore, unraveling their role in seeds can also be useful for improving seed traits. For example, the overexpression of *MIR* genes in an organ- or time-dependent manner can improve agronomic traits such as grain quality, yield, and drought and cold tolerance (Djami-Tchatchou et al., 2017; Tang and Chu, 2017). Nonetheless, caution should be taken when designing artificial miRNAs, as pleiotropic phenotypes can also be produced by transgenic events because of the broad-acting network of miRNAs.

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AUTHOR CONTRIBUTIONS

Both authors contributed equally to this work.

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