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Review Article

An overview of the molecular and biochemical components of seed dormancy and germination in *Brassica napus*

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ABSTRACT

Seed dormancy and germination determines the ecological adaptation and sustainability of seed plants. Intensive research efforts have identified the role of several factors in seed dormancy and germination. The major factors are phytohormones, dormancy-specific genes, chromatin factors, developmental and/or structural components of seeds, and exogenous environmental cues, which have been well studied in model plants like *Arabidopsis* and rice. In general, *Brassica napus* L. (canola) cultivars and its interspecific hybrids show seed heterogeneity and varying degrees of dormancy, and germination potentials. However, detailed research on understanding the molecular mechanisms of seed dormancy and germination in *B. napus* is limited as compared to othe model crops like *Arabidopsis*. Identification of seed dormancy and germination associated QTLs in concert with environmental factors is essential for better management of seed longevity and vigor in economically important oil-seed crops like *B. napus*. In addition, both maternal and paternal genomes and/or their imprinted genes are often known to influence dormancy and subsequently lead to premature germination in some interspecific hybrids. Thus, in this review we provide an overview on plausible role of genetic, physiological, and environmental factors governing seed dormancy, germination and premature germination traits in *B. napus*.

1. Introduction

Oilseed rape (*Brassica napus* L.), also known as canola, is a relatively recent domesticate and the second-largest oilseed crop globally, trailing only soybean (Sohn et al., 2016; Kourani et al., 2022). The eco-physiological adaptation to temperate climates has solidified canola's position as the dominant oil crop in Europe (Namazkar et al., 2016). However, *B. napus* is cultivated worldwide for its high-quality oil, vegetables, fodder, and biodiesel production (Raboanatahiry et al., 2021; Sohn et al., 2022a) thus indicating the economic importance. Seed dormancy, a multifaceted adaptive trait, serves as a critical persistence strategy for numerous temperate annual weeds (Baskin and Baskin 1998). Both seed dormancy and germination are inter-related and play crucial roles in seed quality or for its chemical compositions, seedling establishment/eco-physiological adaptation, thereby protecting crop yield (Shu et al., 2015). Research has significantly advanced our understanding of dormancy expression in several species, revealing its modulation by various factors like genotype, progeny placement on the mother plant, and environmental influences (Gutterman 1981; Nimer et al., 1983). Notably, dormancy can be further shaped by post-dissemination environmental conditions (Hazebroek and Metzger, 1990). Based on the maturation stage, *B. napus* exhibits two types of dormancy. Primary dormancy, characterized by high abscisic acid (ABA) levels, prevents premature germination within the pod and persists from early seed development to seed maturation (Sano et al., 2021; Brown et al., 2022). Secondary dormancy, induced by unfavorable germination conditions after seed dispersal, allows mature seeds to persist in the soil for extended periods (Buijs 2020). *B. napus*, classified

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as a non-deep dormant species, exhibits inhibited radicle protrusion within the embryo under conditions unfavorable for germination, such as continuous darkness, freezing temperatures, or low moisture (Pekrun et al., 1997). Brief periods of imbibition under cold stratification or during ripening typically suffice to break seed dormancy in this species (Baskin and Baskin 1998; Brown et al., 2022). Non-deep physiological dormancy presents a dynamic scenario where *B. napus* seeds can transition between completely dormant, non-dormant, and conditionally dormant states (Sohn et al., 2021; Brown et al., 2022). Conditional dormancy can be broken within constrained environmental settings, enabling seed bank populations to proliferate (Brown et al., 2022). In the non-dormant state, germination is permitted across a broader range of conditions (Baskin and Baskin 1998).

On the other hand, preharvest pod shattering and harvest-related disturbances make *B. napus* susceptible to seed dispersal (Sohn et al., 2021; Brown et al., 2022). Up to 10,000 seeds/m^2 can fall onto the soil surface after harvest (Sohn et al., 2021). While early germination of dispersed seeds allows for control through post-harvest tillage, unfavorable conditions (osmotic stress, oxygen deficiency) in darkness can trigger secondary dormancy and enable seed persistence for years (Sohn et al., 2021; Brown et al., 2022). In fact, a study by Beckie and Warwick (2010) revealed that persistent or dormant seeds can remain viable in the soil for up to 7 years after entering this cycle, creating weed control and contamination issues in subsequent crops. Upon encountering optimal conditions, these dormant seeds can germinate and emerge as volunteer plants, subsequently impacting the yield and quality of newly planted *B. napus* through cross-pollination (Brown et al., 2022). Various strategies have been investigated for mitigating the persistence of dormant canola seeds in the soil, which can subsequently lead to volunteer oilseed rape emergence in future crops (Schwabe et al., 2019). These strategies, tested in both laboratory and field experiments, include seed coating with KNO_3, micronutrients, or gibberellic acid (GA), and pre-harvest spraying of urea ammonium nitrate (UAN) or GA on oilseed rape plants (Schwabe et al., 2019). Interestingly, seed coating treatments were found to reduce secondary dormancy, but paradoxically, they also increased seed persistence in the soil by up to 99 %. Among the coating materials, GA proved most effective in reducing dormancy. However, directly harvested *B. napus* seeds are generally considered non-dormant and do not require light for germination (Baskin and Baskin 1998; Soltani et al., 2018). Nevertheless, seeds possessing low dormancy or lacking dormancy can lead to preharvest sprouting, which poses significant challenges for cereal crop quality and production (Tuan et al., 2018). Therefore, it is evident that dormancy levels are key trait linked to seedling growth and thereby the yield potential of crop plants.

2. Molecular basis of ABA and GA-dependent signal transduction pathway in seed dormancy and germination

Seed germination in canola is a crucial determinant of crop success, as seedlings must rapidly establish self-sufficiency for survival (Iqbal et al., 2022). This process initiates with water imbibition by the quiescent seed and culminates in the expansion of the embryonic axis within the seed coat (Boter et al., 2019). The well-characterized model plant *Arabidopsis thaliana* shares over 86 % of its protein-coding regions with *B. napus*, making it a valuable tool for studying seed germination in the latter species (Cavell et al., 1998). This genetic and physiological similarity has informed much research, directing investigations into *B. napus* seed germination responses (Zhang et al., 2004). Notably, hormones like gibberellic acid (GA) and abscisic acid (ABA) exhibit antagonistic effects on seed germination, highlighting the complex interplay between internal and external factors (Shu et al., 2018). Despite these shared mechanisms, significant differences exist between the two species in terms of seed size, nutrient content, and dormancy characteristics. These findings emphasize the need for a comprehensive framework encompassing both shared and species-specific regulatory systems governing seed germination in *B. napus* (Finch-Savage and Footitt 2017; Boter et al., 2019). The intricate interplay of exogenous factors, such as light, temperature, and soil moisture, with endogenous factors like plant hormones (GA, ABA, ethylene, and auxin) and endosperm breakdown, underscores the complexity of the seed germination process (Carrera-Castaño et al., 2020) (Fig. 1). Therefore, a deeper understanding of these interlinked internal and external influences is crucial for optimizing seed germination potential and ultimately, crop yields.

The delicate balance between two prominent and antagonistic phytohormones, such as GA and ABA, primarily dictates seed dormancy and germination (Zhou et al., 2015). While ABA suppresses germination by inhibiting radicle elongation, cell wall loosening, and the mobilization of stored proteins required for seedling establishment, GA counteracts these effects by promoting testa degradation and facilitating radicle emergence (Dekkers et al., 2016). The necessity of GA for seed germination is influenced by the ABA concentration within the seeds, as evidenced by the fact that GA-deficient mutants are able to germinate even when ABA is absent. High-dormancy genotypes exhibit greater ABA sensitivity, while germination in low-dormancy genotypes can occur even within the seed due to their inherent ABA insensitivity (Gulden et al., 2004). The concentration of ABA in seeds is regulated not only by the control of ABA biosynthesis but also by its conversion into phaseic acid, which results in ABA inactivation. This conversion is facilitated by ABA-8$'$ hydroxylases, which are P450 cytochromes encoded by the genes CYP707A1 and CYP707A2 (Kushiro et al., 2004). Several key regulatory proteins governing seed germination in *Arabidopsis* have been identified by integrating data from mutant studies and omics approaches (Bassel et al., 2011). For successful seed germination, downregulation of ABA signaling is crucial. This process involves the endoplasmic reticulum (ER)-localized bZIP17 protein translocating to the Golgi apparatus via membrane-anchored transcription factor peptidases like S1P (Site-1 Protease) and S2P. Subsequently, bZIP17 reaches the nucleus where it activates the transcription of anti-ABA signaling regulators (Zhou et al., 2015). The main pathway of ABA signaling relies on the PYR/PYL/RCAR-PP2C-SnRKs cascade (Tuan et al., 2018). In the absence of ABA, seed dormancy promoting SnRK2 proteins are inhibited by PP2Cs through dephosphorylation of their kinase activation loop (Ng et al., 2014). However, ABA binding to its receptors, PYR/PYL/RCAR, forms a complex with PP2C, hindering its phosphatase activity and thereby activating SnRK2s (Ng et al., 2014). These activated SnRK2s then stimulate the transcription of ABA-responsive genes through the activation of ABRE-binding protein/ABRE binding factor (AREB/ABF) transcription factors. Among AREB/ABFs, ABA insensitive 3, 4, and 5 (ABI3, ABI4, and ABI5) have been documented to trigger ABA-responsive gene expression, thus controlling seed dormancy (Nambara, and Marion-Poll, 2005). The ABI3 gene, in combination with the seed maturation genes LEAFY COTYLEDON 1 and 2 (LEC1/2) and FUSCA3 (FUS3), makes up the LAFL regulatory network, consisting of LEC1, ABI3, FUS3, and LEC2. ABI3 directly targets several genes, including ABI5, DELLAs, and the bHLH transcription factor PIL5 (PHYTOCHROME INTERACTING FACTOR-LIKE 5) (Tian et al., 2020). ABI 3, ABI5, and DELLAs collaboratively activate SOMNUS, which encodes a C3H zinc finger protein that regulates genes responsible for ABA synthesis and GA catabolism in imbibed seeds, leading to the suppression of germination (Lim et al., 2013). The ABI4 gene encodes a transcription factor of the APETALA2/ethylene response factor family TF that influences various processes by modulating gene expression, including that of ABA degradation genes such as CYP707A1 and CYP707A2 (Chandrasekaran et al., 2020). ABI5 encodes a bZIP transcription factor that binds to ABA Responsive Elements in promoters and interacts with ABI3 through its B1 domain. Additionally, the protein interacts with ABA binding proteins (AFPs), facilitating further protein interactions (Skubacz et al., 2016). In *Arabidopsis*, AFP2 acts as a negative regulator of primary seed dormancy by inhibiting the expression of DELAY OF GERMINATION 1 (DOG1), a key regulator of seed dormancy. The TF WRKY36 can interact with AFP2 to co-repress TOPLESS RELATED PROTEIN 2 and epigenetically silence DOG1 by

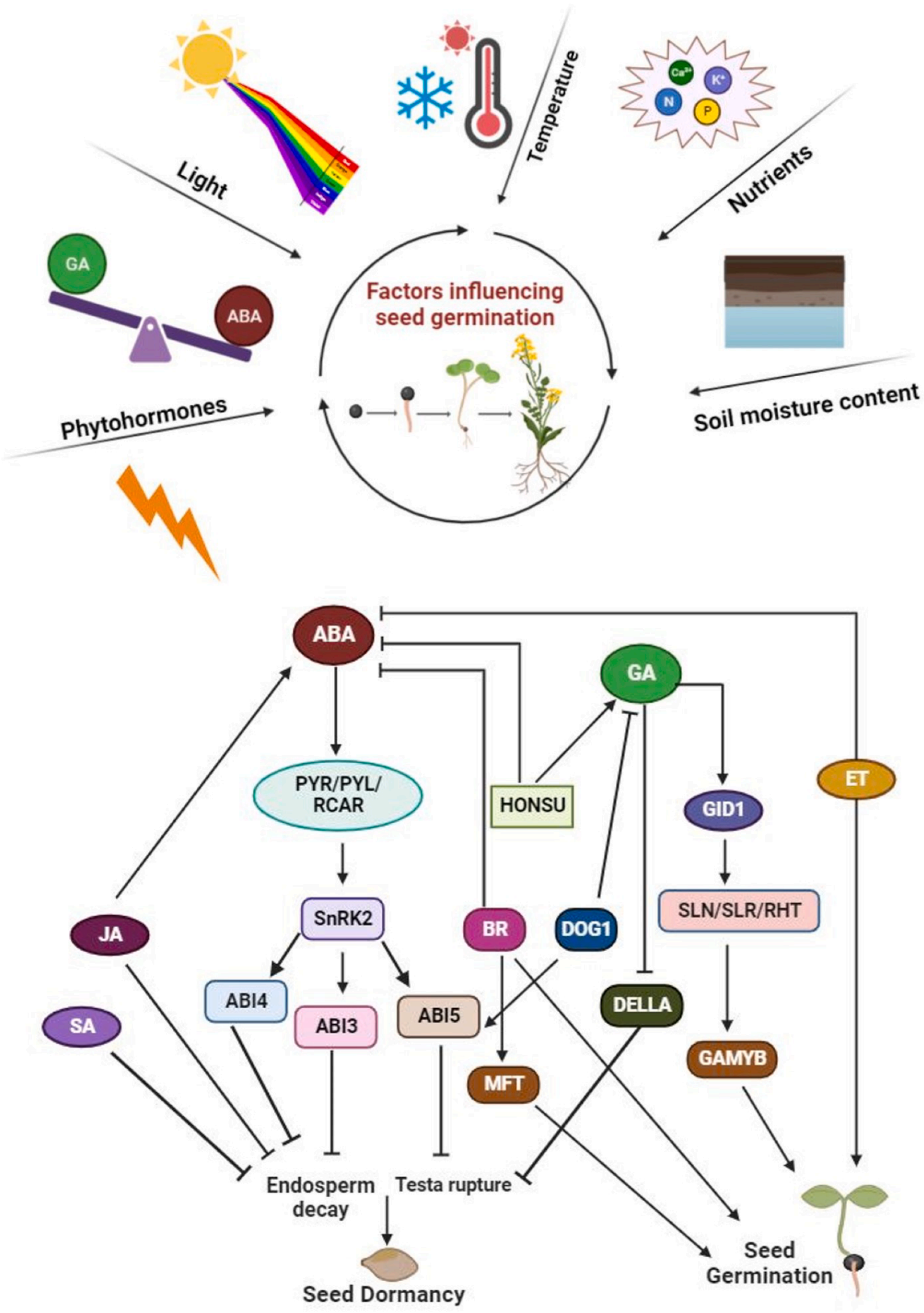

Fig. 1. The exogenous and endogenous driving factors of seed germination. a) The external factors influencing seed germination, which are the priming sources for the hormonal gene regulations. Seed germination is affected by different factors such as soil moisture content, nutrients, temperature, light and hormone contents and expression of their respective genes. b) A pathway of genes promoted by different phytohormones for seed germination and dormancy. Repressor of GA biosynthesis, delay of germination 1 (DOG1), activates ABI3 and ABI5 which prevent the testa rupture thereby lead to the dormancy.

decreasing histone acetylation (Deng et al., 2023). Finally, ABA signaling is terminated by the binding of PP2C proteins, namely ABI1 and ABI2, to the ABA receptors (Cutler et al., 2010). The dominant negative mutants *abi1-1* and *abi2-2* exhibit reduced seed dormancy due to impaired interaction between their mutated PP2C proteins and ABA receptors, confirming the negative role of ABI1 and ABI2 in this process (Zhou et al., 2015). Similarly, the PP2C gene, RD05 reportedly promotes seed germination in *Arabidopsis* by suppressing ABA signaling (Xiang et al., 2014). Another PP2C protein, HONSU, positively regulates GA signaling while downregulating ABA, thereby favoring seed germination (Kim et al., 2013). Table 1 summarizes key mutants studied in relation to seed dormancy and germination.

In *B. napus*, severe hormonal imbalances caused by crosstalk between ABA and auxin, along with downregulation of negative regulators *Bna.*

Table 1
List of various genes involved in the ABA/GA signaling regulation and their impact on seed dormancy and germination in *B. napus* and its closely related plants.

S. No	Gene name	Name of the protein encoded	Type of study	Dormancy level	Effect/type of interaction with ABA/GA signaling	References
1.	*ABI4*	ABA-INSENSITIVE 4	Mutant	Reduced	Positively regulates ABA by inhibiting the gene expression of ABA catabolic genes viz., CYP707A1 and CYP707A2	Shu et al., 2013
2.	*ABI4 and ABI5*	ABA-INSENSITIVE 4 and 5	Mutant	Reduced	Positively regulates ABA signaling and exhibit similar phenotypes with *ABI3* mutants	Finkelstein 1994
3.	*NCED*	9-*cis*-epoxycarotenoid dioxygenase	Mutant	Reduced	Positively regulates ABA biosynthesis and increases ABA levels in response to water deficit	Frey et al., 2012; Xu and Cai, 2017
4.	*GID1, GID2,* and *GID3*	GA INSENSITIVE DWARF	Mutant	Enhanced	Inability of GA to destroy DELLA proteins	Willige et al., 2007
5.	*CYP707A2*	Cytochrome P450	Mutant	Enhanced	ABA catabolic gene that reduces the levels of bioactive ABA	Matakiadis et al., 2009
6.	*WRKY41*	WRKY41 transcription factor	Mutant	Reduced	Directly regulates the transcription of *ABI3*	Ding et al., 2014
7.	*DOG1*	DELAY OF GERMINATION 1	Mutant	Reduced	Controls seed dormancy by temperature-dependent alteration of the GA metabolism	Graeber et al., 2014
8.	*SIZ1*	SUMO (small ubiquitin-related modifier) E3 ligase	Mutant	Enhanced	Regulates ABA signalling by inducing the expression of *ABI5*-dependent signaling genes such as *RD29A*, *Rd29B*, *AtEm6*, *RAB18* and *ADH1*	Miura et al., 2009
9.	*NF-YC3, NF-YC4 and NF-YC9*	NUCLEAR FACTOR Y C	Mutant	Reduced	Alters ABA and GA signaling	Liu et al., 2016
10.	*HONSU*	Protein phosphatase 2C (PP2C)	Mutant	Enhanced	A PP2C protein that inhibits ABA signaling	Kim et al., 2013
11.	*S2P*	Site-2 protease	Mutant	Enhanced	Antagonizes ABA signaling by controlling the activation of the membrane-associated transcription factor bZIP17	Zhou et al., 2015
12.	*RDO5*	Reduced dormancy 5 (Protein phosphatase 2C)	Mutant	Reduced	Positively regulates seed dormancy without influencing ABA or DOG1 but requires expression of the *APUM9* and *APUM11* genes that encode RNA binding proteins	Xiang et al., 2014
13.	*PIL5*	PHYTOCHROME INTERACTING FACTOR 3-LIKE 5	Overexpression	Enhanced	Inhibits seed germination by activating GA catabolic gene (*GA2ox2*) and repressing GA biosynthesis genes *GA3ox1* and *GA3ox2*	Chen et al., 2008
14.	*DAG1*	DOF AFFECTING GERMINATION 1	Mutant	Enhanced	Negatively regulates GA biosynthesis and acts downstream of *PIL5*	Oh et al., 2007
15.	*CHO1*	CHOTTO1, a putative double APETALA2 repeat transcription factor	Mutant	Reduced	Acts downstream of ABA to inhibit GA biosynthesis during seed germination	Gabriele et al., 2010
16.	*DDF1*	DWARF AND DELAYED LOWERING 1	Overexpression	Enhanced	Decreases the levels of bioactive GA	Yano et al., 2009
17.	*RAF10/RAF11*	MAP Kinase Kinase Kinases	Mutant	Reduced	Positively regulates the transcription of ABI3, *ABI5* and other ABA related genes	Magome et al., 2004
18.	*KYP/SUVH4*	Histone methyltransferase	Mutant	Enhanced	Negatively regulates ABA signaling by repressing the transcription of *DOG1* and *ABI3*	Lee et al., 2015
19.	*MYB96*	MYB DOMAIN PROTEIN 96 (transcription factor)	Mutant	Enhanced	Positively regulates the transcription of *ABI4* and some ABA biogenesis genes	Magome et al., 2004
20.	*FHY3* *FAR1*	FAR-RED ELONGATED HYPOCOTYL3, FAR-RED IMPAIRED RESPONSE1	Mutant	Reduced	Positive regulator of ABA signaling by directly activating the transcription of *ABI5*	Zheng et al., 2012
21.	*CSN1* *CSN5A*	COP9 Signalosome	Mutant	Enhanced	Represses the transcription of *RGL2* (repressor of *ga1-3* like 2) and *ABI5*	Tang et al., 2013
22.	*HY5*	bZIP transcription factor	Mutant	Reduced	Directly induces the transcription of *ABI5*	Jin et al., 2018
23.	*ELF3, PKL, LUX*	EARLY FLOWERING 3, PICKLE, LUX ARRHYTHMO	Mutant	Enhanced	Directly represses the transcription of *DOG1*	Zha et al., 2020

ARF10 and *Bna.GH3.5*, have been linked to disrupted seed germination and development (Nguyen et al., 2016). Interestingly, overexpression of the fatty acid desaturase 2 (FAD2) gene promotes hypocotyl elongation and seed germination, suggesting its potential as a downstream component of both GA and light signaling pathways, influencing various physiological traits (Wang et al., 2010). GDSL lipases, which are enzymes involved in seed development, lipid metabolism, stress response, and pathogen defense, also play a role in seed germination. Overexpression of *BnGDSL* in *B. napus* increased germination rate while decreasing oil content, highlighting its role in regulating both processes via transcriptional control (Ding et al., 2019). Recent studies have shown that the expression of Ca^{2+}-dependent RSH (CRSH) proteins during *B. napus* seed maturation leads to the accumulation of alarmones that inhibit plastid and nuclear DNA replication, ultimately preventing seed germination (Turkan et al., 2023). Desiccation plays a crucial role in regulating seed dormancy. During this stage, the expression of CRSH proteins remains low, creating a permissive environment for germination (Turkan et al., 2023). In contrast, seed maturation is characterized by high CRSH levels, leading to the accumulation of alarmones that inhibit DNA replication and prevent germination.

Gibberellic acid (GA) reigns as the principal phytohormone governing seed germination. Its biological activity, however, hinges on a delicate balance between its biosynthesis and inactivation (Vishal and Kumar, 2018). GA20ox and GA3ox enzymes catalyze reactions for GA production, while GA2ox controls its breakdown. Through the activation of GA-responsive genes, it induces cell-wall remodeling enzymes, facilitating embryo expansion and breaching the seed coat. The GA signaling cascade commences with the binding of bioactive GA to its receptor, GIBBERELLIN INSENSITIVE DWARF1 (GID1). This interaction triggers the degradation of DELLA proteins, potent repressors of seed germination via GA-GID1-DELLA complex formation. Further, F-box protein, $SCF^{SLY1/GID2}$ E3 ubiquitin ligase, interacts with the complex GA-GID1-DELLA, causing DELLA to degrade through the ubiquitin- 26S proteasome pathway (Murase et al., 2008). Following DELLA degradation, GAMYB, a downstream effector of GA signaling, becomes activated. This crucial protein orchestrates numerous downstream processes vital for germination (Ravindran et al., 2017). Interestingly, GAMYB also interacts with GATA family transcription factors, which positively regulate seed dormancy. Additionally, it is negatively regulated by KINASE ASSOCIATED WITH GAMYB1 (KGM), leading to the suppression of hydrolase genes in the aleurone layer, further contributing to dormancy control (Woodger et al., 2003). The pivotal role of GA in germination is underscored by gibberellic acid-deficient mutants like *ga1* and *ga2*. These mutants exhibit profound dormancy and can only germinate in the presence of externally applied GA (Zhang et al., 2020). DELLA proteins, critical antagonists in GA signaling, play a pivotal role in seed dormancy. Notably, mutations in two key DELLA genes, RGA-LIKE2 (RGL2) and SPINDLY (SPY), can bypass the non-germination phenotype of the *ga1* mutant, demonstrating their inhibitory effect on germination (Liu et al., 2013). Germination is influenced not solely by the GA response but also by the combined actions of GA and BR (brassinosteroids) signaling. In the BR signaling pathway, two essential basic helix-loop-helix transcription factors, BRASSINOSTEROID ENHANCED EXPRESSION 2 (BEE2) and BEE2 interacting with INCREASED LEAF INCLINATION 1 BINDING bHLH1 (HBI1) play a crucial role in controlling the process of endosperm rupture (Zhong et al., 2021). Moreover, BRI1-EMS-SUPPRESSOR 1 (BES1), which influences BR signaling, has been demonstrated to physically interact with ABI5, reducing its ability to bind to DNA. This interaction diminishes the ABA-mediated inhibition of seed germination by decreasing the expression of ABI5 target genes. Conversely, BIN2, an inhibitor of BR signaling, enhances ABA responses (Zhao et al., 2019).

Reports on the role of auxin in seed dormancy have also emerged, although the precise mechanisms remain unclear. Auxin's role in seed germination varies with concentration, having both stimulatory and inhibitory effects. High levels of auxin have been found to promote seed dormancy through the activation of ABI3, mediated by the AUXIN RESPONSE FACTOR 10 transcription factor and IAA8 (Liu et al., 2013; Hussain et al., 2020). This process results in increased ABI3 expression, although it does not involve direct binding to the ABI3 promoter. Studies on winter-type *B. napus* genotypes demonstrated that upregulation of auxin biosynthesis pathway genes and exogenous application of indole-3-acetic acid (IAA) increased the seed dormancy (Fei et al., 2009; Lui et al., 2020). Further analysis examining the upstream gene signaling pathways resulting in hormonal modifications may delineate the significant insights into the initiation and regulation of dormancy and germination (Zhong et al. 2021). Ethylene (ET) functions as a crucial antagonist of ABA, promoting seed germination and breaking dormancy. A mutant with a loss-of-function in the ethylene receptor ETHYLENE RESPONSE FACTOR 1 (ETR1), known as reduced dormancy 3, exhibited reduced seed dormancy. ETR1 normally represses ERF12, which forms a repressor complex with TOPLESS that binds to the DOG1 promoter, reducing DOG1 expression and thus seed dormancy (Li et al. 2019). Recently, Guo et al. (2023) reported that EIN2, a key player in ethylene signaling, can inhibit a histone H3 acetylase encoded by HOOKLESS 1 (HLS1) independently of the standard ethylene pathway, preventing the upregulation of ABA signaling genes ABI5 and ABI3, and thus promoting germination.

Mutations in the negative ET regulator Ctr1 (Constitutive Triple Response 1) lead to premature or accelerated germination, underscoring its role in suppressing ET signaling (Liu et al., 2013). Conversely, alterations in positive ET signaling components can induce extreme dormancy. This emphasizes the delicate balance between ET and ABA pathways in regulating seed fate. Secondary seed dormancy in *B. napus* is partly attributed to the ABA-dependent upregulation of the MFT (MOTHER OF FT and TFL1) gene. Interestingly, brassinosteroids (BRs) counteract ABA's dormancy-promoting effects partly via MFT regulation, creating an anti-ABA signaling feedback loop. This suggests a complex interplay between MFT, ABA, and BRs in controlling seed dormancy dynamics in *B. napus* (Holdsworth et al., 2008; Lei et al., 2020). The identification of DOG family genes has illuminated the genetic control of dormancy in various plant species (Greaber et al., 2014). In *Arabidopsis*, the DOG1 gene holds primary responsibility for both primary and secondary seed dormancy (Alonso-Blanco et al., 2003). Interestingly, DOG1 expression exhibits a dynamic pattern, peaking during seed maturation and reaching its minimum during ripening (Greaber et al., 2014). This regulation is further influenced by temperature sensitivity and enhanced ABA sensitivity. Higher levels of DOG1 protein accumulation, encoded by the gene, directly impede seed germination, and conversely, lower levels facilitate it (Greaber et al., 2014). Three copies of DOG1 genes were observed in *B. napus* (Née et al., 2015), and their transcript and protein expression were elevated after the induction of secondary dormancy, suggesting functional similarity between *Arabidopsis* and *B. napus* (Née et al., 2015). Two other genes responsible for inducing dormancy in seeds (the *MFT* gene) and for regulating germination (*TFL1*) have been identified in wheat and *Arabidopsis* (Lui et al., 2020). Genes homologous to *MFT* and *TFL1* have been identified in *B. napus* and referred to as *BnaMFTs*. Induction of secondary dormancy using polyethylene glycol resulted in 3.5- fold increased transcripts of *BnaMFTs* (Lui et al., 2020).

3. Imprinted genes modulate seed dormancy and germination through regulating seed development

Among the different genetic factors, the expression of maternally imprinted genes and/or paternally imprinted genes in endosperm of developing seeds play a role in seed dormancy and germination traits. Interestingly, genomic imprinting reveals high plasticity within and between species indicating the biological significance of imprinted genes rarely conserved among closely related species. There were efforts to identify genomic imprinting in *B. napus*, which results in parent-of-origin specific differential expression of maternally and paternally inherited alleles (Feng et al., 2009). Recently, 297 imprinted genes, including 283 maternal expressed genes (MEGs) and 14 paternal expressed genes (PEGs) were identified in endosperm at 20 and 25 days after pollination (DAP) through transcriptome analysis (Rong et al., 2021). Interestingly, the imprinted genes were found to be enriched with transposable elements which might enable rapid molecular evolution and preferential expression in endosperms (Yoshida et al., 2018). The clustering of imprinted genes indicates their genome-wide distribution in rapeseed (Liu et al., 2018). Moreover, 11 genes comprised of MEGs (7) and PEGs (4) were observed with differentially methylated regions. Most imprinting in plants occurs in endosperm, therefore, it can be reasoned that endosperm can influence the embryogenesis and seed maturation, thereby influencing the seed dormancy as well as germination efficiencies. Seed coat and its chemical constituents (e.g. flavonoids) known to alter the dormancy levels and germination process. A study comparing the permeability of yellow seed-coated (low in flavonoids and thinner seed coat) and black seed coated (high in flavonoids) rape seed cultivars revealed substantial difference between seed coat of YS and BS, which could affect their germination status (Xuan et al., 2015). Another study dealing with epigenetic regulation of the yellow and black seeded characteristics of *B. napus* identified extensive methylation changes, responsible for seed-coat variation (Wang et al., 2016). In particular, 10 % of demethylation and 5 % of hypermethylation were detected in yellow rapeseeds compared with black rapeseeds. In fact, two and 13 unique flavonol derivatives were detected in black seeded and yellow seeded rapeseeds. The transcript expression analyses further confirmed that expression of common phenylpropanoid biosynthetic genes (*BnPAL* and *BnC4H*), common flavonoid biosynthetic genes (*BnTT4* and *BnTT6*), anthocyanin and proanthocyandin specific genes (*BnTT3* and *BnTT18*), proanthocyandin specific genes (*BnTT12*, *BnTT10*, and *BnUGT2*) and three transcription factor genes (*BnTTG1*, *BnTTG2*, and *BnTT8*) that function in the flavonoid biosynthetic pathway were significantly different between yellow and black seeds (Qu et al., 2013). Altogether, it is clear that the inherent dormancy and germination potential constituted by genomic elements of seeds, in concert with physiological and agronomic factors, determine the seedling adaptability and sustainability.

4. Environmental signals transduced through phytohormones determine seed dormancy levels and their germination efficiencies

Environmental factors like sunlight, temperature, nutrients, and soil water content profoundly influence seed germination by modulating the crucial signaling and metabolic pathways of GA and ABA (Holdsworth et al., 2008). Extensive research in *B. napus* has identified a network of regulatory genes involved in various stages of germination, encompassing protein biosynthesis, degradation of storage reserves, water transport, cell elongation, oxidative stress response, the ubiquitin system, and the secretory pathway (Ge et al., 2013). Aquaporins (AQPs) play a critical role in water movement across cell membranes during seed imbibition and early embryo growth (Wang et al., 2014). Supporting this, studies have shown that ten AQP genes upregulated during germination and in young *B. napus* seedlings (Barrero et al., 2010). Light acts as a crucial regulator of numerous plant processes, including photomorphogenesis, phototropism, and flowering, and it also serves as a key determinant of seed germination and dormancy (Lymperopoulos et al., 2018; Saleem et al., 2020). Cryptochromes (CRYs) and phototropins act as photosensory receptors sensitive to blue light (320–500 nm), which has been linked to the inhibition of seed germination (Fig. 2) (Farooq et al., 2022). Through CRY1 (cryptochrome circadian regulator 1), the blue light receptor, blue light stimulates the expression of NCED1 (9-CIS-EPOXYCAROTENOID DIOXYGENASE 1), leading to elevated ABA levels and ultimately inhibiting seed germination (Tuan et al. 2019). Similar findings have been observed in wheat, where blue light upregulates ABA biosynthesis genes and downregulates ABA catabolism genes, preventing germination (Saleem et al., 2020; Yang et al., 2020). In contrast to blue light's inhibitory effect, the initial stages of seed germination are often triggered by phytochromes like PhyB. Furthermore, PhyA mediates the very low fluence response (VLFR) to UV-A-FR light spectra and the R/FR high irradiance response (R/FR-HIR) to accelerate germination when active PhyB is absent (De Wit et al., 2016). Red light, in contrast to far-red light which can exhibit negative effects, has been shown to promote seed germination in various studies (Wang et al., 2012).

Temperature deviations from the optimal range (15–30 °C) can drastically impede seed germination through various mechanisms (Carruggio et al., 2021). Excessively high or low temperatures can suppress seed viability, induce thermo-inhibition, or trigger thermodormancy, effectively halting the germination process. High temperatures pose a particular threat to seed development by promoting the detrimental reactive oxygen species (ROS) accumulation via lipid peroxidation. This oxidative stress damages crucial cellular components like cell walls, membranes, organelles, and mitochondria, ultimately leading to endosperm decay (Braybrook et al., 2006). FUS3, a gene regulatory protein, plays a pivotal role in modulating the ABA/GA ratio under high temperatures. It negatively regulates GA biosynthesis while enhancing ABA production during post-embryonic development, further contributing to thermodormancy and germination inhibition (Malek et al., 2022). Studies in *B. napus* have investigated the impact of high-temperature stress (HTS) on triggering thermo-dormancy and thermo-inhibition, as well as the potential of hydropriming as a mitigating strategy. These experiments successfully demonstrated hydropriming's ability to improve germination rates under HTS conditions (Née et al., 2015). While exogenous GA application has shown some success in reducing thermodormancy, it can paradoxically lead to increased seed death and compromised germination in certain *B. napus* cultivars. Therefore, soil moisture content-mediated priming emerges as a more promising approach for enhancing germination under HTS, albeit with potential trade-offs for seed longevity (Née et al., 2015).

Low temperatures exert a powerful influence on seed dormancy by promoting the accumulation of DOG1 (DELAY OF GERMINATION 1) transcripts (Farooq et al., 2022). This gene plays a crucial role in prolonging dormancy, acting within the zygotic tissues of the embryo rather than the surrounding seed coat. Intriguingly, BnaDOG1 transcript levels have been shown to increase specifically during secondary dormancy in *B. napus*, highlighting its involvement in this complex dormancy mechanism (Xia et al., 2018). Endosperm decay, a critical step in seed germination, unfolds in three distinct phases (Sachet et al., 2016). Phase I involves imbibition, where the seed absorbs water rapidly while maintaining its original size and shape. Phase II marks the initiation of testa rupture at the micropylar end surrounding the radicle, and Phase III culminates in the rupture of the endosperm and the emergence of the radicle. This coordinated process provides the seedling with essential nutrients and space for initial growth. One of the key prerequisites for successful germination lies in the breakdown of the endosperm cell wall. This task is primarily accomplished by cell-wall-remodeling enzymes (CWREs) such as expansins and xyloglucan *endo*-transglucosylases (Lee

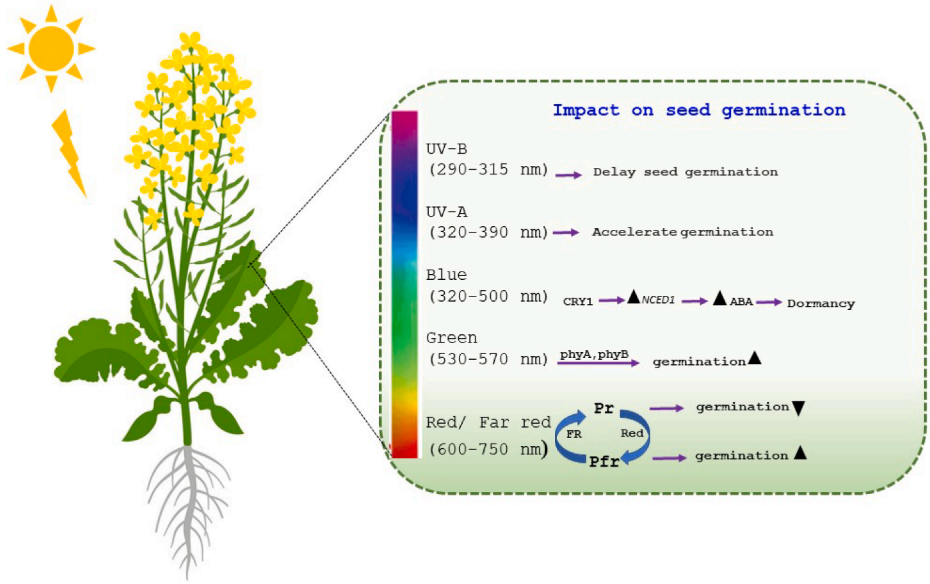

Fig. 2. Schematic representation of potential impact of light at different wavelengths during seed germination sourced from literature in different crops. Pr and Pfr represent inactive and active phytochromes.

et al., 2015). Gibberellic acid (GA) acts as a vital orchestrator in this process, promoting the expression and activity of CWREs. Conversely, abscisic acid (ABA) plays an antagonistic role, suppressing the loosening of the endosperm and hindering germination. Interestingly, studies have shown that at 24 °C, DOG1 specifically targets expansin 2 (EXPA2), expansin 9 (EXPA9), and *xyloglucan endo-transglucosylase 19* (XTH19) genes, key CWREs involved in endosperm breakdown (Sachet et al., 2016; Farooq et al., 2022). This inhibition occurs through DOG1′s differential regulation of GA biosynthesis genes, highlighting its multifaceted role in controlling germination. Hence, achieving the exact balance between GA and ABA signaling becomes crucial for successful seed germination and seedling emergence.

5. Other factors influencing the seed dormancy

Seed dormancy in canola is under the influence of various factors, *viz*., genetic factors as described previously, physiological, and agronomic factors (Fig. 3). (See Fig. 4).

5.1. Agronomic factors of seed dormancy: Secondary dormancy

5.1.1. Seed storage after harvesting

Environmental factors, particularly storage duration and temperature, significantly influence the development and intensity of secondary dormancy in *B. napus* (Gulden et al., 2003; Nguyen et al., 2015). Interestingly, even at extremely low temperatures like −70 °C, seed dormancy can be maintained, highlighting its remarkable resilience (Gulden et al., 2004). Cold storage at varying temperatures over extended periods can effectively preserve the degree of secondary dormancy (Momoh et al., 2002). Studies by Vail and Headley (2018) further revealed that temperature cycling between 25 °C and 45 °C induced the most significant changes in dormancy, particularly in spring *B. napus* genotypes. These findings underscore the importance of considering pre-screening seed storage conditions and potential temperature fluctuations to avoid erroneous interpretation of secondary dormancy levels during subsequent assessments.

5.1.2. Seedbank addition

Seed losses during canola harvest represent a primary pathway for seed contamination and seed bank establishment in previously uninfested fields (Gulden et al., 2003). These losses often occur in two critical phases: first, during seed maturation when fragile pods are susceptible to breakage and seed dispersal, and second, during harvest when seeds escape the combine harvester (Haile and Shirtliffe, 2014). Estimates suggest that losses can reach 5.8 % of the total yield, significantly contributing to seedbank additions. Interestingly, researchers observed variations in dormancy levels among seeds collected at different stages. Seeds harvested before full maturity exhibited higher primary dormancy, while those collected at maturity displayed stronger secondary dormancy (Gulden et al., 2003). This finding reveals the potential mechanism for enhanced resilience of seeds that are lost at various stages of harvest. Reducing seed losses and minimizing their influence on seedbank establishment requires a multifaceted approach. As Raman et al. (2014) pointed out, incorporating pod-shattering tolerant cultivars and implementing appropriate farm management practices can significantly reduce harvest losses and contribute to sustainable canola production.

5.1.3. Tillage regime

Tillage timing and depth can play crucial roles in managing volunteer *B. napus* populations. Delaying tillage practices until after volunteer emergence can significantly reduce their numbers (Gruber et al., 2005). Additionally, increasing tillage depth to 15 or 25 cm can effectively bury volunteer seeds deeper, further limiting their emergence and survival. Huang et al. (2018) highlight the importance of considering both tillage timing and seed burial depth when managing volunteer populations. Tillage conducted after the autumn season, compared to earlier timings, can significantly reduce seed persistence in the soil seed bank. The optimal tillage regime for managing volunteer *B. napus* depends on several factors, including climatic conditions and the specific growth

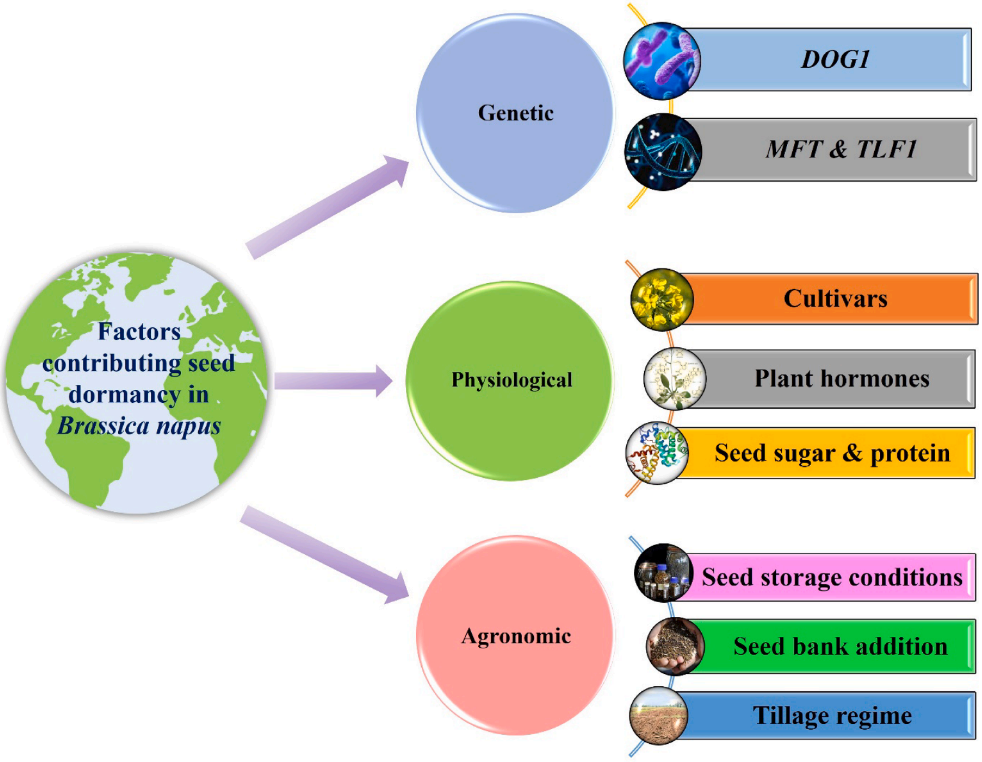

Fig. 3. An overview of the factors contributing to seed dormancy in *Brassica napus* L.

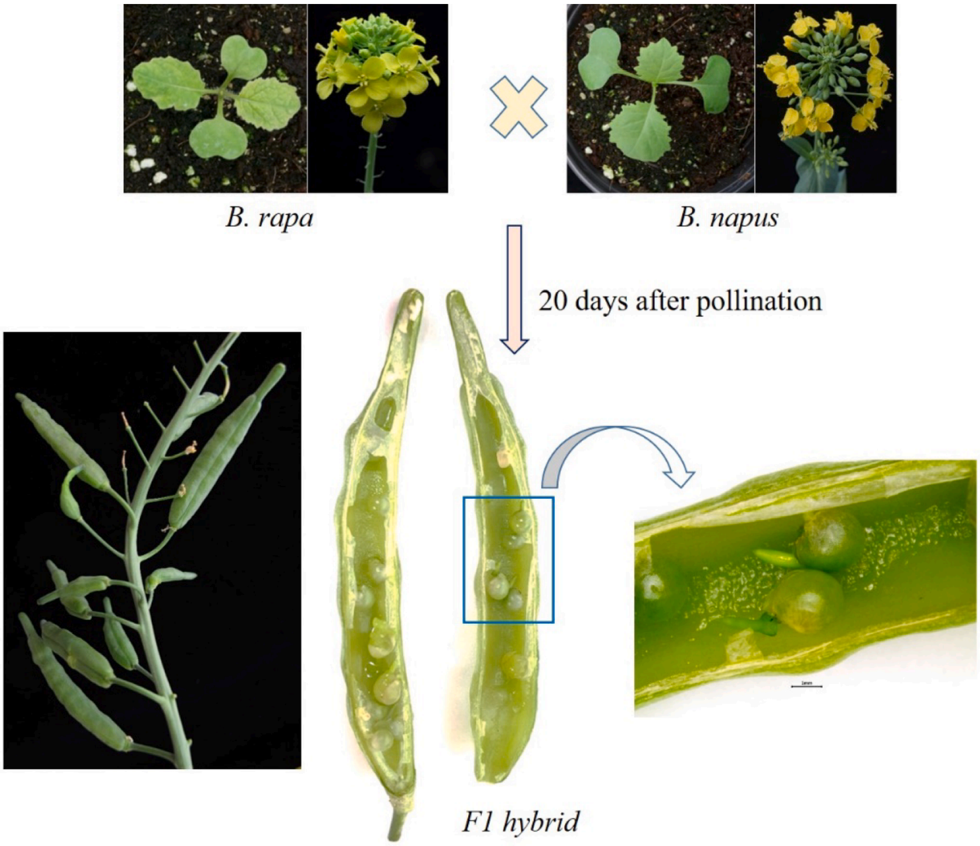

Fig. 4. Precocious germination in the interspecific hybrids of *B. rapa* and *B. napus.* The F1 hybrids between *B. rapa* and *B. napus* was found to have preharvest sprouts after 20 days after pollination.

patterns of the crop variety being planted (2017). Based on these factors, tillage strategies can be tailored to mitigate soil disturbance and conserve significant resources, all while helping in the efficient management of volunteer populations.

5.2. *Physiological factors of seed dormancy: (Physiological dormancy)*

5.2.1. *Physiological changes during winter and spring*

Physiological factors, particularly differences in growth types, influence seed dormancy potential in *B. napus*. Spring varieties generally exhibit higher dormancy potential compared to winter types (Momoh et al., 2002). This enhanced dormancy in spring genotypes serves as a protective mechanism to prevent premature germination in the fall, which could potentially lead to frost damage. In contrast, winter genotypes possess the ability to germinate during the fall period to experience vernalization, a chilling requirement for subsequent flowering in the spring. Consequently, winter type varieties exhibit a greater sensitivity to environmental cues that regulate dormancy break and timing of flowering (Momoh et al., 2002).

5.2.2. *Seed sugar, protein and metabolites*

Sugars and proteins are two crucial components of seeds, playing distinct roles in germination and seedling establishment. Glucose acts as a germination inhibitor by influencing ABA signaling pathways, while seed storage proteins contribute to seedling vigor, dormancy, and seed longevity (Dekkers et al., 2004). Cruciferin and napin are the primary seed storage proteins in *B. napus*, with their relative proportions determined by both genetic and environmental factors. Previous research suggests an inverse relationship between cruciferin and napin content, with napin levels potentially decreasing indirectly due to the selection for low-glucosinolate varieties (Schatzki et al., 2014). If this negative correlation holds true across all *B. napus* species, modern spring-type low-glucosinolate varieties might be predicted to exhibit higher dormancy levels. However, further studies are necessary to fully explore this association and its underlying mechanisms (Baskin and Baskin, 1998; Schatzki et al., 2014).

Among the several chemical constituents of seed coats/seeds, flavonoids were known to be associated with seed dormancy. In particular, proanthocyanidins (PA) which accumulate during early embroyogenesis until seed maturation, play a crucial role in reinforcing the seed-coat-imposed dormancy. Previous studies suggest that PAs and their precursors inhibit germination by acting as structural barriers and as biochemical inhibitors of GA metabolism. A study investigating flavonoid profiles in yellow-coated and black-coated rapeseeds found that the flavonoid biosynthetic genes, anthocyanin and proanthocyanidin specific genes, as well as regulators in the flavonoid synthetic pathway were relatively repressed in yellow seeds (Chen et al., 2023). In fact, later, it was found that *BnTT8* mutation suppressed the expression of phenylpropanoid and flavonoid biosynthetic genes, inhibited proanthocyanidin accumulation in rape seed coats (Zhai et al., 2020). Also, a total of 35 flavonols were identified in the seed coat of *B. napus* (Qu et al., 2013). The predominant flavonols are kaempferol derivatives, quercetin derivatives, isorhamnetin derivatives, and epicatechin glucosides. However, the role of flavonols in seed dormancy and germination in rapeseeds has yet to be identified.

6. Precocious germination/vivipary is correlated with seed dormancy?

Precocious germination, also referred to as premature germination, pre-harvest sprouting, or vivipary, describes seed germination within the maternal plant during its maturation phase. To prevent premature germination, primary dormancy is a prevalent mechanism in maturing *B. napus* seeds, although it diminishes significantly in mature seeds (Feng et al., 2009). However, in certain genotypes and under specific environmental conditions, this dormancy can be insufficient, leading to seed germination on the mother plant and potential yield losses. Premature germination is also a quantitative trait influenced by the interplay of genetics, environment, and their interactions (Ren and Bewely, 1998). Excessive moisture and humidity are environmental factors known to promote higher rates of precocious germination (Feng et al., 2009). Additionally, prematurely germinated seeds typically exhibit lower abscisic acid (ABA) concentrations and altered osmotic potential (Johnson-Flanagan et al., 1991). Another significant environmental factor promoting premature germination is heat stress (Brunel-Muguet et al., 2015). This phenomenon likely arises from a decline in the ABA: GA ratio, leading to reduced primary dormancy and increased germination potential (Fahad et al., 2017). While rare in mature *B. napus* seeds, premature germination may become more frequent if secondary dormancy is compromised, as both primary and secondary dormancy may share similar physiological mechanisms (Feng et al., 2009). Mácová et al., (2022) have found the cultivar-specific premature germination and ABA level reductions in different *B. napus* cultivars, thus indicating the role of genome composition among others. Premature germination and lower ABA levels in heat stress indicate that seeds did not progress into the dormancy phase but continued directly to germination. Interestingly, the interspecific hybridization between *B. napus* and *B. rapa* often exhibits the phenotypic expression of vivipary (Sohn et al. 2022a; Sohn et al. 2022b). Sohn et al. (2022b) observed a higher rate of premature germination in F1 hybrids arising out of *B. rapa* (maternal) and *B. napus* (paternal) crosses (Fig. 3). However, the reverse crossing between them (*B. napus* being maternal parent) do not show vivipary, possibly suggesting the importance of maternal or paternal excess genomes/ploidy levels and also the role of imprinted genes from either parents. However, the precise molecular basis of vivipary except for hormone imbalance in *B. napus,* is unknown. There was a previous attempt to identify QTLs responsible for vivipary in rapeseed (Feng et al., 2009). They found at least five putative QTLs which were designated as qPHS-2-a, qPHS-2-b, qPHS-2-c, qPHS-2-d and qPHS-7, located in the vicinity of A3G12700, A13C1500, P3C4180 and T2G13420 on LG2 (N11) and P1G8300 on LG7 (N3) rapeseed genome. The accumulated contribution of these five QTLs explained 75.63 % of the phenotypic variance, and individual QTL explained 4.11–50.78 % of the phenotypic variance. Genetic markers are associated with better seed longevity and vigor could lead to the development of targeted agronomic strategies, such as optimized storage conditions or specific treatments during seed maturation that can help to minimize the premature germination.

7. Conclusion and future perspectives

To date, significant progress has been made in elucidating the molecular pathways regulating ABA/GA balance and driving seed dormancy-to-germination transitions in model plant, Arabidopsis. However, research reports on seed germination mechanisms in *B. napus* is only emerging and it is clear that several QTLs in concert with external and internal cues participating in seed-related traits, including dormancy and germination. Therefore, comprehensive molecular investigations are essential to elucidate the complex dormancy behaviors in *B. napus*, influenced by various physiochemical factors. Harnessing genetic factors that contribute to sufficient seed vigor can further enhance yield and stability. Genome-wide association studies (GWAS) can identify QTLs and candidate genes associated with seed germination, facilitating gene introgression to expand the genetic and molecular foundation for rapeseed breeding. To unravel the intricate molecular mechanisms underlying seed dormancy and germination, emerging breeding approaches like genomic selection (GS), speed breeding, and Multi-parent advanced generation intercross (MAGIC) populations should be integrated. Additionally, exploring the role of epigenetic factors in *B. napus* seed dormancy and germination is crucial for a comprehensive understanding of these complex traits. The preharvest sprouting in some of the intersepcific hybrids in rapeseed open up new avenues in research where parental genome conflict theory takes centre place, thus indicating the importance of future studies revolving around the identification of biological significance of materal and paternal imprinted genes or the importance of maternal- or paternal-excess genome contribution towards seed development as it provides the cues for dormancy levels and germiantion pontentials. Similar to primary dormancy, secondary dormancy in rape seeds also play a role in environmental adaptation and seedling vigor. Secondary dormancy is also a result of complex interactive responses among the genome, environment, and agronomic practices. However, considering the fair amount of success achieved with exogenous application of dormancy-breaking substances or treatment that remove the seed-coat imposed dormancy or precise envirnomental monitoring measures, secondary dormancy can be fairly manipulated to meet the requirements. Therefore it is important for future farming practices should consider the temporal and geographic dimensions of environmental sensing, along with the distinct functions and detection mechanisms of environmental factors throughout seed development, storage, and germination. Furthermore, integrating genetic, physiological, and multi-omics data with cutting-edge advancements like artificial intelligence (AI) – machine learning (ML) will speed up the identification of precise molecular basis of these key traits. This significant combination holds the potential to uncover personalized seed treatments tailored to impute specific hormonal needs, biosensors for monitoring hormonal dynamisms, CRISPR mediated gene editing for altering the dormancy related genes for on-demand hormone biosynthesis, and smart agriculture systems for optimizing the success frequency of germination and manage dormancy at scale. These advancements can empower farmers with data-driven insights to improve decision making and eventually enhance agricultural productivity and future food security.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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