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Cold Influences Male Reproductive Development in Plants: A Hazard to Fertility, but a Window for Evolution

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Being sessile organisms, plants suffer from various abiotic stresses including low temperature. In particular, male reproductive development of plants is extremely sensitive to cold which may dramatically reduce viable pollen shed and plant fertility. Cold stress disrupts stamen development and prominently interferes with the tapetum, with the stress-responsive hormones ABA and gibberellic acid being greatly involved. In particular, low temperature stress delays and/or inhibits programmed cell death of the tapetal cells which consequently damages pollen development and causes male sterility. On the other hand, studies in Arabidopsis and crops have revealed that ectopically decreased temperature has an impact on recombination and cytokinesis during meiotic cell division, implying a putative role for temperature in manipulating plant genomic diversity and architecture during the evolution of plants. Here, we review the current understanding of the physiological impact of cold stress on the main male reproductive development processes including tapetum development, male meiosis and gametogenesis. Moreover, we provide insights into the genetic factors and signaling pathways that are involved, with putative mechanisms being discussed.

Keywords: Cold stress • Meiotic cytokinesis • Meiotic recombination • Phytohormone • Pollen development • Tapetum.

Introduction

Seed plants sexually reproduce through development of sex organs that host the precursor cells engaging in the production of the male and female gametes. After differentiation of stamen tissues, pollen mother cells (PMCs) in locules of developing anthers produce daughter cells with halved chromosome sets through meiosis; afterwards, the haploid microspores undergo a series of physiological activities including mitotic division and pollen wall formation to develop into mature pollen grains for fertilization (Wilson and Yang 2004). Formation of viable haploid gametes is essential for the constancy of the genome ploidy level over generations and the fertility of seed plants. However, cold stress has a great impact on male reproductive development (De Storme and Geelen 2014) and dramatically reduces crop yield (e.g. 20–30% yield reduction in rice) (Ghadirnezhad and Fallah 2014). To understand the mechanism controlling male reproductive development in response to cold stress is pivotal for agriculture/economic safety and the breeding of cold-tolerant cultivars. In this review, we first briefly introduce the key signaling pathways involved in cold perception and response of plants. Thereafter we outline the impact of low temperature stress on the main male reproductive development processes including tapetum development, male meiosis and gametogenesis. Moreover, we provide insights into the latest understanding of the underpinning genetic mechanisms.

Molecular Mechanisms Controlling Cold Sensitivity and Response of Plants

A myriad of changes are triggered upon cold stress, all to engage in repair of damaged cell structures or to adapt cells to avoid future damage. Many of these changes relate to direct alteration of the cell structure components such as membrane composition and trafficking, or the structure of the cytoskeleton, dependent on an arsenal of enzymes present at the moment when damage is inflicted (Ruelland et al. 2009, Miura and Furumoto 2013). On the other hand, plants have developed complex genetic mechanisms for responding to cold stress through reprogramming gene expression (Barrero-Gil and Salinas 2017, Shi et al. 2018).

The pathway dependent on C-repeat binding factors/dehydration-responsive element-binding proteins (CBFs/DREBs) is considered a master cold signaling pathway that plays a major role in cold tolerance of plants (Thomashow 2010, Zhou et al. 2011, Shi et al. 2018). In Arabidopsis, there are three cold-inducible *CBF* genes, i.e. *CBF1*, 2 and 3, also referred to as *DREB1b*, *DREB1c* and *DREB1a*, respectively (Stockinger et al. 1997, Gilmour et al. 1998, Liu et al. 1998). The CBF proteins are transcription regulators that, together with the binding site CRT/DRE present in the promoter region of their targets, are conserved in different plant species (Gilmour et al. 1998, Jaglo et al. 2001). They form a self-regulatory module whereby CBF2 negatively regulates the expression of *CBF1* and 3 (Novillo et al.

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2004). Cold-induced expression of *CBF* activates downstream cold-responsive (COR) genes to enhance cold tolerance of plants, and ectopically activated CBF can induce COR gene expression under normal temperature conditions (Jaglo-Ottosen et al. 1998). The CBF–COR module is activated by an upstream helix–loop–helix transcription factor, Inducer of CBF Expression 1 (ICE1), a MYC-like protein that binds specifically to the MYC recognition sequences in the promoter region of *CBF* genes (Chinnusamy et al. 2003). The expression of ICE1 is cold insensitive; its function, however, relies on its phosphorylation status (Chinnusamy et al. 2003, H. Li et al. 2017, Zhao et al. 2017). In Arabidopsis, a Ser/Thr protein kinase Open Stomata 1 (OST1) phosphorylates ICE1, and stabilizes it by disrupting its interaction with HOS1, an E3 ligase that mediates the degradation of ICE1 via the 26S–proteasome pathway (Dong et al. 2006, Ding et al. 2015). The mRNA of both *CBF1* and *ICE1* is present in floral tissues (Chinnusamy et al. 2003, Sakata et al. 2014, Liu et al. 2018). Members of the *CBF* gene family positively control cold tolerance of pollen development by acting downstream of a transcription module comprised of cold-inducible MADS Intervening Keratin-Like and C-Terminal* (MIKC*) proteins and the group I WRKY transcription factor WRKY34 (see below for details). These suggest that CBF signaling plays a role in cold tolerance of male reproductive development.

Another important cold signaling pathway is the mitogen-activated protein kinase (MAPK) cascade that is activated by low temperature and acts upstream of CBF signaling (Mizoguchi et al. 1996, Ichimura et al. 2000, Liu and Zhou 2018). At low temperature, the plasma membrane stiffens, which activates Ca^{2+}-permeable, mechanosensitive channels and this causes a rapid increase in cytosolic Ca^{2+} and MAPKKK protein MEKK1 phosphorylation through Ca^{2+}/calmodulin-dependent kinase 1 (CRLK1) (Furuya et al. 2013, Furuya et al. 2014). Afterwards, activated MEKK1 phosphorylates MKK2 that in turn activates MPK4 and MPK6 which subsequently induces the cold response (Teige et al. 2004, Furuya et al. 2013). It is suggested that MPK4 may regulate cold tolerance by modulating ethylene biosynthesis (Zhao et al. 2013). In Arabidopsis, MKK4/5–MPK3/6 phosphorylates ICE1 and promotes its degradation to reduce the expression of CBFs, suggesting a negative role for MKK4/5–MPK3/6 in the cold response. The MEKK1–MKK2–MPK4 pathway has been found to suppress the inhibitory effect of the MKK4/5–MPK3/6 module constitutively and confers plants with cold tolerance (Zhao et al. 2017). In rice, however, OsMPK3 stabilizes OsICE1/OsbHLH002 using a similar mechanism to OST1, and positively contributes to enhanced cold tolerance (Zhang et al. 2017), suggesting that the mode of action of the MAPK factors in responding to cold may differ among plant species.

At the third level, cold-responsive phytohormones, e.g. (GA) gibberellic acid, ABA and brassinosteroid (BR), participate in cold signaling (Krishna 2003, Colebrook et al. 2014, Shi and Yang 2014, Eremina et al. 2016). GA and ABA are the prevailing hormones in the response of male reproductive development to a decrease in temperature. In both Arabidopsis and crops, the effect of cold stress on stamen development, pollen maturation and male fertility is often associated with alterations in GA and ABA signaling (Oliver et al. 2007, Baron et al. 2012, Sakata et al. 2014, Liu et al. 2018). Whether and how the CBF, MAPK and hormone-dependent signaling coordinately regulate the cold response is an important topic currently under investigation. Here we focus on what is known about the signaling mechanisms that take place during male reproductive development in plants.

Cold Stress Disrupts Tapetum Development

The male reproductive organs, or stamens, consist of a filament bearing the anther at the top end in which the microsporocytes give rise to male gametes. For anther development we refer to excellent reviews (McCormick 2004, Scott et al. 2004, Wilson and Yang 2004). Tapetum surrounds and nurses the developing meiocytes and/or microspores by supplying nutrition and enzymes required for microsporogenesis and pollen development. Degeneration of tapetum through programmed cell death (PCD) is crucial for pollen development, and is particularly important for pollen wall formation (Li et al. 2006b, Niu et al. 2013). In Arabidopsis, Dysfunctional Tapetum 1 (DYT1), Defective in Tapetal Development and Function 1 (TDF1), Aborted Microspore (AMS), Male Sterility 188 (MS188) and Male Sterility 1 (MS1) constitute a signaling pathway playing a central role in controlling tapetum development (D.D. Li et al. 2017). *DYT1* and *TDF1*, respectively, encode a basich helix–loop–helix (bHLH) and a R2R3 MYB transcription factor that regulate early tapetum development. The R2R3 MYB transcription protein MS188 and PHD-finger protein MS1 are involved in later stages including tapetum PCD and pollen exine formation (Vizcay-Barrena and Wilson 2006, Zhang et al. 2006, Yang et al. 2007, Zhu et al. 2008, Gu et al. 2014, Lou et al. 2014, Lou et al. 2017). The bHLH transcription factor AMS regulates both early and late pollen development by competitively binding to other bHLH proteins that are interacting partners of DYT1. The sequestering of DYT1-binding factors suppresses DYT1-mediated transcription regulation and AMS is negatively regulated by MS1 (Ferguson et al. 2017). These interactions form multiple feedback loops to ensure proper protein dynamics and tapetum development.

Cold stress predominantly affects the functioning tapetum in the anther (**Fig. 1**), and the transition from tetrads to young microspores is believed to be most cold sensitive (Oliver et al. 2005). Cold disrupts induces PCD-based degeneration of the tapetal cells, leading to vacuolization and hypertrophy of the tapetum (Mamun et al. 2006, Gothandam et al. 2007, Oda et al. 2010). The 'surviving' tapetum shows irregular organization of the endoplasmic reticulum (ER), with the formation of ER bodies, both of which may affect secretion and the release of chemicals or enzymes that interfere with progression of microsporogenesis (Gothandam et al. 2007, Li et al. 2012). The cold-inducible receptor-like kinase Thermo-Sensitive Genic Male Sterile10 (TMS10) and its homolog TMS10-Like (TMS10L) were recently found to play a redundant role in rice tapetum development under low temperature (Yu et al. 2017a), but the mechanism involved is unclear.

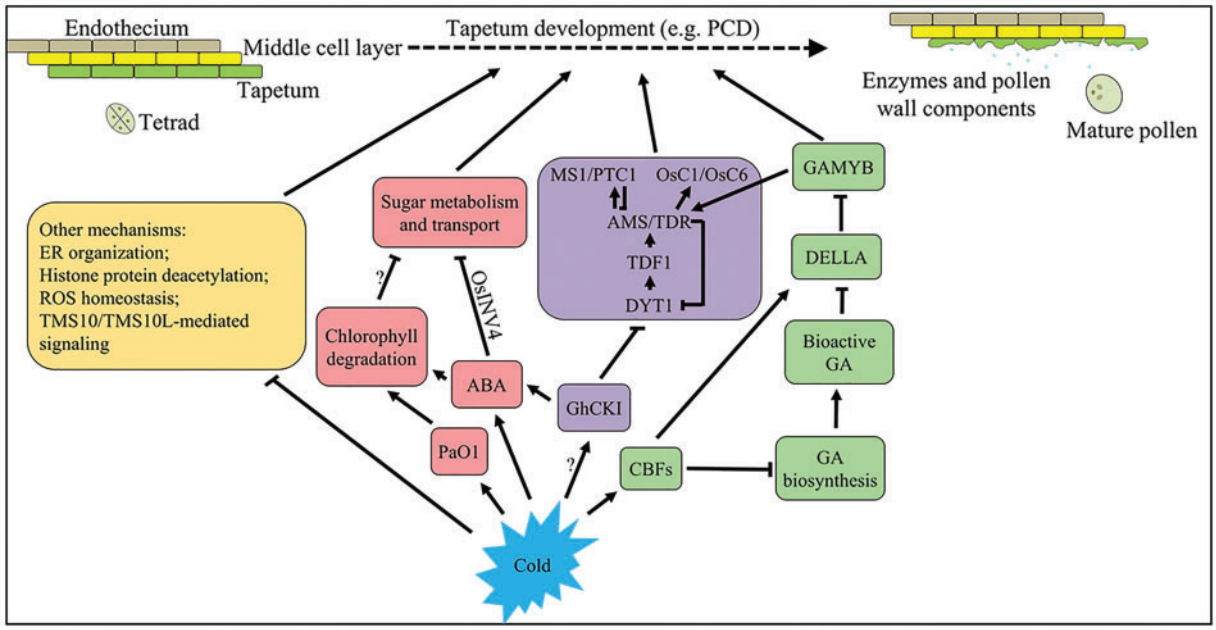

Fig. 1 Cold disrupts tapetum development. Tapetum development, which is controlled by the DYT1–TDF1–AMS–MS1 regulatory module, is crucial for pollen development and maturation. Cold stress affects tapetum function by different mechanisms including lowering the GA level and activating ABA signaling that positively and negatively regulate tapetum PCD, respectively. In addition, cold reduces sugar abundance which subsequently interferes with tapetum development. Moreover, some other physiological activities, such as ER organization and ROS homeostasis, are involved in tapetum development under low temperature stress.

In Arabidopsis, low temperature was found to increase the abundance of the stress-responsive phytohormone ABA in reproductive organs by stimulating the expression of genes involved in ABA biosynthesis (Baron et al. 2012). In addition, ABA is negatively linked with anther development and its tolerance to cold (Nayyar et al. 2005, Oliver et al. 2007, Hirano et al. 2008, Ji et al. 2011, Baron et al. 2012, Kovaleva et al. 2018). It is thus considered that development of cold-affected anthers is at least partially attributed to increased ABA levels in the flowers. It was proposed that ABA mediates development of anthers affected by cold by interfering with carbohydrate/triacylglycerol metabolism and reducing sugar abundance in the anthers, which consequently reduces male fertility (Oliver et al. 2005, 2007, Sharma and Nayyar 2014). In thermo-sensitive genic male sterility (TGMS) wheat plants, pheophorbide *a* oxygenase (PaO) was found to mediate cold-induced senescence-related cell death of anthers under low temperature stress (Yuan et al. 2018). Cold preferentially increases the expression of *TaPaO1* in wheat anthers at the late meiosis stage, and transgenic tobacco plants expressing *TaPaO1* under the control of a cold-responsive promoter *RD29A* exhibit failed pollen shed and strong male sterility under cold stress (Yuan et al. 2018). The function of PaO in chlorophyll degradation suggests that chlorophyll may be involved in the cold tolerance of anther development. Both cold stress and ABA application have been reported to reduce the content of chlorophyll (Battal et al. 2008, Pál et al. 2011, Liu et al. 2013). It will be of interest to study whether and how PaO participates in ABA signaling and regulates anther development under cold stress.

ABA prevents the execution of PCD in tapetal cells (Wang et al. 1999, Zhu et al. 2010, Min et al. 2013, Kovaleva et al. 2018), and thus the elevation of the ABA level in the anther may be the cause of cold-induced aberrant tapetum PCD. In cotton, a casein kinase, *Gossypium hirsutum* Casein Kinase I (GhCKI), has been found to prevent the occurrence of tapetal PCD and it influences the carbohydrate profile in the anther (Min et al. 2013). An expression study revealed that ectopically increased GhCKI leads to reduced expression of ubiquitin-specific protease and aspartyl protease, the mammalian homologs of which are involved in PCD. Additionally, overexpression of GhCKI decreases the expression of *DYT1*, *AMS* and *MS1*, and induces the expression of genes involved in ABA biosynthesis, suggesting that GhCKI may act upstream of the DYT1–AMS–MS1 module and ABA signaling to suppress tapetum degeneration (Min et al. 2013). The putative role of GhCKI and its homologs in other plant species in cold-induced tapetum PCD should be examined in the future study.

In contrast to ABA, GA plays a positive role in regulating male reproductive development, and is especially required for tapetum PCD (Plackett et al. 2011). The accumulation of GA is positively correlated with post-meiotic anther development in rice (Chhun et al. 2007, Hirano et al. 2008). Notably, GA promotes tapetum PCD by regulating its downstream GAMYB proteins (Millar and Gubler 2005, Aya et al. 2009, Zhenhua et al. 2010, Plackett et al. 2012). The lipid transfer protein OsC6 and the cysteine protease OsC1 are required for tapetum PCD in rice, and the expression of OsC6 is up-regulated by GAMYB, suggesting that they are downstream targets of GA (Li et al. 2006a, Aya et al. 2009, Zhang et al. 2010). At the same time, the activity of OsC6 and OsC1 is regulated by Tapetum Degeneration Retardation (TDR), a homolog of AMS in Arabidopsis (Li et al. 2006a, Zhang et al. 2010). In addition,

the PHD-finger protein Persistent Tapetal Cell 1 (PTC1), an ortholog of Arabidopsis MS1, controls tapetum PCD, and its expression is largely suppressed in the *gamyb-2* mutant (Aya et al. 2009, Li et al. 2011). These findings suggest that GA–GAMYB signaling may promote tapetum PCD by regulating the AMS/TDR–MS1/PTC1–OsC6/OsC1 module. On the other hand, in maize, GA-mediated PCD in aleurone cells requires deacetylation of histone proteins catalyzed by histone deacetylases, and ABA application has an opposite effect (Hou et al. 2017). Whether this histone modification mechanism is also involved in GA-induced PCD in the tapetum is not clear.

Low temperature stress may disrupt anther development by lowering the level of bioactive GA that subsequently affects sporogenous cell proliferation and tapetum PCD (Sakata et al. 2014). In Arabidopsis seedlings, low temperature has been reported to lower GA by promoting CBF-stimulated expression of *GA 2-oxidase*, a GA catabolic gene (Achard et al. 2008, Zhou et al. 2017). Similarly, in both Arabidopsis and rice anthers, reduced expression of GA biosynthesis genes due to cold is associated with increased activity of CBFs (Sakata et al. 2014, Liu et al. 2018), suggesting that the effect of low temperature on GA accumulation in both somatic and reproductive tissues is conserved. The accumulation of DELLA through a decrease in GA positively enhances CBF activity using a feedback mechanism and by interacting with jasmonate (JA) signaling (Zhou et al. 2017). Therefore, it is likely that cold stress interferes with tapetum PCD and anther development by manipulating the CBF–GA–DELLA module. On the other hand, it is proposed that GA triggers PCD in the aleurone cells by activating the reactive oxygen species (ROS)-mediated signaling that increases the concentration of ROS molecules (e.g. H_2O_2) (Hou et al. 2017). Studies in different plant species have revealed that a spatiotemporal production of ROS in the tapetum is required for the PCD of the tapetal cells (Xie et al. 2014, Yi et al. 2016, Yu et al. 2017b). These findings may favor the hypothesis that cold disrups tapetum PCD by negatively contributing to GA accumulation and to the production of a proper level of ROS in the anther. Moreover, in Arabidopsis, the GAMYB-like proteins MYB33 and MYB65 are involved in temperature-dependent fertility as the double mutant displays dramatically reduced seed set when growing under normal temperature conditions (22°C), whereas fertility is partially restored at low temperature (16°C) (Millar and Gubler 2005). Further studies are required to understand how GAMYB proteins control plant fertility under low temperature, and whether this is a downstream event of GA signaling.

Cold Manipulates Meiosis: A Window for Genomic Evolution

Low temperature reshapes the landscape of meiotic recombination

At the early stage of meiosis, homologous chromosomes pair, synapse and undergo meiotic recombination, reshuffling genetic material through formation of crossovers (COs). For details on the meiosis process, we refer to excellent reviews (Mercier et al. 2015, Melamed-Bessudo et al. 2016, Lambing et al. 2017). Studies of different plant species suggest that nearly every aspect of meiosis is potentially affected by low temperature stress (**Fig. 2A**). In apricot (*Prunus armeniaca* L.), chilling breaks anther endodormancy and stimulates initiation of meiosis (Julian et al. 2014). In *Lilium longiflorum*, a high level of chromosome contraction at the pre-leptotene stage occurs under low temperature (Walters 1977). The temperature at which plants are incubated during the process of meiosis does not, however, always exert a consistent effect. The frequency of COs, as measured by the occurrence of chiasmata, has been shown either to increase or decrease, depending on the species analyzed. In Pitic wheat and Rosner triticale, low temperature (15°C) from pre-meiosis to maturity leads to a higher incidence of aneuploidy in meiocytes due to unbalanced chromosome segregation in meiosis I, presumably because of the formation of univalents (Boyd et al. 1970). Similarly, in bluebell, *Endymion nonscriptus* and *Hyacinthus orientalis*, low temperatures, installed prior to meiosis, resulted in the lowest number of chiasmata per chromosome and univalent formation (Elliott 1953, Elliott 1955, Wilson 1959). In *Triticum aestivum*, a cold-induced decrease of chiasma frequency was found to be correlated with interference with chromosome pairing at the zygotene stage, suggesting that low temperature may manipulate CO formation by affecting chromosome dynamics (Bayliss and Riley 1972). In maize, on the other hand, chromosome 5 showed an increased number of chiasmata at low temperature (Khan 1955), which contrasts with what has been observed in inversion heterozygote barley (Powell and Nilan 1963). Incubation of barley at 12, 18 and 24°C did not significantly alter the CO rate at two loci on chromosome 6 of barley (Jensen 1981), suggesting that the influential pattern of cold stress on meiotic recombination in barley is genomic region dependent. Moreover, in Arabidopsis, both low and high temperature stresses were found to increase the recombination rate, which also relies on the age of plants, whether the stressed parent was male or female and the genomic position (Francis et al. 2007, Saini et al. 2017, Lloyd et al. 2018). Collectively, the findings of the large number of reports on recombination at different temperatures indicate that plants have evolved to respond differentially to temperature stress. Whether these responses are strategic adaptations to modulate the genetic diversity of progeny produced during temperature stress remains to be demonstrated. A first step toward unveiling possible specific adaptations in the recombination machinery requires the identification of genetic factors affecting temperature sensitivity of the recombination process.

Compared with the recording of chiasmata and COs at various temperatures, very few studies have addressed the molecular mechanisms putatively involved. Cyclin-dependent kinase G1 (CDKG1) controls synapsis and recombination in Arabidopsis in a temperature-dependent fashion. At normal temperature (23°C), the *cdkg1* null mutant displays regular double strand break (DSB) formation and RAD51/DMC1-dependent DSB repair, but exhibits failure of homology pairing

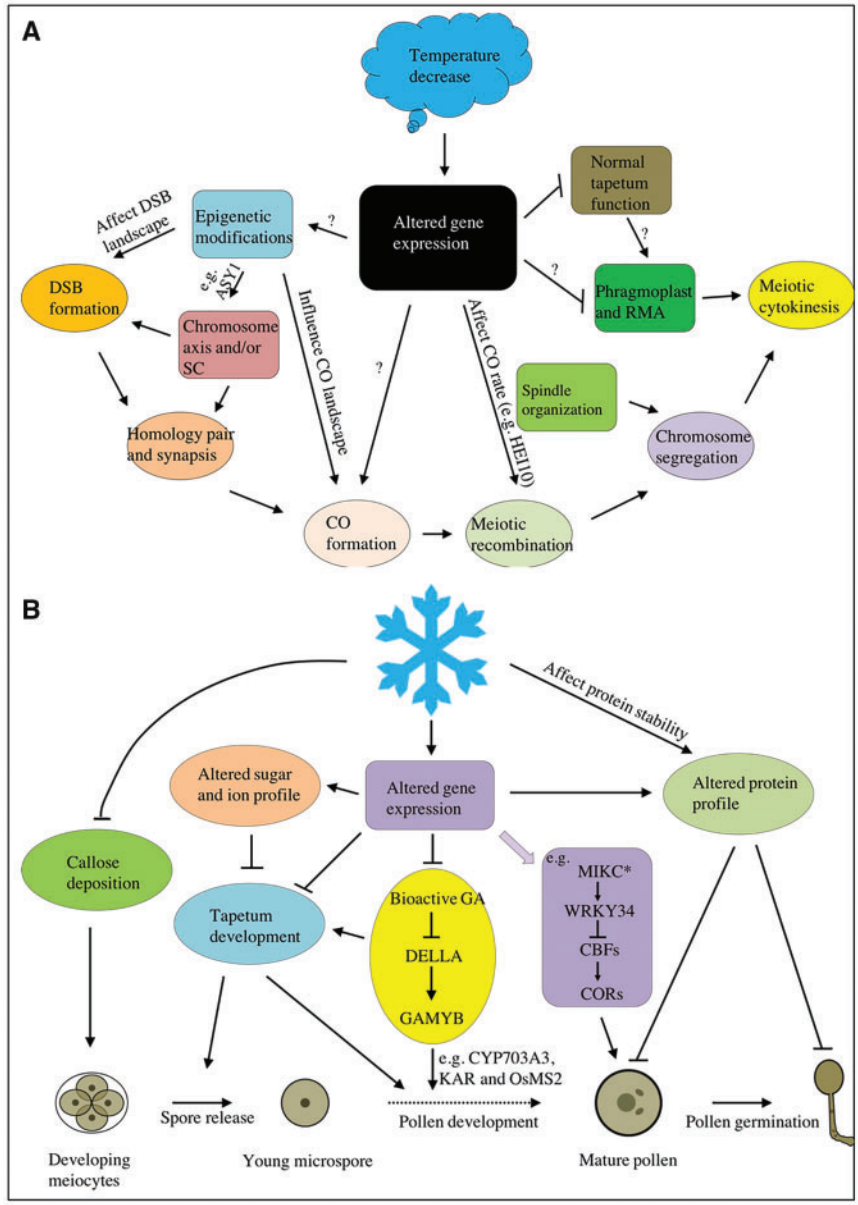

Fig. 2 (A) Low temperature influences male meiotic recombination and cell division. Cold stress has an impact on CO formation, but the underlying molecular mechanism is not clear. Since DSB formation and distribution, homologous chromosome pairing and synapsis, the activity of meiotic recombination-related proteins and the epigenetic modifications of the chromatins can affect the landscape of COs, cold may have an influence by interacting with one or more of these aspects during the progression of meiotic recombination. On the other hand, cold stress interferes with cytoskeleton (phragmoplast)-based meiotic cytokinesis which consequently leads to unreduced gamete production. In addition, tapetum plays a potential role in the regulation of male meiotic cell division and may mediate its cold response. The question marks indicate an uncertain and/or unclear mechanism. (B) Cold influences gametogenesis. The impact of cold stress on pollen development occurs at multiple levels, by which gene expression, protein profile, sugar metabolism and hormone signaling are altered, which coordinately leads to affected pollen development (e.g. pollen wall formation) and maturation.

and synapsis, resulting in decreased COs and univalents at diakinesis, whereas a lower temperature (12°C) complements these meiotic lesions, which is reflected by recovered loading of the synaptonemal complex protein ZYP1 on zygotene and pachytene chromosomes (Zheng et al. 2014). It has been proposed that CDKG1 protein may be dynamically thermosensitive, in which case the high temperature further decreases the function CDKG1 that is maintained at an undetectable level in the background of the *cdkg1* insertion mutant (Zheng et al. 2014). Although not that much is known about how cold stress influences meiotic recombination, some speculation could be made according to what has been reported for heat stress. In barley, Higgins et al. observed a shift of class I COs to proximal regions and an increased recombination rate as temperature rises, and they proposed that this effect is mediated by enhanced homolog pairing and altered chromosome cycling

(Higgins et al. 2012, Phillips et al. 2015). Immunolocalization revealed that the loading and distribution of barley ZYP1 and the chromosome axis protein ASY1 are altered under heat stress (Higgins et al. 2012), and the expression of *ASY1* is up-regulated at higher temperature (Oshino et al. 2007). Morgan et al. have proposed a hypothesis that may explain how heat interferes with meiotic recombination: under heat stress, chromosome structural proteins Rec8, ASY1 and ZYP1 may be misfolded, abnormally denatured and/or functionally suppressed, and these changes may consequently lead to interference with chromosome pairing, synapsis and recombination, as well with COs (Morgan et al. 2017). However, in contrast to barley, where the length of the synaptonemal complex (SC) is positively correlated with rising temperature, total SC length in Arabidopsis is significantly decreased as the temperature increases (Higgins et al. 2012, Lloyd et al. 2018), suggesting that the response pattern of chromosome structures (e.g. the SC) during meiotic recombination depends on plant species. Cold stress does not seem to affect chromosome axis formation and SC construction (Zheng et al. 2014), and how cold affects the meiotic recombination pattern is not clear.

It is proposed that temperature-dependent variation of the recombination rate displays a 'U-shaped' curve. In this model, the recombination rate increases when the temperature declines and/or rises, and then the rate decreases once the temperature reaches an unbearable point (Bomblies et al. 2015, Morgan et al. 2017). A recent study in Arabidopsis supports this hypothesis showing that within a fertile temperature range, both low and high temperatures increase the meiotic recombination rate primarily through enhanced class I CO formation (Lloyd et al. 2018). However, the higher temperature- (28°C) induced promotion of the recombination rate in Arabidopsis is probably through a MLH1-mediated pathway, whereas the lower temperature (8°C) seems to act in a HEI10-dependent fashion (Lloyd et al. 2018). Modliszewski et al. further demonstrated that in Arabidopsis, high temperature promotes CO through the class I CO formation pathway, and suggested that increased CO is derived from a triggered bias of NCOs turning into COs, but not an elevated DSB generation (Modliszewski et al. 2018). It seems that the influence of low temperature on meiotic recombination is channeled by a different pathway from that of high temperature. Nevertheless, examination within limited genomic regions and in a narrow range of temperatures may not represent a universal temperature-responsive pattern of meiotic recombination in plants. Analysis of more genomic intervals and testing of a wider range of temperatures would contribute to a better understanding of how meiotic recombination responds to temperature changes.

On the other hand, chromatin features are temperature sensitive and are key determinants of meiotic recombination patterning (Mirouze et al. 2012, Kim et al. 2015, Shilo et al. 2015, He et al. 2017, Marand et al. 2017, Choi et al. 2018, Underwood et al. 2018). For instance, meiotic recombination hotspots tend to localize at genomic regions with a lower CHG DNA methylation status (Mirouze et al. 2012, Yelina et al. 2015, He et al. 2017, Marand et al. 2017); and DNA methylation can be modified along with an alteration of temperature (Pan et al. 2011, Shan et al. 2013, Naydenov et al. 2015). The temperature-dependent meiotic recombination pattern hence may partially result from a reprogrammed DNA methylation and/or other epigenetic modifications of chromatins and the recombination proteins. Study of DNA methylation mutants and examination of their meiosis behavior under cold stress would help in understanding how cold stress manipulates the meiotic recombination landscape.

Cold reshapes the cytoskeleton during meiotic cell division

Meiotic processes taking place post-recombination are also sensitive to cold (**Fig. 2A**). Meiotic cytokinesis appears vulnerable to cold-induced defects, which has been reported in TGMS wheat (10°C) and Arabidopsis (4°C) (Tang et al. 2011, De Storme et al. 2012). Meiotic cytokinesis is either of the successive type, which occurs in grasses, whereby the first cell plate forms at the end of meiosis I and the second plate is constructed at the end of meiosis II, or of the type that occurs in dicots simultaneously at the tetrad stage separating the four spores in one step (De Storme and Geelen 2013a). In the wheat TGMS line, cold causes the phragmoplast to form abnormally, possibly because of altered actin dynamics, leading to defective meiosis I cytokinesis (Tang et al. 2011, Xu et al. 2013). In Arabidopsis, which executes simultaneous cytokinesis, radial microtubule arrays (RMAs) at the end of male meiosis maintain the distal position of the four haploid nuclei in the tetrad meiocytes. The RMAs are then converted into mini-phragmoplasts that deposit callose between the nuclei (De Storme et al. 2012). In both grasses and dicots, the effect of cold stress on the cytoskeleton seems specific for the phragmoplast as the spindles and chromosome dynamics appear normal. The dyads that are formed because of cold-induced meiosis I cytokinesis defects correspond to second division restitution (SDR) (Tang et al. 2011). It is interesting that cold stress also primarily induces SDR dyad pollen in Arabidopsis despite the fact that cytokinesis is simultaneous and all phragmoplast microtubules occur in a single cytoplasmic space (De Storme et al. 2012). Dyads can progress to form viable pollen and hence may contribute to polyploidization or interspecies hybridization (Bretagnolle and Thompson 1995) or abort, indicating that cold may also affect other vital processes in some species or varieties (Barton et al. 2014). Some of these lethal effects may relate to cytokinesis, as was shown in Australian spring wheat where the incidence of irregular cytomixis was increased under cold temperatures (Barton et al. 2014). In general, it appears that plants show distinct cold responses during meiosis, and this often results in meiotic restitution, which in some cases leads to viable, unreduced or diploid pollen (Mason et al. 2011).

Wheat was shown to adapt to cold under continuous low temperature conditions as microsporogenesis proceeds to form viable pollen (Barton et al. 2014). Genes and derived proteins involved in the adaptation process are potentially up-regulated in the anther. A transcriptome study of cold-

treated wheat revealed differential expression of genes involved in tapetum development, cell cycle progression and many signal transduction cascades that affect cytoskeletal reorganization (Tang et al. 2011). By and large, most of these were genes involved in actin dynamics such as, for example, *Profilin*, *Actin-depolymerization factor* (*ADF*), *Villin*, *Arp2/3*, *Fimbrin* and *WLIM1* and a homolog of the MEKK1-like MAPKKK Nicotiana Protein Kinase 1 (NPK1) that is required for outward expansion of phragmoplast microtubules and the transport of vesicles to the equatorial plane to form the cell plate (Tang et al. 2011). Actin filaments, microtubules, vesicle trafficking and fusion proteins coordinately interact at the phragmoplast, and alteration of one of these components may require multiple adjustments for the system to work at reduced temperature. These changes may not be readily installed during a sudden drop in temperature, which may explain why cold spells cause defects in cytokinesis but continuous cold does not.

Constitutively activated GA signaling induces abnormal meiotic cytokinesis that phenotypically mimics what cold does (Liu et al. 2017). The DELLA protein Repressor of *ga1–3* (RGA) is expressed in somatic anther tissues including the tapetum, but not in meiocytes, suggesting that regulation of meiotic cytokinesis through DELLA depends on a cell–cell communication between tapetal cells and the PMCs. This finding corroborates with arrested male meiosis prior to cytokinesis in mutants with defective tapetal cell differentiation (Zhao et al. 2002, Yang et al. 2003, Zhang et al. 2006). A role for the tapetum in meiotic cytokinesis is also supported by the cytokinesis defects in loss-of-function mutants of AtMYB33 and AtMYB65, two GAMYB-like proteins required for PCD of tapetal cells (Millar and Gubler 2005, Liu et al. 2017). Although the cold-induced defects in cytokinesis do not depend on GA signaling (Liu et al. 2018), these findings indicate that defective meiotic cytokinesis may be due to malfunctioning of the tapetum.

During meiosis, meiotic recombination propels novel combinations of gene alleles in progeny which enable natural selection to occur (Melamed-Bessudo et al. 2016, Lambing et al. 2017). At the same time, production of a polyploid gamete is considered the main source of whole-genome duplication, which is a prominent contributor to genome complexity and diversification of plants (Cui et al. 2006, De Storme and Geelen 2013b, Lu et al. 2013, De Storme and Mason 2014, Barker et al. 2016, McAllister and Miller 2016, Panchy et al. 2016, Zhan et al. 2016, Ren et al. 2018). Temperature decrease thus may drive plant evolution by influencing recombination and cell division during male meiosis.

Cold Disrupts Gametogenesis: A Direct Threat to Plant Fertility

The impact of cold stress on pollen development occurs at multiple levels (**Fig. 2B**). In rice, cold induces accumulation of sucrose at the microspore stage but causes depletion of starch in mature pollen, with cold-tolerant rice plants harboring relatively stable sugar metabolism (Oliver et al. 2005). A proteomic study of rice revealed that cold reprograms the protein profile in the tricellular stage anther and induces degradation of proteins at later anther development stages (Imin et al. 2004). In line with this, proteins required for cold acclimation, lipid transfer and pollen tube growth are substantially reduced in cold-stressed Arabidopsis pollen grains (Lee and Lee 2003). An expression study found that genes required for protein stability against oxidative stress (e.g. *OsFKBP65*) are up-regulated in chilling-stressed rice anthers at the booting stage, and a pre-treatment by chilling water before panicle initiation suppresses the expression of anti-oxidative genes which results in more severe male sterility (Noctor 2015, Suzuki et al. 2015). This suggests that oxidation tolerance may be important for cold tolerance of male fertility in rice, and a low temperature occurring during vegetative development may also have an impact on pollen development. Moreover, cold affects pollen development prominently by interfering with pollen wall formation. In rice, the callosic cell layer surrounding developing meiocytes undergoes premature degeneration under low temperature (22/12°C day/night for 4 d), which results in defective deposition of cell wall components on the surface of developing microspores, leading to pollen sterility (Mamun et al. 2006).

GA plays a key role in regulating pollen wall formation. In Arabidopsis and rice, a proper GA homeostasis is required for pollen wall construction since mutant plants with alterations in GA content and/or signaling pathway exhibit a disrupted pollen coat (Aya et al. 2009, Aya et al. 2011, Plackett et al. 2014). In rice, under the control of GA signaling, GAMYB positively regulates the expression of Cyt P450 hydroxylase *CYP703A3*, *β-Ketoacyl Reductase* (*KAR*) and *Male Sterility 2* (*OsMS2*) that are involved in the synthesis of pollen wall components (Aya et al. 2009). This regulatory pattern is conserved during the evolution of land plants (Aya et al. 2011). It is thus likely that cold affects pollen wall formation by undermining GA signaling (Sakata et al. 2014). Interestingly, although cold suppresses the expression of GA biosynthesis genes, it also deregulates the expression of GA catabolic genes (e.g. *OsGA2OX1*) in rice flowers (Sakata et al. 2014). It could be that cold interferes with GA-dependent gametogenesis using a complicated mechanism, and the variation of the bioactive GA level depends on a modulation of the entire GA metabolism network. An in vivo determination of GA gradients may contribute to the understanding of how GA is controlled in reproductive tissue in response to cold stress (Rizza et al. 2017). In Arabidopsis, a group I WRKY family transcription factor, WRKY34, plays a negative role in mediating cold tolerance of pollen grains by suppressing the expression of *CBF* genes (Zou et al. 2010). The activity of WRKY34 is negatively regulated by three cold-inducible MIKC* proteins, Agamous-Like 65 (AGL65), AGL66 and AGL104, which harbor functional redundancy (Zou et al. 2010). Whether the MIKC*–WRKY34–CBF module acts cooperatively with GA signaling should be addressed. Meanwhile, since the fates of tapetum and pollen development are tightly linked, interference in pollen development by cold temperatures may partially result from a secondary effect of the disturbed tapetum function.

Conclusion and Perspectives

Extreme temperature decrease has a huge impact on haploid gamete formation and yield of crops by interfering with male reproductive development. In recent decades, good progress has been made in deciphering the molecular factors and signaling pathways that are involved in cold tolerance of plants (e.g. CBF and MAPK signaling), as well as the mechanisms controlling plant male reproduction (e.g. GA and ABA signaling). However, much remains unclear regarding what molecular signaling pathways mediate the male development of plants in responding to cold, and how these molecular determinants coordinately act with each other. The tapetum plays a central role in controlling the development of microsporogenesis and gametogenesis, and the response to cold stress. Remarkably, hormones play a major role in male reproductive development under both natural and low temperature conditions. Moreover, accumulated evidence points to the fact that low temperature also influences meiotic recombination and meiotic cytokinesis, two important processes that contribute to genomic diversity and ploidy consistency, respectively. Therefore, from a broader and evolutionary perspective, low temperature stress may play a potential role in manipulating genomic complexity and stability of plants over generations. On the other hand, temperature alterations have an impact on the distribution of COs along the plant chromosomes, which may influence the recombination ratio of the genes that are located at regions considered as CO 'hot-spots' or 'cold-spots'. Whether manipulation of the incubation temperature (at a fertile range) with the aim of modifying the combination of agricultural-related genes could be used as a potential breeding tool is of particular interest to study. However, despite the progress that has been achieved, there are still some important questions which need to be addressed. (i) How does temperature alteration affect the landscape of meiotic recombination in plants? (ii) What is the role of chromosome structures (e.g. the axis) and the central element in controlling meiotic recombination under natural and extreme temperature conditions? (iii) What molecular determinants mediate the cold sensitivity and response of the meiotic cytoskeleton? (iv) How do hormones coordinately regulate male reproductive development under cold stress? (v) How does the tapetum play a role in the regulation of meiosis and its response to cold stress?

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The authors have no conflicts of interest to declare.

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