Gene Reports 43 (2026) 102512

Contents lists available at ScienceDirect

Gene Reports

journal homepage: www.elsevier.com/locate/genrep

Molecular regulation of pollen responses to abiotic stress in flowering plants: Mechanisms, models and future directions

Nadiyah Thajudeen [a], Deepika Vasudevan [a], V. Ramesh Kumar [a], Prakash Pandurangan [a,*], Meenambiga Setti Sudharsan [b], Ravindran Jaganathan [c]

[a] Department of Biotechnology, Sathyabama Institute of Science and Technology, Chennai, 600119, India
[b] Department of Bioengineering, School of Engineering, Vels Institute of Science, Technology and Advanced Studies (VISTAS), Chennai, 600117, India
[c] Preclinical Department, University of Kuala Lumpur, Royal College of Medicine, Perak, Malaysia

ARTICLE INFO

Edited by Ziqing Li

Keywords:
Pollen
Abiotic stress
Molecular mechanisms
Climate change

ABSTRACT

Pollen development and function are highly sensitive to abiotic stresses such as heat, drought, salinity, and cold, making pollen one of the most vulnerable stages in the life cycle of a plant. These stress factors affect pollen viability and disrupt pollen tube growth and germination, directly impacting fertilization success and thereby reducing crop yield. Advances in plant molecular biology have helped identify several stress-responsive genes and regulatory mechanisms that govern pollen responses to stress, including transcription factors, hormonal signalling components, ion transporters, and epigenetic regulators. Studies across different model plants and crop species have utilized techniques like RNA sequencing, qRT-PCR, multi-omics, and in vitro assays to unravel gene expression changes and molecular pathways associated with pollen responses to abiotic stress. However, molecular insights into pollen responses to salinity, cold, and oxidative stress remain comparatively limited in contrast to heat and drought stress. This mini-review provides a gene-centred synthesis of the molecular mechanisms underlying pollen responses to abiotic stress and highlights shared regulatory nodes that integrate multiple stress-response pathways. By comparing mechanisms reported across different plant species and stress types, this review also emphasizes understudied areas such as pollen responses to cold, salinity, and oxidative stress, and outlines key knowledge gaps that must be addressed to improve pollen adaptability and reproductive stability under changing climatic conditions.

1. Introduction

Pollen plays a vital role in the reproduction of flowering plants. They not only act as carriers for the male gamete, but also serve as links between phenotype and plant fitness (Opedal et al., 2023). The key driver responsible for delivering the sperm cell to the ovule is the pollen tube, whose growth is highly sensitive to environmental stressors (Cai and Del Duca, 2019). Due to the stress-sensitivity of pollen development and fertilization, it presents a growing concern regarding reproductive success, as even short-term fluctuations in the environment can cause irreversible impairment. This presents a challenge when it comes to growing plants for ornamental purposes and food crop production under fluctuating conditions (Pereira and Coimbra, 2019). Since pollen development happens within a very tightly controlled time period that involves coordinated meiotic and post-meiotic stages, even short-term environmental stress can interfere with pollen viability and successful fertilization. As a result, this disruption can negatively affect the overall reproductive fitness of the plant (Singh et al., 2021; Begcy and Dresselhaus, 2018).

Among abiotic stresses, heat is a major factor impacting pollen development, and significant temperature rise can hamper the process, leading to a decrease in the viability of pollen, impacting germination and ultimately yield loss (Chaturvedi et al., 2021; Santiago and Sharkey, 2019). High temperatures can disrupt several key processes during pollen development, including meiotic progression, proper functioning of the tapetum, and the formation of the pollen wall. These disruptions

---

Abbreviations: RNAs, ribonucleic acids; DNA, deoxyribose nucleic acid; HSP, heat shocking proteins; HSFA, heat shock transcription factors; CRISPR, Clustered Regularly Interspaced Short Palindromic Repeats; ATAC, Assay for Transposase-Accessible Chromatin u; qRT-PCR, quantitative Reverse Transcription-Polymerase Chain Reaction.

* Corresponding author.
E-mail address: kpprakashmtech@gmail.com (P. Pandurangan).

https://doi.org/10.1016/j.genrep.2026.102512
Received 28 November 2025; Received in revised form 13 April 2026; Accepted 22 April 2026

often lead to pollen sterility under heat stress conditions. In addition to heat stress, other prominent factors affecting pollen are drought (Dong et al., 2017; Yu et al., 2019), salinity (Khaleghi et al., 2019; Razzaq et al., 2019), cold (Huang et al., 2022), and oxidative stress, which often arises as an effect of other stressors (Jia et al., 2017). Pollen has a limited ability to recover from stress in contrast to vegetative tissues; therefore, changes in temperature, water scarcity, and salinity that arise due to climate change pose a great risk to plant reproductive success. In the context of ongoing climate change, the viability of pollen and its response mechanisms against abiotic stress critically determine the efficiency of fertilization and reproductive success across plants (Pacini and Dolferus, 2019).

The response is regulated by a complex and interconnected network of molecular mechanisms that maintain homeostasis and reproductive function, making the pollen resilient to induced stress. This network includes a wide range of transcription factors, such as *bZIP60* (Chaturvedi et al., 2021) and certain members of the Ethylene Response Factors (*ERF*) family (Jin et al., 2018), heat-shock proteins (Singh et al., 2021), stress-responsive enzymes, including *IRE1* (Ren et al., 2021; Chaturvedi et al., 2021; Raja et al., 2019), and hormonal signals (Jegadeesan et al., 2018) that work seamlessly together to protect pollen from damage. Along with gene-specific stress response, larger regulatory systems also help maintain pollen stability during environmental stress. These include signalling through reactive oxygen species (ROS), calcium-mediated signalling pathways, and interactions between different plant hormones, all of which work together to support pollen homeostasis (Jia et al., 2017; Singh et al., 2021). Emerging evidence also highlights the role of epigenetic modifications (Chaturvedi et al., 2021) and non-coding RNAs (Jha et al., 2020; Keller et al., 2020) contributing to pollen stress response. Furthermore, large-scale datasets like the GloPL datasets have shown that pollen limitation is a common issue across ecosystems and taxa (Bennett et al., 2018), thereby emphasizing the criticality of analyzing and maintaining the molecular resilience of pollen and its strong ecological and agricultural relevance.

Though there are growing insights into the molecular basis of pollen stress responses, the current understanding and its depth remain dispersed across the types of stress and different plant species. Additionally, although many studies have identified stress-responsive gene expression patterns in pollen using transcriptomic analyses, only a limited number of studies provide direct functional genetic evidence that clearly connects specific regulatory genes to pollen fertility outcomes under stress conditions. Accordingly, this review examines the current knowledge on molecular mechanisms underlying pollen responses to abiotic stresses, with a focus on key pathways, genes, and regulatory components identified across model plants and crops, while also highlighting conserved signalling pathways and shared molecular regulators that integrate stress perception with reproductive development.

Despite significant advances in transcriptomic and multi-omics technologies, several limitations constrain the interpretation of pollen stress-response datasets. Comparative analyses across studies are complicated by variability in species, stress intensity, developmental timing, and experimental design. Importantly, many studies utilize whole-anther samples, which comprise multiple cell types including the tapetum and anther wall layers. As a result, gene expression profiles derived from such samples may not accurately represent pollen-intrinsic responses. This limitation is particularly relevant when inferring mechanisms of stress tolerance, as reproductive phenotypes may arise from indirect effects mediated through tapetal dysfunction rather than direct effects on pollen cells. Therefore, careful consideration of tissue specificity and experimental context is essential when interpreting existing datasets.

2. Pollen development

Pollen development is a tightly regulated process that takes place within the anther and results in the formation of viable male gametophytes. It begins with microsporogenesis, during which diploid pollen mother cells undergo meiosis to produce haploid microspores. These microspores then enter the microsporogenesis stage, where they develop into mature pollen grains capable of fertilization. The successful progression of these stages depends on coordinated gene expression, proper cellular differentiation, and precise developmental timing (Begcy and Dresselhaus, 2018; Singh et al., 2021).

During microsporogenesis, meiotic division produces tetrads of haploid microspores that are temporarily enclosed within a callose wall. The degradation of this callose layer releases individual microspores into the anther locule, where they undergo expansion and differentiate. Early anther and tapetum development is regulated by several transcription factors, including *DYT1* (Dysfunctional Tapetum1) and *TDF1* (Defective in Tapetal Development and Function1), which control the expression of genes involved in tapetal function and microspore maturation (Zhang et al., 2006; Xu et al., 2010).

The tapetum, the innermost anther wall, plays a critical role in supporting developing microspores by providing nutrients, enzymes, and precursors required for pollen wall formation. Transcription factors such as *AMS* (Aborted Microspores), *MYB80*, and *MS1* (Male Sterility1) regulate key processes including sporopollenin biosynthesis, pollen coat formation, and the programmed cell death of tapetal cells (Sorensen et al., 2003; Xu et al., 2010; Zhu et al., 2011). Proper pollen wall formation, particularly the deposition of sporopollenin in the exine layer, is essential for protecting pollen and ensuring fertility.

Following differentiation, pollen grains proceed through a maturation phase and typically contain a vegetative cell and two sperm cells enclosed within a protective pollen wall. Because pollen development involves highly coordinated cellular and molecular processes, it is particularly sensitive to environmental stress. Abiotic stresses such as heat, drought, and salinity can disrupt meiotic progression, impair tapetum function, and reduce pollen viability, ultimately affecting plant reproductive success (Chaturvedi et al., 2021; Huang et al., 2022).

Key transcriptional regulators of pollen development, including *DYT1, TDF1, AMS, MYB80* and *MS1*, form a well-defined regulatory cascade controlling tapetum function and microspore maturation. Functional genetic studies have demonstrated that disruption of these genes leads to defective pollen development and male sterility, highlighting their central role in reproductive success. Integrating these developmental regulators with stress-responsive pathways is essential to understanding how environmental stress impacts pollen viability at different developmental stages (Zhang et al., 2006; Ko et al., 2014; Zhu et al., 2011).

3. Overview of abiotic stresses

Given the changing climate, including global warming, reduced precipitation, and rising sea levels, abiotic stress such as heat, drought, and salinity significantly affect the growth, development, and reproduction of a plant. These stress factors affect the overall developmental processes of a plant (Table 3.1), and the effect on pollen is a potential threat that affects crop yield, which leads to food demands.

3.1. Heat stress

Heat is a major threat to plant reproductive success. This has been demonstrated in various studies. Simulation of heatwaves showed a decrease in pollen production of *Brassica napus* by about 20% and a sharp decrease in pollen vigor, resulting in an 87% decrease in seed set (Rosenberger et al., 2024). Heat stress is shown to cause early tapetal degradation and carbohydrate depletion in pollen (Chaturvedi et al., 2021). In maize, a transient heat-wave has been shown to cause long-term damage to the pollen, resulting in reduced starch accumulation, altered pollen composition, and poor seed set (Smith, 2019).

Heat stress during critical stages such as microsporogenesis and

Table 3.1
Effect of abiotic stress on pollen development.

Abiotic stress	Major effect on pollen	Changes	Reference
Heat stress	Reduced pollen viability, decreased pollen production, and poor seed set	Early tapetal degeneration, carbohydrate depletion, and reduced starch accumulation	Rosenberger et al., 2024; Chaturvedi et al., 2021; Smith, 2019
Drought stress	Pollen abortion, reduced germination, reduced pollen tube growth	Tapetal disruption, limited starch accumulation, altered ABA signalling	Yu et al., 2019; Dong et al., 2017
Salinity stress	Reduced pollen viability and fertility	Cellular shrinkage, membrane damage, ionic imbalance, and ROS accumulation	Khaleghi et al., 2019; Razzaq et al., 2019
Cold stress	Pollen sterility, reduced fertilization efficiency	Impaired meiosis, disrupted tapetal activity, and delayed anther dehiscence	Huang et al., 2022; Parrotta et al., 2019; Jia et al., 2017

microgametogenesis can interfere with normal meiotic progression, disrupt tapetum function, and alter pollen wall development. These disturbances ultimately affect pollen viability and its ability to germinate. The tapetum, which plays a crucial role in supplying nutrients and materials required for pollen wall formation, is particularly sensitive to high temperatures. As a result, premature or delayed degeneration of the tapetum is often associated with heat-induced male sterility (Chaturvedi et al., 2021).

3.2. *Drought stress*

Drought can cause structural damage and physiological changes in pollen, showing evident differences between normal and drought-stricken pollen. Drought stress disrupts tapetal integrity and limits starch accumulation in pollen, resulting in reduced nutrient availability and compromised pollen performance. Comparable pollen damage has also been reported under polyethylene glycol (PEG)-induced drought stress conditions. Prolonged or severe water deficit can eventually lead to pollen abortion and yield reduction; however, drought-tolerance species are able to maintain pollen viability under limited water availability (Yu et al., 2019; Dong et al., 2017).

In addition to causing structural damage, drought stress can disrupt carbohydrate metabolism and hormonal signalling within the anther. Reduced transport of assimilates to reproductive tissues limits the accumulation of essential reserves in developing pollen grains, which in turn affects pollen germination and pollen tube growth. Moreover, drought conditions can induce oxidative stress and alter abscisic acid (ABA) signalling pathways, and these changes together contribute to reduced reproductive success under water-limited conditions (Yu et al., 2019).

3.3. *Salinity stress*

Salinity stress induces morphological alterations in pollen, including cellular shrinkage and membrane disruption, resulting in a marked decline in pollen viability. Pollen viability is closely linked to salinity tolerance and is frequently used as a marker of stress-tolerant genotypes (Khaleghi et al., 2019; Razzaq et al., 2019). Notably, certain aquatic plant species, such as *Ruppia* and *Althenia,* regulate aperture opening and closure in response to fluctuating salinity, reflecting adaptation to saline environments (Severova et al., 2022).

At the cellular level, salinity stress can disrupt ionic balance and osmotic homeostasis in developing pollen grains. High salt concentrations often lead to increased production of reactive oxygen species (ROS), which can damage cellular membranes and interfere with metabolic pathways involved in pollen maturation. These disruptions ultimately reduce pollen germination efficiency and fertilization potential in salt-affected environments (Khaleghi et al., 2019; Razzaq et al., 2019).

3.4. *Cold stress*

Cold stress interferes with another development and pollen maturation, resulting in pollen abortion and decreased fertilization efficiency (Huang et al., 2022; Parrotta et al., 2019). Cold-related pollen damage is often linked to elevated cellular stress, which further exacerbates pollen injury under low-temperature exposure (Jia et al., 2017).

Low temperatures can disrupt meiotic division, impair tapetal activity, and interfere with pollen wall formation, leading to abnormal pollen development and reduced viability. In many crop species, exposure to cold during early stages of pollen development has been linked to delayed anther dehiscence and reduced pollen germination, ultimately affecting fertilization success and seed formation (Huang et al., 2022; Parrotta et al., 2019).

4. Molecular mechanisms regulating pollen response

In this section, stress-responsive mechanisms affecting pollen development are synthesized in a structured framework based on stress type, developmental stage, tissue specificity, and level of experimental evidence. For each stress condition, regulatory pathways are discussed with emphasis on gene-specific functions, distinguishing between mechanisms acting directly within pollen and those mediated through surrounding anther tissues such as the tapetum. Furthermore, evidence supporting gene-function relationships is critically evaluated to differentiate experimentally validated regulators from those inferred primarily from transcriptomics or correlative studies. This integrative approach enables a more systematic and mechanistic understanding of pollen stress responses across species.

It is important to note that a substantial proportion of reported stress-responsive genes are identified through transcriptomic profiling or association studies. Therefore, unless supported by direct genetic or functional validation, these relationships should be interpreted as indicative rather than definitive, and conclusions regarding gene function are presented with appropriate caution throughout the text.

4.1. *Heat stress response*

Heat stress triggers a multilayered response in pollen, referred to as the heat stress response, which supports pollen viability. This process begins with heat perception through calcium ion ($Ca^{2+)}$ fluxes and the accumulation of misfolded proteins within the endoplasmic reticulum (ER). These signals activate the unfolded protein response (UPR), mainly mediated through *IRE1*-dependent splicing by *bZIP60*, which controls the expression of stress-responsive genes. Moreover, the transcription factors *bZIP17* and *bZIP28* participate in ER homeostasis and promote pollen tolerance to elevated temperatures. These ER-localized signalling pathways primarily function to restore protein-folding capacity and maintain secretory pathway integrity during heat stress. Although these processes underscore the importance of ER-mediated stress signalling, how ER stress responses are coordinated with cytosolic heat shock pathways in pollen remains largely unclear (Chaturvedi et al., 2021; Singh et al., 2021).

Alongside ER-mediated signalling, the cytosolic heat stress response in pollen is governed by the heat shock factor-heat shock proteins (HSF-HSP) axis, which limits protein misfolding by stabilizing native protein structures, refolding denatured proteins, and restricting protein aggregation. This process involves increased expression of heat shock proteins, including *HSP70* and *HSP90*, under the control of heat shock transcription factors, particularly *HSFA1* and *HSFA2* (Raja et al., 2019). Recent studies also highlighted the role of *HSP101* in maintaining meiotic thermotolerance in rice and *Arabidopsis*. Disruption of this chaperone has been shown to reduce pollen viability under high-temperature conditions (Li et al., 2025). In addition, cytosolic heat stress responses interact with ROS signalling and Ca^{2+} homeostasis, which together regulate pollen tube growth and cellular stability under stress. These coordinated molecular responses ultimately help maintain pollen viability, germination capacity, and successful fertilization under elevated temperature conditions.

Heat stress also promotes elevated production of reactive oxygen species (ROS) in pollen, leading to oxidative injury and pollen abortion. Activation of antioxidant enzymes, such as catalase, reduces this damage by sustaining cellular redox balance. Other antioxidant enzymes, such as superoxide dismutase *(SOD)* and ascorbate peroxidase *(APX),* have also been reported to help reduce the accumulation of reactive oxygen species (ROS) in heat-stressed reproductive tissues. Nevertheless, the relative influence of ROS-mediated injury versus protective antioxidant responses to pollen thermotolerance appears to differ among plant species (Chaturvedi et al., 2021). Notably, heat-induced reproductive failure often arises from premature tapetum degeneration; however, direct effects on pollen cells, including protein misfolding, oxidative stress, and impaired metabolism, also contribute significantly to thermosensitivity.

Recent developments in multi-omics technologies have revealed key molecular components governing pollen thermotolerance. Integrated studies in cotton have identified genes associated with metabolic regulation, hormonal signalling, lipid synthesis, and transcriptional control, while also emphasizing the role of epigenetic modifications, including DNA and RNA methylation and histone acetylation, in modulating gene expression under heat stress (Ijaz et al., 2024). For example, chromatin remodelling mediated by the ALBA protein *GhAL5* has been shown to regulate thermotolerant male fertility in cotton by influencing chromatin organisation and modulating the stress-responsive genes (Li et al., 2026).

Moreover, appropriate regulation of endoplasmic reticulum chaperones and protein disulfide isomerases is critical for preserving pollen viability, as these proteins maintain quality control during heat-induced protein stress (Singh et al., 2021). Taken together, these processes support pollen heat tolerance and offer potential targets for enhancing crop resilience and fertilization success under global warming.

Recent pollen-focused transcriptomic analyses further support the central role of ER stress signalling in thermotolerance. RNA-seq studies in Arabidopsis and maize pollen under heat stress identified significant upregulation of the *IRE-bZIP60* pathway components along with downstream chaperons, including *HSP70*, *HSP90,* and protein disulfide isomerases, highlighting coordinated regulation of protein quality control during stress (Chaturvedi et al., 2021; Y. Zhang et al., 2022; H. Zhang et al., 2022). In addition, GWAS and transcriptome-wide association studies in cotton revealed multiple heat-responsive loci associated with pollen stability, including genes involved in ER homeostasis, hormonal signalling, and carbohydrate metabolism (Ma et al., 2021; Ijaz et al., 2024), reinforcing the importance of integrated molecular pathways in pollen heat tolerance.

The significance of translation in pollen thermotolerance has been emphasised by recent research. By encouraging the overexpression of heat shock proteins like *HSP70,* the eukaryotic translation initiation factor *eIF3M2* plays a critical role in preserving pollen tube integrity under heat stress. Translational control is a crucial regulatory layer in pollen stress adaptation, as functional investigations have demonstrated that disruption of *eIF3M2* impairs pollen tube development and reduces thermotolerance. Furthermore, *HSP90* has been functionally identified as a crucial element of stress resilience in the male gametophyte, where it supports cellular homeostasis under high temperatures, regulatory protein stabilisation, and protein folding (Kahrizi et al., 2025a, 2025b).

Nevertheless, most multi-omics insights into pollen thermotolerance originate from a limited number of species, and their broader relevance across diverse crop plants has yet to be fully clarified.

4.2. Drought stress response

Drought-tolerance genotypes activate multiple protective molecular responses to preserve pollen viability under water-deficit conditions. Genes associated with abscisic acid (ABA) biosynthesis, osmoprotectant accumulation (such as proline), antioxidant enzymes, including superoxide dismutase and heat shock proteins, are upregulated, while aquaporin expression is maintained in pollen, as demonstrated in tomato (*Solanum lycopersicum*) (Lamin-Samu et al., 2021).

ABA plays a central role in coordinating drought responses and has been implicated in regulating pollen tube growth by modulating cellular hydration status and metabolic activity under stress conditions. Key components of the ABA-signalling pathway, including *PYR/PYL* receptors and downstream *SnRK2* kinases, play an important role in regulating drought-responsive gene expression and carbohydrate metabolism in pollen (Zhang et al., 2021).

Drought-induced pollen abortion is largely associated with tapetal degeneration, and transcription factors such as NAC have been shown to regulate redox homeostasis and metabolic balance, thereby protecting pollen development (Yu et al., 2019). These effects reflect both direct impacts on pollen physiology, such as a dehydration-induced metabolic disruption, and indirect effects mediated through altered tapetum function, which is essential for nutrient supply and pollen maturation.

In maize, drought tolerance involves the activation of stress-sensing enzymes such as histidine kinases, which trigger downstream signalling cascades mediated by transcription factors, including *WRKY* (Singh et al., 2023; Y. Zhang et al., 2022; H. Zhang et al., 2022). Tolerant lines display sustained expression of sugar transporters, starch biosynthetic enzymes, and cell wall-modifying proteins, thereby maintaining adequate carbohydrate supply to developing pollen. Increased antioxidant capacity further reduces drought-induced oxidative damage. Drought stress also affects the expression of genes associated with tapetum development and hormonal regulation, including ABA, gibberellic acid, and indole-3-acetic acid pathways, along with small RNAs, indicating the participation of epigenetic and post-transcriptional regulatory mechanisms in pollen drought tolerance.

In addition, ABA signalling components, including *PYR/PYL* receptors and *SnRK2* kinases, have been implicated in regulating pollen tube growth and carbohydrate metabolism under drought stress, indicating direct hormonal control of pollen performance (Zhang et al., 2021).

Collectively, these coordinated molecular responses contribute to the maintenance of pollen viability under drought conditions. However, despite the recognized importance of ABA signalling in drought responses, its direct and dynamic regulation of pollen tube growth under field-relevant drought stress remains insufficiently understood.

4.3. Salt stress response

Pollen under salinity shows decreased germination and abnormal wall formation, particularly in sensitive lines. Olive cultivars show varying tolerance to salinity, which causes deformation in pollen and lowers viability, due to different genotypes (Khaleghi et al., 2019). Na^{+}/K^{+} imbalance occurs as a result of ionic stress induced by salinity, which disrupts membrane integrity and metabolism. Na^{+} and K^{+} transporters, for example, *HKT* and components of the *CBL-CIPK* signalling pathway, have been shown to regulate ion homeostasis in plant tissues, including the anther (Ketehouli et al., 2019). Other ion transport regulators, including *NHX* antiporters and components of the *SOS* signalling pathways, have also been shown to play a role in maintaining cellular ion balance under salt stress. While ionic imbalance and osmotic stress directly affect pollen cells, salinity-induced changes in anther tissue physiology, including disruption of tapetal function, may also indirectly influence pollen development and fertility.

Pollen viability is considered a marker of sensitivity to salt stress, and the response can be enhanced by the upregulation of antioxidant enzymes or by breeding plants for increased osmoprotectant production and accumulation (Razzaq et al., 2019). Apart from inducing changes in pollen, salinity also disrupts pollen-pistil interaction by altering calcium signalling. In sunflowers, the expression of enzymes and molecules involved in ion transport and membrane stability required for pollen tube growth, such as annexins and H^+ -ATPase, is altered, and sunflower seedlings exposed to 120 mM NaCl exhibit high proteolytic degradation of OB membrane proteins, indicating membrane destabilisation (Bhatla et al., 2021).

Salinity stress response is largely mediated through ion homeostasis and hormonal regulation, particularly involving Na^+/H^+ exchanges (NHX), high-affinity potassium transporters (HKT), and the SOS signalling pathway. In addition, ABA-dependent signalling pathways contribute to stress adaptation by modulating gene expression and cellular responses. However, the specific functional roles of these pathways in pollen development and viability under salinity stress remain insufficiently characterised (Deinlein et al., 2014; Van Zelm et al., 2020; Ismail and Horie, 2017).

Abscisic acid (ABA), which accumulates under salinity stress, further regulates pollen tube elongation through modulation of Ca^{2+} signalling and cytoskeletal dynamics. Apart from molecular defence mechanisms against salt stress, certain plants have developed morphological adaptations through evolution. Harmomegathy, observed in some aquatic plants, helps maintain pollen viability by reducing the impact of fluctuating salinity. These plants have developed dynamic apertures that adjust water volume in response to osmotic changes. At the cellular level, salt stress induces endoplasmic reticulum (ER) stress related to protein folding, which is distinct from the cytosolic heat stress response mediated by heat shock proteins (Severova et al., 2022).

Although ion transporters such as HKT, NHX, and components of the SOS signalling pathways are well characterised in vegetative tissues, their direct functional roles in pollen remain less clearly defined. Current evidence in reproductive tissues is largely based on gene expression patterns and physiological correlations rather than targeted genetic validation. This indicates that the molecular mechanisms underlying pollen-specific salinity tolerance are still not fully resolved (Van Zelm et al., 2020; Ismail and Horie, 2017).

Compared to heat stress, molecular mechanisms underlying responses to salinity remain less well characterised. Much of the availability evidence is derived from vegetative tissues or whole-anther analyses, with limited studies focusing specifically on pollen, highlighting a specific gap in current understanding.

4.4. Cold stress response

Cold stress significantly affects pollen development by disrupting cellular metabolism, membrane fluidity, and cytoskeletal organisation, which ultimately reduces pollen viability and impairs fertilization. Low temperatures can also interfere with microsporogenesis and pollen maturation, often leading to delayed anther dehiscence and abnormal pollen germination.

One of the key molecular pathways involved in plant cold stress tolerance is the ICE–CBF–COR signalling cascade. In this pathway, the transcription factor *ICE1* activates C-repeat binding factors (*CBF1/CBF2/CBF3*), which in turn regulate the expression of cold-responsive (COR) genes associated with membrane stabilisation, osmoprotection, and antioxidant defence. Studies in *Arabidopsis* have shown that pollen-specific overexpression of CBF1 can improve fertility under temperature stress, suggesting that the CBF pathway plays an important role in maintaining reproductive resilience (Yun et al., 2025). The ICE-CBF-COR signalling pathway represents a central regulatory module in cold stress response, where ICE transcription factors activate *CBF* genes, which in turn regulate downstream *COR* genes involved in cellular protection. While this pathway is well established in vegetative tissues, its functional role in pollen remains less clearly defined, with most evidence based on expression studies rather than direct genetic validation in reproductive tissues (Shi et al., 2018; Ding et al., 2019). Cold stress therefore impacts reproductive success through both direct inhibition of pollen development and indirect effects mediated by altered tapetum activity and anther tissue organisation.

Cold stress can also disrupt reactive oxygen species (ROS) homeostasis and antioxidant defence systems. Under low-temperature conditions, increased ROS accumulation can damage cellular membranes and impair pollen tube growth. Therefore, the activation of antioxidant enzymes such as *SOD*, *CAT,* and *APX* plays an important role in protecting pollen from oxidative damage during cold stress.

Hormonal signalling pathways also play an important role in cold stress response. Auxin-mediated regulation of ROS homeostasis has been linked to reproductive thermotolerance through genes such as *OsLEML2* in rice, which helps regulate auxin signalling and maintain redox balance under stress conditions (Sun et al., 2025). In addition, cold stress can disrupt carbohydrate metabolism and sugar transport within the anther, reducing the energy available for pollen germination and pollen tube elongation.

Although considerable progress has been made in understanding cold stress responses in vegetative tissues, the molecular mechanisms that regulate cold tolerance during pollen development remain relatively less explored. Future studies that integrate transcriptomics, proteomics, and epigenetic profiling will be important for identifying pollen-specific regulators of cold tolerance across different crop species.

In addition to the ICE-CBF-COR pathway, functional studies in *Arabidopsis* have demonstrated that overexpression of *CBF* genes can partially restore pollen fertility under temperature stress, supporting a direct regulatory role in reproductive resilience. However, a substantial portion of current knowledge regarding cold-responsive genes is derived from studies in vegetative tissues, and pollen-specific functional validation remains limited. This highlights a critical gap in understanding the molecular basis of cold tolerance in reproductive development (Ding et al., 2019; Dong et al., 2022).

Although key cold-responsive pathways have been identified, including ICE-CBF-COR signalling, their specific roles in pollen development remain incompletely understood. Most insights are extrapolated from vegetative tissues, and direct evidence in pollen systems is still limited.

4.5. Shared response

As discussed in the previous sections, abiotic stresses, including heat, drought, and salinity, disrupt pollen development and can significantly impact fertilization success. To cope with these stress factors, plants exhibit certain responses that appear to be commonly expressed across stresses. Epigenetic modulations, such as DNA methylation and histone acetylation, as well as the role of miRNAs and other small RNAs in regulating gene expression under stress, are shown to contribute to stress resilience. Chromatin remodelling during meiosis and tapetum development aims to maintain fertility under stress in cereals (Begcy and Dresselhaus, 2018), while heat has been shown to alter histone methylation in pollen, affecting tapetum functioning and reducing viability (Chen et al., 2016).

Apart from epigenetic responses, redox signalling pathways are activated to combat oxidative damage in plants. Although reactive oxygen species (ROS) are toxic at higher concentrations, they also play a role in activating heat shock proteins and antioxidant enzymes, which protect pollen plasma membranes, organelles, and DNA. The systems are shared across major stress factors (Xie et al., 2022). Transcription factors such as *bZIP* and *WRKY* help connect ROS signalling with the regulation of stress-responsive genes, thereby contributing to tolerance against multiple environmental stresses (Shriti et al., 2024).

The central role of (ROS) and Ca^{2+} homeostasis in pollen survival has been demonstrated by increased antioxidant capacity and restored Ca^{2+} signalling in maize pollen under oxidative stress following treatment with selenium-fortified emmer wheatgrass extracts (Del Pino et al., 2022). These signalling pathways not only protect cellular structures but also maintain pollen viability, germination ability, and pollen tube growth, which are critical determinants of fertilization success.

Taken together, ROS signalling, Ca^{2+} homeostasis,s and epigenetic regulation emerge as common molecular nodes integrating stress perception with gene regulation and cellular protection, thereby providing mechanistic clarity on how diverse abiotic stresses converge on conserved pathways controlling pollen viability and fertilization success.

The genes summarised in Table 4.1 indicate that several molecular mechanisms regulating pollen stress tolerance are conserved across different plant species and stress conditions. For instance, transcription factors such as heat shock factors (HSFs) and other stress-responsive regulators have been reported to play key roles in pollen thermotolerance in multiple species, including *Arabidopsis thaliana*, rice, and tomato. Similarly, mechanisms involving reactive oxygen species (ROS) homeostasis, calcium signalling, and hormonal pathways appear to influence pollen viability and pollen tube growth under diverse abiotic stresses. However, the extent to which these regulatory pathways are conserved or diversified among crop species remains unclear. Moreover, comparable molecular studies investigating pollen responses to salinity, cold, and oxidative stress are relatively limited, highlighting important gaps in our understanding of pollen stress adaptation across plant systems.

It is important to note that while several genes discussed above have been identified through transcriptomic and association-based studies, only a subset have been validated through direct functional genetic approaches. Therefore, interpretations of gene function should be considered in the context of the type and strength of supporting evidence, particularly when extrapolating their roles in pollen stress tolerance (Atanasov et al., 2021).

Table 4.1

Key genes regulating pollen responses to abiotic stress.

Gene/protein	Stress type	Molecular function	Plant species	Evidence	Reference
IRE1	Heat	ER stress sensor activating unfolded protein response (UPR)	*Arabidopsis thaliana, Zea mays* (maize)	Mutant phenotype, RNA-seq	Chaturvedi et al., 2021
bZIP60	Heat	Transcription factor regulating UPR gene expression	*Arabidopsis thaliana*	Mutant phenotype, transcriptomics	Chaturvedi et al., 2021
bZIP17	Heat	ER stress signalling and protein quality control	*Arabidopsis thaliana*	Mutant phenotype	Singh et al., 2021
bZIP28	Heat	ER stress signalling and thermotolerance regulation	*Arabidopsis thaliana*	Mutant phenotype	Singh et al., 2021
HSFA1	Heat	Master heat shock transcription factor activating HSP genes	*Arabidopsis thaliana, Triticum aestivum* (wheat)	Mutant phenotype, expression analysis	Raja et al., 2019
HSFA2	Heat	Heat stress transcription factor involved in acquired thermotolerance	*Arabidopsis thaliana, Solanum lycopersicum* (tomato)	Overexpression, transcriptomics	Raja et al., 2019
HSP70	Heat	Molecular chaperone preventing protein misfolding	*Arabidopsis thaliana, Zea mays* (maize)*, Oryza sativa* (rice)	Transcriptomic association	Chaturvedi et al., 2021
HSP90	Heat	Protein folding and stabilisation mediate stress resilience in the male gametophyte	*Arabidopsis thaliana*	Functional study	Kahrizi et al., 2025a
HSP101	Heat	Protein disaggregation and protection of pollen viability	*Arabidopsis thaliana,* rice *(Oryza sativa)*	Mutant phenotype	Li et al., 2025
GhAL5	Heat	Chromatin remodelling regulates the thermotolerant male fertility	*Gossypium hirsutum* (cotton)	Mutant analysis, chromatin assays	Li et al., 2026
SOD (superoxide dismutase)	Heat, drought, cold	Detoxification of superoxide radicals	*Zea mays* (maize), *Oryza sativa* (rice), *Triticum aestivum* (wheat)	Enzyme activity assays	Xie et al., 2022
CAT (catalase)	Heat, drought, cold	Decomposition of hydrogen peroxide	*Arabidopsis thaliana, Oryza sativa* (rice)	Enzyme activity assays	Xie et al., 2022
APX (ascorbate peroxidase)	Heat, drought, cold	ROS scavenging and redox balance	*Oryza sativa* (rice), *Triticum aestivum* (wheat)	Enzyme activity assays, transcriptomics	Xie et al., 2022
PYR/PYL receptors	Drought	ABA perception and signal transduction	*Arabidopsis thaliana, Oryza sativa* (rice)	Mutant phenotype, biochemical assays	Zhang et al., 2021
SnRK2	Drought	Kinase regulating ABA-responsive transcription	*Arabidopsis thaliana, Zea mays* (maize)	Mutant phenotype	Zhang et al., 2021
WRKY TFs	Drought	Regulation of stress-responsive gene expression	*Zea mays* (maize)	Transcriptomics, functional validation	Singh et al., 2023
NAC TFs	Drought	Regulation of redox balance and tapetal stability	*Oryza sativa* (rice), *Triticum aestivum* (maize)	Mutant phenotype	Yu et al., 2019
HKT1	Salinity	Na^+ transporter regulating ion homeostasis	*Arabidopsis thaliana, Triticum aestivum* (maize)	Mutant phenotype	Ketehouli et al., 2019
CBL	Salinity	Calcium sensor in stress signalling pathways	*Arabidopsis thaliana, Oryza sativa* (rice)	Mutant phenotype	Ketehouli et al., 2019
CIPK	Salinity	Kinase interacting with CBL proteins for ion regulation	*Arabidopsis thaliana, Oryza sativa* (rice)	Mutant phenotype	Ketehouli et al., 2019
NHX	Salinity	The vacuolar Na^+/H^+ antiporter maintains ionic balance	*Arabidopsis thaliana, Solanum lycopersicum* (tomato)	Mutant phenotype	Razzaq et al., 2019
SOS1	Salinity	Plasma membrane Na^+/H^+ exchanger	*Arabidopsis thaliana, Oryza sativa* (rice)	Mutant phenotype	Razzaq et al., 2019
ICE1	Cold	Transcription factor initiating cold signalling	*Arabidopsis thaliana*	Mutant phenotype	Yun et al., 2025
CBF1/CBF2/ CBF3	Cold	Regulator of cold-responsive gene expression/ Cold stress transcriptional regulator/ Activation of cold-responsive genes	*Arabidopsis thaliana*	Overexpression study/ Expression analysis/ Overexpression study	Yun et al., 2025
OsLEML2	Heat, cold	Regulation of auxin signalling and ROS homeostasis	*Oryza sativa* (rice)	Mutant phenotype	Sun et al., 2025
eIF3M2	Heat	Translational regulation, maintains pollen tube integrity via *HSP70* upregulation.	*Arabidopsis thaliana*	Functional study, mutant phenotype	Kahrizi et al., 2025b

5. Model systems and experimental tools

Different plants have been used to study the pollen response to abiotic stressors, and this has been achieved by integrating molecular, physiological, and imaging strategies. The model system selected for the study has been crucial to unfold the response mechanisms to stress at distinct regulatory levels.

Recent advances in molecular biology and genomics have enabled the use of multiple experimental tools to investigate pollen stress responses at the transcriptomic, epigenetic, and functional levels. Techniques such as RNA sequencing (RNA-seq), chromatin accessibility profiling (ATAC-seq), genome editing, and quantitative gene expression analysis are widely applied to identify stress-responsive genes, regulatory networks, and functional pathways in pollen development. However, each methodological approach presents specific advantages and limitations that must be considered during experimental design and interpretation of results. A comparison of commonly used tools in pollen stress research is summarised in the table below (Table 5.1).

Arabidopsis thaliana (Thale Cress) is one of the primary genetic models employed for the study of pollen response to heat and is particularly useful due to its short life cycle, access to a wide range of mutant types, and its suitability for functional genomic analyses. This plant model has been specifically used to confirm the mechanistic role of transcription factors and signalling pathways of the endoplasmic reticulum in stress response. In-depth analysis of heat shock transcription factors and epigenetic modifications has been possible in *Arabidopsis* using tools like CRISPR-Cas9, RNA sequencing, and methylation assays, often performed at defined stages of pollen development to capture stage-specific transcriptional responses to stress. Additionally, the expression of genes under stress has been validated through qRT-PCR (Chaturvedi et al., 2021; Chen et al., 2016). However, direct physiological and biochemical assays are limited due to the small pollen size of the plant.

Table 5.1
Experimental tools used to study pollen stress responses and their advantages and disadvantages.

Tools	Advantage	Limitation	Reference
RNA-seq	Enables genome-wide identification of stress-responsive genes and transcriptional changes during pollen development.	Measures gene expression but cannot directly establish gene function or causal relationships.	Stark et al., 2019
ATAC-seq	Identifies chromatin accessibility and regulatory elements controlling stress-responsive gene expression.	Requires high-quality nuclei isolation and careful sample preparation, which can be challenging for small reproductive tissues.	Shaw et al., 2021
CRISPR/Cas genome editing	Allows precise functional validation of candidate genes involved in pollen development and stress tolerance.	Potential off-target mutations and requirements for efficient plant transformation systems.	Wang et al., 2022
qRT-PCR	Provides sensitive validation of gene expression	Limited to targeted genes and does not provide genome-wide expression information.	Upton et al., 2023
Proteomics	Identifies stress-responsive proteins and post-translational modifications involved in pollen stress responses.	May fail to detect low-abundance regulatory proteins and requires complex protein extraction procedures.	Tu et al., 2022
Metabolomics	Reveals metabolomic changes associated with pollen stress tolerance and energy metabolism.	Data interpretation is complex, and metabolite identification may be incomplete.	Tu et al., 2022

Oryza sativa (Rice) has been used to study the effect of cold and heat stress during flowering because the plant is known for its agronomic relevance and has well-defined reproductive development. Transcriptomic analysis, hormonal analysis, and ultrastructure studies of the tapetum have revealed the roles of abscissic acid and the sugar transport system in pollen sterility caused by stress (Begcy and Dresselhaus, 2018). These studies show that the effect of stress in the tissues surrounding the pollen also contributes to pollen failure, complementing pollen-focused analyses in *Arabidopsis.* In many studies, sampling is aligned with specific stages of anther and pollen development to ensure that stress-induced transcriptional and physiological responses are accurately captured.

Drought and heat stress responses have been investigated in *Zea mays* (Maize) pollen using RNA-sequencing, metabolomics, and pollen viability assay. These approaches have unveiled the disruption of sugar metabolism, accumulation of reactive oxygen species, and hampered pollen germination under field-relevant conditions. Such multi-omics analyses are often combined with physiological measurements and targeted validation experiments to strengthen the interpretation of stress-induced molecular changes. The expression of sugar transporters and antioxidant enzymes has been further confirmed with qRT-PCR validation (Y. Zhang et al., 2022; H. Zhang et al., 2022; Del Pino et al., 2022).

The large anthers of *Solanum lycopersicum* (Tomato) make it suitable for in vitro germination studies, imaging, and proteomics to analyse heat and salinity response. Under stress, it has been shown that the remodelling of the cell walls and hampered growth of pollen tubes limit fertility success (Parrotta et al., 2019). These traits allow direct visualisation of pollen tube growth under stress, which is difficult in models with smaller flowers.

Genome-wide association studies and Transcriptome Wide Association Studies of *Gossypium hirsutum* (Cotton) have been used to identify genes involved in male sterility due to heat (Ma et al., 2021). Although functional validation of the genes remains limited, these studies serve as a bridge between regulation at the molecular level and crop performance. *Nicotiana tabacum* (Tobacco) has been studied under cold stress to observe pollen tube integrity and growth disruption with the help of confocal microscopy and staining techniques owing to its large pollen grains and fast-growing pollen tubes (Parrotta et al., 2019).

Studies across various models and crop species suggest that several core stress-response mechanisms, such as heat shock protein response, detoxification of reactive oxygen species, hormonal regulation, and calcium signalling, are broadly conserved in pollen across flowering plants. However, the regulation and extent to which these pathways contribute to stress response vary among species, and the different developmental stages, and some of these responses may be specific to the species or influenced by surrounding reproductive tissues.

While these experimental systems and molecular tools have significantly advanced our understanding of pollen stress responses, high-throughput approaches such as RNA-seq, ATAC-seq, and other multi-omics technologies require careful experimental design for reliable interpretation. This includes precise developmental staging of anthers and pollen, appropriate biological replication, and standardised stress treatments. Detailed reporting of experimental conditions and metadata is also important to ensure reproducibility and enable meaningful comparisons across studies and species.

6. Gap and future directions

Significant progress has been made in understanding the molecular mechanisms underlying pollen responses to abiotic stress. However, most studies remain focused on the responses to heat and drought stress, while pollen responses to cold, salinity, and oxidative stress are comparatively understudied, particularly with respect to epigenetic regulation and the role of non-coding RNAs in stress response. In addition, although several molecular regulators such as heat shock transcription factors (*HSFs*), unfolded protein response components (*bZIP60*, *IRE1*), and ABA signalling regulators (*PYR/PYL* receptors and *SnRK2* kinases) have been implicated in pollen stress responses, many of these relationships are derived primarily from transcriptomic or association studies rather than direct functional genetic validation. Moreover, current knowledge is largely based on a limited number of model species, such as *Arabidopsis thaliana,* rice, and maize, while many agriculturally important and stress-adapted crops remain poorly explored.

Future research should focus on expanding the studies on pollen-specific stress to include cold, salinity, and oxidative stress responses, especially in understudied crops and plants that naturally adapt to extreme environmental conditions. Particular emphasis should be placed on identifying pollen- and tapetum-specific regulatory genes and transcriptional networks that control microspore development, pollen maturation, and pollen tube growth under abiotic stress conditions. Integration of advanced molecular approaches, including multi-omics analyses like transcriptomics, epigenomics [e.g., Assay for Transposase Accessible Chromatin using sequencing (ATAC-seq)], proteomics, and metabolomics, will be key to capturing the complex network of pollen stress-response. Emerging tools and technologies, such as single-cell and spatial transcriptomics, also offer opportunities to unravel responses specific to a particular cell type or developmental stage during the development of pollen under abiotic stress. These approaches may help distinguish molecular responses occurring in different anther tissues, such as the tapetum, developing microspores, and mature pollen grains, which often exhibit distinct stress sensitivities.

Additionally, comparative analyses of cultivated crop species with their wild relatives may reveal conserved and novel regulatory pathways with respect to tolerance of pollen against stress. Genome editing technologies such as CRISPR/Cas systems also provide promising opportunities to functionally validate candidate genes and to engineer crops with improved reproductive stress tolerance. Finally, the gap between molecular insights derived from laboratory experiments and their confirmation at the field level, along with plant breeding strategies, must be bridged as a crucial step to translate fundamental knowledge into approaches for developing plants for the future, which are climate resilient and reproductively stable. Bridging this gap will require coordinated studies integrating molecular genetics, physiological analyses, and field-based validation to determine whether stress-responsive genes of candidate plants identified under controlled conditions contribute to improved pollen fertility under realistic environmental conditions.

7. Conclusion

Abiotic stresses, including heat, drought, salinity, cold, and oxidative stress, pose a significant threat to pollen development, viability, and germination, thereby causing a direct impact on plant fertilization success and crop yield. Studies to date have identified several key stress-responsive genes and regulatory networks controlling pollen responses, including transcription factors, hormonal signalling, ion transporters, and epigenetic modifications, with most insights into these mechanisms derived from model plant systems such as *Arabidopsis*, rice, e and maize. However, the depth of understanding remains unevenly spread across the different stress types, molecular and genetic mechanisms governing pollen responses to salinity, cold, and oxidative stress remaining comparatively less explored.

Particularly, the roles of epigenetic regulation and non-coding RNAs in modulating pollen stress tolerance remain poorly understood. Addressing these gaps will require the integration of gene-focused molecular studies with advanced multi-omics approaches, including transcriptomics, epigenomics, proteomics, and metabolomics, combined with cell-type-specific analyses of pollen development under stress conditions. Furthermore, functional characterisation of stress-responsive genes identified in different plant species and field-level validation of findings will be essential to translate fundamental insights into strategies that can improve the fertility of pollen grains and reproductive stability in crops under the changing climate.

Future research should prioritise pollen-specific functional validation of candidate genes across diverse abiotic stress conditions to establish causal regulatory mechanisms and improve their translational potential in crop improvement programs.

CRediT authorship contribution statement

Nadiyah Thajudeen: Conceptualization. **Deepika Vasudevan:** Data curation. **V. Ramesh Kumar:** Formal analysis. **Prakash Pandurangan:** Supervision. **Meenambiga Setti Sudharsan:** Validation. **Ravindran Jaganathan:** Project administration.

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.

Data availability

No data was used for the research described in the article.

References

Atanasov, A.G., Zotchev, S.B., Dirsch, V.M., Supuran, C.T., 2021 Mar. Natural products in drug discovery: advances and opportunities. Nat. Rev. Drug Discov. 20 (3), 200–216.

Begcy, K., Dresselhaus, T., 2018. Epigenetic responses to abiotic stresses during reproductive development in cereals. Plant Reprod. 31 (4), 343–355.

Bennett, J.M., Steets, J.A., Burns, J.H., Durka, W., Vamosi, J.C., Arceo-Gómez, G., Burd, M., Burkle, L.A., Ellis, A.G., Freitas, L., Li, J., 2018 Nov 20. GloPL, a global data base on pollen limitation of plant reproduction. Sci. Data 5 (1), 180249.

Bhatla, S.C., Gogna, M., Jain, P., Singh, N., Mukherjee, S., Kalra, G., 2021. Signalling mechanisms and biochemical pathways regulating pollen-stigma interaction, seed development, and seedling growth in sunflower under salt stress. Plant Signal. Behav. 16 (11), 1958129.

Cai, G., Del Duca, S., 2019. Pollen tube and plant reproduction. Int. J. Mol. Sci. 20 (3), 531.

Chaturvedi, P., Wiese, A.J., Ghatak, A., Zaveska Drabkova, L., Weckwerth, W., Honys, D., 2021. Heat stress response mechanisms in pollen development. New Phytol. 231 (2), 571–585.

Chen, Y., Müller, F., Rieu, I., Winter, P., 2016. Epigenetic events in plant male germ cell heat stress responses. Plant Reprod. 29 (1–2), 21–29.

Deinlein, U., Stephan, A.B., Horie, T., Luo, W., Xu, G., Schroeder, J.I., 2014 Jun 1. Plant salt-tolerance mechanisms. Trends Plant Sci. 19 (6), 371–379.

Del Pino, A.M., Falcinelli, B., D'Amato, R., Businelli, D., Benincasa, P., Palmerini, C.A., 2022. In Vitro oxidative stress threatening maize pollen germination and cytosolic Ca2+ can be mitigated by extracts of emmer wheatgrass biofortified with selenium. Plants 11 (7), 859.

Ding, Y., Shi, Y., Yang, S., 2019 Jun. Advances and challenges in uncovering cold tolerance regulatory mechanisms in plants. New Phytol. 222 (4), 1690–1704.

Dong, B., Zheng, X., Liu, H., Able, J.A., Yang, H., Zhao, H., Zhang, M., Qiao, Y., Wang, Y., Liu, M., 2017 Jun 20. Effects of drought stress on pollen sterility, grain yield, abscisic acid and protective enzymes in two winter wheat cultivars. Front. Plant Sci. 8, 1008.

Dong, Q., Wallrad, L., Almutairi, B.O., Kudla, J., 2022 Feb. Ca2+signalling in plant responses to abiotic stresses. J. Integr. Plant Biol. 64 (2), 287–300.

Huang, B., Fan, Y., Cui, L., Li, C., Guo, C., 2022. Cold stress response mechanisms in anther development. Int. J. Mol. Sci. 24 (1), 30.

Ijaz, A., Anwar, Z., Ali, A., Ditta, A., Shani, M.Y., Haidar, S., Wang, B., Fang, L., Khan, S. M., Khan, M.K., 2024 Jun 11. Unraveling the genetic and molecular basis of heat stress in cotton. Front. Genet. 15, 1296622.

Ismail, A.M., Horie, T., 2017 Apr 28. Genomics, physiology, and molecular breeding approaches for improving salt tolerance. Annu. Rev. Plant Biol. (68), 405–434.

Jegadeesan, S., Beery, A., Altahan, L., Meir, S., Pressman, E., Firon, N., 2018. Ethylene production and signalling in tomato (Solanum lycopersicum) pollen grains are responsive to heat stress conditions. Plant Reprod. 31 (4), 367–383.

Jha, U.C., Nayyar, H., Jha, R., Khurshid, M., Zhou, M., Mantri, N., Siddique, K.H., 2020. Long non-coding RNAs: emerging players regulating plant abiotic stress response and adaptation. BMC Plant Biol. 20 (1), 466.

Jia, M.X., Shi, Y., Di, W., Jiang, X.R., Xu, J., Liu, Y., 2017. ROS-induced oxidative stress is closely related to pollen deterioration following cryopreservation. In Vitro Cell. Dev. Biol. Plant 53 (4), 433–439.

Jin, Y., Pan, W., Zheng, X., Cheng, X., Liu, M., Ma, H., Ge, X., 2018. OsERF101, an ERF family transcription factor, regulates drought stress response in reproductive tissues. Plant Mol. Biol. 98 (1), 51–65.

Kahrizi, Z., Michailidis, C., Raabe, K., Kumar, V., Honys, D., Hafidh, S., 2025 Jan. The translation initiation factor eIF3M2 upregulates HEAT SHOCK PROTEIN 70 to maintain pollen tube membrane integrity during heat shock. Plant Physiol. 197 (1), kiae643.

Kahrizi, Z., Michailidis, C., Raabe, K., Fíla, J., Klodová, B., Steinbachová, L., Rudolf, J., Schrumpfová, P.P., Honys, D., Fragkostefanakis, S., 2025 Oct 30. HSP90-mediated stress resilience in male gametophyte of Arabidopsis thaliana. Plant Stress 101114.

Keller, M., Schleiff, E., Simm, S., 2020. miRNAs involved in transcriptome remodeling during pollen development and heat stress response in Solanum lycopersicum. Sci. Rep. 10 (1), 10694.

Ketehouli, T., Idrice Carther, K.F., Noman, M., Wang, F.W., Li, X.W., Li, H.Y., 2019. Adaptation of plants to salt stress: characterization of Na+ and K+ transporters and role of CBL gene family in regulating salt stress response. Agronomy 9 (11), 687.

Khaleghi, E., Karamnezhad, F., Moallemi, N., 2019. Study of pollen morphology and salinity effect on the pollen grains of four olive (Olea europaea) cultivars. S. Afr. J. Bot. 127, 51–57.

Ko, S.S., Li, M.J., Sun-Ben, Ku M., Ho, Y.C., Lin, Y.J., Chuang, M.H., Hsing, H.X., Lien, Y. C., Yang, H.T., Chang, H.C., Chan, M.T., 2014 Jun 1. The bHLH142 transcription factor coordinates with TDR1 to modulate the expression of EAT1 and regulate pollen development in rice. Plant Cell 26 (6), 2486–2504.

Lamin-Samu, A.T., Farghal, M., Ali, M., Lu, G., 2021. Morpho-physiological and transcriptome changes in tomato anthers of different developmental stages under drought stress. Cells 10 (7), 1809.

Li, Y., Yang, J., Zhang, J., Xin, Z., Xu, R., Qiu, K., Wang, F., Sun, F., Jiang, H., Jin, W., Jiang, P., 2025 Dec 16. Heat shock protein 101 safeguards meiotic thermotolerance of male germlines in rice and Arabidopsis. Crop J.

Li, Y., Yang, J., Wang, W., Zuo, C., Pei, L., Ma, Y., Zhang, R., Fan, Y., Ma, H., Li, Y., Liu, R., 2026 Jan 4. Chromatin topology reconfiguration orchestrates thermotolerant male fertility via GhAL5 in cotton. Adv. Sci. 13, e07766.

Ma, Y., Min, L., Wang, J., Li, Y., Wu, Y., Hu, Q., Ding, Y., Wang, M., Liang, Y., Gong, Z., Xie, S., 2021 Jul. A combination of genome-wide and transcriptome-wide association studies reveals genetic elements leading to male sterility during high temperature stress in cotton. New Phytol. 231 (1), 165–181.

Opedal, Ø.H., Pérez-Barrales, R., Brito, V.L., Muchhala, N., Capó, M., Dellinger, A., 2023. Pollen is the link between floral phenotype and fitness. Am. J. Bot. 110 (6), e16200.

Pacini, E., Dolferus, R., 2019. Pollen developmental arrest: maintaining pollen fertility in a world with a changing climate. Front. Plant Sci. 10, 679.

Parrotta, L., Faleri, C., Guerriero, G., Cai, G., 2019. Cold stress affects cell wall deposition and growth pattern in tobacco pollen tubes. Plant Sci. 283, 329–342.

Pereira, A.M., Coimbra, S., 2019. Advances in plant reproduction: from gametes to seeds. J. Exp. Bot. 70 (11), 2933–2936.

Raja, M.M., Vijayalakshmi, G., Naik, M.L., Basha, P.O., Sergeant, K., Hausman, J.F., Khan, P.S.S.V., 2019. Pollen development and function under heat stress: from effects to responses. Acta Physiol. Plant. 41 (4), 47.

Razzaq, M.K., Rauf, S., Khurshid, M., Iqbal, S., Bhat, J.A., Farzand, A., Riaz, A., Xing, G., Gai, J., 2019 Dec 1. Pollen Viability an Index of Abiotic Stresses Tolerance and Methods for the Improved Pollen Viability. Pak. J. Agric. Res. 32 (4).

Ren, R., Li, Z., Zhang, L., Zhou, H., Jiang, X., Liu, Y., 2021. Enzymatic and nonenzymatic antioxidant systems impact the viability of cryopreserved Paeonia suffruticosa pollen. Plant Cell Tissue Organ Cult. 144 (1), 233–246.

Rosenberger, N.M., Hemberger, J.A., Williams, N.M., 2024. Heatwaves exacerbate pollen limitation through reductions in pollen production and pollen vigour. AoB Plants 16 (5), plae045.

Santiago, J.P., Sharkey, T.D., 2019. Pollen development at high temperature and role of carbon and nitrogen metabolites. Plant Cell Environ. 42 (10), 2759–2775.

Severova, E.E., Rudall, P.J., Macfarlane, T.D., Krasnova, E.D., Sokoloff, D.D., 2022. Pollen in water of unstable salinity: evolution and function of dynamic apertures in monocot aquatics. Am. J. Bot. 109 (4), 500–513.

Shaw, R., Tian, X., Xu, J., 2021 Jan 4. Single-cell transcriptome analysis in plants: advances and challenges. Mol. Plant 14 (1), 115–126.

Shi, Y., Ding, Y., Yang, S., 2018 Jul 1. Molecular regulation of CBF signaling in cold acclimation. Trends Plant Sci. 23 (7), 623–637.

Shriti, S., Bhar, A., Roy, A., 2024. Unveiling the role of epigenetic mechanisms and redox signaling in alleviating multiple abiotic stress in plants. Front. Plant Sci. 15, 1456414.

Singh, A., Pandey, H., Pandey, S., Lal, D., Chauhan, D., Aparna, Antre, S.H., Kumar, A., 2023 Dec. Drought stress in maize: stress perception to molecular response and strategies for its improvement. Funct. Integr. Genomics 23 (4), 296.

Singh, M.B., Lohani, N., Bhalla, P.L., 2021. The role of endoplasmic reticulum stress response in pollen development and heat stress tolerance. Front. Plant Sci. 12, 661062.

Smith, L.M., 2019. The heat is on: maize pollen development after a heat wave. Plant Physiol. 181 (2), 387–388.

Sorensen, A.M., Kröber, S., Unte, U.S., Huijser, P., Dekker, K., Saedler, H., 2003. The Arabidopsis ABORTED MICROSPORES (AMS) gene encodes a MYC class transcription factor. Plant J. 33 (2), 413–423.

Stark, R., Grzelak, M., Hadfield, J., 2019 Nov. RNA sequencing: the teenage years. Nat. Rev. Genet. 20 (11), 631–656.

Sun, X., Wang, Y., Chen, Y., Zhang, P., Li, Y., Ouyang, T., Li, L., Zhu, J., Jia, X., Ye, X., Zhu, J., 2025 Dec. OsLEML2 Regulates Rice Thermotolerance Through Auxin and ROS Homeostasis. Rice 18 (1), 99.

Tu, M., Zeng, J., Zhang, J., Fan, G., Song, G., 2022 Dec 8. Unleashing the power within short-read RNA-seq for plant research: beyond differential expression analysis and toward regulomics. Front. Plant Sci. (13), 1038109

Upton, R.N., Correr, F.H., Lile, J., Reynolds, G.L., Falaschi, K., Cook, J.P., Lachowiec, J., 2023 Jun 30. Design, execution, and interpretation of plant RNA-seq analyses. Front. Plant Sci. (14), 1135455

Van Zelm, E., Zhang, Y., Testerink, C., 2020 Apr 29. Salt tolerance mechanisms of plants. Annu. Rev. Plant Biol. 71 (1), 403–433.

Wang, Y., Zafar, N., Ali, Q., Manghwar, H., Wang, G., Yu, L., Ding, X., Ding, F., Hong, N., Wang, G., Jin, S., 2022 Dec 5. CRISPR/Cas genome editing technologies for plant improvement against biotic and abiotic stresses: advances, limitations, and future perspectives. Cells 11 (23), 3928.

Xie, D.L., Zheng, X.L., Zhou, C.Y., Kanwar, M.K., Zhou, J., 2022. Functions of redox signaling in pollen development and stress response. Antioxidants 11 (2), 287.

Xu, J., Yang, C., Yuan, Z., Zhang, D., Gondwe, M.Y., Ding, Z., Liang, W., Zhang, D., Wilson, Z.A., 2010 Jan 1. The ABORTED MICROSPORES regulatory network is required for postmeiotic male reproductive development in Arabidopsis thaliana. The Plant Cell 22 (1), 91–107.

Yu, J., Jiang, M., Guo, C., 2019. Crop pollen development under drought: from the phenotype to the mechanism. Int. J. Mol. Sci. 20 (7), 1550.

Yun, S.D., Kim, E.Y., Oh, S.A., Park, S.K., 2025. Targeted overexpression of CBF1 using a pollen-specific promoter enhances fertility in heat-stressed Arabidopsis. J. Plant Biol. 68 (5), 389–401.

Zhang, H., Zhu, J., Gong, Z., Zhu, J.K., 2022b. Abiotic stress responses in plants. Nat. Rev. Genet. 23 (2), 104–119.

Zhang, W., Sun, Y., Timofejeva, L., Chen, C., Grossniklaus, U., Ma, H., 2006. Regulation of Arabidopsis tapetum Development and Function by DYSFUNCTIONAL TAPETUM1 (DYT1) Encoding a Putative bHLH Transcription Factor.

Zhang, Y., Soualihou, S., Li, J., Xu, Y., Rose, R.J., Ruan, Y.L., Li, J., Song, Y., 2022 May 11. Transcriptome analysis of maize pollen grains under drought stress during flowering. Crop Pasture Sci. 73 (9), 1026–1041.

Zhang, Z., Hu, M., Xu, W., Wang, Y., Huang, K., Zhang, C., Wen, J., 2021. Understanding the molecular mechanism of anther development under abiotic stresses. Plant Mol. Biol. 105 (1), 1–10.

Zhu, J., Lou, Y., Xu, X., Yang, Z.N., 2011. A genetic pathway for tapetum development and function in Arabidopsis. J. Integr. Plant Biol. 53 (11), 892–900.