

REVIEW

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The neglected other half - role of the pistil in plant heat stress responses

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Abstract

Heat stress coinciding with reproductive stage leads to a significant loss in reproductive organs viability, resulting in lower seed-set and crop productivity. Successful fertilization and seed formation are determined by the viability of male and female reproductive organs. The impact of heat stress on the male reproductive organ (pollen) is studied more often compared to the female reproductive organ (pistil). This is attributed to easier accessibility of the pollen coupled with the notion that the pistil's role in fertilization and seed-set under heat stress is negligible. However, depending on species and developmental stages, recent studies reveal varying degrees of sensitivity of the pistil to heat stress. Remarkably, in some cases, the vulnerability of the pistil is even greater than the pollen. This article summarizes the current knowledge of the impact of heat stress on three critical stages of pistil for successful seed-set, that is, female reproductive organ development (gametogenesis), pollen-pistil interactions including pollen capture on stigma and pollen tube growth in style, as well as fertilization and early embryogenesis. Further, future research directions are suggested to unravel molecular basis of heat stress tolerance in pistil, which is critical for sustaining crop yields under predicted warming scenarios.

KEYWORDS

embryo formation, female reproductive organ, fertilization, heat stress, ovule development, pistil, pollination

1 | INTRODUCTION

An exponential increase in human population accompanied by a rapidly changing climate is increasing the demand for food and, at the same time, destabilizing global agricultural production (Bajželj et al., 2014; Wiebe, Robinson, & Cattaneo, 2019). Among the major drivers of climate change, increasing temperature leading to heat stress is emerging as a primary factor affecting crop yields negatively (Ortiz-Bobea, Wang, Carrillo, & Ault, 2019). This has increased the need to better understand mechanisms that are important for adapting plants to heat stress or heat waves (Jagadish, Way, & Sharkey, 2021). Knowledge generated can be used for developing crop varieties that can maintain productivity under heat stress

conditions, to ensure sustained food supply in the future (Hammer et al., 2020; Wang et al., 2020).

Among the critical developmental stages, sexual gametogenesis and flowering are known to be extremely sensitive to heat stress in crop plants, negatively affecting seed-set and ultimately grain yield (Prasad, Bheemanahalli, & Jagadish, 2017). The increase in intensity and frequency of heat stress coinciding with these reproductive stages increases spikelet sterility by reducing the viability of male and female reproductive organs (Jagadish, 2020; Lohani, Singh, & Bhalla, 2020; Pfliegerer, Schleussner, Kornhuber, & Coumou, 2019).

Thus far, the pollen, or male reproductive organ, has often been investigated for its response to heat stress. This is because it is easily accessible compared to the ambiguous nature of female reproductive

organ (gametophytes/embryo sacs/ovules/ovaries) coupled with the observation that pollen exhibits greater sensitivity to heat stress than the female reproductive organ in different crop plants such as maize (*Zea mays* L.; Wang et al., 2019), sorghum (*Sorghum bicolor* L. Moench; Djanaguiraman, Perumal, Jagadish, et al., 2018), canola (*Brassica napus* L.; Young, Wilen, & Bonham-Smith, 2004) and chickpea (*Cicer arietinum* L.; Devasirvatham et al., 2013). The pronounced heat-sensitivity of pollen grain could be due to the direct exposure to heat and dry air (Jagadish, 2020; Westgate & Boyer, 1986).

Ovules, in contrast, are enclosed within ovaries, thus the impact of stress on ovules is considered to be relatively less (Gasser & Robinson-Beers, 1993). Nevertheless, recent studies suggest a greater sensitivity of the female compared with male reproductive organ in some plant species such as pearl millet (*Pennisetum glaucum* L. [R.]; Djanaguiraman, Perumal, Ciampitti, Gupta, & Prasad, 2018; Gupta et al., 2015) and provide the impetus for a more detailed account on the current status of heat stress impact on the female reproductive organ.

The female reproductive organ in an angiosperm flower is commonly referred to as the pistil, which is composed of stigma, style and ovary, wherein the gametophyte (i.e., embryo sac or

megagametophyte) develops within the ovule (Figure 1; Yadegari & Drews, 2004). On the basis of physiological processes associated with the pistil development and function, three distinct stages are apparent, namely, gametophyte development, pollen–pistil interactions including pollen capture on stigma and pollen tube growth in style and fertilization and early embryogenesis. It appears that each of these stages have differential sensitivities and distinct responses during heat stress, which also show variation among different plant species.

In this review, the current status of morphological, anatomical, physiological and molecular changes of the pistil subjected to heat stress has been summarized. In addition, future research directions to better understand the role of the pistil in maintaining fertility and seed-set under heat stress are proposed.

2 | FEMALE GAMETOPHYTE DEVELOPMENT (PRE-POLLINATION)

Upon exposure to heat stress, the female organ sterility has been shown to partly contribute to a decrease in seed-set percentage,

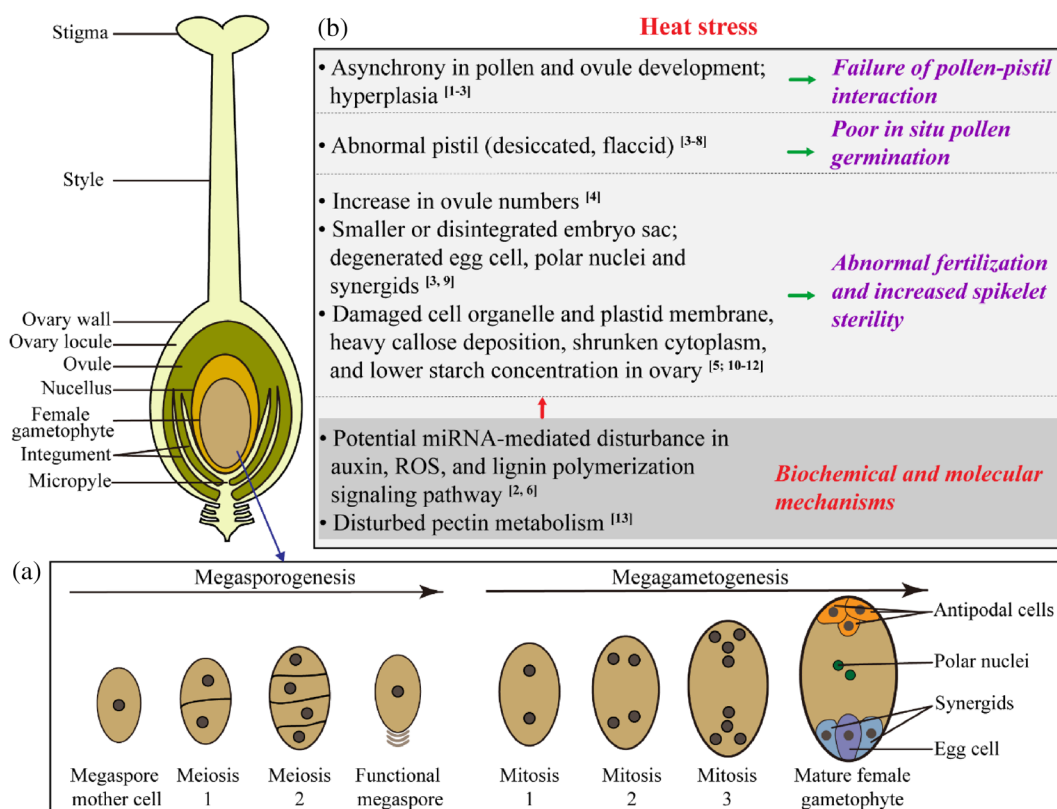


FIGURE 1 Female reproductive organ (pistil) development (a) and responses to heat stress in plants (b). The female gametophyte developmental stages are replicated from Yadegari and Drews (2004), with modification. Studies from which the morphological, anatomical and molecular responses are summarized are referenced according to the crop, with the numbers in parenthesis in the legend aligned with the number and related change listed above in the grey box. Crops and related references: maize—[1] (Cicchino, Edreira, Uribealarea, & Otegui, 2010); tomato—[2] (Pan et al., 2017); canola—[3] (Polowick & Sawhney, 1988); chickpea—[4] (Devasirvatham et al., 2013); sorghum—[5] (Djanaguiraman, Perumal, Jagadish, et al., 2018); [10] (Chiluwal et al., 2020); wheat—[6] (Prasad & Djanaguiraman, 2014); [9] (Saini, Sedgley, & Aspinall, 1983); apricot—[7] (Rodrigo & Herrero, 2002); rice—[8] (Takeoka, Hiroi, Kitano, & Wada, 1991); [13] (Wu et al., 2015); pea—[11] (Jiang et al., 2019); sweet cherry—[12] (Zhang, Ferguson, & Whiting, 2018) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]



which has been quantified by cross-pollination techniques, that is, by pollinating unstressed pollen on pistils exposed to heat stress (common bean [*Phaseolus vulgaris* L.], 32/27°C, Gross & Kigel, 1994; wheat [*Triticum aestivum* L.], 30°C, Saini & Aspinall, 1982). Heat stress derailed the rate of pistil development, which in turn resulted in asynchronous development of the male and female reproductive organs, leading to poor pollination (Cicchino et al., 2010; Rodrigo & Herrero, 2002; Figure 1).

An abnormal pistil including stigma, style and ovule was observed in some species under heat stress (Table 1). Morphological changes such as protruded stigma hindered pollen capture (Polowick & Sawhney, 1988), shorter styles (Devasirvatham et al., 2013; Rodrigo & Herrero, 2002) and shrunken ovaries (Rodrigo & Herrero, 2002) with desiccated and flaccid stigma and style (Djanaguiraman, Perumal, Jagadish, et al., 2018; Prasad & Djanaguiraman, 2014) negatively affected pollination (Table 1 and Figure 1).

The cellular organization within the ovary is also impacted by heat stress during ovule development, including smaller or complete disappearance of embryo sac, decreased starch accumulation (Saini et al., 1983), impaired cell membrane, shrunken cytoplasm, disrupted nucleolus and nucleus and damaged organelle decreased plastid membrane integrity (Chiluwal et al., 2020; Djanaguiraman, Perumal, Jagadish, et al., 2018). Further, heavy callose (β -1,3-glucan) deposition (Jiang et al., 2019; Zhang, Ferguson, & Whiting, 2018) was observed in ovaries under heat stress (Table 2). In several angiosperms, it has often been observed that the pollen tube fails to penetrate the callose deposition leading to sterility (Vishnyakova, 1991). Taken together, several morphological and anatomical changes induced by heat stress could affect ovule viability and accelerate ovule senescence (Figure 1).

Thus far, few investigations have attempted to analyse the molecular responses of pistils exposed to heat stress (Figure 1). Wu et al. (2015) have analysed the gene expression profiles in spikelets of rice (*Oryza sativa* L.) exposed to heat stress (38°C), which revealed differential regulation of various cellular and metabolic processes under heat stress. Five pectinase genes were increased in expression (12–14 times) under heat stress including *Hy4* (pectinesterase 67-like protein), *Hy5* (invertase/pectin methylesterase inhibitor family proteins), *Hy6* (pectinase), *Hy9* (pectinase) and *Hy10* (pectinesterase family protein). In general, pectin (a mixture of heterogeneously branched polysaccharides) rich in galacturonic acids [namely homogalacturonan (HGA), rhamnogalacturonan-I (RG-I), rhamnogalacturonan-II (RG-II) and xylogalacturonan (XGA)] is an important component of plant cell walls (Mohnen, 2008). Furthermore, the reproductive tissues contain higher proportion of pectin in their cell walls (Lord, 2000). Specifically, the pectin content was shown to greatly differ between rice pollen (about 12–15%) and pistil (43%) (Hasegawa et al., 2020). Pectinases were significantly upregulated under heat stress in both the reproductive organs (Wu et al., 2015).

Pectinases are wall-softening enzymes that degrade complex pectin into simple molecules like galacturonic acids. Incidentally, the pectinase activity was shown to differ between young and mature ovary; maximal activity in very young ovaries decreased as ovaries developed in day lily (*Hermerocallis fulva*; Konar & Stanley, 1969). On the other hand, pectinases play important roles in pollen germination (Konar & Stanley, 1969). An increase in pectinases could lead to altered pectin levels in the pistil/pollen tube under heat stress (Wu et al., 2015).

TABLE 1 Pistil morphological responses to pre-pollination heat stress exposure. Temperature presented are in the day/night format

Species	Temperature	Responses	References
Apricot (<i>Prunus armeniaca</i> L.)	6–7°C higher than the ambient conditions	Shorter styles and shrunken ovaries	Rodrigo and Herrero (2002)
Canola	32/26°C	Majority of stigmas were protruded significantly out of the closed flower buds, and ovules were abnormal	Polowick and Sawhney (1988)
Chickpea	Field-38/25.2°C Controlled environments-40/25°C	Shorter styles and increased ovule number in heat sensitive genotypes	Devasirvatham et al. (2013)
Maize	>35°C around noon	Exhibited delayed silking and repressed silk extrusion from the husks	Cicchino et al. (2010)
Rice	>45/30°C	About 56% of pistils developed hyperplasia including multiple stigmas and/or ovaries, profuse swelling of parenchymatous tissue from inside the ovule and unusual trichome growth from the epidermis of the ovary	Takeoka et al. (1991)
Sorghum	39/29°C	Desiccated, flaccid and damaged style and ovary	Djanaguiraman, Perumal, Jagadish, et al. (2018)
Tomato (<i>Lycopersicon esculentum</i> Mill.)	35/30°C	Stigma hyperplasia hindered self-pollination	Pan et al. (2017)
Wheat	35/25°C	Desiccated stigma and style with no pollen grains and flaccid and dried ovary	Prasad and Djanaguiraman (2014)

TABLE 2 Pistil anatomical responses to pre-pollination heat stress. Temperature presented is in the day/night format

Species	Temperature	Responses	References
Pea (<i>Pisum sativum</i>)	35/18°C	Callose (β -1,3-glucan) deposition in ovaries	Jiang et al. (2019)
Sorghum	39/29°C	Decreased cell shape and size in transmitting style tissue, programmed cell death induced in pistil including impaired cell membrane, protoplasm, nucleolus, plastid, mitochondria and endoplasmic reticulum, no starch granules were formed	Djanaguiraman, Perumal, Jagadish, et al. (2018)
	40/22°C	Shrunk cytoplasm and disrupted nucleolus and nucleus in ovary tissue near the micropylar region	Chiluwal et al. (2020)
Sweet cherry (<i>Prunus avium</i> L)	24/12°C	Heavy callose deposition in ovaries	Zhang, Ferguson, and Whiting (2018)
Wheat	30°C	Poor nucellus development, smaller or even a complete disappearance of the embryo sac, complete absence or an inconspicuous nuclei in the embryo sac and decreased starch accumulation in the egg and central cell	Saini et al. (1983)

Taken together, the altered pectin metabolism under heat stress could play an important role both during initial stages of pollination and fertilization, which require an active intercellular communication and cell-wall changes both in pistil and pollen. However, the spikelet analysis as studied in Wu et al. (2015) does not provide the opportunity to distinguish whether the pectinase genes up-regulation is occurring in the pistils or pollen tubes or both. Hence, future studies involving unpollinated and pollinated pistils exposed to heat stress will help clarify the importance of pectin alteration, exclusively in pistils.

Another possible cause of heat induced poor pollination could be insufficient pollen deposition on the stigma. In general, such negative effects of heat can be compensated by exerted stigmas (i.e., stigma surface is exerted above the anther promoting outcrossing, for example, wild tomato), which can promote female reproductive success and even corresponding QTLs are identified in tomato (Chen & Tanksley, 2004; Pan et al., 2017).

Abnormal stigma exertion under heat stress (35/30°C) in cultivated tomato was observed and microRNA (miRNA) analysis in such pistils revealed a significant downregulation of miR398b-3p and miR397-5p (with short-term heat stress—2 days) and miR172b, miR167a, miR319b and miR482a (with long-term heat stress—12 days) (Pan et al., 2017). Their analysis revealed an important role for miRNAs (miRNA-mediated altered auxin signalling pathway via miR393-5p/*SIT1R1* and miR160a/*SIARF10/16*; reactive oxygen species [ROS] signalling pathway via miR398b-3p/*SICSD1*; and lignin polymerization via miR397-5p/*LACs*) in pistils exposed to heat stress (Pan et al., 2017). Several previous studies have implicated a larger role played by auxin and ROS in the reproductive organs exposed to heat stress (Sakata et al., 2010; Zhang et al., 2017; Zhang, Li, et al., 2018). The altered expression of miRNAs that are involved in these same signalling pathways (auxin and ROS) in pistils exposed to heat stress further supports the importance of auxin and ROS homeostasis in reproductive organs exposed to heat stress.

Recent studies revealed that the heat-induced stigma exertion was largely due to shortened stamen length, which can be rescued by jasmonic acid application (Pan et al., 2019). Furthermore, the exerted stigmas were not always positively correlated with female

reproductive success in other plant species such as rice subjected to heat stress (Wu et al., 2019). Intriguingly, the hidden (enclosed) stigma contributed to higher spikelet fertility and heat tolerance in rice (Wu et al., 2019). These observations suggest that the importance of heat-induced stigma exertion is unclear.

3 | POLLEN–PISTIL INTERACTIONS—A VIEW FROM THE FEMALE REPRODUCTIVE ORGAN'S PERSPECTIVE

During flowering, mature pollen grains shed from dehiscent anthers are captured by the stigmatic surface. Adhered pollen grains germinate on stigma and the pollen tube penetrates into the style. It then grows and enters the female gametophyte, finally leading to double fertilization (Figure 2; Lord & Russell, 2002). Both pollination and fertilization processes are extremely sensitive to heat stress. For instance, heat stress decreased the number of pollen grains that adhered to the stigmatic surface affecting pollen receptivity in different plant species (*Arabidopsis* [*Arabidopsis thaliana*], 40/21°C, Katano et al., 2019; chickpea, 40/30°C and 45/35°C, Kumar et al., 2013; peach [*Amygdalus persica* L.], 30°C, Carpenedo et al., 2020; wheat, 35/25°C, Prasad & Djanaguiraman, 2014). In canola, increased temperature shortened the stigma nectar secretion period, which contributed to a gradual decrease in effectiveness of the pollinator-based pollination (Chabert et al., 2018). After pollination, reduced pollen germination and restricted pollen tube growth in the style under heat stress are major bottlenecks for fertilization in crop plants (Figure 2; cotton [*Gossypium hirsutum* L.], 37/30°C and 40/34°C, Song et al., 2015; cotton, 34.6°C, Snider, Oosterhuis, & Kawakami, 2011b; pea, 35/18°C, Jiang et al., 2019; rice, 38°C, Shi et al., 2018; sorghum, 38/28°C, Djanaguiraman, Prasad, Murugan, Perumal, & Reddy, 2014).

During pollen tube growth in the transmitting stylar tract, the pistil plays a key role in supporting and providing a favourable environment, adequate nutrition and signal-based directional cues (Herrero & Hormaza, 1996). For accurate delivery of sperm cells to the female gamete, the style generates attractants that include transmitting

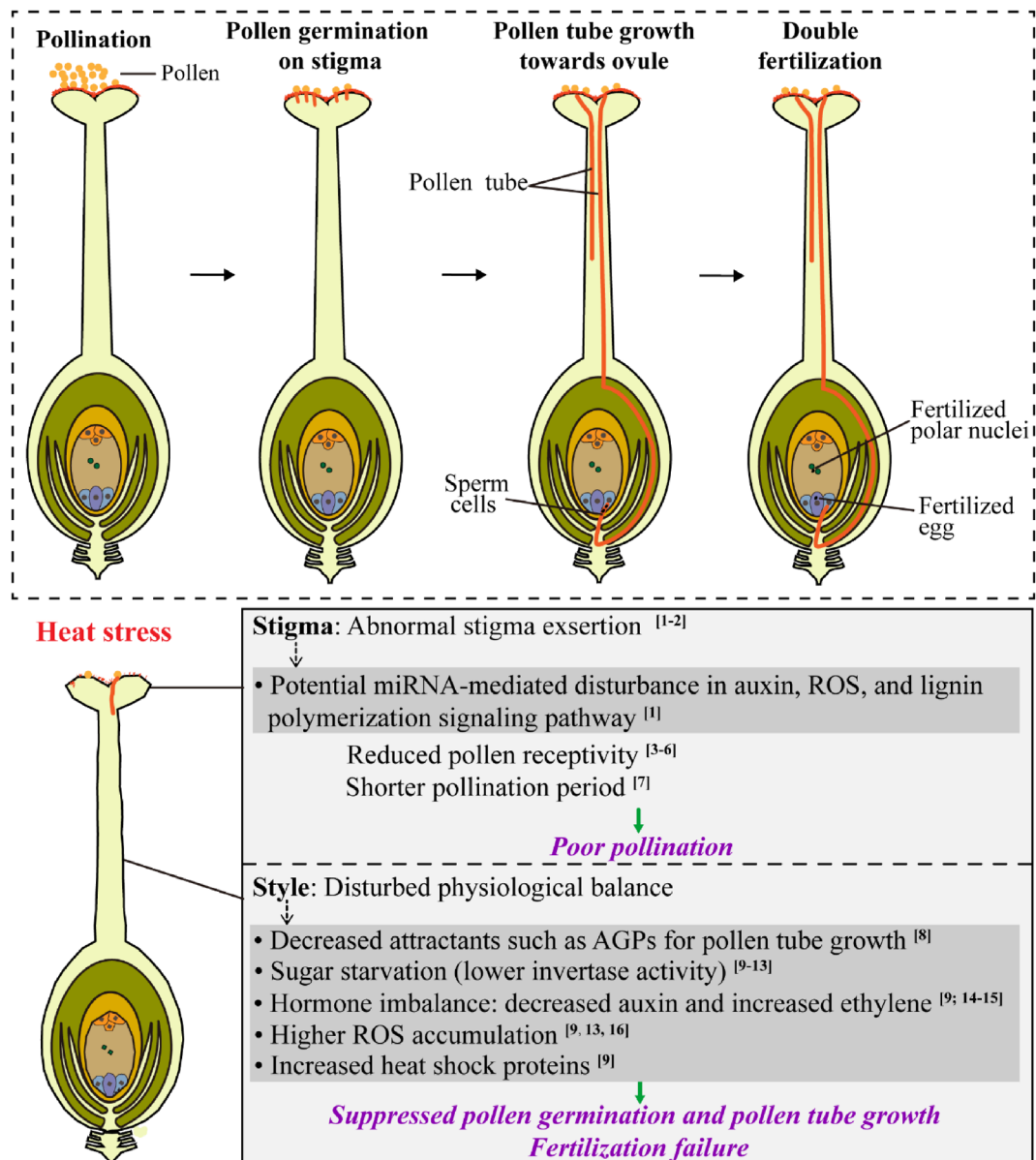


FIGURE 2 Pollination, pollen tube growth in style and fertilization processes affected by heat stress. Studies are referenced according to the crop, with numbers in parenthesis in the legend aligned with the number and related change listed above in the grey box. Crops and related references: tomato—[1] (Pan et al., 2017); [8] (Mareri et al., 2016); [9] (Liu, Offler, & Ruan, 2016); rice—[2] (Wu et al., 2019); [13] (Jiang et al., 2020); [14] (Zhang, Li, Chen, et al., 2018); chickpea—[3] (Kumar et al., 2013); wheat—[4] (Prasad & Djanaguiraman, 2014); arabidopsis—[5] (Katano, Oi, & Suzuki, 2019); peach—[6] (Carpenedo, Bassols, Franzon, Byrne, & Silva, 2020); canola—[7] (Chabert, Lemoine, Cagnato, Morison, & Vaissière, 2018); cotton—[10] (Loka & Oosterhuis, 2016); [11] (Snider, Oosterhuis, Skulman, & Kawakami, 2009); [12] (Snider, Oosterhuis, Loka, & Kawakami, 2011a); pea—[15] (Savada, Ozga, Jayasinghege, Waduthanthri, & Reinecke, 2017); pearl millet—[16] (Djanaguiraman, Perumal, Ciampitti, et al., 2018). AGP, Arabinogalactan Proteins; ROS, Reactive Oxygen Species [Colour figure can be viewed at wileyonlinelibrary.com]

tissue-specific arabinogalactan proteins (AGP) and AGP-calcium to guide the growing pollen tube (Lopes, Moreira, Ferreira, Pereira, & Coimbra, 2019).

Five days prior to anthesis, heat stress (42°C) imposition for 3 hr significantly decreased the distribution and content of AGPs in stigma and ovules, which in turn reduced stigma receptivity and pollen tube guidance to the ovule, respectively, in tomato (*Solanum lycopersicum*; Mareri et al., 2016). Cytosolic calcium levels play an important role not only in pollen germination and directing pollen tube growth in the

style towards ovule but also during the fusion of gametes (Johnson, Harper, & Palanivelu, 2019; Zheng, Su, Xiao, & Tian, 2019). Consistent with this, total and water-soluble calcium contents were found to be significantly higher in the heat-tolerant cotton cultivar than in the sensitive cultivar under heat stress (38/20°C; Snider et al., 2009).

Additionally, cytoskeleton and mechanical properties of the cell wall of stigma/style also play a key role in pollen germination and directing pollen tube growth (Riglet et al., 2020). Recently, Katanin 1 (KAT 1), a microtubule-severing enzyme, has been identified to



properly guide the early pollen tube growth in the stigma papillae in *Arabidopsis* (Riglet et al., 2020). Interestingly, KAT1 has been shown to be important for salt tolerance in *Arabidopsis* (Yang, An, Luo, He, & Wang, 2020), but whether the KAT1 also plays a role during heat stress in guiding the pollen tube growth is unknown. Similarly, the synergid cells that lie adjacent to the egg cells that are primarily responsible for the reception and micropylar guidance of pollen tube into the embryo sac and the MYB98 and its gene regulatory networks (GRNs) in synergids play an important role in these processes (Berger, Hamamura, Ingouff, & Higashiyama, 2008; Higashiyama & Yang, 2017; Lopes et al., 2019). The MYB98 and its GRNs analysis in heat-exposed pistils will help us better understand the roles of these genes in final stages of fertilization.

Apart from directing pollen tube growth, the pistil also provides adequate nutrition including carbohydrates and free amino acids to support pollen tube growth, which is an extremely energy-consuming process (Herrero & Hormaza, 1996). Snider, Oosterhuis, Loka, and Kawakami (2011a) observed a positive correlation between slower pollen tube growth rate and reduced soluble carbohydrate concentration in the pistil in cotton subjected to moderate heat stress (34.6°C). Similarly, cotton exposed to severe heat stress (38/20°C) for a week prior to flowering (sampled after fertilization) recorded a significant decline in soluble carbohydrates (mainly sucrose) and adenosine triphosphate (ATP) content in the pistil, leading to a decrease in ovule number and fertilization efficiency (Snider et al., 2009).

Further, sugar starvation in the pollinated pistil was identified as the major reason leading to fertilization failure in rice exposed to heat stress during flowering (Li et al., 2015). The significance of sugars in pollen tube growth in the pistil exposed to heat stress was further supported by the manipulation of enzymes associated with the sugar hydrolysis and release. For instance, invertases are important metabolic enzymes that hydrolyze sucrose into hexoses (glucose and fructose) and are actively involved in supplying carbohydrates from the transmitting tissue to support pollen tube growth (Goetz et al., 2017; Ruan, 2014). The invertase activity in female reproductive organs was significantly decreased under heat stress, thus limiting the supply of hexose sugars (Jiang et al., 2020; Liu et al., 2016). Application of exogenous acid invertase resulted in a balanced energy production and significantly increased spikelet fertility under heat stress (38/28°C) in rice (Jiang et al., 2020).

In fact, tomato cultivars with elevated cell wall invertase activity in reproductive organs were found to be more tolerant to heat stress than the cultivars with lower cell wall invertase activity (Li et al., 2012). Corroborating this, the improved heat tolerance was observed in genetically manipulated transgenic tomato in which the cell wall invertase activity was elevated both in ovaries and fruits by silencing the cell wall invertase inhibitor. The tolerance was associated with better sucrose import into fruits (sampled 2 days after pollination) and elevated hexokinase and fructokinase activities in ovaries (sampled 2 days before pollination) under long-term moderate heat stress (28/20°C), which was imposed on the 3 mm long first flower bud in the first formed inflorescence and lasted until the end of its life cycle (Liu et al., 2016). In addition, the elevated cell wall invertase

activity in these transgenics suppressed programmed cell death in tomato fruit and alleviated fruit-set failure, by promoting auxin signaling (through higher expression of auxin biosynthesis gene *FZY6*) in the fruits and increased heat shock protein gene expression (*HSP90* and *HSP100*) in ovaries and (*Hsp117.6*) in the fruit (Liu et al., 2016). Interestingly, heat stress tolerance of these transgenic tomato exposed to heat stress was associated with the improved/changed above-mentioned attributes in ovaries and fruits but not in pollen (Liu et al., 2016).

Taken together, insufficient carbohydrate metabolism and decreased invertase activity during daytime heat stress is a critical factor that limits sugar/energy contributed by the pistil to support pollen tube growth, thus leading to fertilization failure (Figure 2). These observations suggest the possibility that cell wall invertase gene expression or enzyme activity in the pistil can serve as a potential marker for heat tolerance in tomato and has the potential to be extended to other plants.

Unlike the high day-time temperature, which is often the subject of study, the damage caused by high night-time temperature is also being currently scrutinized. In this context, accumulation of polyamines (putrescine and spermine) as well as glucose, sucrose and starch in cotton pistils exposed to high night-time temperature was observed (Loka & Oosterhuis, 2016). These findings point to the potential differences in physiological responses under high day-time or high night-time temperature stress conditions, an interesting area that warrants detailed investigation.

The major plant hormones such as auxins, cytokinins and ethylene, whose levels are often altered under stress conditions, play critical roles in pollen–pistil interactions and pollen tube growth in the style as well as the ovary development (Deb, Bland, & Østergaard, 2018; Wu, Qin, & Zhao, 2008). Auxin levels were significantly decreased in heat-susceptible rice pistils exposed to heat stress (40°C for 2 hr), and an external spraying of 1-naphthaleneacetic acid (NAA) alleviated the restriction on pollen tube growth (Zhang, Li, et al., 2018). Ethylene was shown to be produced in the stigma/style to coordinate reproductive physiology in plants. Expression of ethylene biosynthesis genes *PsACS* and *PsACO* was increased in pre-pollinated ovaries under heat stress (33–35°C for 6 hr/day for 4 days) that promoted ovary senescence in pea (Savada et al., 2017). On the other hand, heat stress in post-pollinated pea plants suppressed the *PsACO* expression leading to reduced ethylene in style/stigma, suggesting that the ethylene-dependent pollen germination and pollen tube growth on stigma and style are inhibited under heat (Savada et al., 2017).

ROS levels have been shown to increase whereas antioxidant enzymes decreased in pistils exposed to heat stress (pearl millet, 36/26 and 40/30°C, Djanaguiraman, Perumal, Ciampitti, et al., 2018; rice, 38/28°C, Jiang et al., 2020), rendering pistils and the fertilization process vulnerable. Interestingly, the induction of programmed cell death in tomato under long-term moderate heat stress (28/20°C from flowering to maturity) was independent of ROS accumulation; however, short-term severe heat stress (36/30°C for 24 hr during flowering) damage was associated with significant increase in ROS

levels (Liu et al., 2016). These findings suggest that the impact of heat stress is dependent on the intensity and duration, but additional studies are expected to shed more light on such differences or commonalities among different plant species.

Taken together, besides the restricted stigma receptivity, sugar metabolism, hormonal and ROS levels in the style hinder pollen tube growth, coupled with the deterioration of ovary, collectively leading to spikelet sterility under heat stress (Figure 2). Although the involvement of different processes mentioned above is known, a detailed account on the extent of their involvement and interactions leading to loss in seed-set is poorly understood.

4 | POST-FERTILIZATION AND EARLY EMBRYOGENESIS

After the fertilization, fertilized egg cell (zygote) and fertilized polar nuclei (primary endosperm cell) undergo cell division and differentiation and finally form the embryo and endosperm, respectively (Figure 3; Sliwinska et al., 2014). Initial stages of seed development (post-fertilization) are highly sensitive to heat stress (Folsom et al., 2014). Exposure to heat stress after fertilization can inhibit the development of endosperm and promote the degeneration of embryo sac (bush bean [*Phaseolus vulgaris* L.]; 35/26.5°C; Ormrod et al., 1967) or restrict the development of fertilized ovules (tomato; 40°C; Iwahori, 1966). A study revealed that the

endosperm development was comparatively more sensitive to heat stress than the early embryo formation (Iwahori, 1966).

Efforts to understand the epigenetic responses (DNA methylation, histone modification) to abiotic stresses during gametogenesis and early seed development are only beginning to emerge (Begcy & Dresselhaus, 2018, references within). The reduced seed size and/or weight in rice exposed to heat stress during early seed development was attributed to delayed endosperm cellularization as revealed by histochemical analysis (Paul et al., 2020). Interestingly, moderate heat stress (34°C) shortened syncytial stage of endosperm and precocious cellularization, whereas severe heat stress (42°C) resulted in failure of the endosperm cellularization (Folsom et al., 2014). Several imprinted genes control endosperm cellularization in plants (Gehring, 2013), and their mis-regulation under heat stress contributes to the developmental abnormalities of the endosperm (Chen et al., 2016).

Among the many imprinted genes, a few were examined for their function under heat stress. One such gene is the *fertilization-independent endosperm1* (*OsFIE1*), a critical subunit of the polycomb-repressive complex 2 (PRC2), which is responsible for causing repressive mark (H3K27me3) on the target genes leading to their transcriptional repression (Folsom et al., 2014). The expression of rice *FIE1* is restricted to the endosperm (from 4 to 10 days after fertilization) and strongly increased under moderate heat stress (34°C) but repressed at severe heat stress (42°C; Folsom et al., 2014). Such an altered expression of *OsFIE1* under heat stress is correlated with decreasing DNA methylation as well as H3K9me2 (dimethylation of H3K9,

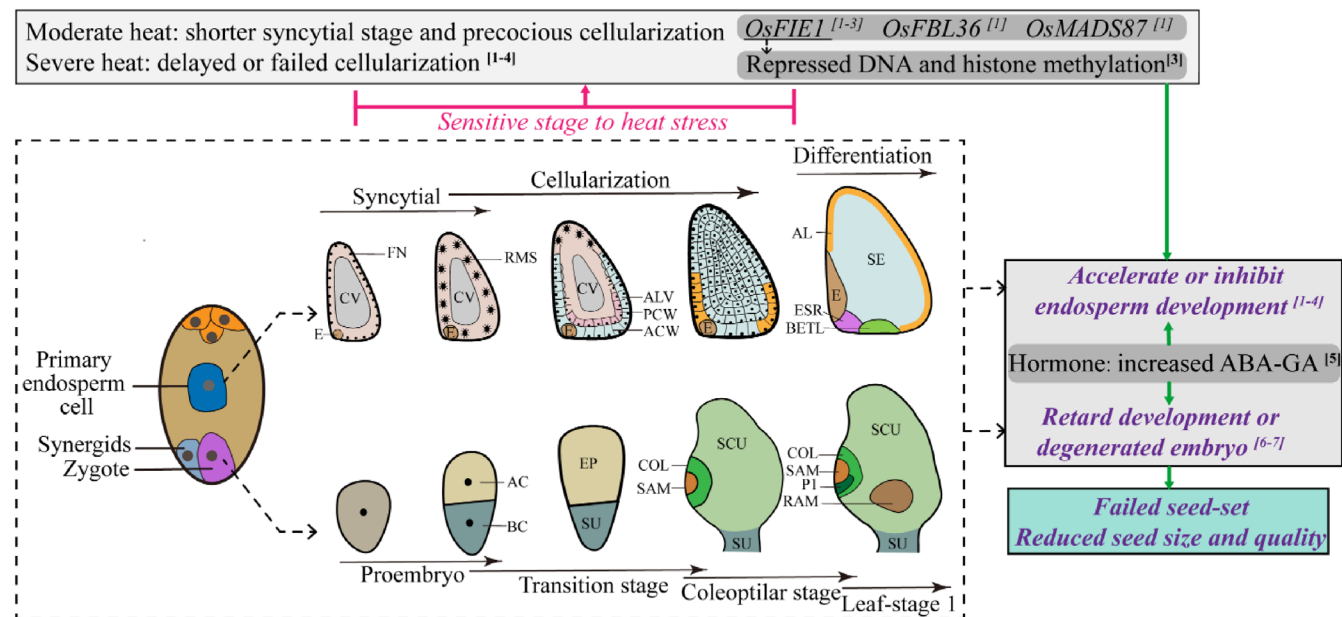


FIGURE 3 Post-fertilization early embryo development and changes induced by heat stress. Early embryogenesis development stages in the above diagram are drawn based on Sliwinska, Bewley, and Gallagher (2014), with modifications. Studies indicated with numbers in parenthesis in the legend are aligned with the number and related change listed above. In endosperm: ACW, anticlinal cell; ALV, alveolus; AL, aleurone layer; BETL, basal endosperm transfer layer; CV, central vacuole; E, embryo; ESR, embryo-surrounding region; FN, free nuclei; PCW, periclinal cell; RMS, radial microtubular systems; SE, starchy endosperm. In embryo: AC, axial cell; BC, basal cell; COL, coleoptile; EP, embryo proper; P1, leaf stage 1; RAM, root apical meristem; SU, suspensor; SCU, scutellum; SAM, shoot apical meristem. Crops and heat stress references: rice—[1] (Chen et al., 2016); [2] (Dhatt et al., 2020); [3] (Folsom, Begcy, Hao, Wang, & Walia, 2014); [4] (Paul et al., 2020); [5] (Begcy, Sandhu, & Walia, 2018); tomato—[6] (Iwahori, 1966); bush bean—[7] (Ormrod, Woolley, Eaton, & Stobbe, 1967) [Colour figure can be viewed at wileyonlinelibrary.com]



another transcriptional repressive mark) implying that *FIE1* gene regulation itself is epigenetically controlled (Folsom et al., 2014).

A recent study analysed early grain development (1–10 days after fertilization) in rice subjected to high night temperature (28°C) that generally affects rice grain chalkiness (Dhatt et al., 2020). This study further identified *FIE1* as a key regulator of grain width since knock-out mutants recorded decreased grain size under high night temperature (Dhatt et al., 2020). Moreover, the *FIE1* was shown to be pleiotropically involved in rice grain chalk formation as reduced *FIE1* recorded a significant increase in grain chalkiness under heat stress, attributed to abnormal starch packing (Dhatt et al., 2020). Interestingly, another imprinted gene, *OsFBL36* (F-box domain and LRR containing protein), displayed similar regulation like *OsFIE1* under heat stress, that is, up-regulation under moderate (35/30°C) and down-regulation under severe (39/34°C) heat stress (Chen et al., 2016).

The *OsMADS87* is yet another imprinted gene in rice, a member of type I MADS-box gene, specifically expressed at the syncytial stage also exhibited strong heat sensitivity during the transition from syncytium to cellularization. This heat stress sensitivity was associated with accelerated endosperm cellularization and decreased seed size suggesting a potential role for these MADS-box genes in endosperm cellularization during heat stress responses (Chen et al., 2016).

Several putative development-related genes like cell cycle-related genes were down-regulated both under moderate and severe heat stress, with a higher fold change under severe stress, resulting in accelerated and arrested syncytium/cellularization and endosperm transition (Chen et al., 2016). Together, these observations suggest an important role for the maternally imprinted genes in the endosperm cellularization under heat stress (Figure 3). Functional analysis of other imprinted genes is likely to reveal additional genes that could be associated with the heat stress responses in plants.

Even heat stress (moderate—35°C and severe—39°C) lasting only for 24 to 72 hr (transient heat stress) during post-fertilization (initial stage of embryo and endosperm development) in rice led to malformed embryos (Begcy et al., 2018). This was further coupled with altered expression of gibberellin and abscisic acid biosynthesis genes leading to decreased gibberellin biosynthesis and increased abscisic acid biosynthesis (Begcy et al., 2018). In the same study, *OsAP2-39*, an *APETALA2* (*AP2*) class family transcription factor that orchestrates both abscisic acid increase and gibberellin decrease was up-regulated more than twofold under heat stress (Begcy et al., 2018). All these studies suggest that the heat stress during early seed development mainly disrupts endosperm development especially during the transition of syncytial to cellularization stage (Figure 3). Despite the fact that the sensitive events during early seed development have been identified, information about the embryo response and the pathways and genes that interfere with the embryogenesis and endosperm development under heat stress is limited.

5 | CONCLUSION AND FUTURE PERSPECTIVES

Overall, the discussion presented here suggests a complex but well-coordinated regulatory network involving genes, metabolites,

signalling molecules and hormones that play critical roles in female gametophyte development, pollen–pistil interactions and fertilization as well as early embryogenesis and endosperm development. Heat stress appears to affect almost all of these processes although to a different degree depending on the heat stress intensity and duration coupled with the differences in plant species responses.

A clear identification of sensitive events in female reproductive organ development under heat stress and determining their contribution to yield loss is important to develop stress resilient crops for the future. For instance, a higher pistil temperature was recorded in cotton and rice flowers exposed to ambient conditions (Shi, Ishimaru, Gannaban, Oane, & Jagadish, 2015; Snider, Oosterhuis, Loka, & Kawakami, 2011a). These differences suggest the need for identifying temperature thresholds specifically related to female reproductive organ, but thus far no such study has been undertaken. Furthermore, most information that was obtained on pistil response to heat stress was largely obtained from controlled environments, and very little is known about these responses under field conditions. Studies under realistic field conditions will help identify knowledge gaps which is important for translating the findings. Accessing the female reproductive organ compared to the anther/pollen is a major challenge but novel sensor-based phenotyping methods can potentially help explore genetically diverse germplasm (see Luria, Rutley, Lazar, Harper, & Miller, 2019 for high-throughput phenotyping for pollen viability) and advance our understanding of pistil's response to heat stress. A list of intriguing questions that can help advance our understanding of the pistil's response to heat stress and help breed heat resilient crops are listed below.

6 | OUTSTANDING QUESTIONS

1. What is the range of critical temperature and VPD-based thresholds in different crops/plants after which pistil viability decreases leading to loss in seed-set?
2. What is the quantitative contribution of different physiological factors such as sugar starvation, ROS and hormonal signalling in style and synergids to pollen tube growth inhibition and fertilization failure under heat stress?
3. What are the different molecular and biochemical changes (gene expression profiles including miRNAs, sugar and hormonal signalling) that induce heat tolerance or rapid recovery in pistils exposed to heat stress?
4. How different are the responses and regulatory mechanisms in pistils exposed to short- and long-term day-time vs night-time heat stress?
5. Is it possible to modify the floral tissue surface stomatal characteristics to maintain favorable tissue temperature, to protect reproductive organs from heat stress-induced damage?

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable and no new data generated.

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