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EDITED BY
Raju Datla,
Global Institute for Food Security, Canada

REVIEWED BY
Nasreen Bano,
University of Pennsylvania, United States
Waqas Shafqat Chattha,
University of Agriculture, Faisalabad, Pakistan

*CORRESPONDENCE
Yunfei Jiang
✉ yunfei.jiang@dal.ca

†PRESENT ADDRESS
Mohammad Erfatpour,
Department of Plant Agriculture, University of Guelph, Guelph, ON, Canada

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Ovule and seed development of crop plants in response to climate change

Mohammad Erfatpour[1†], Dustin MacLean[1], Rachid Lahlali[2] and Yunfei Jiang[1*]

[1]Department of Plant, Food, and Environmental Sciences, Faculty of Agriculture, Dalhousie University, Truro, NS, Canada, [2]Department of Plant Protection, Phytopathology Unit, École Nationale d'Agriculture de Meknès, Rte. HajKaddour, Meknes, Morocco

The ovule is a plant structure that upon fertilization, transforms into a seed. Successful fertilization is required for optimum crop productivity and is strongly affected by environmental conditions including temperature and precipitation. Climate change refers to sustained changes in global or regional climate patterns over an extended period, typically decades to millions of years. These shifts can result from natural processes like volcanic eruptions and solar radiation fluctuations, but in recent times, human activities—especially the burning of fossil fuels, deforestation, and industrial emissions—have accelerated the pace and scale of climate change. Human-induced climate change impacts the agricultural sector mainly through global warming and altering weather patterns, both of which create conditions that challenge agricultural production and food security. With food demand projected to sharply increase by 2050, urgent action is needed to prevent the worst impacts of climate change on food security and allow time for agricultural production systems to adapt and become more resilient. Gaining insights into the female reproductive part of the flower and seed development under extreme environmental conditions is important to oversee plant evolution, agricultural productivity, and food security in the face of climate change. This review summarizes the current knowledge on plant reproductive development and the effects of temperature and water stress, soil salinity, elevated carbon dioxide, and ozone pollution on the female reproductive structure and development across grain legumes, cereal, oilseed, and horticultural crops. It identifies gaps in existing studies for potential future research and suggests suitable mitigation strategies for sustaining crop productivity in a changing climate.

KEYWORDS

abiotic stress, climate change, ovule development, seed development, seed production

1 Introduction

Climate change has exacerbated the adverse effects of environmental stress on crop production worldwide. Extreme weather events like heat waves, extreme droughts, and floods are becoming more frequent and more intense across the globe. For example, July 2023 was the hottest month on record since 1880 (National Aeronautics and Space Administration, 2023). Extreme weather can result in poor yields, or worse, crop failures. The average yield loss of cereal crops due to drought and heat stress was estimated at 9%–10% in recent decades, and the impact was greatest in developing nations compared to developed countries (Lesk et al., 2016). Together, these impacts pressure domestic and global food systems and increase the likelihood of supply chain disruptions and competition for increasingly limited resources (https://www.ccacoalition.org).

Grain (or seed) number and grain weight are two key yield components in grain crops. A grain is developed through the union of two sperm cells delivered by a pollen grain and two female gametes (the egg and central cells) in the ovule in a process known as double fertilization (Davies et al., 2018). The world's leading crops - cereals, oilseeds, and pulses, are produced through sexual reproduction, which involves the fusion of male and female gametes to form seeds. These seeds are the grains or edible parts of the crops that ultimately contribute to the world's food supply. Successful pollination and fertilization (seed set) play a key role in crop productivity and depend greatly on the environmental conditions in which these processes take place.

Reproduction is the most sensitive developmental stage to hot and cold temperatures, drought, combined heat and drought, and salinity stresses (Zinn et al., 2010; Suzuki et al., 2014). Adverse impacts of high-temperature stress on the morphological and quantitative parameters of pollen grains have been reported in many crops, such as maize (*Zea mays*) (Wang et al., 2019, 2021b), wheat (*Triticum aestivum*) (Khan et al., 2022), barley (*Hordeum vulgare*) (Sakata et al., 2010), rice (*Oryza sativa*) (Endo et al., 2009), field pea (*Pisum sativum*) (Lahlali et al., 2014; Jiang et al., 2015, 2019a,b), common bean (*Phaseolus vulgaris*) (Porch and Jahn, 2001; Prasad et al., 2002), peanut (*Arachis hypogaea*) (Prasad et al., 1999), cotton (*Gossypium hirsutum*) (Song et al., 2015), flax (*Linum usitatissimum*) (Cross et al., 2003), tomato (*Solanum lycopersicum*) (Giorno et al., 2013), and pepper (*Capsicum annum*) (Erickson and Markhart, 2002). Drought, like heat stress, can adversely impact male and female organs and contribute to yield reduction in crops (Ishimaru et al., 2022). The effects of drought stress during the reproductive stage are manifested in the form of degenerated meiocytes, disorientated microspores, expanded anther wall layers with a vacuolized tapetum, early anther dehiscence, and non-viable pollen (Giorno et al., 2013; De Storme and Geelen, 2014).

Depending on its concentration, the duration of exposure, the plant's sensitivity, and the plant's developmental stage, tropospheric ozone (O_3) can be a source of stress and can have damaging effects on reproductive development in flowering plants (Pasqualini et al., 2011; Duque et al., 2021b). Some of the proposed mechanisms by which ozone might affect reproductive performance include (i) reduction in photosynthetic efficiency through damaging chloroplasts and reducing the plant's overall energy production (ii) inhibition of assimilate translocation, and (iii) reduction in pollen viability (Pasqualini et al., 2011), pollen germination, and pollen tube growth and increase in abscission of reproductive sites (Fiscus et al., 2005; Leisner and Ainsworth, 2012). Ozone has been shown to alter the timing of the flowering onset (Rämö et al., 2007; Hayes et al., 2012; Duque et al., 2021a) and to decrease the number of flowers (Hayes et al., 2012; Duque et al., 2021a), which may alter reproductive success. According to Stabler (2016), exposure of broad bean (*Vicia faba*) plants to ozone reduced the amount of pollen produced and decreased its protein content.

Since the start of the industrial revolution, burning fossil fuels like coal and oil has increased the concentration of atmospheric carbon dioxide (CO_2). In flowering plants, elevated levels of CO_2 can have both positive and negative effects on reproductive development, depending on the plant species (C3 or C4), environment, and interaction with other factors such as temperature and nutrient availability. In theory, elevated levels of CO_2 increase photosynthesis if the other essential factors such as sunlight, water, temperature, or nutrients are available in abundance (Boretti and Florentine, 2019). This can lead to a slower increase in the atmospheric concentration of CO_2, compared to what would be expected solely based on global CO_2 emissions (Le Quéré et al., 2009). Additionally, higher atmospheric CO_2 levels have been shown to reduce the water plants lose through transpiration, allowing plants to survive in drier conditions (Swann et al., 2016). These two processes can improve the uptake of CO_2 by the biosphere, thus increasing the land carbon stock—a phenomenon known as the CO_2 fertilization effect (Chen et al., 2022). Across 79 crop and undomesticated (wild) species, CO_2 enrichment (500–800 $\mu L\ l^{-1}$) resulted in substantial increases in number of flowers (+19%), fruits (+18%), and seeds (+16%) as well as greater individual seed mass (+4%) and total seed mass (+25%) than control treatments (Jablonski et al., 2002). Similarly, elevated CO_2 significantly increased the number of flowers for the tropical legume forage species *Stylosanthes capitata* Vogel (Alzate-Marin et al., 2021). Even though the weight of evidence favors the idea that the male reproductive organ is more sensitive to abiotic stress than its female counterpart in several crops such as maize (Wang et al., 2019), sorghum (*Sorghum bicolor*) (Djanaguiraman et al., 2018b), barley (Callens et al., 2023), and field pea (Jiang et al., 2019a), evidence for species-specificity of reproductive organs' sensitivity to abiotic stress is accumulating (Hedhly, 2011; Wang et al., 2021a,b). This review focuses on the status of the pistil's morphological, physiological, and molecular changes subjected to abiotic stress, and bridging the gap between basic research and the applied field of agronomy.

2 Plant reproductive development

2.1 Male gametophyte development

Male gametophyte (also referred to as microgametophyte or pollen grain) development in anthers occurs over two distinct sequential phases, microsporogenesis and microgametogenesis (Huang et al., 2021). During microsporogenesis, diploid microspore mother cells (also called pollen mother cells or microsporocytes) undergo meiotic division to produce tetrads of haploid microspores. Unicellular microspores are released from tetrads and undergo microgametogenesis (Pandey et al., 2022). This process involves asymmetric mitosis (mitosis I) that generates two unequal cells, the larger vegetative and the smaller generative cells. The generative cell goes through symmetric mitosis (mitosis II) to produce two sperm cells (Figure 1A). Approximately 70% of male gametophytes of flowering plants have a sexually immature bicellular state when they are dispersed as pollen. The remainder have tricellular pollen containing fully formed sperm at anthesis (Williams et al., 2014). In species with bicellular pollen grains, pollen mitosis II occurs in the growing pollen tube within the pistil (Berger and Twell, 2011; Dresselhaus and Franklin-Tong, 2013), such as in field pea (Jiang et al., 2019b).

2.2 Female gametophyte development

The gynoecium is the female reproductive portion and the innermost whorl of the flower in angiosperms (or flowering plants) and predominantly consists of one pistil (Cucinotta et al., 2020). The

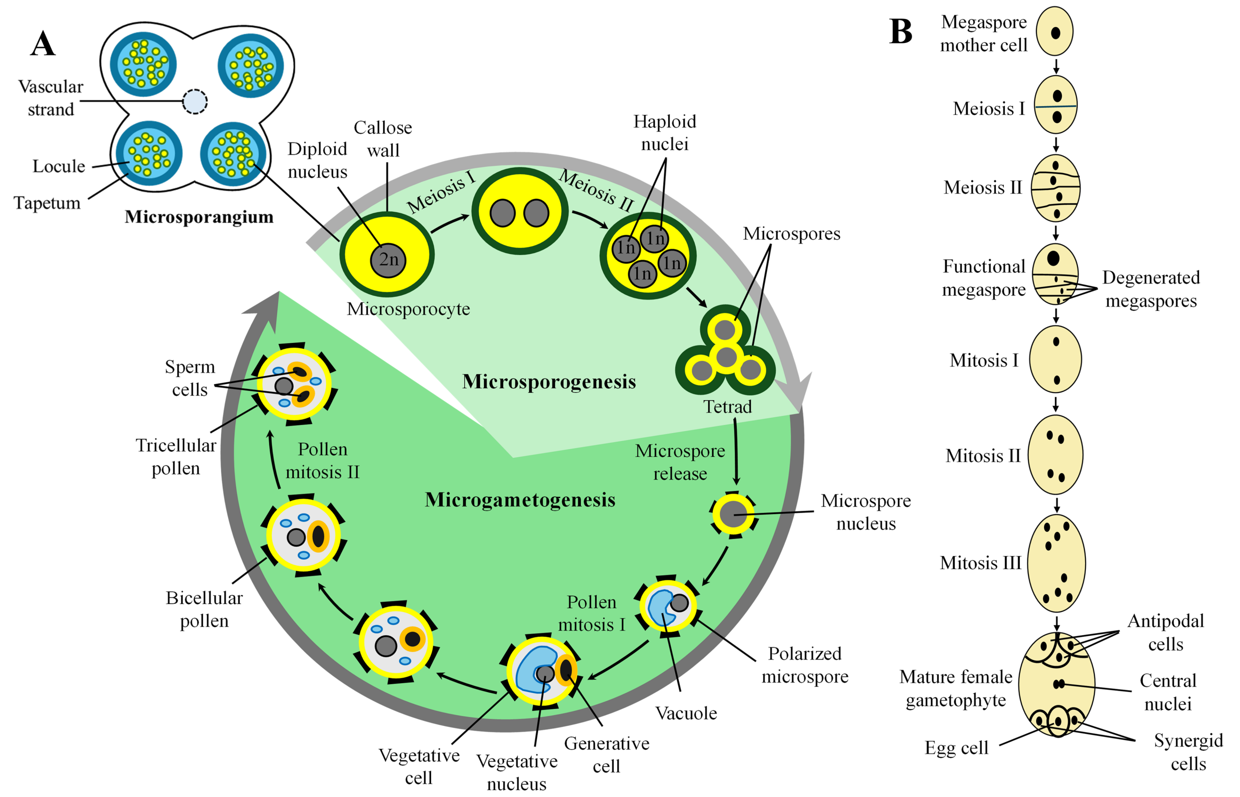


FIGURE 1
Schematic of **(A)** male gametophyte (pollen grain) development and **(B)** female gametophyte (embryo sac) in flowering plants.

pistil has three main parts: the ovary at the base where ovules are housed, the style through which the pollen tubes grow, and the stigma on which the pollen grains germinate. The female gametophyte (also called embryo sac or megagametophyte) develops within the ovule over two phases, megasporogenesis and megagametogenesis. More than 15 different patterns of female gametophyte development have been characterized based on the variations in cytokinesis during meiosis, the number and pattern of mitotic divisions, and the pattern of cellularization (Yadegari and Drews, 2004). The Polygonum-type female gametophyte is the most typical type of embryo sac in many economically important families including Gramineae, Leguminosae, Solanaceae, Brassicaceae, and Malvaceae (Willemse and Van Went, 1984; Haig, 1990; Huang et al., 1998; Drews and Koltunow, 2011). It possesses seven cells with four cell types: one egg cell and two synergid cells at the micropylar pole, one big central cell with two polar nuclei in the middle, and three antipodal cells at the chalazal pole. Chalaza is the basal part of the body of the ovule from which the inner and outer integuments develop, and these finally envelop and protect the embryonic sac (Figure 1B). It is present opposite the micropylar end of an ovule (Davies et al., 2018).

During megasporogenesis, the diploid megaspore mother cell (megasporocyte) undergoes meiosis resulting in the formation of four megaspore nuclei (Drews and Koltunow, 2011). There are three main types of megasporogenesis in angiosperm, namely monosporic, bisporic, and tetrasporic (Haig, 2020). These three types differ mainly in whether cell plate formation occurs after these divisions, thus determining the number of meiotic products that affect the development of the mature female gametophyte (Yadegari and Drews, 2004). In the monosporic type of megasporogenesis, meiosis is followed by cytokinesis, leading to four megaspore cells. Subsequently, three megaspores, generally the micropylar-most megaspores, undergo cell death (Drews and Koltunow, 2011). In the bisporic type of megasporogenesis, meiosis I is followed by cytokinesis, but not meiosis II, which leads to two-nucleate megaspores, one of which degenerates. In the tetrasporic pattern, cytokinesis does not occur at all after meiosis, resulting in a single cell with four haploid nuclei. Thus, these three patterns give rise to a single functional megaspore that contains one (monosporic), two (bisporic), or four (tetrasporic) haploid megaspore nuclei (Haig, 2020). The monosporic pattern is the most common form and is represented within the Polygonum pattern (Willemse and Van Went, 1984; Haig, 1990; Yadegari and Drews, 2004). The monosporic, Polygonum type of female gametophyte is typically a seven-celled structure at maturity (Yadegari and Drews, 2004). However, this structure may be modified by cell death or cell proliferation events in various species (Grossniklaus and Schneitz, 1998; Yadegari and Drews, 2004; Friedman, 2006; Drews and Koltunow, 2011; Endress, 2011a,b).

2.3 Pollination and sexual reproduction in flowering plants

Efficient and successful pollination and fertilization are key processes for crop productivity (Suzuki, 2009; Bleckmann et al., 2014). Pollination is initiated after a pollen grain is transferred from the anther to a receptive stigma via various agents, such as pollinators, wind, or direct contact. Most pollen grains are metabolically quiescent and highly desiccated, ranging from 15 % to 35% water content when released from the anthers (Heslop-Harrison, 1979; Buitink et al., 2000). Stigma plays an important role in pollination and is composed of stigmatic papillae, which are divided into wet and dry types depending on the presence or absence of secretions at the stigma surface (Heslop-Harrison and Shivanna, 1977; Heslop-Harrison, 1981). Wet stigmas are covered with surface cells that often lyse to release a viscous surface secretion containing proteins, lipids, polysaccharides, and pigments (Edlund et al., 2004). Pistils in Leguminosae, Solanaceae, and Orchidaceae have wet stigmas (Zheng et al., 2018). Dry stigmas lack copious surface secretion (Edlund et al., 2004) and are further divided into unicellular and multicellular types (Katano and Suzuki, 2021). Stigmas in Gramineae, Brassicaceae, and Asteraceae are of the dry type (Elleman et al., 1992; Zheng et al., 2018).

Upon pollen adhesion, water, nutrients, and other small molecules are transported rapidly into the pollen grain from the stigma exudate (in the wet stigma type), leading to pollen hydration (Richards, 1997; Edlund et al., 2004). Following pollen hydration, the pollen tube germinates and penetrates the stigma cell wall and then passes through the nutrient-rich extracellular matrix of the transmitting tract toward the female gametophyte (Johnson and Preuss, 2002; Rejón et al., 2016). The pollen tube eventually enters the embryo sac in the ovule from the micropyle by growing between the two halves of the filiform apparatus of the synergid cells. Just after passing the filiform apparatus, wall deposition at the tip of the pollen tube appears disordered, resulting in pollen tube discharge. One of the two sperm cells fuses with the egg cell to develop into the embryo, and the other sperm cell fuses with the polar nuclei to develop into the endosperm during double fertilization (Faure, 2001; Higashiyama, 2010; Drews and Koltunow, 2011).

The ovule is the structure that gives rise to and contains the female reproductive cells. It consists of three parts: the integument, forming the outer layer; the nucellus (or remnant of the megasporangium), a diploid nutritive tissue; and the female gametophyte in the center of the ovule. Embryo development in a typical dicot includes the proembryo stage, globular stage, cotyledon stage, and mature seed. In contrast, embryo development in a typical monocot includes proembryo stage, globular stage, scutellar stage, coleoptilar stage, and mature seed stage (Davies et al., 2018). In most cases, antipodals at the chalazal end degrade soon before or soon after fertilization (Panoli et al., 2015). In other cases (such as many monocots, particularly grasses), the antipodals can continue to divide and develop 40–100 antipodal cells, for example in maize (*Zea mays*) (Diboll, 1968). For the latter, antipodals may provide nutrition for endosperm and embryo development (Davies et al., 2018).

3 Effects of abiotic stress on female reproductive organ

The pistilar sporophytic tissues provide an optimal environment to support several key events during plant reproductive development, including gametophyte development, pollen germination, pollen tube growth, and fertilization. To fulfill these roles, the pistil acquires adequate levels of enzymes (e.g., invertase and antioxidant enzymes), phytohormones, soluble carbohydrates, free amino acids, adenosine triphosphate (ATP), and lipids (Herrero and Hormaza, 1996; Jain et al., 2007; Deb et al., 2018; Liu et al., 2022; Shi et al., 2022). However, the pistil is prone to irreversible morphological and physiochemical changes due to changes or disruptions in climate variables (heat and drought stress, flooding, ozone pollution, and elevated CO_2), which results in up to 100% yield loss depending on crop species, genotype, and stress conditions (Table 1). These disruptions collectively contribute to reduced fertilization success and can limit seed production and fruit set through different mechanisms such as impaired pollen tube growth and ovule number. For example, heat stress modifies source-sink relations, reduces the kernel-filling stage, and produces unfilled or aborted seeds in several globally important crops (Kaushal et al., 2016). Exposure to high temperatures during seed filling can accelerate the senescence of seeds, decrease seed set and seed weight, and lead to yield loss because plants tend to divert energy and resources such as photosynthates to deal with heat stress (Bueckert and Clarke, 2013). Schematic of some major impacts of changes or disruptions in climate variables (heat and drought stress, flooding, ozone pollution, and elevated CO_2) on female reproductive organs in major food sources selected in this review is shown in Figure 2.

3.1 Effect of abiotic stress on the female reproductive organ in grain legumes

Heat-induced morphological changes in the pistil were reported in several crops. Exposure of a heat-sensitive chickpea (*Cicer arietinum*) genotype, 'ICC 4567', to high temperatures (39.4/27.2°C day/night temperatures) against a control treatment (27/16°C) for 7 days during pre-anthesis shortened the style length and led to ovule and ovary abnormalities (Devasirvatham et al., 2013). Heat stress accelerated seed abortion in all ovule positions within pods in field pea (Jiang et al., 2020). In half of the cultivars tested, ovules at the pod's medial and stylar-end positions were more likely to develop into seeds compared to basal ovules. Pea cultivars with small seed size such as '40–10' and 'Naparnyk' were able to retain the most ovules and seeds per pod compared to large seed size cultivars, and large-seeded cultivars like 'MFR043' aborted seeds when exposed to heat in growth chambers (Jiang et al., 2020). Under field conditions, the field pea cultivars 'CDC Meadow', 'CDC Sage', and 'Carnival' (identified as having a low and medium proportion of ovules developing into seeds per pod) which were subjected to heat stress during flowering phases displayed higher levels of ovule abortion and a significant decrease in ovaries, ovules, and embryo sac size than cultivars '40–10', 'Naparnyk', and 'MFR043' (identified as having a high proportion of ovules developing into seeds per pod) (Osorio et al., 2023). Heat stress (>32/20°C) accelerated pod abortion as well as shortened the duration of seed set, leading to yield loss in lentil (Bhandari et al., 2016). In addition, heat stress was reported to decrease ovule number and ovule viability, and result in fertilization failure in common bean (Monterroso and Wien, 1990; Ormrod et al., 1967). Cold stress may also cause morphological changes in female reproductive cells and organs. Exposure of sensitive chickpea genotypes to low temperatures (15/0°C) significantly reduced ovary and style size and delayed floral development (Srinivasan et al., 1999).

Seed-filling processes are adversely affected by heat and drought stress in all crop species, including grain legumes, resulting in reduced seed yields and quality. For example, drought stress significantly reduced seed weight per plant, average seed weight, average seed size,

TABLE 1 Effects of abiotic stress on ovule/seed development and seed yield reduction in different field crops.

Crops	Growth stage	Stress conditions	Effects on ovule/ seed	Seed yield reduction ()	References
Flax (*Linum usitatissimum*)	Post-anthesis	Heat, 40/18°C (day/night) for 7 d or 14 d	Reduced seed number, single seed weight, increased % malformed seed	ns	Cross et al. (2003)
Field pea (*Pisum sativum*)	Flowering	Heat, 35/24°C (day/night) for 7 d	Reduced seed number and seed to ovule ratio	15	Jiang et al. (2020b)
Maize (Zea Mays)	Reproduction	Heat, 40/30°C (day/night)	Reduced kernel number	28	Wang et al. (2021b)
Chickpea (*Cicer arietinum*)	-	Heat, >35°C in the field	Reduction in pod set	39	Devasirvatham et al. (2015)
Oilseed rape (*Brassica napus*)	Seed filling	Heat, 33/19°C (day/night)	Reduced seed number	40	Brunel-Muguet et al. (2015)
Sorghum (*Sorghum bicolor*)	Anthesis	Heat, 38/22°C (day/night)	Reduced grain number, damaged ovule cells	50	Chiluwal et al. (2020)
Wheat (*Triticum aestivum*)	Seeding to maturity	Salinity, 15 dS m^{-1}	Reduced seed weight	58	Abbas et al. (2013)
Camelina (*Camelina sativa*)	Post-anthesis	Heat, 34/24°C (day/night) for 7 d or 14 d	Reduced seed oil accumulation	85	Nadakuduti et al. (2023)
Pearl millet (*Pennisetum glaucum*)	Seeding to maturity	Heat, 42/32°C (day/night)	Reduced seed number	85	Djanaguiraman et al. (2018a)
Chickpea (*Cicer arietinum*)	Seeding to maturity	Salinity, 40 mM NaCl	Reduced seed number	20d–98 depending on genotype	Turner et al. (2013)
Kidney bean (*Phaseolus vulgaris*)	Reproduction	Heat, 40/30°C (day/night) and CO_2 (700 µmol mol^{-1})	Reduced seed number	100	Prasad et al. (2002)

ns, seed yield between control and stressed treatments not significant.

and number of pods in chickpeas (Nayyar et al., 2006). Drought stress during pod-filling resulted in significant reductions in seed minerals (i.e., Fe, Zn, P, and N) and seed protein content in common bean (Ghanbari et al., 2013a, 2013b). Similarly, drought stress at seed filling stage led to significant reductions in starch, protein, amino acids, and minerals (Ca, P, and Fe) in chickpea seeds (Nayyar et al., 2006).

Salinity stress is another major abiotic factor that has adverse effects on reproductive processes through ionic imbalance, osmotic stress, and oxidative stress, leading to a reduction in nutrient uptake, cell division and expansion, and photosynthesis and photoassimilates (Khataar et al., 2018; Kumari et al., 2022; Atta et al., 2023). In sensitive chickpea genotypes, reproductive development related traits, such as flower number, ovule fertilization, pod development and retention, seed number, and seed size are highly sensitive to salt stress (Flowers et al., 2010). According to Khan et al. (2017), saline stress reduced photosynthesis and decreased tissue sugars by 22%–47%; both vegetative and reproductive development were severely impaired. Turner et al. (2013) reported that salt stress increased pod abortion in sensitive chickpea genotypes, but pollen viability, *in vitro* pollen germination, and *in vivo* pollen growth was not affected.

3.2 Effect of abiotic stress on the female reproductive organ in cereals

In maize, ovule development, ear growth, and ovary/kernel size and number were highly sensitive to heat and drought stress (Danilevskaya et al., 2019; Wang et al., 2019). Exposure of maize plants to low water potentials (Ψ_w) for 6 days during flowering [from silk emergence (day -5 from pollination to day 1 after pollination)] led to leaf Ψ_w of -1.25 MPa in water-stressed plants in comparison to leaf Ψ_w of 0.45 MPa in control plants at pollination, resulting in embryo abortion and a substantial reduction in kernel number, with abortion being linked to restricted carbon flow to the young ovaries due to impaired photosynthesis (Zinselmeier et al., 1999). Heat stress has negatively impacted ovule development in wheat, leading to yield loss (Saini and Aspinall, 1982; Saini et al., 1983). One-third of heat-stressed ovaries before anthesis in wheat exhibited an abnormal nucellus or embryo sac (Saini et al., 1983). Some of these abnormal ovules contained small embryo sacs without complete cellular organization or lacking any recognizable cells; the development of the nucellus degenerates in some of the ovules (Saini et al., 1983). In the wheat cultivar 'Chinese spring', short episodes (2 d or 5 days) of heat stress (35/25°C) during reproductive development (first at 8–6 days before anthesis and second at 2–0 days before anthesis) resulted in desiccated stigmas and styles with no pollen grains and flaccid and dried ovaries (Prasad and Djanaguiraman, 2014). Likewise, exposure of pearl millet (*Pennisetum glaucum*) to heat stress (39/29°C) against a non-stressed treatment (30/20°C) from gametogenesis through flowering in both controlled and field environments led to deformed and desiccated styles and ovaries (Djanaguiraman et al., 2018a). Six days of heat stress (38°C and 40°C) during megasporogenesis of a heat-tolerant rice genotype, 'N22', and a heat-sensitive genotype, 'IR64', resulted in degeneration of all four megaspores instead of just three nuclei, formation of mature embryo sacs without the female germ unit, improper positioning of nuclei, and shrunken embryo sacs in the sensitive IR64 as compared to the control (30°C) treatment (Shi et al., 2022).

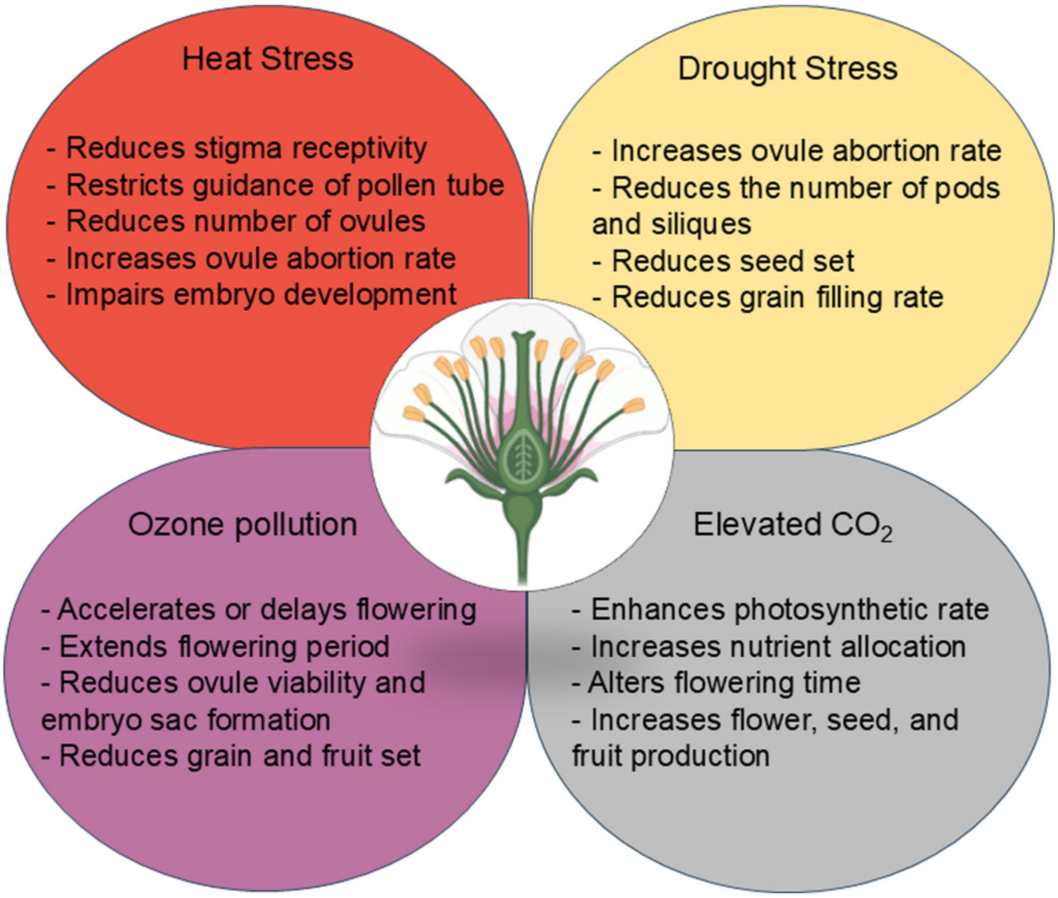


FIGURE 2
Schematic of some major impacts of climate change on female reproductive organs in crop species.

Cell wall invertases are important metabolic enzymes that hydrolyze sucrose into glucose and fructose and play an important role in apoplasmic unloading of sucrose and hexoses to the elongating pollen tubes and developing seeds and hence crop yield (Shen et al., 2019). The invertase activity in female reproductive organs was significantly decreased under heat stress, thus limiting the supply of sucrose and hexoses to rice spikletes (Jiang et al., 2020) and tomato fruits (Liu et al., 2016). Severe drought stress significantly reduced the invertase activity in the placental region and the ovary dry mass, leading to poor grain set and grain yield in maize (Andersen et al., 2002). Drought stress caused inhibition of invertase enzymes, downregulation of genes encoding sucrose processing enzymes, and expression of senescence-related genes in the ovary of maize, leading to ovary abortion (McLaughlin and Boyer, 2004).

Metabolite profiling of pistils during the gametogenesis stage of a heat-sensitive rice genotype, IR64, and a heat-tolerant rice genotype, N22, grown under control (30°C) and two high-temperature treatments (38°C and 40°C) for 6 days, revealed significant reductions in starch content, TCA cycle (citrate cycle) related metabolites (i.e., citric acid, fumaric acid, and succinic acid), and amino acid metabolites (i.e., 3-cyanoalanine, proline, aspartic acid, lysine, valine, and isoleucine) in the developing pistils of IR64 than N22 (Shi et al., 2022). According to Zinselmeier et al. (1995), water deficit conditions, particularly during flowering and early embryo growth, contributed to arrested embryo growth, a decreased sucrose flux, and an altered carbohydrate metabolism in the ovaries of maize.

Long-term drought stress from growth stage V7 (the beginning of the rapid growth phase and stem elongation) through R1 (silking) under field conditions caused significant transcriptional changes in ears but only minor changes in the tassel of the maize 'B73' inbred line (Danilevskaya et al., 2019). Many key genes involved in DNA replication, cell cycle, cell division, floral development (e.g., MADS-box and non-MADs genes), and embryo sac development (i.e., *IG1*; *indeterminate gametophyte*) were suppressed under drought stress, which ultimately led to the formation of defective ovaries and a failure to produce kernels (Danilevskaya et al., 2019). In rice, the pectinase gene family overexpressed in the male and female floral organs by high-temperature treatments and was suggested to be the direct cause of rice floral organ abortion during heat stress (Wu et al., 2015). Previous research showed that *ribosome inactivating protein* (*RIP2*) and *phospholipase D* (*PLD1*) genes were transcriptionally activated under stress conditions due to a lack of carbon sources, leading to early senescence and ovule abortion in maize (Boyer and McLaughlin, 2007). A summary of the adverse effects of heat on drought stress on the female reproductive phase, crop productivity, and grain quality in grain legumes and cereal crops is included in Figure 3.

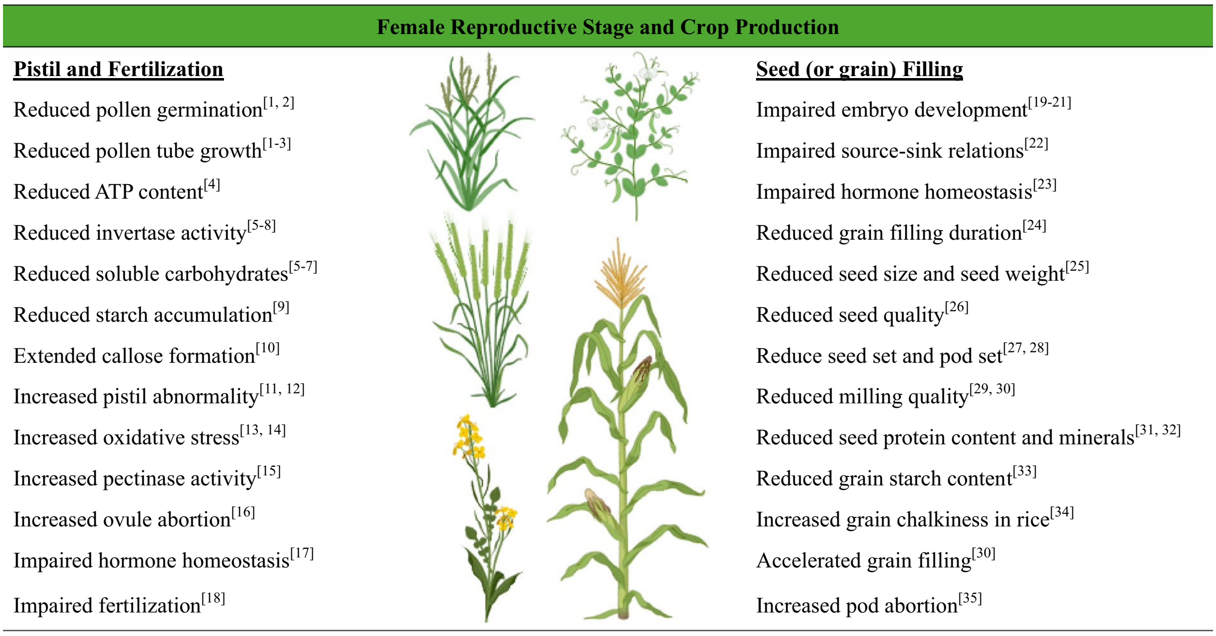
Salinity stress significantly reduced the growth and productivity of cereal crops (Munns et al., 2006). In maize, salinity stress considerably reduced grain yield of maize by decreasing the number of grains and grain weight during the reproductive growth stage (Schubert et al., 2009). This was attributed to reduced photosynthesis and photoassimilates (Lohaus et al., 2000; Hiyane et al., 2010) and impaired translocation of assimilates from source to developing grains (sink) under salt stress. In wheat, salinity stress accelerates all phenological phases (Grieve et al., 1994), decreases the number of spikelets number per spike (Frank et al., 1987), and reduces grain yield (Abbas et al., 2013; Sorour et al., 2019), and grain quality traits (El Sabagh et al., 2021).

3.3 Effect of abiotic stress on female reproductive organ in oilseed crops

Under high-temperature conditions (32/26°C) most stigmas protruded significantly out of the closed flower buds in rapeseed (*Brassica napus*) (Polowick and Sawhney, 1988). Heat stress (32/26°C) caused abnormal embryo sac development in rapeseed – the ovule growth was not uniform along the length of the ovaries of both pollinated and unpollinated flowers (Polowick and Sawhney, 1988). Heat stress in rapeseed was associated with asynchronous embryo development, a high rate of defective embryos, accelerated embryo development, altered seed quality, induced pre-harvest sprouting, and decreased abscisic acid (ABA) levels in mature seeds (Brunel-Muguet et al., 2015; Mácová et al., 2022). Heat stress decreased seed oil content by 52% in canola, but the protein content increased under heat, drought, and a combination of heat and drought (Elferjani and Soolanayakanahally, 2018). Heat stress reduced seed oil content but increased seed sugar content in rapeseed, suggesting that the conversion of carbohydrates into triacylglycerols was affected under heat stress (Huang et al., 2019). The authors also found that reduced seed production was caused by the impairment of photosynthesis and downregulation of *BnWRI1* and its downstream genes. Fewer fertile pods and seeds per pod were produced by canola florets under heat stress (Hu et al., 2024). Further, heat stress during seed development was reported to induce changes in the biosynthesis from polyunsaturated fatty acid synthesis to more monounsaturated fatty acid accumulation in camelina (*Camelina sativa*), leading to membrane stability to protect cell function and embryo development (Nadakuduti et al., 2023).

3.4 Effect of abiotic stress on the female reproductive organ in other horticulture crops

In apricots (*Prunus armeniaca*), mild heat stress (an average of 3°C higher than the control) during the last week of flower development shortened the style length and led to abnormal ovary development (Rodrigo and Herrero, 2002). Heat stress reduced ovule longevity in plum (*Prunus mume*) (Cerovic et al., 2000). Fertilized ovules may stop swelling rapidly in tomatoes due to high temperatures (Kinet and Peet, 1997). Heat stress also decreased ovule number and



Female Reproductive Stage and Crop Production

Pistil and Fertilization

Reduced pollen germination[1, 2]
Reduced pollen tube growth[1-3]
Reduced ATP content[4]
Reduced invertase activity[5-8]
Reduced soluble carbohydrates[5-7]
Reduced starch accumulation[9]
Extended callose formation[10]
Increased pistil abnormality[11, 12]
Increased oxidative stress[13, 14]
Increased pectinase activity[15]
Increased ovule abortion[16]
Impaired hormone homeostasis[17]
Impaired fertilization[18]

Seed (or grain) Filling

Impaired embryo development[19-21]
Impaired source-sink relations[22]
Impaired hormone homeostasis[23]
Reduced grain filling duration[24]
Reduced seed size and seed weight[25]
Reduced seed quality[26]
Reduce seed set and pod set[27, 28]
Reduced milling quality[29, 30]
Reduced seed protein content and minerals[31, 32]
Reduced grain starch content[33]
Increased grain chalkiness in rice[34]
Accelerated grain filling[30]
Increased pod abortion[35]

FIGURE 3
Adverse effects of heat and drought stress on female reproductive organs and seed (or grain) filling in crop plants. Chickpea-[1] (Kumar et al., 2013); pearl millet-[2] (Gupta et al., 2015); rice-[3] (Zhang et al., 2018a); cotton-[4] (Snider et al., 2009); tomato-[5] (Liu et al., 2016); cotton-[6] (Loka and Oosterhuis, 2016); rice-[7] (Jiang et al., 2020a); maize-[8] (Andersen et al., 2002); rice-[9] (Shi et al., 2022); pea-[10] (Jiang et al., 2019b); rice-[11] (Takeoka et al., 1991); chickpea [12] (Devasirvatham et al., 2013); pearl millet-[13] (Djanaguiraman et al., 2018a); rice-[14] (Jiang et al., 2020a); rice-[15] (Wu et al., 2015); *Arabidopsis*-[16] (Whittle et al., 2009); pea-[17] (Savada et al., 2017); rice-[18] (Li et al., 2015); rice-[19] (Begcy et al., 2018); spring wheat [20] (Prasad et al., 2008); common bean [21] (Vargas et al., 2021); common bean [22] (Soltani et al., 2019); pea-[23] (Ozga et al., 2009); wheat-[24] (Wardlaw, 2002); lentil-[25] (Kumar et al., 2016); soybean-[26] (Teixeira et al., 2016); common bean-[27] (Gross and Kigel, 1994); soybean-[28] (Liu et al., 2003, 2004); wheat-[29] (Hernández-Espinosa et al., 2018); [30] (Mahdavi et al., 2022); common bean- [31] (Ghanbari et al., 2013a); [32] (Ghanbari et al., 2013b); rice-[33] (Yamakawa et al., 2007); rice-[34] (Nakata et al., 2017); cool-season pulses-[35] (Bhandari et al., 2016) Created in BioRender.

viability of tomato plants (Din et al., 2015). Similarly, a reduction of seed set under heat stress was associated with a decreased amount of carbohydrates and growth regulators in plant sink tissues in tomato (Kinet and Peet, 1997).

3.5 Callose deposition as a biomarker in response to abiotic stress in female reproductive organs

Callose is a polysaccharide β-1,3-glucan synthesized by a family of callose synthases and deposited in specialized cell walls or cell wall-associated structures such as cell plates, outer walls of pollen grains, pollen tubes, and plasmodesmata in a wide variety of higher plants (Nishikawa et al., 2005). Plant cell walls contain only small amounts of callose, ranging from 0.2%–0.5% in *Arabidopsis* and food crops to about 5% in energy crops under normal growth conditions (Wang et al., 2022). However, heavy callose deposition in cell walls may occur due to abiotic stress, wounding, and pathogen infection (Chen and Kim, 2009; Luna et al., 2011). Callose in the cell wall, plasmodesmata, and sieve pores contribute to the internal stabilities of cells during water stress and heat (Wang et al., 2022). In angiosperms with monosporic or bisporic embryo sac development, callose is formed in the megaspore mother cell walls (Rodkiewicz, 1970). Callose also accumulates in the walls of megaspore tetrads, the four haploid cells produced by the meiotic division of megaspore mother cells. Under optimal growth conditions, the callose begins to degrade when the functional megaspore undergoes its first mitosis and throughout the process of embryo sac development (Shi et al., 2016; Zhou et al., 2016; Brzezicka and Kozieradzka-Kiszkurno, 2024). However, callose accumulation can be extended around the synergid and at the micropylar in response to stress which can lead to ovule abortion and embryo senescence likely by hindering signals required for the pollen tube to enter the embryo sac and reducing sugar transport into ovules (Rodrigo and Herrero, 1998; Sun et al., 2004). A higher amount of callose deposition were observed in ovules of field pea under heat stress (Jiang et al., 2019b) and in sweet cherry (*Prunus avium*) (Zhang et al., 2018). A similar observation was reported in salt-stressed *Arabidopsis* plants (Sun et al., 2004). Callose has been used as a biomarker for embryo senescence such as in *Arabidopsis* (Sun et al., 2004) and field pea (Jiang et al., 2019b).

3.6 Effect of heat stress on reactive oxygen species (ROS) in female flower organs

Plants convert 1%–2% of consumed oxygen into reactive ROS, such as hydrogen peroxide (H_2O_2), singlet oxygen ($^1O_2$), superoxide radicals ($O2^{\bullet-}$), and hydroxyl radicals ($^{\bullet}OH$) as a byproduct of aerobic metabolism in several cellular compartments such as the chloroplast, mitochondria, and peroxisomes (Sachdev et al., 2021). ROS are important signaling molecules that are involved in reproductive processes such as megagametogenesis, pollen-pistil interaction, and degeneration of synergids (Zinta et al., 2016). ROS levels surge beyond physiological thresholds in response to environmental stressors which can cause irreversible damage to DNA, lipids, and proteins, leading to cell death (Dat et al., 2000; Zafar et al., 2022; Hong et al., 2024). To counteract these deleterious effects, plants have evolved a regulatory network comprising enzymatic [e.g., superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT)] and non-enzymatic (e.g., ascorbic acid, glutathione, flavonoids, carotenoids, proline, and ubiquinone) antioxidant systems tends to keep the magnitude of ROS within plant cells to a non-damaging level (Zafar et al., 2023). However, antioxidants may fail to scavenge excess ROS. For example, under high-temperature stress, prolonged accumulation of ROS and low antioxidant activity in the pistils was suggested to be responsible for low fertilization rate and/or high rate of early embryo abortion in heat-sensitive genotypes of sorghum (Djanaguiraman et al., 2018b) and pearl millet (Djanaguiraman et al., 2018a). In contrast, the heat-tolerant rice genotype N22 maintained ROS homeostasis and antioxidant enzyme activities in its female gametophytes better than IR64, especially during post-stress recovery (Shi et al., 2022).

3.7 Effect of heat stress on phytohormones in female reproductive organs

Plant phytohormones such as abscisic acid (ABA), auxins, cytokinins, and ethylene play important roles in pollen-pistil interactions, pollen tube growth, and ovary development (Wu et al., 2008; Deb et al., 2018) and are altered to regulate the physiological and biochemical processes in response to environmental stresses (Zhang et al., 2023). Under high-temperature (34/18°C) conditions, pistils in a heat-sensitive rapeseed cultivar., ‘Westar’, had significantly lower levels of ABA than those developed under optimal (21/14°) conditions, suggesting that they are less protected against temperature stress (Mácová et al., 2022). Auxin plays an essential role in embryonic patterning at the early stage of seed development (Verma et al., 2021). Auxin levels were significantly decreased in heat-susceptible rice pistils due to high-temperature treatment (40°C for 2 h), and exogenous application of NAA (1-naphthaleneacetic acid) alleviated the restriction on pollen tube growth (Zhang C. et al., 2018). Ethylene may play a role in reproductive processes and seed development. It may also promote, inhibit or induce senescence depending upon the optimal or sub-optimal ethylene levels (Iqbal et al., 2017). The ethylene biosynthesis gene, 1-aminocyclopropane-1-carboxylic acid (ACC) oxidase (*ACO*) was expressed in early developing stigma, style, and ovary in tobacco (*Nicotiana tabacum*) (De Martinis and Mariani, 1999). In tomato, *LeACO1,2,3,* and *4* and *LeACS1A* transcripts were detected in pistils (Llop-Tous et al., 2000). In China rose (*Hibiscus rosa-sinensis*), ACC synthase (*ACS*) and *ACO* were found to be specifically expressed in developing style-stigma and ovary tissues (Trivellini et al., 2011). Ethylene seems to be involved in the senescence of unpollinated pistils in peas (Savada et al., 2017), tomato (Shinozaki et al., 2018), and *Arabidopsis* (Carbonell-Bejerano et al., 2011). In pea, *PsACS* and *PsACO* were differentially expressed in pre-pollinated ovaries under heat stress (33°C–35°C 6 h/day for 4 days) that promoted ovary senescence (Savada et al., 2017). The authors also suggested that the ethylene-dependent pollen germination and pollen tube growth on stigma and style were inhibited under heat (Savada et al., 2017).

4 Stress adaptation mechanisms during sexual reproduction

Plants can escape from environmental stress or resist it by avoidance or tolerance (Bueckert and Clarke, 2013). Management and breeding approaches, such as shifting planting date and genetic manipulation of crop phenology, have been used to facilitate plants to escape from heat stress (Sadras et al., 2015). Stress avoidance is the ability of plants to avoid stress conditions through some physiological mechanisms (Bueckert and Clarke, 2013). Stress tolerance is the ability of plants to survive under stress conditions and usually produce lower economic yield compared to optimal conditions (Hasanuzzaman et al., 2013). The terms, stress tolerance and stress resistance, are also used in the literature interchangeably to mean a trait with stress robustness compared to heat susceptibility. For example, dryland cereals (e.g., wheat, sorghum, and pearl millet) usually flower early morning or late evening during the cool hours of the day to avoid higher temperatures (Jagadish, 2020). In sorghum, 100% flowering was completed within 1 h before dawn, which helped sorghum plants escape dryer and hotter conditions during the day (Chiluwal et al., 2020).

Under stress conditions, several mechanisms are employed to maintain homeostasis and normal cellular functions. The strategy termed "differential transpiration" was recently reported by Sinha et al. (2023) – under combined heat and drought conditions, soybean plants prioritized their transpiration in flowers by opening flower stomata on sepals to have a cooling effect and kept their leaf stomata closed. The authors proposed that manipulating flower stomatal parameters (such as size and density) could be used as a strategy to enhance crop resilience to climate change (Sinha et al., 2023).

Heat shock proteins (HSPs) are a unique family of proteins produced in plant cells in response to environmental stresses (Singh et al., 2024). HSPs play a crucial role in conferring plant tolerance to heat and drought stress by maintaining the function of proteins and integrity of various biomembranes (Zhang et al., 2015; Liu et al., 2019). The application of genetic manipulation approach to enhance heat and drought tolerance in crops species has mainly focused on HSP encoding genes. For example, constitutive expression of *Arabidopsis AtHsp101* (Katiyar-Agarwal et al., 2003) and *OsHSP18.6* (Wang et al., 2015) increased thermotolerance in transgenic rice plants. Overexpression of small *HSP17.7* enhanced rice tolerance to heat and UV-B exposure (Murakami et al., 2004). Pre-foliage exogenous application of ABA before high-temperature treatment of rice genotypes resulted in enhanced expression levels of *HSP* genes, increased levels of starch and soluble sugars, and proteins involved in sugar transport and conversion, and improved activity of antioxidant enzymes and ATP content in spikelets (Rezaul et al., 2019). Similarly, an auxin application of 1 μM resulted in a greater grain number and grain yield in wheat when plants were exposed to heat stress (34°C–35°C for 6 h for 6 days) (Abeysingha et al., 2021).

Cell wall invertases are involved in carbohydrate partitioning, hormone signaling, and stress responses and play fundamental roles in plant reproductive developments, including ovule development and seed/fruit set (Roitsch and González, 2004; Liu et al., 2022). In *Arabidopsis*, cell wall invertase functions as a positive regulator of ovule initiation through sugar signaling (Liao et al., 2020). In tomato crop, cell wall invertase promotes fruit set under heat stress by suppressing ROS-independent cell death (Liu et al., 2016). According to Li et al. (2012), 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. Similarly, 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 (Liu et al., 2016). In addition, the cell wall invertases-elevated transgenic tomato plants exhibited higher transcript levels of *HSP90* and *HSP100* in ovaries *HspII17.6* in fruits and suppressed programmed cell death in fruits and alleviated fruit-set failure by promoting higher transcript levels of auxin biosynthesis gene *ToFZY6* (Liu et al., 2016).

Recent studies have identified peptide/receptor signaling pathways that contribute to stress adaptation in female organs during sexual reproduction. In *Arabidopsis*, *CLE45* (*CLAVATA3/EMBRYO SURROUNDING REGION-RELATED45*), a post-translationally modified peptide, was preferentially expressed in the stigma at normal temperature. Upon heat stress, the expression of *CLE45* was expanded to the transmitting tract cells where it paired with RLK receptors *SKM1* (*STERILITY-REGULATING KINASE MEMBER1*) and *SKM2* of the male gametophyte to sustain pollen tube growth, leading to adequate fertilization and seed production (Endo et al., 2013). Endoplasmic reticulum-localized DnaJ (ERECTA) family receptor kinases play an important role in heat tolerance; when they are absent, high temperatures aggravate the negative effects on ovule development in *Arabidopsis* (Leng et al., 2022). A recent study showed that *Class II TEOSINTE BRANCHED 1/CYCLOIDEA/ PCF (TCP)* transcription factors protect ovule identity in *Arabidopsis* under high-temperature stress (Lan et al., 2023). Small RNAs play significant roles in ovule development (Petrella et al., 2021). Overexpression of *OsRab7* gene increased the number of filled grains per hill by 35%, the seed filling rate by 21%, and the total grain weight by 27% in rice (El-Esawi and Alayafi, 2019).

5 Discussion

Ovule development is a critical step in plant reproduction, and maintaining optimal conditions during this process is essential for successful seed formation and overall plant productivity. Although a lot of previous work focused on the impact of abiotic stressors on the male gametophyte, several studies from recent years delved into the impact of these stress factors on the development of the female gametophyte (Djanaguiraman et al., 2018a; Jiang et al., 2019b; Wang et al., 2021a). Understanding how ovule and seed development respond to environmental stress is essential for developing effective strategies to enhance crop resilience to climate change. Further research in this field is not only crucial for advancing our knowledge but also for translating this understanding into practical solutions, such as abiotic stress resistance breeding and developing beneficial agronomy practices to mitigate the risk of climate change on crop production. In recent years, several research groups contributed to abiotic stress-resistant breeding (Rao et al., 2016; Gilliham et al., 2017; Derbyshire et al., 2022), such as the efforts in breeding for stress-resilient cultivars of pea (Jiang et al., 2017; Huang et al., 2023), wheat (Mondal et al., 2021; Tanin et al., 2022), and maize (Farooqi et al., 2022). Diversified cropping systems showed their effectiveness in improving crop resilience to climate change (Li et al., 2019). The concept of "green strategies" was proposed by González Guzmán et al. (2022), and they refer to environmentally friendly practices such as the use of beneficial soil microorganisms, chemical priming, and improved water management that aim to enhance plant tolerance to stress factors.

Soil microbes such as rhizobia, arbuscular mycorrhizal fungi, and plant growth-promoting rhizobacteria have shown the ability to improve plant growth and optimize reproductive development and seed set under adverse environmental conditions by employing several mechanisms, such as enhancing water use efficiency and nutrient acquisition through the production of phytohormones hormones, improving photosynthetic rate, balancing ionic equilibrium, producing antioxidants, and improving soil health and fertility (Sagar et al., 2021; Fahde et al., 2023). Salicylic acid is a phytohormone that is involved in plant flowering, pollen germination, pollen tube elongation, and post-fertilization ovary development (Luo et al., 2022). It is evidenced that foliar sprays or soil applications of priming agents like salicylic acid can alleviate yield losses due to heat stress (Zhang et al., 2017; Berková et al., 2023). Mulching is another green strategy that can contribute to the stability of reproductive processes during periods of low rainfall by reducing soil evaporation, conserving moisture, controlling soil temperature, reducing weed growth, and improving microbial activities (Iqbal et al., 2020).

Overall, these strategies optimize nutrient availability, reduce stress, and promote overall plant health, ensuring that ovule development in flowering plants is sustained and successful under changing environmental conditions, leading to improved plant development and reproduction.

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