Plant Science 311 (2021) 111007

Contents lists available at ScienceDirect

Plant Science

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

Review article

The impact of stress combination on reproductive processes in crops

Ranjita Sinha [a], Felix B. Fritschi [a], Sara I. Zandalinas [a], Ron Mittler [a,b,*]

[a] *Division of Plant Sciences, College of Agriculture Food and Natural Resources, and Interdisciplinary Plant Group, Christopher S. Bond Life Sciences Center, University of Missouri, Columbia, MO, USA*

[b] *Department of Surgery, University of Missouri School of Medicine, Christopher S. Bond Life Sciences Center, University of Missouri, 1201 Rollins Street, Columbia, MO, 65201, USA*

ARTICLE INFO

Keywords:
Agriculture
Climate change
Crop
Drought
Flowering
Heat
Global warming
Reproduction
Stress combination
Yield

ABSTRACT

Historically, extended droughts combined with heat waves caused severe reductions in crop yields estimated at billions of dollars annually. Because global warming and climate change are driving an increase in the frequency and intensity of combined water-deficit and heat stress episodes, understanding how these episodes impact yield is critical for our efforts to develop climate change-resilient crops. Recent studies demonstrated that a combination of water-deficit and heat stress exacerbates the impacts of water-deficit or heat stress on reproductive processes of different cereals and legumes, directly impacting grain production. These studies identified several different mechanisms potentially underlying the effects of stress combination on anthers, pollen, and stigma development and function, as well as fertilization. Here we review some of these findings focusing on unbalanced reactive oxygen accumulation, altered sugar concentrations, and conflicting functions of different hormones, as contributing to the reduction in yield during a combination of water-deficit and heat stress. Future studies focused on the effects of water-deficit and heat stress combination on reproduction of different crops are likely to unravel additional mechanisms, as well as reveal novel ways to develop stress combination-resilient crops. These could mitigate some of the potentially devastating impacts of this stress combination on agriculture.

1. Heat and water-deficit combination in a changing climate

The global increase in anthropogenic greenhouse gasses in our atmosphere has adversely impacted agriculture, subjecting crops to multiple combinations of abiotic stresses [1–5]. Average ambient temperatures have been steadily increasing in the past 40 years and are predicted to increase further with frequent occurrences of heat waves and elevated night temperatures [4]. This process, termed global warming, is driving climate changes that lead to frequent episodes of water-deficit stress [6]. As a result, increased ambient temperatures and frequently occurring water-deficit stress episodes are becoming a major threat to yield production [7,8], especially since large areas of agricultural land used for cereal and legume cultivation are rain-fed [9]. Moreover, the simultaneous occurrence of water-deficit stress episodes with heat waves subjects crops to a combination of water-deficit and heat stress in the field [10], and this combination exacerbates the impacts of water-deficit stress, as higher temperatures increase water loss by enhanced evapotranspiration, further impacting limited soil water resources [11]. Historically, the combination of water-deficit and heat stress has greatly reduced crop production [12], with yield losses in the US estimated at 33, 44, 7.6, and 7 billion $ during the summers of 1980, 1988, 2000, 2003 and 2008, respectively [13]. A combination of heat and water-deficit stress in Europe in 2003 has also reduced crop production by 30 % [12]. Although a combination of water-deficit and heat stress can severely reduce seedling emergence and vegetative plant growth, its impacts on reproductive processes of crops, such as cereals and legumes, is thought to be the major cause of agricultural yield losses [1,14,15]. In addition to water-deficit and heat stress combinations, the frequency and intensity of other stress combinations, such as heat and flooding, heat and salinity, and water-deficit and salinity are predicted to increase due to climate change [5]. Moreover, more complex scenarios involving combinations of multiple factors that include abiotic, biotic and man-made pollutants are predicted to occur and adversely impact plants, soils and microbiomes [5,16]. These were recently termed multifactorial stress combinations and shown to have an alarming effect on plant growth and survival [5,17].

* Corresponding author at: Division of Plant Sciences, College of Agriculture Food and Natural Resources, and Interdisciplinary Plant Group, Christopher S. Bond Life Sciences Center, University of Missouri, Columbia, MO, USA.

E-mail address: mittlerr@missouri.edu (R. Mittler).

https://doi.org/10.1016/j.plantsci.2021.111007
Received 1 May 2021; Received in revised form 19 July 2021; Accepted 22 July 2021
Available online 24 July 2021
0168-9452/

2. Plant reproduction is a complex process that is highly sensitive to abiotic stress

Plant reproduction is a complex and highly coordinated process involving specialized organs that display heightened, and sometimes differential, sensitivity to different abiotic conditions (Fig. 1). The development of pollen occurs in anthers inside specialized compartments called locules. This process is divided into two stages: microsporogenesis and microgametogenesis. The maturation of pollen within locules is supported by a highly coordinated process of tapetum layer programmed cell death (PCD) that releases nutrients into the locule compartments. Upon maturation and dehydration, pollen are shed from anthers in a regulated manner (anther dehiscence). Pollen must then land on a compatible female stigma, rehydrate, germinate, and form a pollen tube that grows through the style until it reaches the ovule. At the entrance to the female gametophyte within the ovule, the tube bursts in the synergid cells to release its sperms (one will fuse with the egg cell forming an embryo, and the other will fuse with the polar nuclei forming the endosperm) [18]. In addition to the anther and pollen grain functions described above, pistil (stigma, style, ovary) development and functions, which include pistil-pollen interactions, as well as embryo development and seed filling, are also very sensitive to abiotic stresses. Only upon completion of all the highly coordinated stages described above (Fig. 1), a mature seed will form. As described below and in [14, 15,19–29], many of the processes resulting in the formation of functional seeds (yield in the case of cereals and legumes) are highly sensitive to heat, water-deficit and/or heat and water-deficit combination (Fig. 2). In addition, because certain crops can be self-pollinating (pollination occurs within unopened flower buds), and/or require insect or wind vectors for pollination (cross-pollination), different environmental conditions and stresses, associated with climate change (*e.g.,* drought combined with heat waves or altered insect populations) could affect different crops differently.

3. Occurrence of heat and water-deficit stress combination during flowering time exacerbates yield losses

The co-occurrence of water-deficit and heat stress causes large yield reductions in both cereals and legumes [22–25]. These losses are magnified when the two stresses coincide with different reproductive and/or seed maturation processes [15,19,22–25,30–32]. Indeed, flower development and fertilization, two indispensable processes affecting crop yield production, are exceptionally vulnerable to abiotic stresses [26–29]. The heightened sensitivity of reproductive processes to a combination of water-deficit and heat stress suggests that this stress combination has a unique effect on plant reproduction. However, how these two stresses applied together impact flowering, fertilization, embryogenesis and seed development, and compromise crop productivity is still under investigation (Fig. 2). Moreover, results from studies focusing on reproductive processes under conditions of heat or water-deficit stress, applied individually, can not necessarily be extrapolated to predict responses of reproductive tissues to stress combination, as this response may be unique [33]. It is therefore essential to study the different developmental and physiological processes of reproductive tissues to stress combination at the molecular, proteomic, and metabolic levels, side-by-side with their responses to each of the different stresses applied individually. Flowering and fertilization are complex processes that involve various tissues and molecular responses, and successful fertilization requires the proper development of male and female reproductive organs (anther and carpel), and male and female gametes (pollen and ovule). Here, we review some of the studies conducted on reproductive tissues subjected to water-deficit, heat, and their combination, as well as address some of the major gaps in our understanding of these processes that remain to be studied.

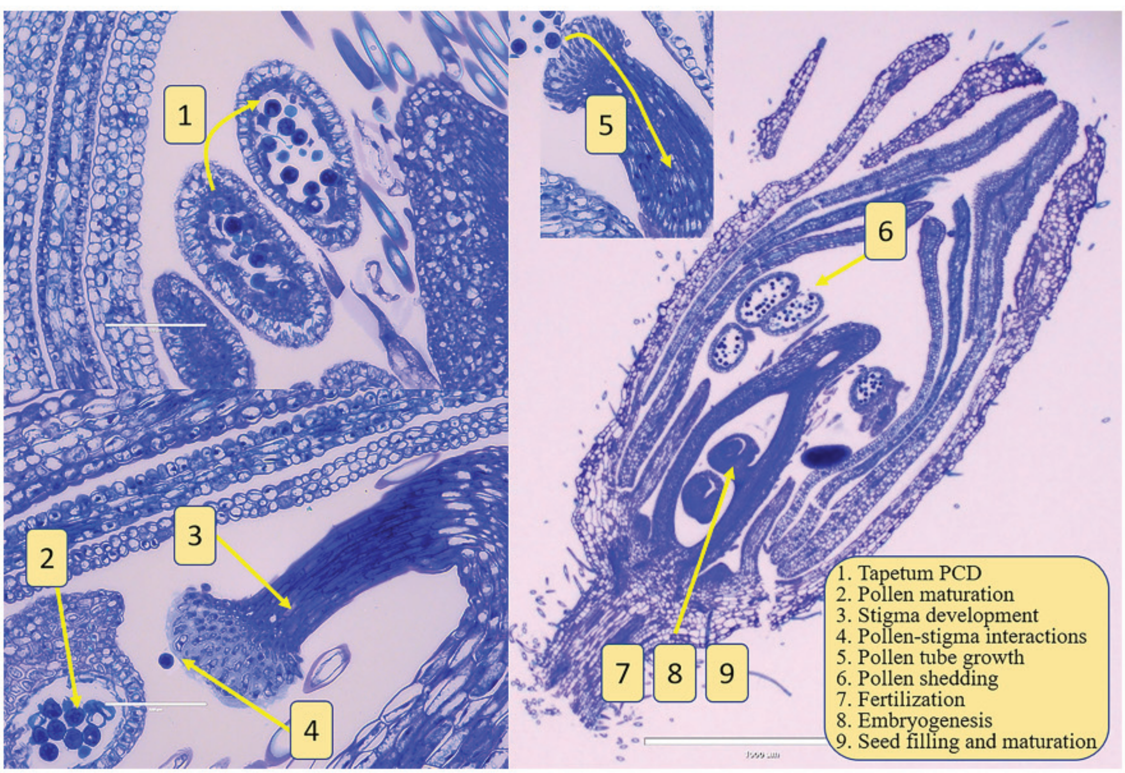

Fig. 1. Light microscopy images depicting different reproductive processes in soybean that could potentially be sensitive to water-deficit, heat stress and/or water-deficit and heat stress combination. Images were obtained from cross-sections of soybean flowers grown under controlled growth conditions and assembled to highlight different reproductive processes. Because in soybean self-pollination is predominating, stigma, pollen grains and pollen sacs can be found in close proximity inside unopen flower buds. *Abbreviations:* PCD, programmed cell death.

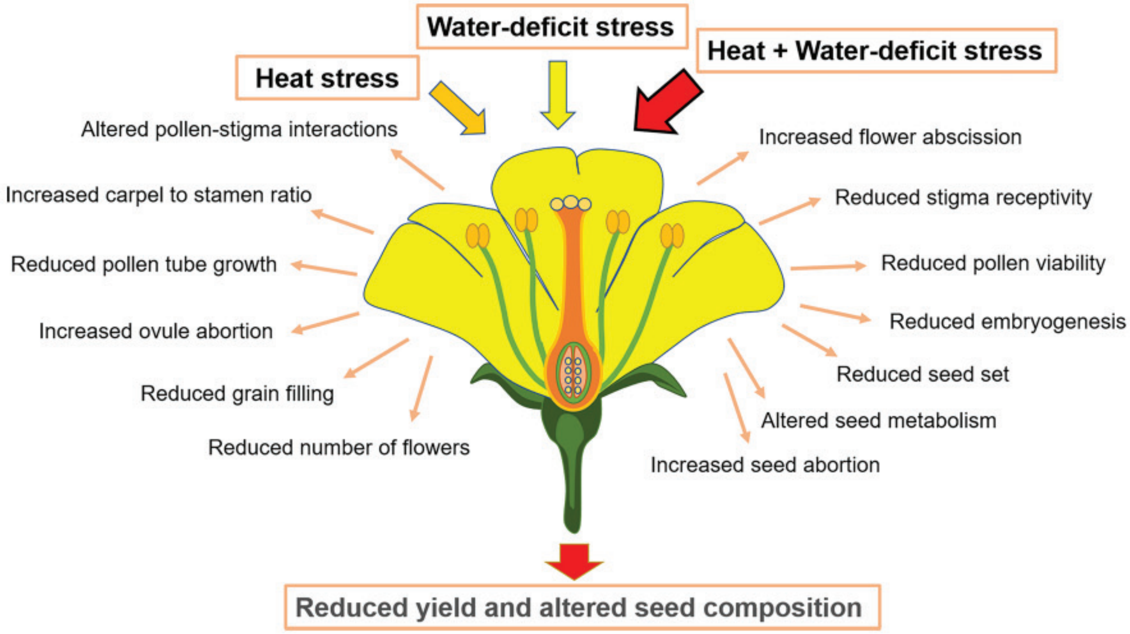

Fig. 2. Different reproductive processes of plants affected by water-deficit, heat stress and/or water-deficit and heat stress combination. The impact of water-deficit, heat and/or water-deficit and heat combination on these processes is shown to result in yield reduction.

4. Impacts of water-deficit and heat stress on flowering time and duration

When water-deficit stress occurs during vegetative development, annual plants often initiate their reproductive development earlier, a phenomenon called drought escape, to ensure some fertilization and seed development before the completion of their life cycle [34,35]. Incidences of water-deficit occurring during floral induction and flower development can cause however a delay in flower development and occasionally lead to complete inhibition [36–39]. In rice (*Oryza sativa*), water-deficit stress around anthesis was reported to prolong anthesis silking intervals [40]. As a part of an avoidance strategy, some plants exposed to high temperatures can change their flowering time to mitigate the potential of heat stress-induced reproductive sterility [41–43]. For example, rice plants shift their flowering time to early morning to accomplish fertilization before the onset of heat stress [41–43], and heat tolerant wheat (*Triticum aestivum*) plants shift their flower opening to the cooler morning or evening hours [44]. Heat stress was found to accelerate flowering time in Arabidopsis (*Arabidopsis thaliana*), but delay it in Brassica (*Brassica rapa*) [45,46]. One of the major questions associated with our current and predicted climate conditions, and the increasing frequency of water-deficit and heat stress combination is: How do plants modulate their flowering time or anthesis when exposed to stress combination? Rang et al., [47], reported that the flowering period is extended under a combination of water-deficit and heat stress in rice. Similarly, Liu et al. [25], reported prolonged silking intervals in maize (*Zea mays*) under combined heat and water-deficit stress. Flowering initiates early under a combination of heat and water-deficit stress in wheat with a decreased duration of microgametogenesis [26]. However, the impact of this combination on many other cereals and legumes is still unknown. It is possible that to avoid and/or minimize the impacts of stress combination on different reproductive processes such as pollen shedding, interactions with stigma and tube elongation, other crops, such as self-pollinating legumes, would also favor morning hours when the temperature is low and humidity is high. However, detailed studies are required to unravel the role of flowering time in enhancing the success of different processes leading up to and associated with fertilization and seed setting. In addition, because night and morning temperatures are also predicted to increase, as a consequence of global warming, shifting flowering time may only work for as long as the temperature threshold for inhibition of reproductive processes will not be crossed during these hours. High night temperatures were found, for example, to affect pollen development and viability, anther dehiscence, and pod development and cause reduced yield in common bean (*Phaseolus vulgaris*), cowpea (*Vigna unguiculata*), and soybean (*Glycine max*) (Reviewed in [15]). Several studies have also identified key differences between the daytime and night heat stress response of plants [48–52], and these could be playing an important role in the protection of reproductive tissues from heat stress during the daytime or at night. Further studies are therefore needed to distinguish between the molecular mechanisms that could protect reproductive tissues during day- or night-time, and these should be utilized in future endeavors to enhance the tolerance of crops to global warming.

5. Impacts of water-deficit and heat combination on flower development

Both water-deficit and heat stress, even when applied alone, significantly impair flower development and fertility [20,38,53,54]. Maize plants exposed to water-deficit stress around anthesis show decreased growth rate of silk and ovary, and aborted kernels [25,54,55]. Similarly, in Arabidopsis, occurrence of water-deficit during flowering causes reduced fertility with arrest of floral development, abnormal anther development, reduced pollen viability, reduced filament elongation, abortion of ovule and suppression of flower opening [38]. Water-deficit can also lead to premature flower abscission due to flower separation at the abscission zone [56]. When exposed to heat stress during flowering, rice plants display spikelet degeneration, reduced floral organ development, decreased pollen viability, reduced anther dehiscence and low pollen shedding, reduced number of spikelets, and reduced grain filling [57–61]. Similarly, Arabidopsis plants under heat stress have impaired anther and pollen development [62]. Heat susceptible plants commonly display reduced pollen grain numbers within their anthers when experiencing high temperatures [30,63–65], and even a transient heat stress at the tetrad stage of pollen development was observed to reduce pollen germination and cause sterility in maize [66]. Under a combination of heat and water-deficit stress, rice spikelets show shorter peduncles, lower pollen counts, and reduced anther dehiscence and spikelet fertility

[47,67]. Similarly, maize plants under combined water-deficit and heat stress exhibit kernel abortion, decreased fertilization, reduced pollen viability and seed setting, and lower starch content in kernels [25]. Water-deficit or heat stress were found to cause an increase in the levels of abscisic acid (ABA) that were accompanied by a decrease in gibberellic acid (GA) and auxin (IAA) concentrations. Enhanced water-deficit or heat induced ABA levels prompted excessive ROS accumulation, which caused oxidative damage to anther tissues and disrupted the normal process of tapetum PCD (Fig. 3). Heat was additionally found to cause the enhanced expression of heat stress-responsive genes in anthers and pollen, including the heat shock transcription factors (HSFs), unfolded protein response (UPR) and multiprotein-bridging factor 1 (MBF1) associated networks (reviewed in [32]). Because heat or water-deficit stress resulted in very similar responses, their combination could overwhelm plant defenses and cause an even more detrimental effect than each of them applied individually. In addition, as described

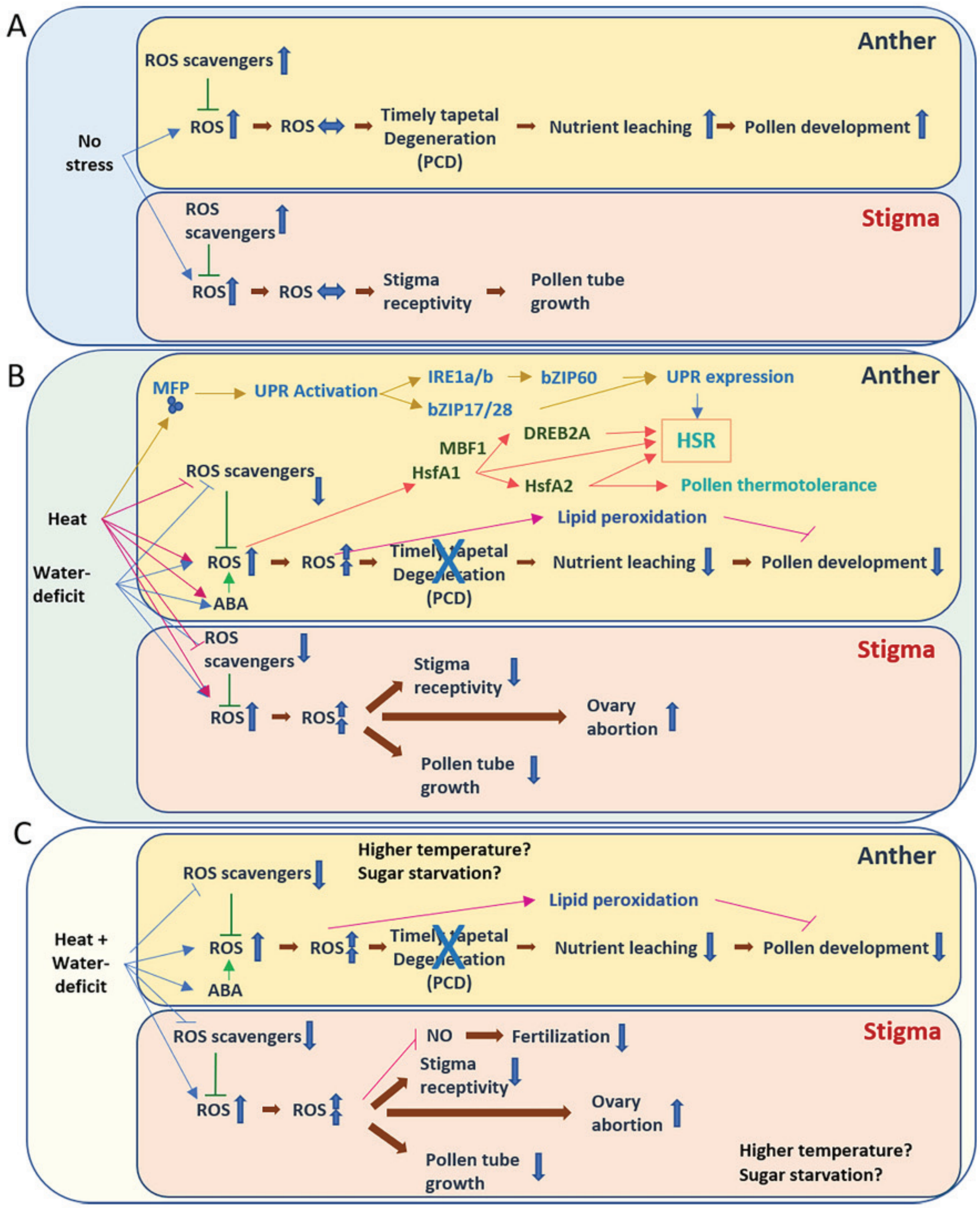

Fig. 3. Reactive oxygen species (ROS) and plant reproduction under water-deficit, heat stress and/or water-deficit and heat stress combination. ROS-mediated floral tissue development in the absence of stress (A), under heat or water-deficit (B) or under a combination of water-deficit and heat stress (C). ROS play a key role in floral tissue development and reproduction. However, under stress, ROS levels increase and impair processes such as tapetum PCD, pollen development, pollen shedding, and pollen tube elongation, stigma receptivity, ovary development, fertilization, and embryogenesis. *Abbreviations:* NO, nitric oxide; PCD, programmed cell death; ROS, reactive oxygen species; MFP, miss-folded proteins; HSR, heat shock response; ABA, abscisic acid; HSFA1, heat shock factor A1; MBF1, multiprotein bridging factor 1; DREB2A, dehydration-responsive element binding protein 2A; IRE1a/b, inositol requiring enzyme 1a/b; UPR, unfolded protein response.

below, the timing of stress occurrence with respect to the different reproductive stages plays a critical role in yield reduction.

6. Impacts of water-deficit or heat stress on sporogenesis

For effective fertilization and seed development, processes such as microsporogenesis, microgametogenesis, megasporogenesis, and megagametogenesis need to be successful, however, water-deficit or heat stress alter these processes in many crop plants [63,68,69]. During microsporogenesis, meiotic crossover frequency has been observed to increase under both heat stress as well as water-deficit [70–74]. Heat stress induces second gamete formation in Rosa (*Rosa rubiginosa*) [75], Populus (*Populus canescens*) [76] and Arabidopsis [77] due to defects in cell wall formation at the end of meiosis II. Draeger and Moore [78] reported that interphase and leptotene are the most affected stages in meiosis under heat stress in wheat, but post zygotene the meiosis of pollen mother cells proceeds normally. Meiotic crossover during microsporogenesis and megasporogenesis under combined heat and water-deficit stress have not been reported yet, however, since meiosis is vulnerable to both water-deficit and heat stress, the combination of these two stresses may make the process even more vulnerable.

7. Impacts of water-deficit or heat stress on tapetum PCD

Tapetum cells accumulate sugars, flavonoids, fatty acids and proteins used to feed the developing pollen [79]. A properly-developed tapetum, coupled with a timely PCD process of this cell layer, is indispensable for sporogenesis and pollen development [80,81]. Under non-stress conditions, tapetum cells are metabolically active, with large numbers of mitochondria and optimum ROS production for timely tapetum degeneration. However, heat stress disrupts ROS homeostasis in anthers inducing lipid peroxidation, and membrane damage, and causing untimely PCD of the tapetal cells [82] (Fig. 3). Under high temperatures tapetum cells become hyper vacuolated, and have deformed chloroplasts, altered rough endoplasmic reticulum, and excessively swollen mitochondria [83], as well as degenerate prematurely [83–85]. This effect delays the maturation of microspores due to the lack of nutrients and other compounds such as flavonoids. The resulting low flavonoid content and improperly developed pollen cell walls impact pollen germination and pollen tube elongation [80,81,84,86]. Tapetum degeneration was found to be either accelerated or delayed under water-deficit stress [38,87,88] and tapetal cells in water-deficit stressed wheat flowers were shown to contain abnormal vacuolization and detached microspores [89]. The development of the tapetum under a combination of heat and water-deficit stress requires further studies. Although a few studies have reported reduced pollen viability, reduced functionality of male and female organs, and reduced flower fertility under a combination of heat and water-deficit stress [26,47], it is largely unknown how this stress combination will impact the PCD process of the tapetum layer. Because the timing of tapetum degradation and other functions are critical for pollen development and maturation, and this timing is dependent on ROS and hormone levels, as well as the availability of different nitrogen and carbon metabolites [29,30], any stress-related alterations in ROS, glucose 6-phosphate and/or other compounds could affect the efficiency of tapetum function and its support of pollen development and maturation, and ultimately result in reduced yield (Fig. 3).

8. The effect of heat and water-deficit combination on flower female reproductive processes

Heat stress reduces female gametophyte expansion, causes malformation and degeneration of the embryo sac, causes incomplete differentiation of eggs, synergid cells, and ovule development, and leads to ovule abortion [90–92]. Heat stress also causes desiccation of stigma, style and ovary along with a reduction in the size of style transmitting tissue [64]. Water-deficit stress leads to abortion of the ovule [38,93], however, the precise impact of water-deficit on female organ development is under investigation. Some reports suggest that female reproductive organs are not significantly affected by water-deficit stress [94, 95], while other studies reported reduced seed set when female flowers from water-deficit-stressed plants were fertilized with pollen from non-stressed plants, indicating that female reproductive organs are impacted by water-deficit stress [53,96]. Not much information is available on the impact of water-deficit and heat stress combination on female gametogenesis and female organ development. In one study, Fabian et al. [26], reported that water-deficit and heat stress combination in wheat did not affect ovule or female gametophyte development processes. However, these two stresses together caused malformation in cortical cells of stylodia and transmitting cells, as stylodia were reduced in size and transmitting cells were crushed [26]. In addition, heat and water-deficit combination reduced the turgor of papilla cells with the resultant shriveling of stigma branches. These changes in female reproductive organs under a combination of heat and water-deficit stress resulted in reduced fertility [26]. Pistils are critical for proper fertilization as they support, recognize, and provide the pollen with anchorage, rehydration and soluble sugars for pollen tube elongation [97–100]. In a recent study [101] it was found that a combination of water-deficit and heat stress reduced seed production in soybean without a significant effect on the number of flowers produced, or pollen viability, further suggesting that female reproductive development processes may be impacted by a combination of water-deficit and heat stress. Further studies are required to understand the impacts of water-deficit and heat stress combination on the different growth and development processes occurring at the female reproductive organs of different crop species.

9. Impacts of heat and water-deficit combination on anther dehiscence and pollen shedding

Following the successful development of male and female reproductive organs, proper orientation of anthers and stigma within the closed flower, a successful release of pollen from anthers, pollen shedding onto stigma, and proper development of pollen tubes are essential. In Arabidopsis, pollination was found to be impacted due to differences in the relative size and position of anther and stigma within the closed flower under heat and water-deficit stresses [38,102]. Pollen release from anther requires successful anther dehiscence. Plants under heat stress show inhibition of anther dehiscence and reduced pollen shedding onto stigma [61,69,103,104]. Heat stress was also shown to reduce the thickenings of the endothecium wall, impair the dissolution of the interlocular septa causing indehiscence of anther in tomato (*Solanum lycopersicum*) and common bean [69,105]. Based on transcriptional data, Endo et al. [106] suggested that pollen adhesion and pollen germination on the stigmatic surface are potentially affected under heat stress in rice. Heat stress also impacts the receptivity of the stigma [90], and reduces pollen tube growth [66,103,107]. Similarly, plants under water-deficit stress show reduced anther dehiscence and reduced pollen tube growth on stigma [53,87,93]. In rice, anther dehiscence and pollen shedding on stigma were observed to decrease and fertilization was reduced under heat and water-deficit stress combination [47,67,108]. Jagadish et al. [108], showed that gene expression of pollen allergens and expansins, which facilitate the loosening and extension of cell wall to aid in the invasion of the pollen tube into the stigma, were down-regulated under combined heat and water-deficit stress suggesting that a combination of these two stresses could negatively affect pollen tube growth [108]. Studying the precise molecular mechanisms involved in the different processes described above would enable targeting these processes to reduce the impacts of heat and water-deficit stress combination on anther dehiscence, pollen shedding and pollen tube growth.

10. Flower temperature under conditions of water-deficit and heat stress

Plants open stomata to cool their leaves by evaporative transpiration during heat stress. In contrast, during water-deficit, plants close their stomata to minimize water loss [109,110]. In general, plants close their stomata under a combination of heat and water-deficit stress to avoid water loss, however, this comes at the price of higher leaf temperature (compared to heat alone) [33,111,112]. In contrast to leaf stomata regulation during stress, much less is known about stomatal activity of flowers under water-deficit, heat, or a combination of these two. Lawas et al. [23], reported decreased stomatal conductance and increased panicle surface temperature in rice under combined water-deficit and heat stress treatment. Wei et al. [113], reported that the number of stomata on anthers decreased in an Arabidopsis mutant deficient in INDUCER OF CBF EXPRESSION 1 (ICE1) and that this reduction was associated with anther indehiscence, as well as decreased pollen viability and germination rate. These findings raise several questions, most importantly, what is the inner temperature of flowers during stress combination, and more specifically that of the male and female reproductive organs? Are flowers using an alternative mechanism to dissipate the heat produced during stress combination if stomata are closed during combination of heat and water-deficit stress? These questions are highly important because the flower inner temperature will directly impact growth and developmental processes leading to gamete formation, as well as fertilization, embryogenesis, and seed production. All processes critical for grain yield formation. If plants are unable to cool their flowers during the stress combination (as is the case for leaves [33,112,114]), then the inner temperature of flowers will be higher during a combination of water-deficit and heat stress, compared to water-deficit or heat stress applied individually (Fig. 2), and yield will suffer even more under the stress combination. Further studies are needed to address this question.

11. Reactive oxygen species and reproductive processes under stress

Reactive oxygen species such as superoxide radicals and hydrogen peroxide play key regulatory roles in pollen development, pollen tube growth and various processes of pollen-stigma communication [115]. ROS are thought to regulate pollen hydration and germination on the stigma, pollen tube growth within the pistil, and pollen tube reception by the female gametophyte. In addition, as described above, ROS are thought to play a key role in regulating the PCD process of the tapetum that controls pollen development and maturation [115–122]. In general, the levels of ROS in these different tissues is controlled by alterations in ROS production through the function of respiratory burst oxidase homolog (RBOH) NADPH oxidases and mitochondrial respiration, as well as the function of different antioxidants and ROS scavengers such as flavonoids and peroxidases [115–122]. The PCD of nutritive tapetum cells requires for example a peak in ROS production [118,119,123] and disruptions in temporal ROS patterns affect the timing of tapetal PCD causing abortion of male gametophytes [118]. ROS production at the tip of the pollen tube is also essential for pollen tube elongation [124] and is required for the release of sperm cells [125]. Water-deficit and heat both induce the accumulation of ROS and reactive nitrogen species (RNS) in plants which can lead to cellular damage if their production exceeds the capacity for scavenging of these compounds [126,127] (Fig. 3). ROS content increases in floral tissues under abiotic stresses, especially in anther and tapetum [30] due to high metabolic activity, higher number of mitochondria, and elevated rate of respiration [30,64]. This imbalance in ROS homeostasis disrupts the process of pollen development, pollen tube elongation and overall fertility of flowers [86,123,128,129]. In rice, water-deficit stress results in higher accumulation of ROS, decreased transcript abundance of antioxidant enzymes, and decreased activity of antioxidant enzymes in anthers, causing pollen sterility [130–132]. If excess ROS is removed by overexpression of peroxidase (POD) genes, flower damage can be prevented under water-deficit stress [88]. ROS has important functions in inducing PCD in stigma and sets a time window for stigma receptivity for pollen [133]. ROS over-accumulation under heat or water-deficit stress can therefore result in an altered time window of stigma receptivity for pollen, reducing the chance of fertilization [134] (Fig. 3). Female reproductive organs in a thermotolerant cotton (*Gossypium hirsutum*) variety were found to have high superoxide dismutase (SOD) and glutathione reductase (GR) activities even prior to heat stress [107], and heat stress further induces GR in pistils [92] indicating crucial involvement of ROS scavenging mechanisms in heat stress tolerance in female reproductive organ function. Fabians et al. [26], reported that when water-deficit and heat stress were applied together during anthesis, the stigmatic papillae of a sensitive variety of wheat generated high amounts of ROS and RNS but reduced amounts of nitric oxide (NO), and displayed compromised flower fertility. ROS production was also higher in mitochondria than in cytoplasm in a sensitive variety of wheat [26]. This study proposed that reduction in NO production due to high ROS levels could impair pollen tube development in stigma and style leading to impaired fertilization [26] (Fig. 3). Further studies are needed to explore the beneficial and damaging roles of ROS [127] during the different reproductive processes of crops under water-deficit, heat, and their combination. Regulating ROS levels through for example controlling RBOH function via calcium signaling and/or altering the content of antioxidants or the expression level of different scavengers could be used as a viable strategy to reduce the impacts of stress combination on plant reproduction. However, such approaches should take into consideration the important role ROS play during non-stress conditions. A drastic suppression in ROS levels could therefore lead to reduced yield under non-stress conditions because ROS are required for pollen-pistil interactions and other important reproduction processes (Fig. 3).

12. Sugar metabolism in flowers during stress combination

Sugars play a key role in many reproductive and developmental processes [99,135,136]. Flower development is energy demanding as evident by the high respiration rates and increased mitochondrial activity of floral organs [98,137–139]. Floral reproductive organs import sugars from leaf tissues and/or sepals symplastically or apoplastically [140–142]. The imported sugars are either stored in the vacuole or cytosol, or metabolized [82]. The rate of sugar import by flower tissues depends on the developmental stage of the flower [139]. Developing anthers and filling grains for example display a very high sink activity [82,95]. The process of sugar import requires enzymes such as cell wall invertases (cwINVs) and sucrose synthases (SUSs), as well as sugar transporters (STPs), to provide sugar monomers for metabolism. Being a nutritive tissue, the tapetum requires high amounts of carbohydrates which are later released into the locular fluid (upon tapetal degeneration) to support pollen cell wall synthesis and accumulation of carbon reserves in pollen for tube development [143,144]. Sugar is essential for the viability of pollen as decreased sugar accumulation in walls of anther and pollen correlates with reduced pollen viability [145]. In addition, higher activities of cwINVs in developing pollen walls during pollen development support the importance of sugars for male gamete formation [135,141]. Goetz et al. [99], reported that pollen tube elongation involves coordinated activity of pollen tube cwINVs and vacuolar invertases (vINVs) of transmitting tissues of the style to acquire sugar resources while the pollen tube is elongating towards an ovule. Deficiencies in sugar metabolism under abiotic stresses are therefore expected to negatively impact the reproductive development and fertilization at several levels [20,66,145,146]. Jin et al. [147], showed that starch granules were abnormally deposited outside of anthers, in the lemma and palea in water-deficit-stressed rice, suggesting impaired tapetal functions under water-deficit stress. The expression of INVs, hexokinases (HXKs) and glycoside hydrolase were also downregulated in rice flowers indicating impaired utilization of sugars in anthers under water-deficit stress [147]. Similarly, in wheat, gene expression and activity of cwINVs and vINVs are reduced under water-deficit and pollen development is impaired [148]. Several studies also reported reduction in sucrose concentrations and reduced gene expression and enzymatic activity of cwINV in microspores and anthers under heat stress [145,146,149–151]. Santiago et al. [30], reported a significant decrease in sucrose and glucose concentrations along with reduced expression of the sucrose transporter PvSUT1.1 in whole flowers and anthers of a heat susceptible genotype of common bean exposed to high temperatures. Tomato flowers under heat stress were reported to have decreased starch granule in pollen grain and increased concentrations of soluble sugars in locular fluid indicating decreased pollen sugar uptake [152]. Mild heat stress for short duration during the tetrad stage in maize resulted in reduced starch content but increased sucrose, glucose, and fructose content in pollen causing impaired pollen tube growth [66]. Continuous mild heat stress during meiotic and microspore stages of flower development was also found to decrease the expression of vINV in anthers [146] and this might have led to reduced pollen viability [153]. A large number of sugar and starch metabolizing genes are expressed if heat stress is applied at the early stage of flower development or if a moderate water-deficit stress is applied [134]. Moreover, heat tolerant genotypes are better able to maintain sugar concentrations [30], with relatively higher expression of cwINV and improved pollen viability under heat stress [67].

Pollen tube growth and successful fertilization require the conversion of sucrose into glucose and fructose. Sugar transport to ovaries decreases under water-deficit stress resulting in decreased ovule fertility [154,155]. Heat stress reduces the concentrations of sucrose and soluble sugars in pistils, which is thought to be the reason for diminished pollen tube growth in the pistil [92,107,156]. Water-deficit and heat were also reported to downregulate the expression of ovary-specific cwINV (*Incw2*), and soluble INV (*Incw2*) in maize which subsequently decreased the ovary sugar pool causing senescence and abortion of ovaries via activation of ribosome-inactivating protein (*RIP2*) and phospholipase D1 (*PLD1*) genes [157]. Under combined water-deficit and heat stress, studies in rice reported depletion of sucrose levels and upsurge of monosaccharides in floral organs of stress sensitive plants [23,67]. Li et al. [67], reported that in floral organs of a sensitive genotype of rice, sucrose concentrations decreased, supported by increased gene expression of stachyose synthase and SUS and decreased expression of the sugar transporter gene *SUT3*. Gene expression of a monosaccharide transporter (*MST8*), a cwINV (*INV4*) and a UDP-glucose pyrophosphorylase (*UGP1*) were also down-regulated in anthers of a susceptible cultivar while gene expression of carbon starved anthers (*CSA*, a MYB family transcription factor) was increased, further supporting reduced sucrose concentration in anthers [67]. Although sugar metabolism was shown to play an important role in anther and pollen functions during stress combination, available information is restricted to only one or a few crop species and little is known about the role of sugar metabolism in pistils, ovules, and styles during stress combination. How conserved are these responses across diverse species? Would sugar levels increase in female reproductive tissues during stress combination? If yes, would they support pollen tube growth and fertilization? Is decreased sugar concentration one of the important reasons for fertilization failure under combined stress? Further studies are needed to address these important questions.

13. Hormone signaling during flowering under stress

Hormones, especially GA, auxin, ABA, jasmonic acid (JA), brassinosteroid (BR), ethylene (ET), and cytokinin, play important roles during flower development [32,158,159]. While GA plays an important role during the transformation of a shoot apical meristem to a floral meristem, it is also essential for anther and pollen development [160,161]. Auxins are required for organogenesis and are crucial for carpel development [160]. Similarly, auxin, GAs and JA are needed for petal development, and GA along with BR, cytokinins, auxins, and JA are involved in anther and pollen development [160,162]. In addition, in many plant species, the sex of the flowers depends on the relative ratios of hormones such as GA and auxin [163].

Heat or water-deficit stress disrupt the hormonal balance of plants and decrease fertility of flowers. Hormones such as salicylic acid (SA), auxin, ABA and ET help in alleviating the damage to pollen caused by heat stress [32,164–166]. A large number of genes involved in the biosynthesis and signal transduction of hormones such auxin, GA, ABA and ET display differential expression in flower tissues under heat stress [104,167]. Unlike vegetative tissues, heat stress was reported to impair auxin biosynthesis in the anthers of rice, barley, cotton, and Arabidopsis and the resultant decrease in auxin levels were observed to cause pollen abortion [168–172]. Reversal of anther development upon external application of auxin [169,172], and increased male fertility by upregulation of auxin biosynthesis genes under heat stress [173], further support the importance of auxin in male gametophyte development and functioning. Auxin homeostasis is also required for pistil function during pollen tube germination and/or tube growth [166,174] and heat stress-mediated decrease in auxin levels in pistils of a susceptible variety of rice resulted in spikelet sterility [166]. Water-deficit stress also decreases endogenous auxin levels in rice spikelets [172]. Heat and water-deficit stress downregulate the expression of the flavin monooxygenase-like enzyme YUCCA (*YUC*), which is involved in auxin biosynthesis and impact the expression of auxin co-receptor genes in rice spikelets [172]. If supplemented externally, auxin decreases water-deficit and heat stress-induced peroxidation of membrane lipids in rice spikelets, in turn rescuing spikelet fertility [172]. Auxin can also modulate ROS homeostasis by enhancing the expression of enzymes involved in ROS detoxification [175–177]. Although unknown at present, the role of auxin may be pivotal for the success or failure of fertilization and ultimately grain yield formation under conditions of water-deficit and heat combination. Heat stress decreases GA and various GA-responsive genes in anthers [106,168]. Similarly, water-deficit stress alters GA biosynthesis and signaling in flower tissues which has been associated with male sterility [147]. Since GA-deficiency leads to abnormal anther development and male sterility [178,179], heat- or water-deficit-induced decreases in GA could be an additional important factor during heat/water-deficit-induced male sterility. Similarly, ABA is a central hormone enhanced during drought stress. Increased ABA and JA signaling in flowers under water-deficit stress is known to cause male sterility and impair reproductive development [147,180]. High temperature increases ABA levels in young rice panicles, rice anthers and Arabidopsis flowers leading to decreased flower fertility [38,168], and ABA was found to play a key role in vegetative plant responses to water-deficit and heat stress combination [111]. It is thought that enhanced ABA levels are driving an increase in ROS levels that could disrupt different reproductive processes during water-deficit or heat stress, and that ABA accumulation suppressed tapetum PCD during heat stress [32]). Cytokinins play protective roles during heat stress or water-deficit [181], however, heat stress decreases cytokinin levels in young panicles causing sterility in rice [182]. Thus far, a comprehensive analysis of flower hormonal homeostasis under combined heat and water-deficit stress is unavailable. Drawing from the few studies conducted on hormone functions during stress combination of vegetative tissues [126,183], it is likely that hormone homeostasis and possible conflicting hormonal interactions would significantly impact crop reproduction and yield under a combination of water-deficit and heat stress. Further studies are of course needed.

14. Potential strategies to mitigate the impact of global warming and climate change on plant reproduction

Developing strategies to enhance the tolerance of reproductive tissues to stress is challenging since many of these processes already involve the activation of multiple stress response programs in the absence of stress. For example, pollen undergo a dehydration and rehydration cycle that involves expression of multiple water-deficit responsive genes [18,184–186]. In addition, pollen were found to express different HSFs, heat shock proteins (HSPs) and UPR genes in the absence of stress [20,187–189]. The timing of stress occurrence with respect to the timeline of the different reproductive processes is also critical. Triggering of a particular stress response pathway at the wrong time might for example interfere with the PCD process of the tapetum or interfere with some of the ROS-dependent signalling processes that determine pollen-pistil compatibility. This situation is further complicated since many stress-response transcripts and proteins are thought to accumulate in pollen in the form of stress granules or RNA-protein complexes/granules [19]. The formation of these granules and the release of their content has to be coordinated with different reproductive processes and disrupting this coordination could also interfere with normal flower development, fertilization and overall yield. Keeping these complex considerations in mind, several different avenues for the development of crops with enhanced yield production under conditions of stress combination could nevertheless be explored. For example, once processes and mechanisms are better understood, it may be possible to manipulate the levels of ROS, different sugars, and/or different plant hormones such as ABA, GA, IAA and SA at the right time in different flower organs using different CRISPR or breeding strategies to mitigate the effects of stress combination on stress sensitive processes such as tapetum PCD, pollen maturation, pollen-pistil interactions, grain filling and more (Fig. 2). In addition, the expression of key regulatory genes that control processes such as the heat stress response (*e.g.,* HSFs, UPR, MBF1 and others), and/or acclimation to water-deficit conditions (*e.g.,* osmoprotectants, dehydrins and others), could be manipulated in different flower organs at specific times to increase their tolerance to stress. Different genes and or acclimation/adaptation strategies could also be adopted from wild plants that evolved to withstand extreme stress conditions during flowering time (*e.g.,* plants grown in arid zones, or different invasive species [5]). A completely different strategy could involve manipulating the plant microbiome (at the root, leaves and/or flowers) to include more beneficial microbes that could enhance plant tolerance to stress [190–193], and/or using different chemical priming molecules [194]. In addition, the function and number of stomata on flowers could be regulated to control the temperature of different flower parts by enhancing transpiration. Of course, as more studies of the effect of stress combination on plant reproduction will become available, more strategies, genes and/or different combinations of strategies and genes are expected to emerge, and these should be tested in crops under field conditions [195].

15. Concluding remarks

Flower development and fertilization, two processes critical for yield production in cereals, legumes, and other crops, are especially vulnerable to abiotic stresses such as water-deficit and heat stress. Recent studies have shown that a combination of water-deficit and heat stress causes a severe reduction in yield and suggest that this yield reduction is the outcome of the stress combination impacting reproductive processes, even more than the individual occurrence of water-deficit or heat (Fig. 2). Because the frequency and intensity of water-deficit and heat stress combination is likely to increase in the coming years due to global warming and climate change [5], understanding the mechanisms underlying the severe effects of stress combination on reproductive processes of different crops, and especially the signaling roles of ROS [127,196] in these processes, are critical to our success in developing crops that are resilient to climate change and global warming. We highlight several possible mechanisms by which water-deficit and heat combination impact reproduction and yield in crops. These include flower temperature, increased production of ROS, altered sugar metabolism, and conflicting functions of different hormones. Future studies of the impacts of stress combination on reproductive processes ought to identify additional mechanisms, as well as reveal ways to counter the negative impacts of stress combination on yield in different crops, opening the way for the development of more resilient crops that will improve our chances to survive the changing climate on our planet [5].

Declaration of Competing Interest

The authors declare no competing interests

Acknowledgements

This work was supported by funding from the National Science Foundation (IOS-2110017, IOS-1353886, MCB-1936590, IOS-1932639, IOS-1557801) and the University of Missouri.

References

[1] S.M. Gourdji, A.M. Sibley, D.B. Lobell, Global crop exposure to critical high temperatures in the reproductive period: historical trends and future projections, Environ. Res. Lett. 8 (2013), https://doi.org/10.1088/1748-9326/8/2/024041.

[2] A. AghaKouchak, L. Cheng, O. Mazdiyasni, A. Farahmand, Global warming and changes in risk of concurrent climate extremes: insights from the 2014 California drought, Geophys. Res. Lett. 41 (2014) 8847–8852, https://doi.org/10.1002/2014GL062308.

[3] T.R. Ault, On the essentials of drought in a changing climate, Science. 368 (2020) 256LP–260, https://doi.org/10.1126/science.aaz5492.

[4] IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzer, n.d.

[5] S.I. Zandalinas, F.B. Fritschi, R. Mittler, Global Warming, Climate Change, and Environmental Pollution: Recipe for a Multifactorial Stress Combination Disaster, Trends Plant Sci. 26 (2021) 588–599, https://doi.org/10.1016/j.tplants.2021.02.011.

[6] J.T. Overpeck, B. Udall, Climate change and the aridification of North America, Proc. Natl. Acad. Sci. U. S. A. 117 (2020) 11856–11858, https://doi.org/10.1073/pnas.2006323117.

[7] C. Lesk, P. Rowhani, N. Ramankutty, Influence of extreme weather disasters on global crop production, Nature. 529 (2016) 84–87, https://doi.org/10.1038/nature16467.

[8] T. Iizumi, N. Ramankutty, Changes in yield variability of major crops for 1981-2010 explained by climate change, Environ. Res. Lett. 11 (2016), https://doi.org/10.1088/1748-9326/11/3/034003.

[9] S.L. Dwivedi, K.H.M. Siddique, M. Farooq, P.K. Thornton, R. Ortiz, Using biotechnology-led approaches to uplift cereal and food legume yields in dryland environments, Front. Plant Sci. 9 (2018) 1–26, https://doi.org/10.3389/fpls.2018.01249.

[10] M.R. Alizadeh, J. Adamowski, M.R. Nikoo, A. AghaKouchak, P. Dennison, M. Sadegh, A century of observations reveals increasing likelihood of continental-scale compound dry-hot extremes, Sci. Adv. 6 (2020) 1–12, https://doi.org/10.1126/sciadv.aaz4571.

[11] A.J. Crawford, D.H. McLachlan, A.M. Hetherington, K.A. Franklin, High temperature exposure increases plant cooling capacity, Curr. Biol. 22 (2012) R396–R397, https://doi.org/10.1016/j.cub.2012.03.044.

[12] P. Ciais, M. Reichstein, N. Viovy, A. Granier, J. Ogée, V. Allard, M. Aubinet, N. Buchmann, C. Bernhofer, A. Carrara, F. Chevallier, N. De Noblet, A.D. Friend, P. Friedlingstein, T. Grünwald, B. Heinesch, P. Keronen, A. Knohl, G. Krinner, D. Loustau, G. Manca, G. Matteucci, F. Miglietta, J.M. Ourcival, D. Papale, K. Pilegaard, S. Rambal, G. Seufert, J.F. Soussana, M.J. Sanz, E.D. Schulze, T. Vesala, R. Valentini, Europe-wide reduction in primary productivity caused by the heat and drought in 2003, Nature 437 (2005) 529–533, https://doi.org/10.1038/nature03972.

[13] O. Mazdiyasni, A. AghaKouchak, Substantial increase in concurrent droughts and heatwaves in the United States, Proc. Natl. Acad. Sci. U. S. A. 112 (2015) 11484–11489, https://doi.org/10.1073/pnas.1422945112.

[14] A.S.M.H.M. Talukder, G.K. McDonald, G.S. Gill, Effect of short-term heat stress prior to flowering and early grain set on the grain yield of wheat, F. Crop. Res. 160 (2014) 54–63, https://doi.org/10.1016/j.fcr.2014.01.013.

[15] Y. Liu, J. Li, Y. Zhu, A. Jones, R.J. Rose, Y. Song, Heat stress in legume seed setting: effects, causes, and future prospects, Front. Plant Sci. 10 (2019), https://doi.org/10.3389/fpls.2019.00938.

[16] M.C. Rillig, M. Ryo, A. Lehmann, C.A. Aguilar-Trigueros, S. Buchert, A. Wulf, A. Iwasaki, J. Roy, G. Yang, The role of multiple global change factors in driving soil functions and microbial biodiversity, Science 366 (2019) 886–890, https://doi.org/10.1126/science.aay2832.

[17] S.I. Zandalinas, S. Sengupta, F.B. Fritschi, R.K. Azad, R. Nechushtai, R. Mittler, The impact of multifactorial stress combination on plant growth and survival, New Phytol. 230 (2021) 1034–1048, https://doi.org/10.1111/nph.17232.

[18] M.A. Johnson, J.F. Harper, R. Palanivelu, A fruitful journey: pollen tube navigation from germination to fertilization, Annu. Rev. Plant Biol. 70 (2019) 809–837, https://doi.org/10.1146/annurev-arplant-050718-100133.

[19] P. Chaturvedi, A.J. Wiese, A. Ghatak, L. Záveská Drábková, W. Weckwerth, D. Honys, Heat stress response mechanisms in pollen development, New Phytol. 231 (2021) 571–585, https://doi.org/10.1111/nph.17380.

[20] I. Rieu, D. Twell, N. Firon, Pollen development at high temperature: from acclimation to collapse, Plant Physiol. 173 (2017) 1967–1976, https://doi.org/10.1104/pp.16.01644.

[21] A. Hedhly, Sensitivity of flowering plant gametophytes to temperature fluctuations, Environ. Exp. Bot. 74 (2011) 9–16, https://doi.org/10.1016/j.envexpbot.2011.03.016.

[22] A. Mahrookashani, S. Siebert, H. Hüging, F. Ewert, Independent and combined effects of high temperature and drought stress around anthesis on wheat, J. Agron. Crop Sci. 203 (2017) 453–463, https://doi.org/10.1111/jac.12218.

[23] L.M.F. Lawas, W. Shi, M. Yoshimoto, T. Hasegawa, D.K. Hincha, E. Zuther, S.V. K. Jagadish, Combined drought and heat stress impact during flowering and grain filling in contrasting rice cultivars grown under field conditions, F. Crop. Res. 229 (2018) 66–77, https://doi.org/10.1016/j.fcr.2018.09.009.

[24] I. Cohen, S.I. Zandalinas, C. Huck, F.B. Fritschi, R. Mittler, Meta-analysis of drought and heat stress combination impact on crop yield and yield components, Physiol. Plant. 171 (2021) 66–76, https://doi.org/10.1111/ppl.13203.

[25] X. Liu, X. Wang, X. Wang, J. Gao, N. Luo, Q. Meng, P. Wang, Dissecting the critical stage in the response of maize kernel set to individual and combined drought and heat stress around flowering, Environ. Exp. Bot. 179 (2020), 104213, https://doi.org/10.1016/j.envexpbot.2020.104213.

[26] A. Fábián, E. Sáfrán, G. Szabó-Eitel, B. Barnabás, K. Jäger, Stigma functionality and fertility are reduced by heat and drought co-stress in wheat, Front. Plant Sci. 10 (2019) 1–18, https://doi.org/10.3389/fpls.2019.00244.

[27] R. Bheemanahalli, V.S.J. Sunoj, G. Saripalli, P.V.V. Prasad, H.S. Balyan, P. K. Gupta, N. Grant, K.S. Gill, S.V.K. Jagadish, Quantifying the impact of heat stress on pollen germination, seed set, and grain filling in spring wheat, Crop Sci. 59 (2019) 684–696, https://doi.org/10.2135/cropsci2018.05.0292.

[28] M. Djanaguiraman, S. Narayanan, E. Erdayani, P.V.V. Prasad, Effects of high temperature stress during anthesis and grain filling periods on photosynthesis, lipids and grain yield in wheat, BMC Plant Biol. 20 (2020) 1–12, https://doi.org/10.1186/s12870-020-02479-0.

[29] J.P. Santiago, T.D. Sharkey, Pollen development at high temperature and role of carbon and nitrogen metabolites, Plant Cell Environ. 42 (2019) 2759–2775, https://doi.org/10.1111/pce.13576.

[30] J.P. Santiago, A. Soltani, M.M. Bresson, A.L. Preiser, D.B. Lowry, T.D. Sharkey, Contrasting Anther Glucose 6-phosphate Dehydrogenase Activities Between Two Bean Varieties Suggest an Important Role in Reproductive Heat Tolerance, 2021, https://doi.org/10.1111/pce.14057.

[31] S. Hafidh, J. Fíla, D. Honys, Male gametophyte development and function in angiosperms: a general concept, Plant Reprod. 29 (2016) 31–51, https://doi.org/10.1007/s00497-015-0272-4.

[32] Z. Zhang, M. Hu, W. Xu, Y. Wang, K. Huang, C. Zhang, J. Wen, Understanding the molecular mechanism of anther development under abiotic stresses, Plant Mol. Biol. 105 (2021) 1–10, https://doi.org/10.1007/s11103-020-01074-z.

[33] R. Mittler, Abiotic stress, the field environment and stress combination, Trends Plant Sci. 11 (2006) 15–19, https://doi.org/10.1016/j.tplants.2005.11.002.

[34] M. Bernal, M. Estiarte, J. Peñuelas, Drought advances spring growth phenology of the Mediterranean shrub Erica multiflora, Plant Biol. 13 (2011) 252–257, https://doi.org/10.1111/j.1438-8677.2010.00358.x.

[35] S.J. Franks, Plasticity and evolution in drought avoidance and escape in the annual plant Brassica rapa, New Phytol. 190 (2011) 249–257, https://doi.org/10.1111/j.1469-8137.2010.03603.x.

[36] V. Mahalakshmi, F.R. Bidinger, Flowering response of pearl millet to water stress during panicle development, Ann. Appl. Biol. 106 (1985) 571–578, https://doi.org/10.1111/j.1744-7348.1985.tb03148.x.

[37] T. Winkel, J.F. Renno, W.A. Payne, Effect of the timing of water deficit on growth, phenology and yield of pearl millet (Pennisetum glaucum (L.) R. Br.) grown in Sahelian conditions, J. Exp. Bot. 48 (1997) 1001–1009, https://doi.org/10.1093/jxb/48.5.1001.

[38] Z. Su, X. Ma, H. Guo, N.L. Sukiran, B. Guo, S.M. Assmann, H. Ma, Flower development under drought stress: morphological and transcriptomic analyses reveal acute responses and long-term acclimation in Arabidopsis, Plant Cell 25 (2013) 3785–3807, https://doi.org/10.1105/tpc.113.115428.

[39] X. Ma, N.L. Sukiran, H. Ma, Z. Su, Moderate drought causes dramatic floral transcriptomic reprogramming to ensure successful reproductive development in Arabidopsis, BMC Plant Biol. 14 (2014) 1–16, https://doi.org/10.1186/1471-2229-14-164.

[40] A. Fuad-Hassan, F. Tardieu, O. Turc, Drought-induced changes in anthesis-silking interval are related to silk expansion: a spatio-temporal growth analysis in maize plants subjected to soil water deficit, Plant, Cell Environ. 31 (2008) 1349–1360, https://doi.org/10.1111/j.1365-3040.2008.01839.x.

[41] T. Ishimaru, H. Hirabayashi, M. Ida, T. Takai, Y.A. San-Oh, S. Yoshinaga, I. Ando, T. Ogawa, M. Kondo, A genetic resource for early-morning flowering trait of wild rice Oryza officinalis to mitigate high temperature-induced spikelet sterility at anthesis, Ann. Bot. 106 (2010) 515–520, https://doi.org/10.1093/aob/mcq124.

[42] H. Hirabayashi, K. Sasaki, T. Kambe, R.B. Gannaban, M.A. Miras, M.S. Mendioro, E.V. Simon, P.D. Lumanglas, D. Fujita, Y. Takemoto-Kuno, Y. Takeuchi, R. Kaji, M. Kondo, N. Kobayashi, T. Ogawa, I. Ando, K.S.V. Jagadish, T. Ishimaru, QEMF3, a novel QTL for the early-morning flowering trait from wild rice, Oryza officinalis, to mitigate heat stress damage at flowering in rice, O. sativa, J. Exp. Bot. 66 (2015) 1227–1236, https://doi.org/10.1093/jxb/eru474.

[43] R. Bheemanahalli, R. Sathishraj, M. Manoharan, H.N. Sumanth, M. Raveendran, T. Ishimaru, J.S.V. Krishna, Is early morning flowering an effective trait to minimize heat stress damage during flowering in rice? F. Crop. Res. 203 (2017) 238–242, https://doi.org/10.1016/j.fcr.2016.11.011.

[44] S. Aiqing, I. Somayanda, S.V. Sebastian, K. Singh, K. Gill, P.V.V. Prasad, S.V. K. Jagadish, Heat stress during flowering affects time of day of flowering, seed set, and grain quality in spring wheat, Crop Sci. 58 (2018) 380–392, https://doi.org/10.2135/cropsci2017.04.0221.

[45] I. del Olmo, L. Poza-Viejo, M. Piñeiro, J.A. Jarillo, P. Crevillén, High ambient temperature leads to reduced FT expression and delayed flowering in Brassica rapa via a mechanism associated with H2A.Z dynamics, Plant J. 100 (2019) 343–356, https://doi.org/10.1111/tpj.14446.

[46] S. Balasubramanian, S. Sureshkumar, J. Lempe, D. Weigel, Potent induction of Arabidopsis thaliana flowering by elevated growth temperature, PLoS Genet. 2 (2006) 0980–0989, https://doi.org/10.1371/journal.pgen.0020106.

[47] Z.W. Rang, S.V.K. Jagadish, Q.M. Zhou, P.Q. Craufurd, S. Heuer, Effect of high temperature and water stress on pollen germination and spikelet fertility in rice, Environ. Exp. Bot. 70 (2011) 58–65, https://doi.org/10.1016/j.envexpbot.2010.08.009.

[48] S.V.K. Jagadish, M.V.R. Murty, W.P. Quick, Rice responses to rising temperatures - challenges, perspectives and future directions, Plant Cell Environ. 38 (2015) 1686–1698, https://doi.org/10.1111/pce.12430.

[49] J. Xu, A. Henry, N. Sreenivasulu, Rice yield formation under high day and night temperatures—a prerequisite to ensure future food security, Plant Cell Environ. 43 (2020) 1595–1608, https://doi.org/10.1111/pce.13748.

[50] R.M. Borges, Dark matters: challenges of nocturnal communication between plants and animals in delivery of pollination services, Yale J. Biol. Med. 91 (2018) 33–42.

[51] S. Hayes, J. Schachtschabel, M. Mishkind, T. Munnik, S.A. Arisz, Hot topic: thermosensing in plants, Plant Cell Environ. (2020) 1–16, https://doi.org/10.1111/pce.13979.

[52] R. Lippmann, S. Babben, A. Menger, C. Delker, M. Quint, Development of wild and cultivated plants under global warming conditions, Curr. Biol. 29 (2019) R1326–R1338, https://doi.org/10.1016/j.cub.2019.10.016.

[53] X. Fang, N.C. Turner, G. Yan, F. Li, K.H.M. Siddique, Flower numbers, pod production, pollen viability, and pistil function are reduced and flower and pod abortion increased in chickpea (Cicer arietinum L.) under terminal drought, J. Exp. Bot. 61 (2010) 335–345, https://doi.org/10.1093/jxb/erp307.

[54] V. Oury, C.F. Caldeira, D. Prodhomme, J.P. Pichon, Y. Gibon, F. Tardieu, O. Turc, Is change in ovary carbon status a cause or a consequence of maize ovary abortion in water deficit during flowering? Plant Physiol. 171 (2016) 997–1008, https://doi.org/10.1104/pp.15.01130.

[55] V. Oury, F. Tardieu, O. Turc, Ovary apical abortion under water deficit is caused by changes in sequential development of ovaries and in silk growth rate in maize, Plant Physiol. 171 (2016) 986–996, https://doi.org/10.1104/pp.15.00268.

[56] S. Reichardt, H.P. Piepho, A. Stintzi, A. Schaller, Peptide signaling for drought-induced tomato flower drop, Science 367 (2020) 1482–1485, https://doi.org/10.1126/science.aaz5641.

[57] K. Kobayashi, T. Matsui, Y. Murata, M. Yamamoto, Percentage of dehisced thecae and length of dehiscence control pollination stability of rice cultivars at high temperatures, Plant Prod. Sci. 14 (2011) 89–95, https://doi.org/10.1626/pps.14.89.

[58] L. Zhao, Z. Zhu, X. Tian, K. Kobayasi, T. Hasegawa, Y. Zhang, Z. Chen, C. Wang, T. Matsui, Inheritance analysis of anther dehiscence as a trait for the heat tolerance at flowering in japonica hybrid rice (Oryza sativa L.), Euphytica 211 (2016) 311–320, https://doi.org/10.1007/s10681-016-1738-7.

[59] O. Coast, A.J. Murdoch, R.H. Ellis, F.R. Hay, K.S.V. Jagadish, Resilience of rice (Oryza spp.) pollen germination and tube growth to temperature stress, Plant Cell Environ. 39 (2016) 26–37, https://doi.org/10.1111/pce.12475.

[60] C. Wu, K. Cui, W. Wang, Q. Li, S. Fahad, Q. Hu, J. Huang, L. Nie, P.K. Mohapatra, S. Peng, Heat-induced cytokinin transportation and degradation are associated with reduced panicle cytokinin expression and fewer spikelets per panicle in rice, Front. Plant Sci. 8 (2017) 1–15, https://doi.org/10.3389/fpls.2017.00371.

[61] Y. Wang, L. Wang, J. Zhou, S. Hu, H. Chen, J. Xiang, Y. Zhang, Y. Zeng, Q. Shi, D. Zhu, Y. Zhang, Research progress on heat stress of rice at flowering stage, Rice Sci. 26 (2019) 1–10, https://doi.org/10.1016/j.rsci.2018.06.009.

[62] A. Hedhly, A. Nestorova, A. Herrmann, U. Grossniklaus, Acute heat stress during stamen development affects both the germline and sporophytic lineages in Arabidopsis thaliana (L.) Heynh, Environ. Exp. Bot. 173 (2020) 1–8, https://doi.org/10.1016/j.envexpbot.2020.103992.

[63] T.L. Sage, S. Bagha, V. Lundsgaard-Nielsen, H.A. Branch, S. Sultmanis, R.F. Sage, The effect of high temperature stress on male and female reproduction in plants, F. Crop. Res. 182 (2015) 30–42, https://doi.org/10.1016/j.fcr.2015.06.011.

[64] M. Djanaguiraman, R. Perumal, S.V.K. Jagadish, I.A. Ciampitti, R. Welti, P.V. V. Prasad, Sensitivity of sorghum pollen and pistil to high-temperature stress, Plant Cell Environ. 41 (2018) 1065–1082, https://doi.org/10.1111/pce.13089.

[65] Y. Jiang, R. Lahlali, C. Karunakaran, T.D. Warkentin, A.R. Davis, R.A. Bueckert, Pollen, ovules, and pollination in pea: success, failure, and resilience in heat, Plant Cell Environ. 42 (2019) 354–372, https://doi.org/10.1111/pce.13427.

[66] K. Begcy, T. Nosenko, L.Z. Zhou, L. Fragner, W. Weckwerth, T. Dresselhaus, Male sterility in maize after transient heat stress during the tetrad stage of pollen development, Plant Physiol. 181 (2019) 683–700, https://doi.org/10.1104/pp.19.00707.

[67] X. Li, L.M.F. Lawas, R. Malo, U. Glaubitz, A. Erban, R. Mauleon, S. Heuer, E. Zuther, J. Kopka, D.K. Hincha, K.S.V. Jagadish, Metabolic and transcriptomic signatures of rice floral organs reveal sugar starvation as a factor in reproductive failure under heat and drought stress, Plant Cell Environ. 38 (2015) 2171–2192, https://doi.org/10.1111/pce.12545.

[68] T. Sakata, H. Takahashi, I. Nishiyama, A. Higashitani, Effects of high temperature on the development of pollen mother cells and microspores in Barley Hordeum vulgare L, J. Plant Res. 113 (2000) 395–402, https://doi.org/10.1007/pl00013947.

[69] T.G. Porch, M. Jahn, Effects of high-temperature stress on microsporogenesis in heat-sensitive and heat-tolerant genotypes of Phaseolus vulgaris, Plant Cell Environ. 24 (2001) 723–731, https://doi.org/10.1046/j.1365-3040.2001.00716.x.

[70] L.A. Verde, The Effect of Stress on Meiotic Recombination in Maize (Zea Mays L.), Iowa State University, 2003. http://lib.dr.iastate.edu/rtd/1397.

[71] K.E. Francis, S.Y. Lam, B.D. Harrison, A.L. Bey, L.E. Berchowitz, G.P. Copenhaver, Pollen tetrad-based visual assay for meiotic recombination in Arabidopsis, Proc. Natl. Acad. Sci. U. S. A. 104 (2007) 3913–3918, https://doi.org/10.1073/pnas.0608936104.

[72] J.D. Higgins, R.M. Perry, A. Barakate, L. Ramsay, R. Waugh, C. Halpin, S. J. Armstrong, F.C.H. Franklin, Spatiotemporal asymmetry of the meiotic program underlies the predominantly distal distribution of meiotic crossovers in barley, Plant Cell 24 (2012) 4096–4109, https://doi.org/10.1105/tpc.112.102483.

[73] D. Phillips, G. Jenkins, M. Macaulay, C. Nibau, J. Wnetrzak, D. Fallding, I. Colas, H. Oakey, R. Waugh, L. Ramsay, The effect of temperature on the male and female recombination landscape of barley, New Phytol. 208 (2015) 421–429, https://doi.org/10.1111/nph.13548.

[74] A. Lloyd, C. Morgan, F.C.H. Franklin, K. Bomblies, Plasticity of meiotic recombination rates in response to temperature in arabidopsis, Genetics 208 (2018) 1409–1420, https://doi.org/10.1534/genetics.117.300588.

[75] Y. Pécrix, G. Rallo, H. Folzer, M. Cigna, S. Gudin, M. Le Bris, Polyploidization mechanisms: temperature environment can induce diploid gamete formation in Rosa sp, J. Exp. Bot. 62 (2011) 3587–3597, https://doi.org/10.1093/jxb/err052.

[76] M. Tian, Y. Zhang, Y. Liu, X. Kang, P. Zhang, High temperature exposure did not affect induced 2n pollen viability in Populus, Plant Cell Environ. 41 (2018) 1383–1393, https://doi.org/10.1111/pce.13165.

[77] N. De Storme, D. Geelen, High temperatures alter cross-over distribution and induce male meiotic restitution in Arabidopsis thaliana, Commun. Biol. 3 (2020) 1–15, https://doi.org/10.1038/s42003-020-0897-1.

[78] T. Draeger, G. Moore, Short periods of high temperature during meiosis prevent normal meiotic progression and reduce grain number in hexaploid wheat (Triticum aestivum L.), Theor. Appl. Genet. 130 (2017) 1785–1800, https://doi.org/10.1007/s00122-017-2925-1.

[79] K. Hsieh, A.H.C. Huang, Tapetosomes in Brassica tapetum accumulate endoplasmic reticulum-derived flavonoids and alkanes for delivery to the pollen surface, Plant Cell 19 (2007) 582–596, https://doi.org/10.1105/tpc.106.049049.

[80] T. Ariizumi, K. Toriyama, Genetic regulation of sporopollenin synthesis and pollen exine development, Annu. Rev. Plant Biol. 62 (2011) 437–460, https://doi.org/10.1146/annurev-arplant-042809-112312.

[81] J. Shi, M. Cui, L. Yang, Y.J. Kim, D. Zhang, Genetic and biochemical mechanisms of pollen wall development, Trends Plant Sci. 20 (2015) 741–753, https://doi.org/10.1016/j.tplants.2015.07.010.

[82] N. De Storme, D. Geelen, The impact of environmental stress on male reproductive development in plants: biological processes and molecular mechanisms, Plant, Cell Environ. 37 (2014) 1–18, https://doi.org/10.1111/pce.12142.

[83] T. Oshino, M. Abiko, R. Saito, E. Ichiishi, M. Endo, M. Kawagishi-Kobayashi, A. Higashitani, Premature progression of anther early developmental programs accompanied by comprehensive alterations in transcription during high-temperature injury in barley plants, Mol. Genet. Genomics 278 (2007) 31–42, https://doi.org/10.1007/s00438-007-0229-x.

[84] S. Ku, H. Yoon, H.S. Suh, Y.Y. Chung, Male-sterility of thermosensitive genic male-sterile rice is associated with premature programmed cell death of the tapetum, Planta 217 (2003) 559–565, https://doi.org/10.1007/s00425-003-1030-7.

[85] M. Abiko, K. Akibayashi, T. Sakata, M. Kimura, M. Kihara, K. Itoh, E. Asamizu, S. Sato, H. Takahashi, A. Higashitani, High-temperature induction of male sterility during barley (Hordeum vulgare L.) anther development is mediated by transcriptional inhibition, Sex. Plant Reprod. 18 (2005) 91–100, https://doi.org/10.1007/s00497-005-0004-2.

[86] J.K. Muhlemann, T.L.B. Younts, G.K. Muday, Flavonols control pollen tube growth and integrity by regulating ROS homeostasis during high-temperature stress, Proc. Natl. Acad. Sci. U. S. A. 115 (2018) E11188–E11197, https://doi.org/10.1073/pnas.1811492115.

[87] C. Guo, X. Ge, H. Ma, The rice OsDIL gene plays a role in drought tolerance at vegetative and reproductive stages, Plant Mol. Biol. 82 (2013) 239–253, https://doi.org/10.1007/s11103-013-0057-9.

[88] C. Guo, L. Yao, C. You, S. Wang, J. Cui, X. Ge, H. Ma, MID1 plays an important role in response to drought stress during reproductive development, Plant J. 88 (2016) 280–293, https://doi.org/10.1111/tpj.13250.

[89] H.S. Saini, M. Sedgley, D. Aspinall, Developmental anatomy in wheat of male sterility induced by heat stress, water deficit or abscisic acid, Aust. J. Plant Physiol. 11 (1984) 243–253, https://doi.org/10.1071/PP9840243.

[90] H.S. Saini, M. Sedgley, D. Aspinall, Effect of heat stress during floral development on pollen tube growth and ovary anatomy in wheat (Triticum aestivum L.), Aust. J. Plant Physiol. 10 (1983) 137–144, https://doi.org/10.1071/PP9830137.

[91] P.L. Polowick, V.K. Sawhney, High temperature induced male and female sterility in canola (Brassica napus L.), Ann. Bot. 62 (1988) 83–86, https://doi.org/10.1093/oxfordjournals.aob.a087639.

[92] J.L. Snider, D.M. Oosterhuis, B.W. Skulman, E.M. Kawakami, Heat stress-induced limitations to reproductive success in Gossypium hirsutum, Physiol. Plant. 137 (2009) 125–138, https://doi.org/10.1111/j.1399-3054.2009.01266.x.

[93] M. Gusmao, K.H.M. Siddique, K. Flower, H. Nesbitt, E.J. Veneklaas, Water deficit during the reproductive period of grass pea (Lathyrus sativus L.) reduced grain yield but maintained seed size, J. Agron. Crop Sci. 198 (2012) 430–441, https://doi.org/10.1111/j.1439-037X.2012.00513.x.

[94] H.S. Saini, Effects of water stress on male gametophyte development in plants, Sex. Plant Reprod. 10 (1997) 67–73, https://doi.org/10.1007/s004970050069.

[95] X. Ji, B. Shiran, J. Wan, D.C. Lewis, C.L.D. Jenkins, A.G. Condon, R.A. Richards, R. Dolferus, Importance of pre-anthesis anther sink strength for maintenance of grain number during reproductive stage water stress in wheat, Plant Cell Environ. 33 (2010) 926–942, https://doi.org/10.1111/j.1365-3040.2010.02130.x.

[96] I. Onyemaobi, H. Liu, K.H.M. Siddique, G. Yan, Both male and female malfunction contributes to yield reduction under water stress during meiosis in bread wheat, Front. Plant Sci. 7 (2017), https://doi.org/10.3389/fpls.2016.02071.

[97] C.M. Rounds, L.J. Winship, P.K. Hepler, Pollen tube energetics: respiration, fermentation and the race to the ovule, AoB Plants 11 (2011) 1–14, https://doi.org/10.1093/aobpla/plr019.

[98] J. Selinski, R. Scheibe, Pollen tube growth: where does the energy come from? Plant Signal. Behav. 9 (2014) https://doi.org/10.4161/15592324.2014.977200 e977200-1-e977200-9.

[99] M. Goetz, A. Guivarćh, J. Hirsche, M.A. Bauerfeind, M.C. González, T.K. Hyun, S. H. Eom, D. Chriqui, T. Engelke, D.K. Großkinsky, T. Roitsch, Metabolic control of tobacco pollination by sugars and invertases, Plant Physiol. 173 (2017) 984–997, https://doi.org/10.1104/pp.16.01601.

[100] L. Parrotta, C. Faleri, S. Del Duca, G. Cai, Depletion of sucrose induces changes in the tip growth mechanism of tobacco pollen tubes, Ann. Bot. 122 (2018) 23–43, https://doi.org/10.1093/aob/mcy043.

[101] I. Cohen, S.I. Zandalinas, F.B. Fritschi, S. Sengupta, Y. Fichman, K. Azad, R. Mittler, The impact of water deficit and heat stress combination on the molecular response, physiology, and seed production of soybean, Physiol. Plant. 172 (2021) 41–52, https://doi.org/10.1111/ppl.13269.

[102] K. Katano, T. Oi, N. Suzuki, Failure of pollen attachment to the stigma triggers elongation of stigmatic papillae in Arabidopsis thaliana, Front. Plant Sci. 11 (2020) 1–12, https://doi.org/10.3389/fpls.2020.00989.

[103] S.V.K. Jagadish, P.Q. Craufurd, T.R. Wheeler, High temperature stress and spikelet fertility in rice (Oryza sativa L.), J. Exp. Bot. 58 (2007) 1627–1635, https://doi.org/10.1093/jxb/erm003.

[104] X. Ding, Q. Guo, Q. Li, J. Gai, S. Yang, Comparative transcriptomics analysis and functional study reveal important role of high-temperature stress response gene GmHSFA2 during flower bud development of CMS-Based F1 in soybean, Front. Plant Sci. 11 (2020) 1–17, https://doi.org/10.3389/fpls.2020.600217.

[105] J. Rudich, E. Zamski, Y. Regev, Genotypic variation for sensitivity to high temperature in the tomato: pollination and fruit set, Bot. Gaz. 138 (1977) 448–452, https://doi.org/10.1086/336947.

[106] M. Endo, T. Tsuchiya, K. Hamada, S. Kawamura, K. Yano, M. Ohshima, A. Higashitani, M. Watanabe, M. Kawagishi-Kobayashi, High temperatures cause male sterility in rice plants with transcriptional alterations during pollen development, Plant Cell Physiol. 50 (2009) 1911–1922, https://doi.org/10.1093/pcp/pcp135.

[107] J.L. Snider, D.M. Oosterhuis, D.A. Loka, E.M. Kawakami, High temperature limits in vivo pollen tube growth rates by altering diurnal carbohydrate balance in field-grown Gossypium hirsutum pistils, J. Plant Physiol. 168 (2011) 1168–1175, https://doi.org/10.1016/j.jplph.2010.12.011.

[108] S.V.K. Jagadish, M. Raveendran, Z.W. Rang, R. Malo, S. Heuer, J. Bennett, P. Q. Craufurd, Spikelet proteomic response to combined water deficit and heat stress in rice (Oryza sativa cv. N22), Rice 4 (2011) 1–11, https://doi.org/10.1007/s12284-011-9059-x.

[109] D. Laffray, P. Louguet, Stomatal responses and drought resistance, Bull. La Soc. Bot. Fr. Actual. Bot. 137 (1990) 47–60, https://doi.org/10.1080/01811789.1990.10826986.

[110] J. Urban, M.W. Ingwers, M.A. McGuire, R.O. Teskey, Increase in leaf temperature opens stomata and decouples net photosynthesis from stomatal conductance in Pinus taeda and Populus deltoides x nigra, J. Exp. Bot. 68 (2017) 1757–1767, https://doi.org/10.1093/jxb/erx052.

[111] S.I. Zandalinas, D. Balfagón, V. Arbona, A. Gómez-Cadenas, M.A. Inupakutika, R. Mittler, ABA is required for the accumulation of APX1 and MBF1c during a combination of water deficit and heat stress, J. Exp. Bot. 67 (2016) 5381–5390, https://doi.org/10.1093/jxb/erw299.

[112] I. Cohen, S.I. Zandalinas, F.B. Fritschi, S. Sengupta, Y. Fichman, R.K. Azad, R. Mittler, The impact of water deficit and heat stress combination on the molecular response, physiology, and seed production of soybean, Physiol. Plant. (2020) 1–12, https://doi.org/10.1111/ppl.13269.

[113] D. Wei, M. Liu, H. Chen, Y. Zheng, Y. Liu, X. Wang, S. Yang, M. Zhou, J. Lin, INDUCER OF CBF EXPRESSION 1 is a male fertility regulator impacting anther dehydration in Arabidopsis, PLoS Genet. 14 (2018), e1007695, https://doi.org/10.1371/journal.pgen.1007695.

[114] S.I. Zandalinas, F.B. Fritschi, R. Mittler, Signal transduction networks during stress combination, J. Exp. Bot. 71 (2020) 1734–1741, https://doi.org/10.1093/jxb/erz486.

[115] M.J. Zhang, X.S. Zhang, X.Q. Gao, ROS in the male–female interactions during pollination: function and regulation, Front. Plant Sci. 11 (2020) 1–8, https://doi.org/10.3389/fpls.2020.00177.

[116] M. Victoria Martin, D. Fernando Fiol, V. Sundaresan, E. Julián Zabaleta, G. C. Pagnussat, Oiwa, a female gametophytic mutant impaired in a mitochondrial manganese-superoxide dismutase, reveals crucial roles for reactive oxygen species during embryo sac development and fertilization in Arabidopsis, Plant Cell 25 (2013) 1573–1591, https://doi.org/10.1105/tpc.113.109306.

[117] R. Lassig, T. Gutermuth, T.D. Bey, K.R. Konrad, T. Romeis, Pollen tube NAD(P)H oxidases act as a speed control to dampen growth rate oscillations during polarized cell growth, Plant J. 78 (2014) 94–106, https://doi.org/10.1111/tpj.12452.

[118] H.T. Xie, Z.Y. Wan, S. Li, Y. Zhang, Spatiotemporal production of reactive oxygen species by NADPH oxidase is critical for tapetal programmed cell death and pollen development in Arabidopsis, Plant Cell 26 (2014) 2007–2023, https://doi.org/10.1105/tpc.114.125427.

[119] D. Zhang, L. Yang, Specification of tapetum and microsporocyte cells within the anther, Curr. Opin. Plant Biol. 17 (2014) 49–55, https://doi.org/10.1016/j.pbi.2013.11.001.

[120] A. Daneva, Z. Gao, M. Van Durme, M.K. Nowack, Functions and regulation of programmed cell death in plant development, Annu. Rev. Cell Dev. Biol. 32 (2016) 441–468, https://doi.org/10.1146/annurev-cellbio-111315-124915.

[121] M.J. Jimenez-Quesada, J.A. Traverso, M. Potocký, V. Žárský, J. de D. Alché, Generation of superoxide by OeRbohH, a NADPH oxidase activity during olive (Olea europaea L.) pollen development and germination, Front. Plant Sci. 10 (2019) 1–17, https://doi.org/10.3389/fpls.2019.01149.

[122] S. Sankaranarayanan, Y. Ju, S.A. Kessler, Reactive oxygen species as mediators of gametophyte development and double fertilization in flowering plants, Front. Plant Sci. 11 (2020) 1199, https://doi.org/10.3389/fpls.2020.01199.

[123] J. Yi, S. Moon, Y.S. Lee, L. Zhu, W. Liang, D. Zhang, K.H. Jung, G. An, Defective tapetum cell death 1 (DTC1) regulates ROS levels by binding to metallothionein during tapetum degeneration, Plant Physiol. 170 (2016) 1611–1623, https://doi.org/10.1104/pp.15.01561.

[124] H. Kaya, R. Nakajima, M. Iwano, M.M. Kanaoka, S. Kimura, S. Takeda, T. Kawarazaki, E. Senzaki, Y. Hamamura, T. Higashiyama, S. Takayama, M. Abe, K. Kuchitsu, Ca2+-activated reactive oxygen species production by Arabidopsis RbohH and RbohJ is essential for proper pollen tube tip growth, Plant Cell 26 (2014) 1069–1080, https://doi.org/10.1105/tpc.113.120642.

[125] Q. Duan, D. Kita, E.A. Johnson, M. Aggarwal, L. Gates, H.M. Wu, A.Y. Cheung, Reactive oxygen species mediate pollen tube rupture to release sperm for fertilization in Arabidopsis, Nat. Commun. 5 (2014) 3129, https://doi.org/10.1038/ncomms4129.

[126] S.I. Zandalinas, R. Mittler, D. Balfagón, V. Arbona, A. Gómez-Cadenas, Plant adaptations to the combination of drought and high temperatures, Physiol. Plant. 162 (2018) 2–12, https://doi.org/10.1111/ppl.12540.

[127] R. Mittler, ROS are good, Trends Plant Sci. 22 (2017) 11–19, https://doi.org/10.1016/J.TPLANTS.2016.08.002.

[128] G. Zinta, A. Khan, H. AbdElgawad, V. Verma, A.K. Srivastava, Unveiling the redox control of plant eproductive development during abiotic stress, Front. Plant Sci. 7 (2016) 1–6, https://doi.org/10.3389/fpls.2016.00700.

[129] B. Zechmann, B.E. Koffler, S.D. Russell, Glutathione synthesis is essential for pollen germination in vitro, BMC Plant Biol. 11 (2011), https://doi.org/10.1186/1471-2229-11-54.

[130] D.S. Selote, R. Khanna-Chopra, Drought-induced spikelet sterility is associated with an inefficient antioxidant defence in rice panicles, Physiol. Plant. 121 (2004) 462–471, https://doi.org/10.1111/j.1399-3054.2004.00341.x.

[131] G.N. Nguyen, D.L. Hailstones, M. Wilkes, B.G. Sutton, Drought-induced oxidative conditions in rice anthers leading to a programmed cell death and pollen abortion, J. Agron. Crop Sci. 195 (2009) 157–164, https://doi.org/10.1111/j.1439-037X.2008.00357.x.

[132] G.F. Fu, J. Song, J. Xiong, Y.R. Li, H.Z. Chen, M.K. Le, L.X. Tao, Changes of oxidative stress and soluble sugar in anthers involve in rice pollen abortion under drought stress, Agric. Sci. China 10 (2011) 1016–1025, https://doi.org/10.1016/S1671-2927(11)60089-8.

[133] Z. Gao, A. Daneva, Y. Salanenka, M. Van Durme, M. Huysmans, Z. Lin, F. De Winter, S. Vanneste, M. Karimi, J. Van De Velde, K. Vandepoele, D. Van De Walle, K. Dewettinck, B.N. Lambrecht, M.K. Nowack, KIRA1 And ORESARA1 Terminate Flower Receptivity by Promoting Cell Death in the Stigma of Arabidopsis, 2018, https://doi.org/10.1038/s41477-018-0160-7.

[134] M. Borghi, L. Perez de Souza, T. Yoshida, A.R. Fernie, Flowers and climate change: a metabolic perspective, New Phytol. 224 (2019) 1425–1441, https://doi.org/10.1111/nph.16031.

[135] M. Goetz, D.E. Godt, A. Guivarc'h, U. Kahmann, D. Chriqui, T. Roitsch, Induction of male sterility in plants by metabolic engineering of the carbohydrate supply, Proc. Natl. Acad. Sci. U. S. A. 98 (2001) 6522–6527, https://doi.org/10.1073/pnas.091097998.

[136] R. Datta, K.C. Chamusco, P.S. Chourey, Starch biosynthesis during pollen maturation is associated with altered patterns of gene expression in maize, Plant Physiol. 130 (2002) 1645–1656, https://doi.org/10.1104/pp.006908.

[137] S.-L.J. Lee, H.E. Warmke, Organelle size and number in fertile and T-Cytoplasmic male-sterile corn, Am. J. Bot. 66 (1979) 141–148, https://doi.org/10.2307/2442516.

[138] R.W. Parish, H.A. Phan, S. Iacuone, S.F. Li, Tapetal development and abiotic stress: a centre of vulnerability, Funct. Plant Biol. 39 (2012) 553–559, https://doi.org/10.1071/FP12090.

[139] N. Lohani, M.B. Singh, P.L. Bhalla, High temperature susceptibility of sexual reproduction in crop plants, J. Exp. Bot. 71 (2020) 555–568, https://doi.org/10.1093/jxb/erz426.

[140] G.N. Nguyen, D.L. Hailstones, M. Wilkes, B.G. Sutton, Role of carbohydrate metabolism in drought-induced male sterility in rice anthers, J. Agron. Crop Sci. 196 (2010) 346–357, https://doi.org/10.1111/j.1439-037X.2010.00423.x.

[141] E. Pressman, R. Shaked, S. Shen, L. Altahan, N. Firon, Variations in carbohydrate content and sucrose-metabolizing enzymes in tomato (Solanum lycopersicum L.) stamen parts during pollen maturation, Am. J. Plant Sci. 3 (2012) 252–260, https://doi.org/10.4236/ajps.2012.32030.

[142] M. Borghi, A.R. Fernie, Floral metabolism of sugars and amino acids: implications for pollinators' preferences and seed and fruit set, Plant Physiol. 175 (2017) 1510–1524, https://doi.org/10.1104/pp.17.01164.

[143] T. Higashiyama, H. Takeuchi, The mechanism and key molecules involved in pollen tube guidance, Annu. Rev. Plant Biol. 66 (2015) 393–413, https://doi.org/10.1146/annurev-arplant-043014-115635.

[144] A.G. Mizukami, R. Inatsugi, J. Jiao, T. Kotake, K. Kuwata, K. Ootani, S. Okuda, S. Sankaranarayanan, Y. Sato, D. Maruyama, H. Iwai, E. Garénaux, C. Sato, K. Kitajima, Y. Tsumuraya, H. Mori, J. Yamaguchi, K. Itami, N. Sasaki, T. Higashiyama, The AMOR arabinogalactan sugar chain induces pollen-tube competency to respond to ovular guidance, Curr. Biol. 26 (2016) 1091–1097, https://doi.org/10.1016/j.cub.2016.02.040.

[145] M. Jain, P.V.V. Prasad, K.J. Boote, A.L. Hartwell, P.S. Chourey, Effects of season-long high temperature growth conditions on sugar-to-starch metabolism in developing microspores of grain sorghum (Sorghum bicolor L. Moench), Planta 227 (2007) 67–79, https://doi.org/10.1007/s00425-007-0595-y.

[146] S. Sato, M. Kamiyama, T. Iwata, N. Makita, H. Furukawa, H. Ikeda, Moderate increase of mean daily temperature adversely affects fruit set of Lycopersicon esculentum by disrupting specific physiological processes in male reproductive development, Ann. Bot. 97 (2006) 731–738, https://doi.org/10.1093/aob/mcl037.

[147] Y. Jin, H. Yang, Z. Wei, H. Ma, X. Ge, Rice male development under drought stress: phenotypic changes and stage-dependent transcriptomic reprogramming, Mol. Plant 6 (2013) 1630–1645, https://doi.org/10.1093/mp/sst067.

[148] P.K. Koonjul, J.S. Minhas, C. Nunes, I.S. Sheoran, H.S. Saini, Selective transcriptional down-regulation of anther invertases precedes the failure of pollen development in water-stressed wheat, J. Exp. Bot. 56 (2005) 179–190, https://doi.org/10.1093/jxb/eri018.

[149] E. Pressman, D. Harel, E. Zamski, R. Shaked, L. Althan, K. Rosenfeld, N. Firon, The effect of high temperatures on the expression and activity of sucrose-cleaving enzymes during tomato (Lycopersicon esculentum) anther development, J. Hortic. Sci. Biotechnol. 81 (2006) 341–348, https://doi.org/10.1080/14620316.2006.11512071.

[150] R. Kaur, T.S. Bains, H. Bindumadhava, H. Nayyar, Responses of mungbean (Vigna radiata L.) genotypes to heat stress: effects on reproductive biology, leaf function and yield traits, Sci. Hortic. (Amsterdam). 197 (2015) 527–541, https://doi.org/10.1016/j.scienta.2015.10.015.

[151] N. Kaushal, R. Awasthi, K. Gupta, P. Gaur, K.H.M. Siddique, H. Nayyar, Heat-stress-induced reproductive failures in chickpea (Cicer arietinum) are associated with impaired sucrose metabolism in leaves and anthers, Funct. Plant Biol. 40 (2013) 1334–1349, https://doi.org/10.1071/FP13082.

[152] E. Pressman, M.M. Peet, D.M. Pharr, The effect of heat stress on tomato pollen characteristics is associated with changes in carbohydrate concentration in the developing anthers, Ann. Bot. 90 (2002) 631–636, https://doi.org/10.1093/aob/mcf240.

[153] L. Wang, Y.L. Ruan, Critical roles of vacuolar invertase in floral organ development and male and female fertilities are revealed through characterization of GhVIN1-RNAi cotton plants, Plant Physiol. 171 (2016) 405–423, https://doi.org/10.1104/pp.16.00197.

[154] P. Mäkelä, J.E. McLaughlin, J.S. Boyer, Imaging and quantifying carbohydrate transport to the developing ovaries of maize, Ann. Bot. 96 (2005) 939–949, https://doi.org/10.1093/aob/mci246.

[155] A. Kakumanu, M.M.R. Ambavaram, C. Klumas, A. Krishnan, U. Batlang, E. Myers, R. Grene, A. Pereira, Effects of drought on gene expression in maize reproductive and leaf meristem tissue revealed by RNA-Seq, Plant Physiol. 160 (2012) 846–867, https://doi.org/10.1104/pp.112.200444.

[156] L. Parrotta, C. Faleri, M. Cresti, G. Cai, Heat stress affects the cytoskeleton and the delivery of sucrose synthase in tobacco pollen tubes, Planta 243 (2016) 43–63, https://doi.org/10.1007/s00425-015-2394-1.

[157] J.S. Boyer, J.E. McLaughlin, Functional reversion to identify controlling genes in multigenic responses: analysis of floral abortion, J. Exp. Bot. 58 (2007) 267–277, https://doi.org/10.1093/jxb/erl177.

[158] A.R. Smith, D. Zhao, Sterility caused by floral organ degeneration and abiotic stresses in Arabidopsis and cereal grains, Front. Plant Sci. 7 (2016) 1503, https://doi.org/10.3389/fpls.2016.01503.

[159] L. Conti, Hormonal control of the floral transition: Can one catch them all? Dev. Biol. 430 (2017) 288–301, https://doi.org/10.1016/j.ydbio.2017.03.024.

[160] J.W. Chandler, The hormonal regulation of flower development, J. Plant Growth Regul. 30 (2011) 242–254, https://doi.org/10.1007/s00344-010-9180-x.

[161] A.R.G. Plackett, Z.A. Wilson, Gibberellins and Plant Reproduction, 2017, https://doi.org/10.1002/9781119312994.apr0540.

[162] S. Song, T. Qi, H. Huang, D. Xie, Regulation of stamen development by coordinated actions of jasmonate, auxin, and gibberellin in arabidopsis, Mol. Plant 6 (2013) 1065–1073, https://doi.org/10.1093/mp/sst054.

[163] V.S. Jaiswal, A. Kumar, M. Lal, Role of endogenous phytohormones and some macromolecules in regulation of sex differentiation in flowering plants, Proc. Plant Sci. 95 (1985) 453–459, https://doi.org/10.1007/BF03053684.

[164] B. Feng, C. Zhang, T. Chen, X. Zhang, L. Tao, G. Fu, Salicylic acid reverses pollen abortion of rice caused by heat stress, BMC Plant Biol. 18 (2018) 1–16, https://doi.org/10.1186/s12870-018-1472-5.

[165] S. Jegadeesan, A. Beery, L. Altahan, S. Meir, E. Pressman, N. Firon, Ethylene production and signaling in tomato (Solanum lycopersicum) pollen grains is responsive to heat stress conditions, Plant Reprod. 31 (2018) 367–383, https://doi.org/10.1007/s00497-018-0339-0.

[166] C. Zhang, G. Li, T. Chen, B. Feng, W. Fu, J. Yan, M.R. Islam, Q. Jin, L. Tao, G. Fu, Heat stress induces spikelet sterility in rice at anthesis through inhibition of pollen tube elongation interfering with auxin homeostasis in pollinated pistils, Rice 11 (2018), https://doi.org/10.1186/s12284-018-0206-5.

[167] G. Liu, Z. Zha, H. Cai, D. Qin, H. Jia, C. Liu, D. Qiu, Z. Zhang, Z. Wan, Y. Yang, B. Wan, A. You, C. Jiao, Dynamic transcriptome analysis of anther response to heat stress during anthesis in thermotolerant rice (Oryza sativa L.), Int. J. Mol. Sci. 21 (2020), https://doi.org/10.3390/ijms21031155.

[168] R.S. Tang, J.C. Zheng, Z.Q. Jin, D.D. Zhang, Y.H. Huang, L.G. Chen, Possible correlation between high temperature-induced floret sterility and endogenous levels of IAA, GAs and ABA in rice (Oryza sativa L.), Plant Growth Regul. 54 (2008) 37–43, https://doi.org/10.1007/s10725-007-9225-8.

[169] T. Sakata, T. Oshino, S. Miura, M. Tomabechi, Y. Tsunaga, N. Higashitani, Y. Miyazawa, H. Takahashi, M. Watanabe, A. Higashitani, Auxins reverse plant male sterility caused by high temperatures, Proc. Natl. Acad. Sci. U. S. A. 107 (2010) 8569–8574, https://doi.org/10.1073/pnas.1000869107.

[170] A. Higashitani, High temperature injury and auxin biosynthesis in microsporogenesis, Front. Plant Sci. 4 (2013) 2007–2010, https://doi.org/10.3389/fpls.2013.00047.

[171] L. Min, Y. Li, Q. Hu, L. Zhu, W. Gao, Y. Wu, Y. Ding, S. Liu, X. Yang, X. Zhang, Sugar and auxin signaling pathways respond to high-temperature stress during anther development as revealed by transcript profiling analysis in cotton, Plant Physiol. 164 (2014) 1293–1308, https://doi.org/10.1104/pp.113.232314.

[172] L. Sharma, M. Dalal, R.K. Verma, S.V.V. Kumar, S.K. Yadav, S. Pushkar, S. R. Kushwaha, A. Bhowmik, V. Chinnusamy, Auxin protects spikelet fertility and grain yield under drought and heat stresses in rice, Environ. Exp. Bot. 150 (2018) 9–24, https://doi.org/10.1016/j.envexpbot.2018.02.013.

[173] S.S. Zhang, H. Yang, L. Ding, Z.T. Song, H. Ma, F. Chang, J.X. Liu, Tissue-specific transcriptomics reveals an important role of the unfolded protein response in maintaining fertility upon heat stress in arabidopsis, Plant Cell 29 (2017) 1007–1023, https://doi.org/10.1105/tpc.16.00916.

[174] J.Z. Wu, Y. Lin, X.L. Zhang, D.W. Pang, J. Zhao, IAA stimulates pollen tube growth and mediates the modification of its wall composition and structure in Torenia fournieri, J. Exp. Bot. 59 (2008) 2529–2543, https://doi.org/10.1093/jxb/ern119.

[175] M.J. Laskowski, K.A. Dreher, M.A. Gehring, S. Abel, A.L. Gensler, I.M. Sussex, FQR1, a novel primary auxin-response gene, encodes a flavin mononucleotide-binding quinone reductase, Plant Physiol. 128 (2002) 578–590, https://doi.org/10.1104/pp.010581.

[176] I.A. Paponov, M. Paponov, W. Teale, M. Menges, S. Chakrabortee, J.A.H. Murray, K. Palme, Comprehensive transcriptome analysis of auxin responses in Arabidopsis, Mol. Plant 1 (2008) 321–337, https://doi.org/10.1093/mp/ssm021.

[177] H. Shi, L. Chen, T. Ye, X. Liu, K. Ding, Z. Chan, Modulation of auxin content in Arabidopsis confers improved drought stress resistance, Plant Physiol. Biochem. 82 (2014) 209–217, https://doi.org/10.1016/j.plaphy.2014.06.008.

[178] K. Aya, M.U. Tanaka, M. Kondo, K. Hamada, K. Yano, M. Nishimura, M. Matsuoka, Gibberellin modulates anther development in rice via the transcriptional regulation of GAMYB, Plant Cell 21 (2009) 1453–1472, https://doi.org/10.1105/tpc.108.062935.

[179] T. Sakata, S. Oda, Y. Tsunaga, H. Shomura, M. Kawagishi-Kobayashi, K. Aya, K. Saeki, T. Endo, K. Nagano, M. Kojima, H. Sakakibara, M. Watanabe, M. Matsuoka, A. Higashitani, Reduction of gibberellin by low temperature disrupts pollen development in rice, Plant Physiol. 164 (2014) 2011–2019, https://doi.org/10.1104/pp.113.234401.

[180] K.D. Sharma, H. Nayyar, Regulatory networks in pollen development under cold stress, Front. Plant Sci. 7 (2016) 1–13, https://doi.org/10.3389/fpls.2016.00402.

[181] R.M. Rivero, M. Kojima, A. Gepstein, H. Sakakibara, R. Mittler, S. Gepstein, E. Blumwald, Delayed leaf senescence induces extreme drought tolerance in a flowering plant, Proc. Natl. Acad. Sci. U. S. A. 104 (2007) 19631–19636, https://doi.org/10.1073/pnas.0709453104.

[182] C. Wu, K. Cui, W. Wang, Q. Li, S. Fahad, Q. Hu, J. Huang, L. Nie, S. Peng, Heat-induced phytohormone changes are associated with disrupted early reproductive development and reduced yield in rice, Sci. Rep. 6 (2016) 1–14, https://doi.org/10.1038/srep34978.

[183] A.R. Devireddy, S.I. Zandalinas, Y. Fichman, R. Mittler, Integration of reactive oxygen species and hormone signaling during abiotic stress, Plant J. 105 (2020) 459–476, https://doi.org/10.1111/tpj.15010.

[184] L. Poidevin, J. Forment, D. Unal, A. Ferrando, Transcriptome and translatome changes in germinated pollen under heat stress uncover roles of transporter genes involved in pollen tube growth, Plant Cell Environ. (2020) 1–18, https://doi.org/10.1111/pce.13972.

[185] M. Borg, L. Brownfield, D. Twell, Male gametophyte development: a molecular perspective, J. Exp. Bot. 60 (2009) 1465–1478, https://doi.org/10.1093/jxb/ern355.

[186] G.G. Franchi, B. Piotto, M. Nepi, C.C. Baskin, J.M. Baskin, E. Pacini, Pollen and seed desiccation tolerance in relation to degree of developmental arrest, dispersal, and survival, J. Exp. Bot. 62 (2011) 5267–5281, https://doi.org/10.1093/jxb/err154.

[187] Y. Wang, W.Z. Zhang, L.F. Song, J.J. Zou, Z. Su, W.H. Wu, Transcriptome analyses show changes in gene expression to accompany pollen germination and tube growth in arabidopsis, Plant Physiol. 148 (2008) 1201–1211, https://doi.org/10.1104/pp.108.126375.

[188] Y. Qin, A.R. Leydon, A. Manziello, R. Pandey, D. Mount, S. Denic, B. Vasic, M. A. Johnson, R. Palanivelu, Penetration of the stigma and style elicits a novel transcriptome in pollen tubes, pointing to genes critical for growth in a pistil, PLoS Genet. 5 (2009), https://doi.org/10.1371/journal.pgen.1000621.

[189] G. Frank, E. Pressman, R. Ophir, L. Althan, R. Shaked, M. Freedman, S. Shen, N. Firon, Transcriptional profiling of maturing tomato (Solanum lycopersicum L.) microspores reveals the involvement of heat shock proteins, ROS scavengers, hormones, and sugars in the heat stress response, J. Exp. Bot. 60 (2009) 3891–3908, https://doi.org/10.1093/jxb/erp234.

[190] H. Liu, L.E. Brettell, Z. Qiu, B.K. Singh, Microbiome-mediated stress resistance in plants, Trends Plant Sci. 25 (2020) 733–743, https://doi.org/10.1016/j.tplants.2020.03.014.

[191] F.T. De Vries, R.I. Griffiths, C.G. Knight, O. Nicolitch, A. Williams, Harnessing rhizosphere microbiomes for drought-resilient crop production, Science 368 (2020) 270–274, https://doi.org/10.1126/science.aaz5192.

[192] S. Bilal, R. Shahzad, M. Imran, R. Jan, K.M. Kim, I.J. Lee, Synergistic association of endophytic fungi enhances Glycine max L. resilience to combined abiotic stresses: Heavy metals, high temperature and drought stress, Ind. Crops Prod. 143 (2020), 111931, https://doi.org/10.1016/j.indcrop.2019.111931.

[193] R. Vescio, A. Malacrinò, A.E. Bennett, A. Sorgonà, Single and combined abiotic stressors affect maize rhizosphere bacterial microbiota, Rhizosphere 17 (2021), 100318, https://doi.org/10.1016/j.rhisph.2021.100318.

[194] A. Savvides, S. Ali, M. Tester, V. Fotopoulos, Chemical Priming of Plants Against Multiple Abiotic Stresses: Mission Possible? Trends Plant Sci. 21 (2016) 329–340, https://doi.org/10.1016/j.tplants.2015.11.003.

[195] R. Mittler, E. Blumwald, Genetic engineering for modern agriculture: challenges and perspectives, Annu. Rev. Plant Biol. 61 (2010) 443–462, https://doi.org/10.1146/annurev-arplant-042809-112116.

[196] F.K. Choudhury, R.M. Rivero, E. Blumwald, R. Mittler, Reactive oxygen species, abiotic stress and stress combination, Plant J. 90 (2017) 856–867, https://doi.org/10.1111/tpj.13299.