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Review

Molecular Basis and Engineering Strategies for Transcription Factor-Mediated Reproductive-Stage Heat Tolerance in Crop Plants

Niharika Sharma [1,*], Lakshay Sharma [2], Dhanyakumar Onkarappa [3,4], Kalenahalli Yogendra [4], Jayakumar Bose [5] and Rita A. Sharma [2]

[1] NSW Department of Primary Industries, Orange Agricultural Institute, Orange, NSW 2800, Australia
[2] Department of Biological Sciences, Birla Institute of Technology & Science Pilani (BITS Pilani), Pilani Campus, Pilani 333031, India
[3] Department of Entomology, Tamil Nadu Agricultural University, Coimbatore 641003, India
[4] International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502324, India; yogendra.kalenahalli@icrisat.org
[5] School of Science, Hawkesbury Institute for the Environment (HIE), Western Sydney University, Richmond, NSW 2753, Australia; j.bose@westernsydney.edu.au
* Correspondence: niharika.sharma@dpi.nsw.gov.au

Abstract: Heat stress (HS) is a major threat to crop productivity and is expected to be more frequent and severe due to climate change challenges. The predicted increase in global temperature requires us to understand the dimensions of HS experienced by plants, particularly during reproductive stages, as crop productivity is majorly dependent on the success of plant reproduction. The impact of HS on crop productivity is relatively less-studied than the other abiotic stresses, such as drought and salinity. Plants have evolved diverse mechanisms to perceive, transduce, respond, and adapt to HS at the molecular, biochemical, and physiological levels. Unraveling these complex mechanisms underlying plant HS response and tolerance would facilitate designing well-informed and effective strategies to engineer HS tolerance in crop plants. In this review, we concisely discuss the molecular impact of HS on plant reproductive processes and yield, with major emphasis on transcription factors. Moreover, we offer vital strategies (encompassing omics studies, genetic engineering and more prominently gene editing techniques) that can be used to engineer transcription factors for enhancing heat tolerance. Further, we highlight critical shortcomings and knowledge gaps in HS tolerance research that should guide future research investigations. Judicious studies and a combination of these strategies could speed up the much-needed development of HS-resilient crop cultivars.

Keywords: heat stress; transcription factors; reproductive stage; omics approaches; CRISPR gene editing

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1. Introduction

The increasing levels of greenhouse gases in the atmosphere indicate that average global temperatures could rise by 0.3–4.8 °C by 2100 [1,2]. Growing concerns over global warming and the increased frequency of severe heat waves have fueled research on the mechanism and tolerance of heat stress [3]. Temperatures exceeding the adaptation threshold adversely affects the plant growth and reproduction [4,5], leading to alterations in phenology, physiology, and crop productivity in response to heat [6]. Thus, heat stress (HS), or a consistent increase in temperature above optimal, is a major abiotic factor affecting crop plants worldwide [7,8]. Significant advances have been made in discovering physiological mechanisms, molecular responses, and HS-regulatory networks, followed by the characterization of genes or quantitative trait loci (QTLs) associated with heat stress response and tolerance in plants [9–13]. In this area, scientists have been trying to identify new alleles for HS-responsive genes [14] and understand how the improved knowledge of cross-talk between physiology and molecular mechanisms can help us develop crop varieties encompassing HS tolerance, adaptation, and recovery [11,15].

HS leads to irreversible damage to cellular components, plant functioning, and development, drastically impacting crop growth and productivity. Wheat productivity is estimated to decrease by 4–6% with a 1 °C rise in global temperature [16], rice by 10% [17] and maize by 80−90% [18]. The severity of HS depends on the frequency, duration, and intensity of the heat waves and the stage of the plant development. Longer HS exposure times and higher temperatures are more damaging to plants than short-term exposures [10,19]. Usually, short-term HS lasts minutes to hours and is defined as the heat shock type [20,21]. Longer-term heat waves expose the plants to higher temperatures, lasting hours to days [7]. Both types of HS have been observed to negatively impact crop growth, reproductive fitness, and yield components [22,23].

Plants adopt variable physiological, cellular, and metabolic acclimation mechanisms to combat HS that vary between crops and genotypes [24–26]. Understanding the molecular mechanisms underlying thermotolerance is imperative for effectively utilizing genetic engineering tools for crop improvement and future yield sustainability. Numerous studies have identified transcription factors (TFs) as the critical regulators of molecular and biochemical processes associated with HS tolerance. TFs perceive the stress signal and regulate specific stress-responsive genes on and off by binding to their *cis* or *trans*-regulatory elements. Thus, insights into the role and regulation of the TFs will facilitate the crop improvement strategies intended to develop and deliver agronomically superior crops [27]. Our review emphasizes the role of TFs that have been exploited in the past and strategies leveraging TFs that can be explored in the future to engineer heat-tolerant crop plants. We have discussed the molecular roles of a few TF families, such as basic leucine zipper (bZIP), heat shock factor (HSF), MYB, NAC, and WRKY, previously associated with HS response based on experimental evidence. Further, we elaborate on challenges and future opportunities leveraging TFs for developing climate-resilient crops. Additionally, this review provides an overview of recent research on molecular, biochemical, and genetic events observed in the reproductive stages of plant development during HS. These events involve the role of transcriptional and post-transcriptional regulators and the small RNA molecules in HS perception, heat-induced signaling, regulating HS-responsive gene expression, and thermotolerance that promote plant adaptation to HS events.

2. Impact of HS on Plant Reproductive Development and Yield

HS can occur during any stage of the plant life cycle. Still, it is most detrimental during reproductive stages of development, such as flowering, male and female gametogenesis, and seed development [8,28–33]. HS during the reproductive stages leads to significant yield losses due to reduced spikelet fertility and pollen viability, compromised seed yield, vigor, and quality [10,18,34–36] (Figure 1). A heat wave could block reproduction or delay reproduction and seed set, perhaps until after the heat wave, in either case, leading to yield loss and lower seed quality. Among the reproductive stages, gametogenesis and flowering in common bean [37,38]; maize [39]; peanut [40]; sorghum [41]; wheat [42–44]; soybean [45,46]; capsicum [47]; *Brassica* [48]; and chickpeas [49] are highly sensitive to HS, leading to reduction in flower number, spikelet sterility, and decreased seed and fruit numbers [28,50,51]. However, there needs to be more studies on the impact of HS on floral meristem development, floral initiation, and panicle initiation [52–54]. HS impairs rice yield by deforming floral organs reducing spikelet number, size, and sterility due to poor panicle initiation and spikelet development [55]. High temperatures also reduce the number of flowering branches and thus the overall floral turnover [48,56].

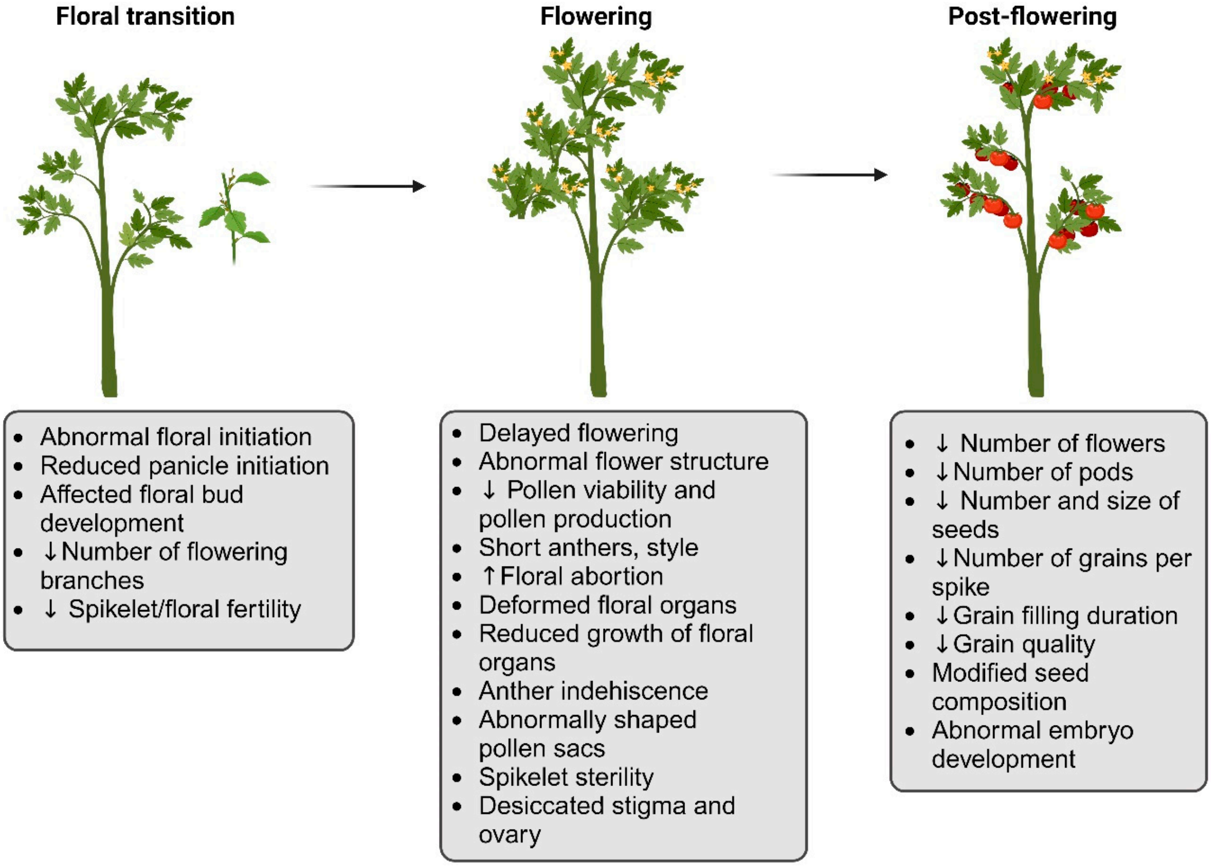

Figure 1. Impact of heat stress on plant development's reproductive stages (floral initiation, flowering, and post-flowering).

HS during the anthesis and grain filling stages led to reduced photosynthetic rate and grain yield in wheat [57] and also caused substantial damage to floret fertility and total crop failure with a mean daily temperature of 35 °C [58]. The intensity of HS affects the floral bud development in cowpeas; flowers developed under high night temperatures (30 °C) set no pods due to low pollen viability and anther indehiscence [59]. HS increased the rate of floral abortion in cotton [60]. In spring barley, an increase in the ambient temperature decreased floret number and grains per spike [61]. Severe HS impacts gametogenesis, ovary growth, and pollen development and transfer, consequently reducing the kernel number [62,63]. HS causes structural abnormalities leading to abnormally shaped microspores and pollen sacs, which cannot accumulate carbohydrates [64]. Pre-anthesis HS decreased seed setting rate and grain quality in rice [65]. In sorghum, HS led to the abortion of florets and decreased pollen production and viability with a significant reduction in seed size and yield [66]. In maize also, pre-anthesis and anthesis stage HS reduced pollen viability [39]. Furthermore, post-anthesis HS in cereals expediates the rate of leaf senescence and reduces the duration of grain filling, resulting in reduced seed size and yields [42,62,67]. High ambient temperature delayed flowering in *Brassica rapa* [68], inhibited anther dehiscence, and shortened anthers with reduced pollen germinability and viability in *B. napus* [13,69]. HS-induced yield decreases will impact all cultivated crops, but crop productivity will also vary across different regions worldwide [70].

HS can cause damage to both microsporogenesis and megasporogenesis, decreasing viable seeds [48,71]. Although female reproductive development is considered less sensitive to HS than male, a few studies have reported a varied response to HS across different crops with a decreased number of ovules and increased abortion rate [72], a reduction in the size of the transmitting tissue in style [73], and desiccated and flaccid stigma, style, and ovary [74]. Few studies directly compared HS effect on pistil and pollen [73,75]. Recently, it has been reported that the female gametophyte possesses a unique and differentially mediated response to HS depending on the identity of the cell, as several essential HS responsive genes were specifically expressed in the central cell but not in the egg cell [76].

HS during pre-anthesis and reproductive development reduces floret fertility and lowers viable seed number [43,77–79]. This consequence cannot be rescued, resulting in irreversible yield loss [34]. Post-anthesis HS, on the other hand, reduces the duration of seed filling, resulting in smaller seeds and lower yields [77,80]. Hence, the thermotolerance of seed setting and filling stages are also crucial in determining grain yield and composition. It was also noted that yield was affected more by HS at the flowering than at the pod development stage, indicating that pods pass a vital developmental threshold contributing to enhanced heat tolerance [81].

In *Brassica*, HS impaired fatty acid biosynthesis and suppressed oil deposition in developing seeds [82]. Also, high temperature during seed development altered seed composition and impaired seed dormancy with a concomitant decrease in the abscisic acid/gibberellic acid (ABA/GA) ratio [83]. In legumes, HS causes abortion during the early stages of embryo development after fertilization [84].

The impact of high temperatures on plant development also varies with the genotype [25,81]. Thus, exploring phenotypic plasticity in different cultivars in response to increasing temperature is critical for leveraging plant breeding techniques and adapting crops to increasing global temperatures [85]. Some strong candidates for thermotolerance traits include the photosynthetic capacity, leaf characteristics, root architecture, flowering traits, size, fitness, metabolite content, and nutrient composition of seeds [32]. However, a higher yield under high temperatures is the goal of plant breeding. Therefore, reproductive traits are the most appealing traits for screening and selection of thermotolerant genotypes. Numerous studies have been conducted to screen the wild relatives of cultivated species to identify heat-tolerant genotypes [42,45,75,86]. An early flowering trait from *Oryza officinalis* was utilized in rice to develop commercial cultivars displaying heat avoidance to ensure successful fertilization [87]. Wild wheat accessions such as *Aegilops speltoides*, and *A. geniculata* also have better thermotolerance than the cultivated varieties [88].

3. Plant Response Mechanisms to HS

Crops have evolved complex mechanisms to sense and respond to HS [89], which are highly conserved and involve multiple pathways, regulatory networks, and cellular compartments [20]. A whole set of genes acting for HS perception and signalling is reviewed here [20,67,90]. Plants respond to high-temperature stress through short-term escape, avoidance, and long-term acclimation mechanisms [5,8,67], as depicted in Figure 2. The escape mechanisms ensure that plants quickly complete their life cycle during favorable temperature conditions, often leading to minor crop yield penalties [67]. Several crop plants mature early under HS, resulting in small yield losses, implying an important heat escape mechanism [91]. Some heat-tolerant rice genotypes have incorporated the early morning flowering trait, which aids plants in avoiding HS damage [92,93]. Heat escape has also been reported in wheat, with peak flowering occurring during cooler hours of the day (i.e.; early in the morning or late in the evening) [42]. This escape mechanism allows plants to finish fertilizing before the onset of harmful (high) temperatures that can cause sterility. High night temperatures induced a shift in *B. napus* peak flower opening time into earlier and cooler morning hours, indicating an adaptation towards the heat escape response, accompanied by a significant yield reduction [94]. There have also been reports that the effect of temperature on reproductive development varies depending on the length of the day, with high temperatures causing rapid progression through reproductive development on long days but inhibiting early stages of reproductive development on short days [95]. These findings indicate that different thermoresponsive floral regulator pathways are active in various crop plants.

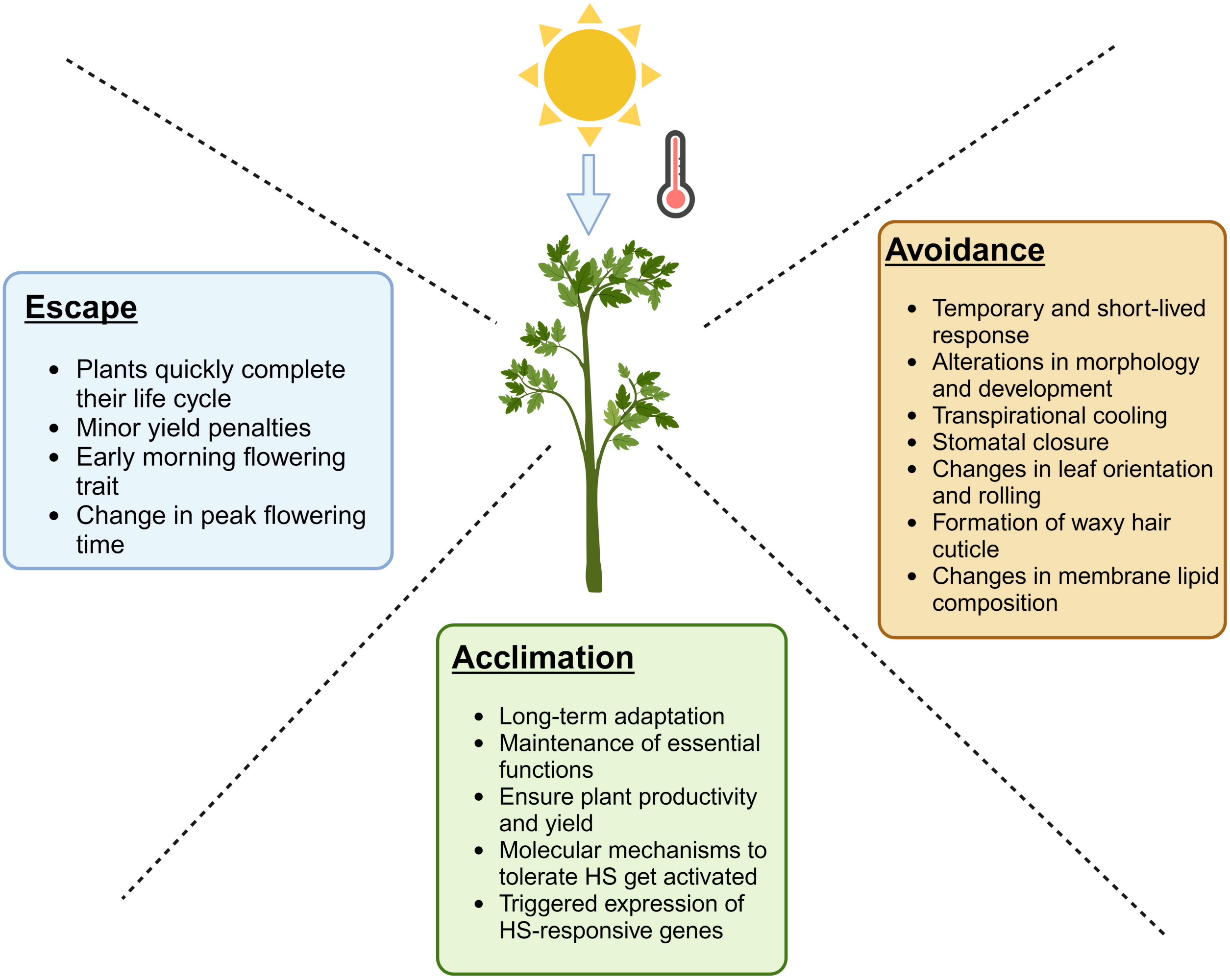

Figure 2. Mechanisms of heat stress response in plants.

Heat avoidance is a temporary and short-lived response elicited by warm ambient temperature conditions, which is usually species-dependent via morphology and development changes [67]. Mildly elevated temperatures can cause significant expression of HS-responsive genes, resulting in visible plant morphological and developmental changes, including accelerated flowering. This response is characterized by thermomorphogenesis [32,96]. Long-term adaptation mechanisms for HS tolerance, on the other hand, entail maintaining essential plant functions and ensuring plant productivity under HS conditions. Furthermore, this improves plant genotype fitness under HS [67] and improves plant adaptation to the HS environment [5].

Because plants are sessile, they have evolved complex signaling and response networks to detect changes in ambient temperature, activating a series of molecular events that modify the plant's cellular metabolism and promote survival and reproduction to better adapt to HS [20,97]. Plants respond to HS by changing their molecular, cellular, biochemical, metabolic, physiological, and morphological responses [98]. HS (a) alters membrane fluidity, which disrupts photosynthesis and respiration, resulting in cell death and plant wilting; (b) alters protein misfolding and protein aggregate accumulation, resulting in proteotoxic stress; (c) induces ROS production and creates hormonal and metabolic imbalance; and (d) alters cytoskeleton dismantling, resulting in several disruptions in plant development [20,99,100]. Activation of the antioxidant defense system, phytohormonal regulation, transcriptional regulation of the HS response, initiation of HS-responsive genes, and maintenance of cellular homeostasis are all components of HS tolerance [101,102]. The expression of HSFs and heat shock proteins (HSPs) and reactive oxygen species (ROS)-scavenging activity play important roles in plant responses and acclimatization to HS [14,103]. Epigenetics, small RNAs (sRNAs), and post-translational modifications have also been implicated in thermotolerance [96,104,105].

3.1. Transcriptomic, Proteomic, and Metabolomic Changes in Response to HS

Plants employ a strategy of modulating multiple genes, proteins, and metabolites to tolerate HS [102]. Omics approaches have contributed significantly to our understanding of plant HS, providing valuable insights into the underlying mechanisms and processes [106]. This section summarizes comparative transcriptomic, proteomic, and metabolomic studies deciphering plant HS response and acclimation in reproductive stages. These studies have identified key differentially expressed genes, proteins and metabolites using contrasting (tolerant and sensitive) genotypes [106].

3.1.1. Changes in Gene Expression Patterns in Response to HS

Transcriptional dynamics in response to HS can help understand the impact of HS on reproductive development in crop plants. For example, transcriptional inhibition in response to HS led to male sterility in barley [107]. Furthermore, transcriptional changes in response to short-term HS influenced caryopsis developmental functions [103]. Failure of transcriptional reactivation following a return to normal average temperatures increased with the duration of elevated temperatures and was strongly associated with male sterility. When exposed to HS, significant differences in gene expression were observed in the early development and differentiation of barley anthers [108]. Transcriptomic studies in tomatoes revealed that TFs and genes involved in HS response differed during microspore stages [109,110]. ROS-related genes, ethylene and ABA signaling genes, HSFs, and carbohydrate metabolism genes are among the primary differentially regulated genes in HS-treated microspores and pollen mother cells. Transcription profiling in *B. napus* seeds revealed that genes encoding ethylene and GA biosynthesis were all downregulated, whereas genes encoding auxin biosynthesis, signaling, and transport were all induced in response to HS [111]. The HS responses involve the activation of specific genes and HSPs via signaling pathways [35]. Improved signal transduction and hormonal regulation under high temperature promote heat tolerance in rice. Simultaneously, abnormal panicle development has been linked to impaired starch and sucrose metabolism under HS [112]. WRKY, HD-ZIP, and ERF TFs were the most prominent among HS-responsive genes in the tolerant genotype, implying a critical role in developing panicle HS tolerance. During anthesis, the RNA sequencing of heat-treated reproductive tissues revealed that TF-encoding genes, signal transduction genes, and metabolic pathway genes were all down-regulated in rice. Simultaneously, the expression of HSFs and HSPs was highly activated, implying that the appropriate expression of protective chaperones in anthers (before anthesis) ensures that stress damage is overcome, and fertilization is successful [113]. Another study that examined the transcriptome profiles of rice grains (at the early milky stage) from heat-tolerant and heat-sensitive cultivars in response to high night temperatures found that high temperature disrupts electron transport in the mitochondria, resulting in changes in hydrogen ion concentration and enzyme activity in the TCA cycle, influencing secondary metabolism in plant cells [114]. A recent comparative transcriptomic study revealed that post-pollination HS in a heat-sensitive cultivar of maize led to kernel abortion due to carbohydrate metabolic disorders [115].

Thermosensitive genic male sterility (TGMS) has also been reported in *B. napus* [69]. HSPs, skeleton proteins, GTPase, and calmodulin genes were discovered to be potentially involved in TGMS under high temperatures. Auxin, gibberellins, jasmonic acid, abscisic acid, and brassinosteroid signaling pathways, as well as some well-known TFs (MADS, NFY, HSF, MYB, and WRKY), were also found to be involved in the regulation of TGMS in the flowers. High night temperature exposure between flowering and seed-filling stages resulted in a significant reduction in total fatty acids and changes in fatty acid composition in susceptible *B. napus* cultivars. In-depth transcriptome analysis revealed that high night temperature increased gibberellin signaling associated with active expression of genes involved in fatty acid catabolism during seed-filling stages [116]. Another transcriptome study of HS on *Arabidopsis* reproductive stages revealed that genes involved in the unfolded protein response (UPR) were enriched in reproductive tissues in response to heat. Furthermore, the UPR-deficient *bzip28 bzip60* double mutant was HS sensitive, with decreased silique length and fertility. These findings show that the UPR plays a protective role in maintaining fertility under HS [30].

3.1.2. Changes in Protein Profiles in Response to HS

A study that looked at changes in anther protein expression in three rice genotypes exposed to HS during anther dehiscence discovered cold and heat shock proteins that are involved in heat tolerance [117]. Under different levels of high temperature, a comparative proteomics analysis on rice anthers between HS-resistant and HS-sensitive cultivars revealed that the resistant cultivar had significantly higher spikelet fertility than the sensitive cultivar [118]. Data suggested that ribosomal protein degradation in the sensitive cultivar negatively impacts the protein biosynthetic machinery. HS, on the other hand, increased HSPs, expansins, and lipid transfer proteins in the resistant cultivar, which likely contributed to its tolerance to HS. Another proteomics study found that ethylene helps enhance thermotolerance in tomato pollen; higher ethylene levels before HS exposure improved pollen quality [119]. Trehalose synthase activity in rice anthers increased significantly after heat treatment, implying that trehalose may play a role in preventing protein denaturation via desiccation [120]. A comparative proteomic analysis of tomato anthers collected from thermotolerant and sensitive genotypes also identified several thermotolerance-associated proteins [121]. During high-temperature stress, comparative proteomic analysis in the early milky stage of rice grains identified proteins involved in biosynthesis, energy metabolism, oxidation, heat shock metabolism, and transcriptional regulation [122]. Photosynthesis, glycolysis, stress, defense response, heat shock, and ATP production proteins were differentially expressed in tolerant and sensitive wheat cultivars during grain filling stages [123].

A comprehensive analysis of tomato pollen collected at different development stages under HS revealed elevated temperature response at both transcriptomic and proteomic levels [124]. The proteins that were found to be differentially regulated were mostly involved in protein synthesis, folding, and degradation. Another study compared the physiological and proteomic profiles of heat sensitive (ICC16374) and tolerant (JG14) chickpea genotypes during anthesis [100]. The analysis identified a set of 482 heat-responsive proteins in the tolerant genotype including acetyl-CoA carboxylase, ATP synthase, sucrose synthase, glycosyltransferase, pyrroline-5-carboxylate synthase (P5CS), ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), phenylalanine ammonia-lyase (PAL) 2, and late embryogenesis abundant (LEA) proteins. High temperatures during seed filling are also detrimental to seed yield and quality [125].

Future research should focus on similar studies to better understand the pathways that lead to decreased crop fertility during HS. The key HS-responsive proteins discovered in these comparative proteomic studies could be used as biomarkers to identify or genetically engineer HS-tolerant cereal crop cultivars.

3.1.3. Changes in Metabolite Accumulation in Response to HS

A comparative metabolomic and transcriptomic study of rice floral organs (anthers and pistils) from a heat-tolerant and a heat-sensitive rice cultivar identified sugar metabolism as the crucial metabolic and transcriptional component differentiating floral organ tolerance or susceptibility to HS [126]. In an untargeted metabolomic analysis of tomato pollen, young microspores accumulated large amount of alkaloids and polyamines, while mature pollen accumulated flavonoids [127]. The accumulation of flavonoids was suggested to protect against oxidative stress during HS. Another untargeted metabolic assessment identified several metabolic markers differentially induced between the heat-tolerant and heat-susceptible genotypes of *B. napus* during the reproduction stage under HS [128]. A comparative metabolomics study of wheat genotypes exposed to post-anthesis HS discovered several metabolites, such as L-arginine, L-tryptophan, L-histidine, and leucine, with significantly higher levels in tolerant genotypes. Furthermore, HS had the most significant impact on the aminoacyl-tRNA biosynthesis and plant secondary metabolite biosynthesis pathways, indicating their importance in post-anthesis HS tolerance in wheat [129]. Another targeted metabolomics study reported that salicylic acid (SA)-treated rice plants exhibited higher pollen viability and seed-setting rates by reducing the excessive ROS and HS-induced tapetum degradation [130]. Another group reported changes in the wheat pollen lipidome during high day- and night-temperature stress, implying that similar lipid changes contribute to adaptive mechanisms in wheat leaves and pollen under high temperature stress. Pollen and leaf lipidomes, on the other hand, have distinct compositions [131].

3.2. Role of Transcription Factors in Mitigating the Impact of HS on Plant Reproductive Development

Plant HS response is regulated by a complex web of transcription factors (TFs) that modulate HS-responsive gene expression [132]. These gene expression changes are the driving force behind cellular, physiological, biochemical, and molecular changes in response to HS [133,134]. Therefore, TFs are important targets for modulating downstream gene regulatory networks and developing climate-resilient crops. TFs typically respond to stress by binding their target sites within cis-acting elements in stress-responsive gene promoter regions. The stress response consists of signal perception, signal transduction, and stress-responsive gene expression [135]. Stress susceptibility or tolerance in plants is primarily determined by the coordinated activity of phytohormones and transcription factors (TFs) that control the spatiotemporal regulation of stress-responsive genes, as shown in Figure 3. Recent reviews [12,102,136] go into great detail about the signaling cascade and phytohormone-mediated regulation of the HS response in plants. This section only includes studies that investigate the role of TFs in plant HS response and acclimation during reproductive stages.

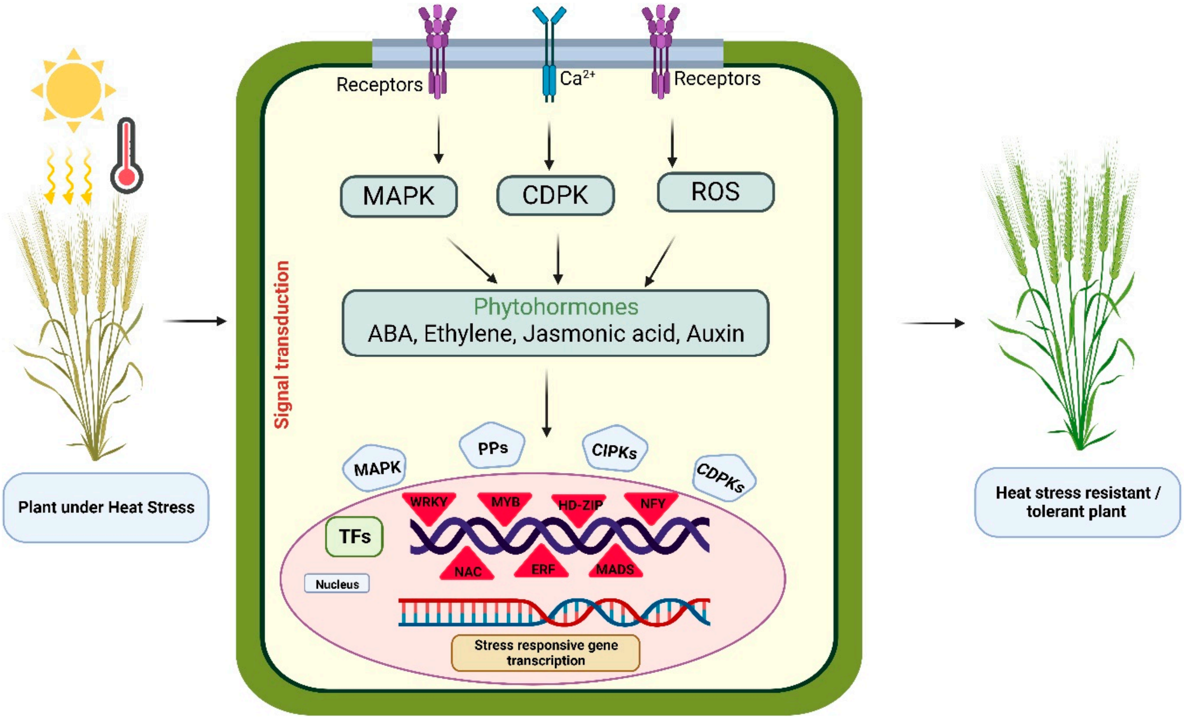

Figure 3. Role of transcription factors in mitigating the effects of HS in plants: TFs as key molecular targets for engineering heat tolerance.

The heat shock response (HSR) during HS in plants is a conserved response where HSFs regulate HSPs by recognizing and binding to the conserved palindromic motifs in their promoter regions [137]. Further, HSPs bind to the denatured proteins and inhibit their aggregation, thereby maintaining the protein homeostasis and thermotolerance [138]. For example, *HSFA2* functions from a heat shock trigger and induces HSP genes to preserve cytosolic protein homeostasis [139]. In a classic HSP-induced HSR model, *HSP70*, *HSP90* and *HSP100* exhibit upregulation to confer HS tolerance in barley reproductive stages [140].

Plant HSFs have been used for gene manipulation and crop tolerance to HS due to their role as central regulators of the HS response [141,142]. The HSFA1 subfamily is a master regulator of HS responses, and *HSFA1a* in tomato has a unique function for acquired thermotolerance [143]. Overexpression of soybean *GmHSFA1* improved transgenic soybean thermotolerance by activating downstream genes such as *GmHsp70*, *GmHsp22*, and other *GmHsps* under HS [135,144]. Recently, it was discovered that HSFA1 interacts with a bHLH TF, BRASSINOSTEROID INSENSITIVE 1 EMS-SUPPRESSOR 1 (BES1) to improve HS tolerance in *Arabidopsis* [145]. Overexpression of *Arabidopsis HSFA2* in the *HSFA1* quadruple knockout (*hsfA1a*,*b*,*d*,*e*) mutant improved thermotolerance, suggesting that *HSFA2* can be active and functional and interact with other HSFs [145]. Meanwhile, *TaHSFA2-10* overexpressing transgenic *Arabidopsis* plants exhibited enhanced HS tolerance because *TaHSFA2-10* regulated the binding and upregulation of AtHSPs [146]. In addition, the ectopic expression of rice *HSFA2e* and lily *HSFA2* in *Arabidopsis* resulted in increased thermotolerance [137,147,148]. Another study demonstrated that *DREB2A* plays a key role in the transcriptional regulation of *HSFA3* to improve plant thermotolerance [149]. Transgenic plants overexpressing *ZmDREB2A* demonstrated improved thermotolerance 150]. Wheat and *Arabidopsis* plants overexpressing wheat *TaHSFA6f* showed improved thermotolerance [150,151]. *ZmHsf05* overexpression in *Arabidopsis* enhanced both basal and acquired thermotolerances in transgenic plants [142]. Expression of maize gene *ZmHsf06* enhances transgenic *Arabidopsis'* thermotolerance and drought-stress tolerance [152]. Also, ectopic expression of tomato *HSFA3* and wheat *HSF3* in *Arabidopsis* enhanced its thermotolerance [153,154]. *HSFB1* of *Arabidopsis* acts as a repressor of HS-inducible HSFs—*HSFA2*, *A7a*, *B1*, and *B2b*—with *hsfb1*, *hsfb2b* knockout mutants exhibiting decreased acquired thermotolerance [155]. Overexpression of *VpHSF1* (HSFB2 family) from Chinese wild *Vitis pseudoreticulata* in tobacco demonstrated the role of *VpHSF1* as a positive regulator of acquired thermotolerance but a negative regulator of basal thermotolerance [156].

Transgenic rice lines overexpressing *AtHSP101* had significantly higher survival rates and growth performance in the recovery phase after HS [157]. Rice HS tolerance is improved by *OsHSP101* [158], while transgenic *Arabidopsis* plants overexpressing *HSP100* induce enhanced thermotolerance [159]. Transgenic plants overexpressing *OsHSP18.6* showed improved tolerance to HS and other abiotic stresses [160]. Furthermore, transgenic *Arabidopsis* plants over-expressing the HS-responsive HSP wheat gene *TaHSP23.9* showed improved tolerance to heat and salt stress, implying that TaHSP23.9 acts as a chaperone to positively regulate plant responses to heat and salt stress [161]. The complex gene regulatory network involved in the transcriptional regulation of HS response is made up of several HSFs and HSPs.

Several other TF families such as WRKY, NAC, MYB, and bZIP also regulate heat-responsive genes [162]. Constitutive expression of *OsWRKY11* using *HSP101* promoter enhanced heat and drought stress tolerance in rice [163]. The transgenic *Arabidopsis* overexpressing maize gene *ZmWRKY106* exhibited improved tolerance to heat and drought stresses [164]. Rice plants overexpressing *SNAC3* showed increased tolerance to HS and oxidative stresses, whereas plants lacking *SNAC3* showed increased sensitivity to these stresses [165]. HS increases the expression of the wheat NAC TF gene *TaNAC2L*, and *TaNAC2L* overexpression in *Arabidopsis* plants improves acquired thermotolerance [166]. The NAC TF gene (*ONAC063*) in rice roots responds to heat stress [167]. Another example is that transgenic *Arabidopsis* plants overexpressing *ANAC042* have higher HS tolerance than wild-type plants [168]. Heat sensitivity was conferred by a loss of function mutation in *OsNTL3*, whereas heat tolerance was increased by inducible expression of the truncated form of *OsNTL3* in rice seedlings [169].

In *Arabidopsis*, a direct mechanism was suggested by which increasing temperature causes the bHLH TF *Phytochrome Interacting Factor 4* (*PIF4*) to activate *Flowering Locus T (FT)*, inducing flowering under short-day conditions [170]. So, *PIF4* controlled thermosensory memory and the reproductive transition in *Arabidopsis*. Also, a variant of *GmPIF4b* in soybean had a unique temperature adaptation at elevated temperatures [171]. PIFs play roles in HS sensing and signalling [172], with *PIF4* as a core thermomorphogenesis signalling hub [173]. Like *PIF4*, *PIF7* promoted thermomorphogenesis in *Arabidopsis* in response to elevated ambient temperature [174].

MADS-box genes, *Flowering Locus M* (*FLM*) and *Short Vegetative Phase* (*SVP*), are also key regulators of temperature-mediated flowering time [32,175,176]. In *Arabidopsis*, *SVP* tends to be unstable and degrade at higher temperatures. *SVP* and FLM-β (alternatively spliced variant of FLM) form a complex that represses flowering, but FLM-β is not produced at warm temperatures, which allows flowering to proceed. However, at lower temperatures, more repressive complex (SVP–FLMβ complex) is present and flowering is delayed [177,178]. In contrast, in barley, elevated expression of the MADS-box floral repressor *HvODDSOC2* at higher temperatures in short days is suggested to be involved in delayed flowering. So, under long-day conditions, high temperature promotes flowering in winter barley, while an opposite response is observed under short days [178].

bZIP17 knockout mutant in *Arabidopsis* exhibit higher sensitivity to HS at the reproductive stage (silique length and fertility), demonstrating the role of *AtbZIP17* in HS tolerance [179]. *SPL1* and *SPL12*, two Squamosa Promoter Binding Protein-like (SPL) TF genes in *Arabidopsis*, act redundantly to confer thermotolerance during the reproductive stage and in inflorescences [180]. Following HS exposure, MYB genes (*BnMYB44* and *BnVIP1*) were simultaneously reprogrammed and induced in the silique wall and seeds of *B. napus* [181]. Ectopic expression of the transcription factor *AtMYB68* in *B. napus* after severe HS during flowering significantly improved pollen viability and yield [182]. Elevated temperatures increase glucosinolate concentrations, which play protective roles in plant stress defense mechanisms against biotic and abiotic stress in *B. rapa* through *BrMYB28*- and *BrMYB34*-mediated regulation [183]. Overexpression of *OsMYB55* improved tolerance to HS and drought in maize [184]. Soybean DREB1/CBF-type TFs are reported to modulate heat-, drought-, and cold-stress-responsive gene expression [185]. The expression of *thermal resistance gene 1* (*BnTR1)* increased rice yield and heat tolerance, suggesting its role in mitigating adverse impacts of HS [186]. Table 1 lists the TFs whose roles have been experimentally validated in promoting plant heat tolerance.

Table 1. List of transcription factors (TFs) with experimentally demonstrated roles in heat tolerance.

S. No.	Gene Name	TF Family	Source Species	Host Species	Strategy Used	Phenotype	References
1	*AF1* and *ANAC055*	NAC	*A. thaliana*	*A. thaliana*	Mutant lines	Knockout mutants showed improved thermomemoryand showed faster seed germination and higher fresh mass ratio than wild type	[187]
2	*ANAC042*	NAC	*A. thaliana*	*A. thaliana*	Overexpression	Overexpressed lines showed increased heat tolerance	[168]
3	*AtWRKY30*	WRKY	*A. thaliana*	*T. aestivum*	Overexpression	Overexpressed lines showed increased heat and drought tolerance	[188]
4	*BnWRKY149*	WRKY	*B. napus*	*A. thaliana*	Overexpression	Overexpression lines were less sensitive to ABA	[189]

Table 1. *Cont.*

S. No.	Gene Name	TF Family	Source Species	Host Species	Strategy Used	Phenotype	References
5	*BZR1*	BZR	*S. lycopersicum*	*S. lycopersicum*	Overexpression and CRISPR/Cas-mediated editing	Overexpressed lines showed increased heat tolerance while knockout lines showed decreased heat tolerance and severe wilting after heat stress	[190]
6	*CaWRKY40*	WRKY	*C. annuum*	*N. tabacum*	Overexpression	Overexpression lines showed increased heat tolerance and enhanced basal defence against virulent *R. solanacearum*	[191]
7	*CBF1*	ERF/AP2	*A. thaliana*	*A. thaliana*	Overexpression and CRISPR/Cas-mediated editing	Ocerexpression lines showed improved heat tolerance and CRISPR-edited lines were extremely sensitive to heat stress	[192]
8	*DgMADS114* and *DgMADS115*	MADS-box	*D. glomerata*	*A. thaliana*	Overexpression	Overexpression lines showed increased tolerance to heat stress and osmotic stress	[193]
9	*HaHB4*	HD-Zip	*H. annuus*	*G. max*	Overexpression	Overexpression lines showed increased heat tolerance and delayed senescence	[194]
10	*BhHSF1*	HSF	*B. hygrometrica*	*A. thaliana* and *N. tabacum*	Overexpression	Overexpression lines showed increased heat tolerance	[195]
11	*OsHSF7*	HSF	*O. sativa*	*A. thaliana*	Overexpression	Overexpression lines showed increased basal thermotolerance	[196]
12	*HSFA1*	HSF	*G. max*	*G. max*	Overexpression	Overexpression lines showed increased heat tolerance	[144]
13	*HSFA2*	HSF	*A. thaliana*	*A. thaliana*	Overexpression	Overexpression lines showed increased heat tolerance	[197]
14	*LlHSFA2b*	HSF	*L. longiflorum*	*A. thaliana*	Overexpression	Overexpression lines showed increased heat and oxidative stress tolerance	[148]
15	*HSFA3*	HSF	*A. thaliana*	*A. thaliana*	Overexpression	Overexpression lines showed increased heat tolerance	[198]
16	*HsfB1*	HSF	*S. peruvianum*	*S. lycopersicum*	Overexpression and Antisense	Overexpression lines showed increased heat tolerance	[199]
17	*HsfC1b*	HSF	*L. perenne*	*A. thaliana*	Overexpression	Overexpression lines showed increased heat tolerance	[200]
18	*HvSHN1*	SHN/WIN	*H. vulgare*	*N. tabacum*	Overexpression	Overexpression lines showed increased heat, drought, and salt tolerance	[201]
19	*LlERF110*	ERF	*L. longiflorum*	*A. thaliana* and *N. benthamiana*	Overexpression	Overexpression lines showed reduced heat tolerance	[202]
20	*LiHsfA4*	HSF	*L. Longiflorum*	*A. thaliana*	Overexpression	Overexpression lines showed increased heat tolerance	[203]

Table 1. *Cont.*

S. No.	Gene Name	TF Family	Source Species	Host Species	Strategy Used	Phenotype	References
21	*MaDREB20*	DREB	*M. acuminata*	*A. thaliana*	Overexpression	Overexpression lines showed increased heat and drought tolerance	[204]
22	*OsNAC063*	NAC	*O. sativa*	*A. thaliana*	Overexpression	Overexpression lines showed tolerance to heat, salinity, and osmotic stress	[167]
23	*OsMYB55*	MYB	*O. sativa*	*Z. mays*	Overexpression	Overexpression lines showed increased heat and drought tolerance	[121]
24	*OsNTL3*	NAC	*O. sativa*	*O. sativa*	Overexpression and CRISPR/Cas-mediated editing	Overexpression lines showed increased heat tolerance while loss of function mutant showed heat sensitivity	[145]
25	*OsWRKY11*	WRKY	*O. sativa*	*O. sativa*	Overexpression	Overexpression lines showed increased heat and drought tolerance	[109]
26	*PpNAC56*	NAC	*P. persica*	*S. lycopersicum*	Overexpression	Overexpression lines showed increased heat tolerance	[205]
27	*SNAC3*	NAC	*O. sativa*	*O. sativa*	Overexpression and RNAi	Overexpression lines showed increased heat and drought tolerance while suppressing *SNAC3* showed decreased heat, drought, and oxidayive stress tolerance	[184]
28	*TabZIP60*	bZIP	*T. aestivum*	*A. thaliana*	Overexpression	Overexpression lines showed increased heat tolerance	[206]
29	*TaHsfA2d*	HSF	*T. aestivum*	*A.thaliana*	Overexpression	Overexpression lines showed increased heat, salinity, and drought tolerance	[207]
30	*TaHsfA6b*	HSF	*T. aestivum*	*A. thaliana*	Overexpression	Overexpression lines performed better in repsonse to stress	[208]
31	*TaHsfA6b*	HSF	*T. aestivum*	*H. vulgare*	Overexpression	Overexpression lines showed improved heat tolerance	[209]
32	*TaHSFA6f*	HSF	*T. aestivum*	*T. aestivum* *A. thaliana*	Overexpression	Overexpression lines showed tolerance to heat, drought and salt stress	[151]
33	*TaNAC2L*	NAC	*T. aestivum*	*A. thaliana*	Overexpression	Overexpression lines showed increased heat, drought, salt and freezing stress	[166]
34	*TaZnF*	Zin finger	*T. aestivum*	*A. thaliana*	Overexpression	Overexpression lines showed tolerance to heat, cold, and oxidative stress	[210]
35	*VpHSF1*	HSF	*V. pseudoreticulata*	*N. tabacum*	Overexpression	Overexpression lines showed tolerance to heat, drought, and salt stress but enhanced susceptibility to *P. parasitica*	[156]

Table 1. *Cont.*

S. No.	Gene Name	TF Family	Source Species	Host Species	Strategy Used	Phenotype	References
36	*ZmDREB2A*	DREB	*Z. mays*	*Zea mays*	Overexpression	Overexpression lines showed tolerance to heat, drought, and salt stress	[211]
37	*ZmHsf05*	HSF	*Z. mays*	*A. thaliana*	Overexpression	Overexpression lines showed increased heat tolerance	[142]
38	*ZmHsf06*	HSF	*Z. mays*	*A. thaliana*	Overexpression	Higher seed germination rate, longer axial root length	[152]
39	*ZmNAC074*	NAC	*Z. mays*	*A. thaliana*	Overexpression	Overexpression lines showed increased heat tolerance	[212]
40	*ZmWRKY106*	WRKY	*Z. mays*	*A. thaliana*	Overexpression	Overexpression lines showed improved drought and heat tolerance	[163]
41	*HSFA1a*	HSF	*S. lycopersicum*	*S. lycopersicum*	Mutants lines	Mutant lines showed strong defects in growth	[213]
42	*OsNAC006*	NAC	*O. sativa*	*O. sativa*	CRISPR/ Cas-mediated gene editing	Knockouts line showed heat and drought sensitivity	[214]
43	*AtMYB68*	MYB	*A. thaliana*	*A. thaliana*	Overexpression	Overexpression lines showed increased heat and drought tolerance	[182]
44	*ONAC127* and *ONAC129*	NAC	*O. sativa*	*O. sativa*	Overexpression and CRISPR/ Cas-mediated editing	Both knockout and overexpression lines show incomplete grain filling and shrunken grains with higher severity of heat stress	[215]
45	*OsMADS87*	MADS-box	*O. sativa*	*O. sativa*	Overexpression and RNAi	Overexpression lines showed increased thermotolerance while suppressor linses were sensitive to heat stress	[216]

3.3. Epigenetic Modifications in Response to HS

Chromatin remodeling, DNA and histone methylation, RNA-mediated DNA methylation, and post-translational modifications—acetylation, methylation, phosphorylation, SUMOylation, ubiquitination, and ribosylation—all play a role in plant survival during HS by regulating HS-responsive gene expression [217–219] (Figure 4). Plants respond to temperature changes, and even minor changes can cause morphological responses associated with flowering. The histone variant H2A.Z has been proposed to act as a molecular enabler of the thermoresponsive flowering pathway in *Arabidopsis* [220]. Alternatively, in *B. rapa*, delayed-flowering, observed under high-temperature treatment, was associated with reduced *BraA.FT.a* mRNA expression. Also, high levels of H2A.Z occupied the *BraA.FT.a* locus, which affected chromatin conformation and hindered its accessibility [68]. This implies that thermosensory pathways behave differently in different crops in order to change flowering time regulators. *Heat shock transcription factor A1* (*HSFA1*), the transcriptional network's master regulator, is involved in the HS response and acts dynamically with H2A.Z histone [221]. As a result, HsfA1s are prime activators in the response to HS, whereas HSPs, such as HSP70 and HSP90, suppress these in normal conditions. *Dehydration-responsive element binding 2A* (*DREB2A*), *heat shock factor A2* (*HsfA2*), *HsfBs*, *DREB2C*, *multiprotein binding factor 1C* (*MBF1C*), and *NAC* are all regulated by these HSPs. At the cellular level, HSPs are involved in homeostasis and plant defense. At the onset of

HS, inactive HSFs are activated through oligomerization and shuttle signalling between the cytoplasm and the nucleus [222].

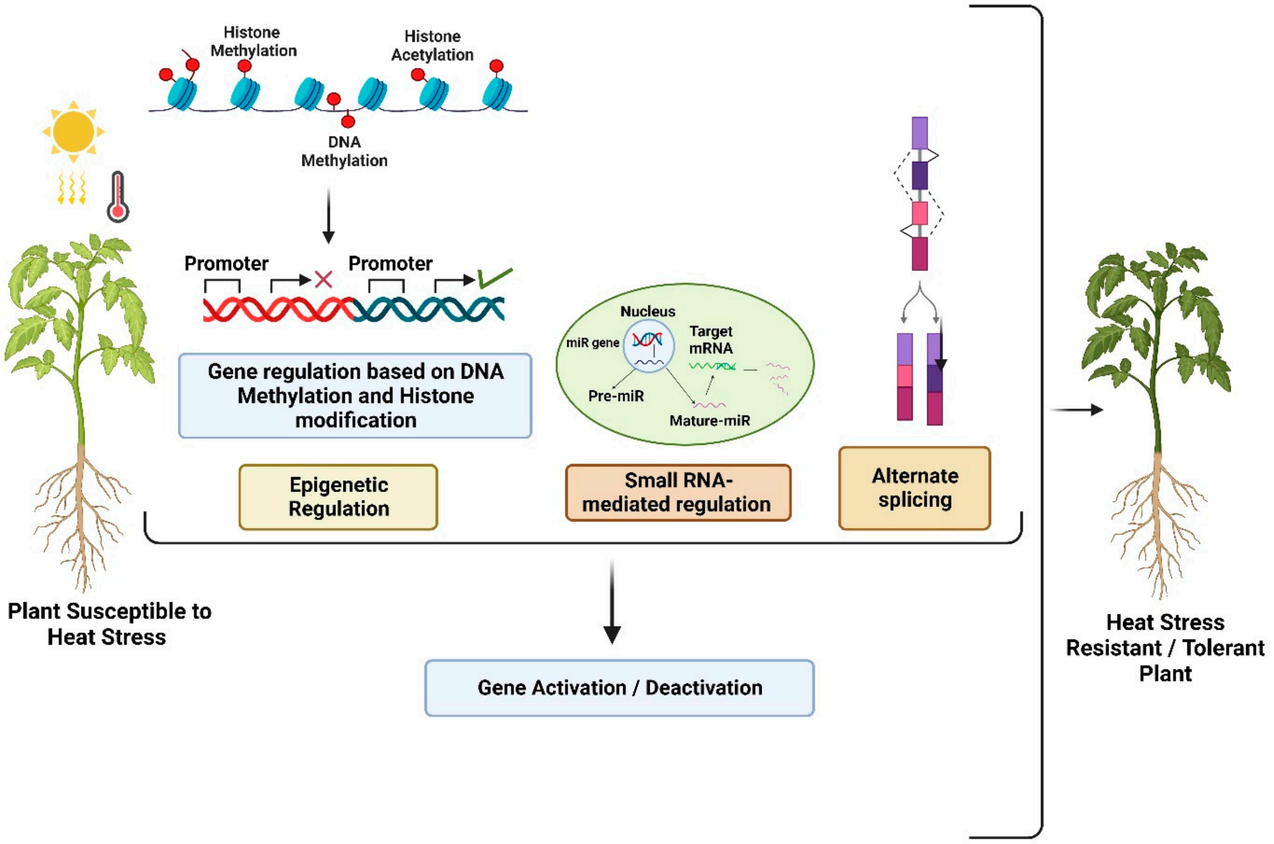

Figure 4. Epigenetic-, small RNA-, and alternative splicing-mediated regulation of heat tolerance.

A study found phenotypic variation in anthers and pollen during heat stress in the heat-sensitive and heat-tolerant cotton lines [223]. In comparison to a heat-sensitive line, the heat-tolerant cotton line had higher levels of genome-wide DNA methylation under HS [224]. These methylation differences have been associated with the differential expression of starch, auxin, and sugar metabolic pathway genes critical for pollen development. Further, to investigate how variation in DNA methylation between these two cotton lines affects their ability to tolerate HS, bisulphite-treated DNA sequencing on tissues from various stages of anther development was performed [225]. The heat-tolerant line was discovered to have an increased abundance of small RNAs, which correlates highly with increased methylation levels uniformly across all chromosomes. Furthermore, in response to heat treatment, more DNA methylation was observed in the heat-sensitive cultivar and more DNA demethylation in the heat-tolerant line in *B. napus* [226]. Furthermore, a significant change in the expression levels of DNA methyltransferase and demethylase enzymes in response to salt and HS have been reported, indicating that the methylation of some genes is required for plant response to abiotic stress [227]. Similarly, under heat stress, position and context-dependent methylation variations were observed in *B. rapa* [228]. More complex implications of DNA methylation on gene expression and stress tolerance have been discovered at the reproductive stages. During gametophytic development and pollen embryogenesis, in vitro-cultured *B. napus* microspores changed their gametophytic developmental pathway towards embryogenesis in response to HS via an epigenetic reprogramming control. This developmental change was linked to decreased global DNA methylation and cell proliferation activation [229]. Conversely, short-term heat shock treatment decreased DNA methylation in cultured microspores of *B. napus* [229]. Another *B. rapa* study found that 15 paralogous pairs of histone methyltransferase and demethylase genes showed significant variation in their expression profiles in response to heat and cold stress. The dynamic differences in gene expression between specific tissues and treatments suggest that these genes may play a role in stress tolerance mechanisms [230]. BAG7, an ER-resident TF, participates in heat and cold stress responses by acting as a co-chaperone and preventing the accumulation of unfolded proteins. BAG7 was sumoylated, released from the ER, and translocated to the nucleus under HS conditions, where it interacts with WRKY29 to regulate gene expression [231].

3.4. Alternative Splicing in Response to HS

Alternative splicing (AS) is an important control mechanism influencing signal-response mechanisms in different developmental stages under stress conditions, and HS has been reported to induce AS events in several genes, such as those related to protein folding [232] (Figure 4). A research group examined HS-induced AS in the pollen tissue of two tomato cultivars [233]. Under control conditions, transcripts with steady expression levels were obtained, and HS revealed a clear difference in the occurrence of specific isoforms (intron retention or exon skipping) with partially or completely missing functional domains. The latter demonstrates that post-transcriptional AS results in the synthesis of transcripts encoding alternative protein isoforms that may be required for HS response. For example, an ER-embedded sensor, Inositol Requiring Enzyme 1 (IRE1), acts as an RNA splicing factor to convert *bZIP60* mRNA into a form that lacks the transmembrane domain. The active bZIP60 TF protein translated from the spliced variant is transported to the nucleus and activates expression of stress-responsive genes [233]. Overexpression of the spliced form of *TabZIP60* (*TabZIP60s*) increased HS tolerance in *Arabidopsis* but not the unspliced form (*TabZIP60u*) [206]. In addition, combined heat and drought stress induced specific AS events in wheat, and 40% of differentially spliced genes overlapped with differentially expressed genes under HS and combined heat and drought conditions [234]. These findings indicate a close relationship between AS and transcriptional regulation in stress tolerance. Recently, *Arabidopsis NTC1-related protein 1* (*NTR1*) was shown to confer heat tolerance by regulating the alternative splicing of several HS-responsive genes, including HSFs and HSPs [235].

In *B. napus*, RNA-Seq analysis of plants treated with cold, heat, and drought stress exhibited A subgenome biases in gene expression and C subgenome biases in the extent of AS [236]. It has been demonstrated that polyploidy can lead to changes in transcriptome repertoire by influencing AS [237,238]. AS in HS was further investigated for the existence of splicing memory for achieving thermotolerance in *Arabidopsis* [239]. Heat-stressed plants were observed to accumulate unprocessed transcripts through splicing repression with intron retention that eventually reached normal levels during recovery. In the second heat exposure, primed plants responded differently from non–primed plants. Under normal conditions, primed plants remembered to undergo splicing and correctly process transcripts. As a result, primed plants retain a splicing memory that can carry out correct splicing and produce the necessary transcripts and proteins for plant growth and development after stress cessation, thus ensuring plant survival following another stress event [240]. More research is needed to determine whether splicing-linked stress memory can be passed down through generations or is limited to the somatic cells of an individual.

3.5. Non-Coding RNA-Mediated Regulation of HS

The role of non-coding RNAs in regulating reproductive-stage stress tolerance is an emerging area [241] (Figure 4). Both omics and single-gene-based studies are being carried out to dissect this area further. For example, small RNA and degradome sequencing have been used to examine the role of miRNAs in male sterility under high temperature stress in cotton [242]. Analyses of known and novel miRNAs and their target genes from anthers of insensitive and sensitive cotton cultivars suggested that miRNA-mediated auxin signalling is essential for cotton anther fertility under high-temperature stress. The maize *Dicer-like 5* (*Dcl5*) is responsible for 24-nt phased small interfering RNA (phasiRNA) biogenesis in meiotic anthers. The null mutants exhibit male sterility with complete loss of 24-nt phasiRNAs under high-temperature conditions, indicating that *Dcl5*-mediated generation of 24-nt phasiRNAs is critical for maintaining male fertility under HS conditions [243]. Five conserved miRNA families and four novel miRNA families were discovered to be HS responsive in *B. rapa* [244]. In *Arabidopsis* and rice, miR159-regulated *GAMYB-like* TF family function in flower development and gibberellin (GA) signalling [245]. *TamiR159*-overexpressing rice lines were more sensitive to HS than the wild type, implying that TamiR159 downregulation in wheat after HS may participate in a heat stress-related signaling pathway, contributing to HS tolerance [246]. In another study, miRNAs mediated thermotolerance in *Arabidopsis* by altering the expression of HSPs and improving seed germination and seedling survival under HS [247]. In plants, research on non-coding RNAs is still in its infancy, with only a few studies showing their role in plant development and adaptation to abiotic stress [248]. Several novel lncRNAs in *B. rapa* in response to heat treatment have been identified using RNA-seq [249]. Similarly, two up-regulated lncRNAs (*TalnRNA27* and *TalnRNA5*—miRNA precursors) were up-regulated in wheat in response to HS [250]. A systematic analysis of pollen development and fertilization in *B. rapa* revealed that 47 cis-acting lncRNAs and 451 trans-acting lncRNAs were highly co-expressed with their target genes [251]. Furthermore, a *B. rapa* coexpression network showed 210 DEGs, 4 miRNAs, and 33 lncRNAs under HS, implying their role in the heat response [252]. These findings suggest that lncRNAs in plants may add complexity to other stress response mechanisms during abiotic stress events. Because of its complexity and poorly understood mechanisms, a more in-depth understanding of these intricate epigenetic components would be a boon for gaining insights into the genomic regulation underlying HS-mediated responses in important crop species.

4. CRISPR-Based Strategies for Targeting TFs Associated with Heat Stress Tolerance

TFs are lucrative candidates for engineering heat tolerance in plants [27]. Advances in sequencing platforms have led to genome-wide identification and analysis of TF families in several plant species. Several dedicated databases have also been developed for TF-encoding genes that serve as valuable resources for candidate gene selection [253,254]. However, as TFs usually comprise large gene families in plants, a high level of redundancy among gene family members hinders shortlisting candidates for characterization and experimental validation. Integrating phylogenomic data with gene expression profiling has been demonstrated as an effective strategy to tackle this challenge [255].

Various forward and reverse genetics strategies have been used to characterize TFs associated with HS tolerance in the past. In forward genetics studies, large-scale mutants are developed and screened for enhanced HS tolerance. A gain-of-function, forward genetic screen in *Arabidopsis* identified *AtMYB68* as a key transcriptional activator responsible for productive seed set after severe HS during flowering [182]. Similarly, reverse genetics strategies using overexpression or knockdown/out strategies have been used for the functional characterization of candidate TF genes associated with heat stress tolerance (Table 1). For example, overexpression of the *BZR1* (*Brassinazole Resistant 1*) TF gene enhanced tomato heat tolerance [190]. Conversely, RNAi-mediated gene silencing of *OsMADS87* decreased the negative impact of HS on grain filling in rice [216]. However, although transgenic approaches have been widely used for functional characterization of genes in crop plants, large-scale cultivation of transgenic plants remains a significant challenge.

Recent technologies such as transcription activator-like nucleases (TALENs) [256], zinc-finger nucleases (ZFNs) [257], and CRISPR/Cas system [258] have completely and revolutionized plant biotechnology. While the first two technologies are more complex to implement, CRISPR/Cas-based editing approaches are at the core of the new age agricultural innovations, enabling efficient and precise trait generation and selection with the scope of commercialization [259–262]. So far, the CRISPR/cas-based knock-out strategy has been mainly employed to characterize TFs acting as positive thermotolerance regulators where knockout plants demonstrate higher heat sensitivity (Table 1). However, this technology can also be applied to negative regulators to obtain heat-tolerant plants (Figure 5). For example, CRISPR-mediated loss-of-function of a stearic acid desaturase gene, *PtSAD*, in *Pinellia ternata* led to enhanced thermotolerance [263]. Alternatively, CRIPSR-mediated activation (CRISPRa) of positive regulators can also be achieved by using a catalytically inactive Cas9, also known as dead Cas9 (dCas9) [264], where both the nuclease domains of Cas9 are mutated. Hence, only the RNA-guided DNA binding activity of Cas9 is retained, but its ability to cleave the DNA is lost. The dCas9 is fused with a transcriptional activator such as simplex Virus Protein (VP16) or Transcriptional Activator Domain (TAD) to enhance target gene expression. Several CRISPRa systems have been developed and evaluated in plants for target gene activation [265]. Similarly, repressors such as SRDX have been recruited to block RNA polymerase elongation, thereby blocking gene transcription known as CRISPR interference (CRISPRi) [266].

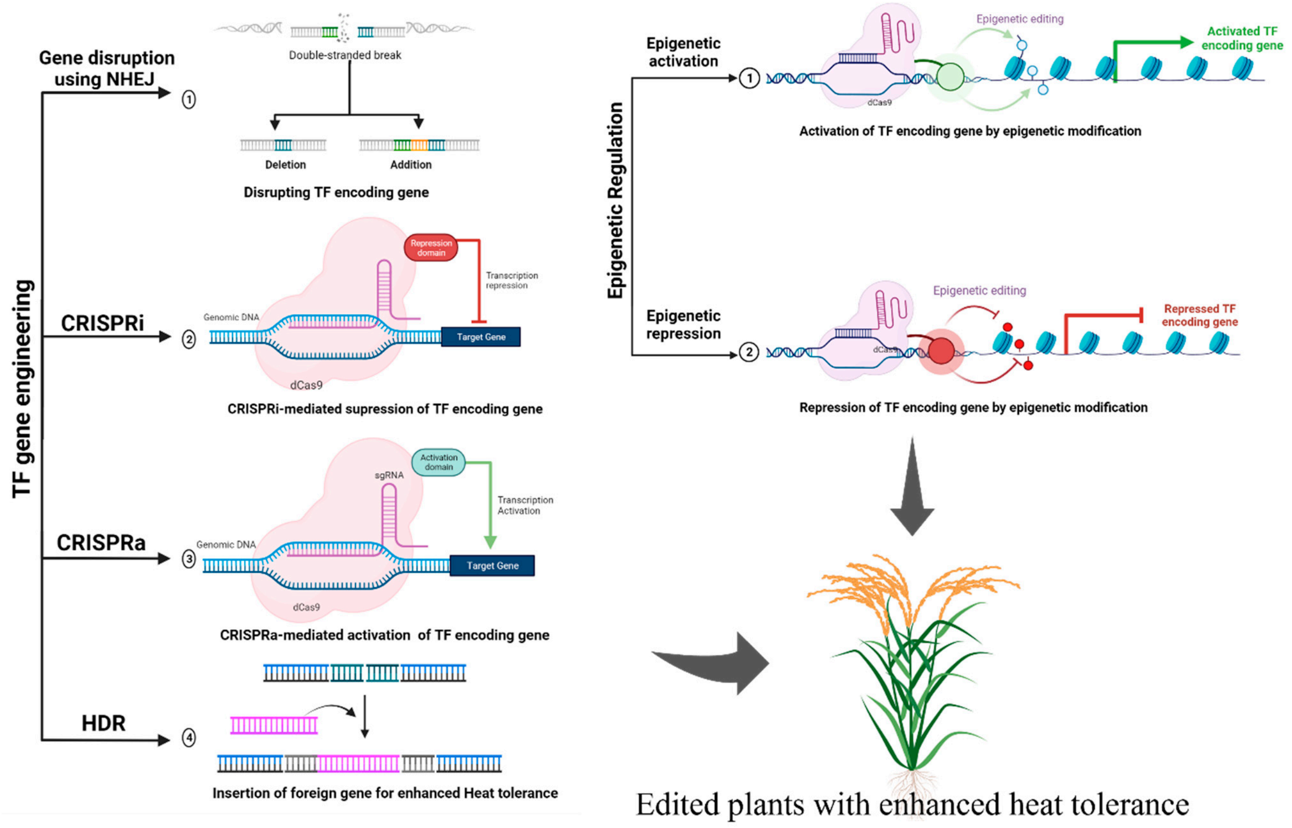

Figure 5. CRISPR-mediated strategies for engineering TF gene expression for enhanced heat tolerance.

Alternatively, homology-directed repair (HDR) can also be leveraged by providing the homologous sequence as a template for repair to insert foreign genes/promoters for enhanced stress tolerance [267] (Figure 5). Although not yet applied for engineering plant heat tolerance, HDR has successfully attempted to replace a native gene/promoter at specific loci in several plant species [268].

The involvement of epigenetic modifications in HS response has been established in plants [269]. HS significantly alters the 3D chromatin organization and interactions between promoters and regulatory elements [213]. The application of the CRISPR activation (CRISPRa) system for generating stress-tolerant plants through epigenetic modification has been demonstrated in *Arabidopsis* [270]. The authors generated chimeric $\text{dCas9}^{\text{HAT}}$ where dCas9 was fused with a catalytic core of *Arabidopsis* histone acetyltransferase that triggers histone acetylation and induces DNA relaxation in the targeted region. Transgenic plants expressing $\text{dCas9}^{\text{HAT}}$ targeting *AREB1* (ABA-responsive element binding protein 1) promoter region enhanced *AREB1* gene expression and drought tolerance [270]. DNA methylation is a particularly vital mechanism plants adopt to manage HS during male gametophyte development [271]. Therefore, CRISPR-mediated activation or repression through epigenetic modifications can be implemented to engineer reproductive stage HS tolerance (Figure 5).

Another prospective approach would be promoter engineering, where CRISPR technology can also incorporate a specific DNA element in the regulatory region for enhanced or decreased transcriptional activity of the target gene (Figure 6). This is facilitated by prime editing that utilizes nicking Cas9 (nCas9), where one of the nuclease domains has been inactivated through point mutation [272]. Unlike Cas9, which creates double-stranded breaks repaired through NHEJ, nCas9 induces single-stranded breaks and promotes homologous recombination [273]. For prime editing, nCas9 is linked to an engineered reverse transcriptase and a prime editing gRNA (pegRNA), specifying the target site and the anticipated editing region [274]. Recently, this strategy has been used to generate disease-resistant rice plants by inserting an effector binding element in the promoter region of a dysfunctional executor gene, *xa23* [275]. Similar strategies can be deployed to incorporate enhancer or suppressor elements into the regulatory regions of TF genes associated with heat tolerance.

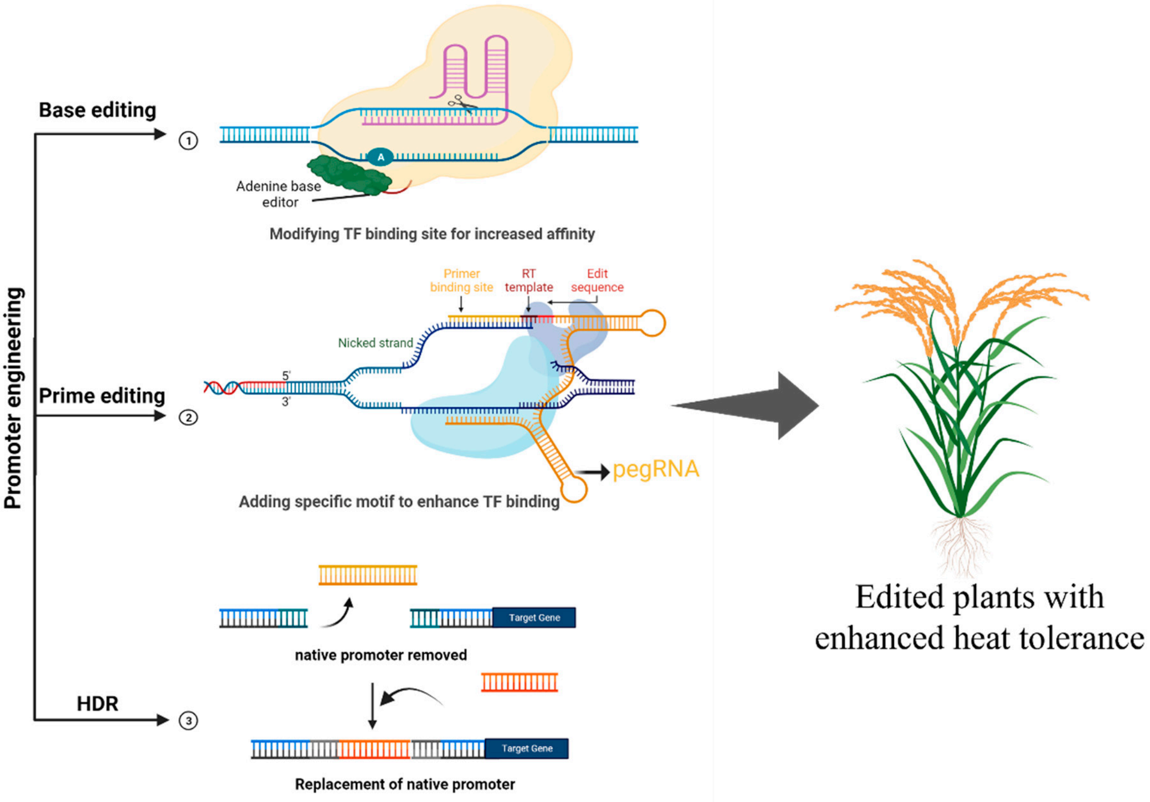

Figure 6. CRISPR-mediated engineering of promoter regions of target TF genes or their targets for enhanced heat tolerance.

Similarly, dCas9 fused with the deaminase enzyme can facilitate C to T or G to A substitution. CRISPR/Cas9-derived Cytidine base editor (CBE) was recently demonstrated to direct a C-to-T base conversion in the *acetolactate synthase* (*ALS*) gene in tomato and potato [276].

Alternatively, HDR can be used to replace the native promoter with a more potent promoter to achieve the desired level of expression of the target gene. Shi and coworkers demonstrated the use of CRISPR-mediated HDR by replacing the native promoter of *ARGO8* (*1-aminocyclopropane-1-carboxylic acid synthase6*) gene of maize with *GOS2* promoter that derives moderately constitutive expression [277]. The ubiquitous expression of *ARGOS8* driven by *GOS2* promoter led to enhanced grain yield under drought conditions. A similar approach can also provide tissue-specific, chemical, light, and hormone-responsive gene expression [278].

5. Conclusions, Challenges, and Future Directions

As climate change intensifies, HS is a major threat to global food security. The yield reduction depends on the plant developmental stage in which HS occurs as well as the frequency, duration, and intensity of HS. Among the developmental stages, the reproductive stages are most sensitive to HS, severely affecting crop yields. To enhance crop HS tolerance, an in-depth understanding is needed of how HS affects different stages of reproduction, including floral meristem development, floral initiation, flowering, male and female gametogenesis, fertilization, seed filling, and seed maturity. In particular, research should identify molecular mechanisms that allow the crops to sense high temperatures and induce thermoresponsive flowering (e.g., early morning flowering to avoid HS during mid-day).

Comparative omics analyses targeting specific reproductive stages would pave the way to unearth essential candidate genes or proteins underpinning heat tolerance at the reproductive stage. Further, studies unraveling the role of non-coding RNAs [279], RNA folding [280] and epigenetics [281] in HS response are pivotal in understanding the events underlying response to HS during sexual reproduction. The proposed thermotolerance mechanisms, such as post-translational modifications, transcription factors regulating flowering, hormonal regulations, heat shock factors (HSFs), heat shock proteins (HSPs), and increased reactive oxygen species (ROS) scavenging ability specific to the reproductive stage will provide better tools for breeders and molecular biologist to develop heat-stress-resilient crops with enhanced crop productivity.

With the increase in night temperatures, there is an emerging interest in investigating the impact of high night temperature stress on plant development and crop productivity in cereals [282–284]. However, to date, our knowledge of the impacts of high night temperatures on reproductive biology is limited, and this topic warrants further research.

As our understanding of TFs and the HS response grows, we expect to see even more innovative and practical approaches to engineering heat tolerance. Crops suffer tissue culture and transformation limitations, which can, fortunately, be overcome by using improved *Agrobacterium*-mediated transformation methods [285] or using innovative approaches to plant transformation and editing [286,287].

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