

Review Article

Response and tolerance mechanism of food crops under high temperature stress: a review

Mecanismo de resposta e tolerância de culturas alimentares sob estresse de alta temperatura: uma revisão

S. Han^a , S. Jiang^{b*}, R. Xiong^a, K. Shafique^c, K. R. Zahid^d and Y. Wang^{a*} 

^aLiupanshui Normal University, School of Biological Sciences and Technology, Liupanshui, China

^bZhengzhou Normal University, Bioengineering Research Center, Zhengzhou, Henan, P.R. China

^cGovernment Sadiq College Women University, Department of Botany, Bahawalpur, Pakistan

^dShenzhen University, Carson International Cancer Center, College of Life Sciences and Oceanography, Shenzhen Key Laboratory of Microbial Genetic Engineering, Shenzhen, Guangdong, China

Abstract

High temperature stress events are critical factors inhibiting crop yield. Meanwhile, world population is growing very rapidly and will be reached up to 9 billion by 2050. To feed increasing world population, it is challenging task to increase about 70% global food productions. Food crops have significant contribution toward global food demand and food security. However, consequences from increasing heat stress events are demolishing their abilities to survive and sustain yield when subjected to extreme high temperature stress. Therefore, there is dire need to better understand response and tolerance mechanism of food crops following exposure to heat stress. Here, we aimed to provide recent update on impact of high temperature stress on crop yield of food crops, pollination, pollinators, and novel strategies for improving tolerance of food crop under high temperature stress. Importantly, development of heat-resistant transgenic food crops can grant food security through transformation of superior genes into current germplasm, which are associated with various signaling pathways as well as epigenetic regulation in response to extreme high temperature stress.

Keywords: high temperature stress, food security, chromatin remodeling, epigenetic, pollen infertility.

Resumo

Eventos de estresse de alta temperatura são fatores críticos que inibem o rendimento das culturas. Enquanto isso, a população mundial está crescendo muito rapidamente e atingirá até 9 bilhões em 2050. Para alimentar a crescente população mundial, é uma tarefa desafiadora aumentar cerca de 70% da produção global de alimentos. As culturas alimentares têm uma contribuição significativa para a procura global de alimentos e a segurança alimentar. No entanto, as consequências do aumento de eventos de estresse por calor estão destruindo suas habilidades de sobreviver e manter a produção quando submetidos a estresse de alta temperatura. Portanto, há uma necessidade urgente de entender melhor o mecanismo de resposta e tolerância das safras de alimentos após a exposição ao estresse por calor. Aqui, nosso objetivo foi fornecer atualizações recentes sobre o impacto do estresse de alta temperatura no rendimento de culturas de alimentos, polinização, polinizadores e novas estratégias para melhorar a tolerância de culturas de alimentos sob estresse de alta temperatura. É importante ressaltar que o desenvolvimento de culturas alimentares transgênicas resistentes ao calor pode garantir segurança alimentar por meio da transformação de genes superiores em germoplasma atual, que estão associados a várias vias de sinalização, bem como à regulação epigenética em resposta ao estresse de alta temperatura extrema.

Palavras-chave: estresse de alta temperatura, comida segura, remodelação da cromatina, epigenética, infertilidade de pólen.

1. Introduction

Rapid climatic changes have increased the magnitude of extreme weather such as precipitation, high temperatures, and drought stress in agricultural regions (Boyer et al., 2013; Lesk et al., 2016). Planet's climate became warm by about 0.6 °C during 1910 and 1945 and it has become

warmer from 1976 onwards as compared to previous 1000 years (Pachauri et al., 2014). According to the IPCC 5th assessment report global average temperature was increased 0.85 °C from 1880–2012 (Pachauri and Meyer, 2014). Recently, the IPCC has anticipated that average

*e-mail: 1211817475@qq.com; 76759258@qq.com

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global temperature will be increased up to 3-6 °C by 2100 (Masson-Delmotte et al., 2018). Recent evidences show that increased climate impacts is because of anthropogenic emission of carbon dioxide and leads to global warming (IPCC, 2013; King et al., 2015).

It has been projected that world population will be exceed above 9 billion by 2050. In order to feed the 9 billion population, about 70% increment in global food production is required (Stratonovitch and Semenov, 2015). Extreme temperature will affect the goal of the target of achieving of 70% global food production for the 9 billion of world population by 2050. Growing evidences show that climate changes have caused significant crop yield losses and also damaged to food security. Various abiotic stresses including high temperature stress and drought have reduced productivity of various field crops over the years (Boyer et al., 2013). Climate changes have also damaged to food production in poor countries (Oseni and Masarirambi, 2011). There is no doubt that agricultural production has been continuously affected owing to climate changes and the average yield of field crops will depend on the regional differences in both the natural and anthropogenic factors that control crops responses (Rustad, 2008; Wei et al., 2014).

Above 200,000 plant species are present on the earth, among them approximately 80,000 plants species are edible to humans. In spite of wide range of plant species, about 95% protein intake and calories of livestock and human have been obtained from only 20 to 25 plant species (Fuleky, 2009). Among major cereal crops, rice, maize, and wheat play central role in food demand across the globe (Hussain et al., 2019; Impa et al., 2021; Tack et al., 2015). However, climate changes have caused yield losses of these three plants species such as wheat, rice, and maize which supply 70% of total grain production worldwide (Iizumi et al., 2013; Liu et al., 2016a; Lobell et al., 2014). Nearly, 820 million population (or 11% of the current global population) are undernourished in terms of food intake, and 1.3 billion people are suffering from micronutrient deficiencies (WHO, 2019). Most of them are living in Sub-Saharan Africa and Asia. However, increment of 3 °C to 4 °C temperatures causes 15 to 35% crop yield losses in Asia and Africa whereas 25-35% in Middle East (Ortiz et al., 2008). There are several review articles which raised general question of how to meet food demand of rising world population in future (Grote, 2014; Le Mouël and Forslund, 2017). Nevertheless, only few articles have been devoted to key role of staple food crops including maize and wheat (Shiferaw et al., 2013; Tadesse et al., 2019). Here, we aimed to provide recent update on impact of high temperature stress on crop yield of food crops, pollination, pollinators, and novel strategies for improving tolerance of food crop under high temperature stress.

2. Review Writing Strategy

To recapitulate and compile the desired literature related to response and tolerance mechanism of food crops, we conducted a literature search by using PubMed, Google, ScienceDirect, and Google Scholar Databases. Moreover, other information was also searched from reliable sources such as IPCC. Keywords used for literature

search included High temperature stress, Food Security, pollination, pollinators, transcriptional factors, noncoding RNAs, Phytohormones, reactive oxygen species, heat shock proteins, chromatin remodeling, epigenetic, synthetic biology, and genome editing.

3. Climate Change Limits Crop Yield

Each year, extreme abiotic stress conditions including heat and drought affect crops productivity across the globe (Devireddy et al., 2021). The effects of these stresses are becoming alarming recent years and pose serious threat for food security across the globe (Degife et al., 2021; Raza et al., 2019). It has been predicted that we should increase crop yield about 25-70% by 2050 without putting pressure on the ecosystem functioning (Hunter et al., 2017; Wang et al., 2019). The largest decline in yields of cereal crops, including rice and wheat has also been observed in South Asia. If current rate of warming remains unchanged, wheat yield will be decreased nearly 50% by 2050. Nearly, 60% decline will be in India and Bangladesh followed by Pakistan at 27%. Rice yield will be decreased 40% in India, followed by Bhutan at 4%, Bangladesh at 10%, and Nepal at 32%. Additionally, yield of sugarcane and maize will also reduced because of global warming. This is disquieting situation for the South Asia and global community. South Asia is not only second leading producer of wheat and rice across the globe, after China, but also the largest consumer of cereal crops. However, India is the second largest and Pakistan the eight largest countries growing wheat worldwide, India and Pakistan are the second largest and fifth largest consumer of wheat. Likewise, India has been reported second largest and Bangladesh the fourth largest rice consuming countries across the globe. Therefore, declining only rice and wheat production in South Asia can, thus, destabilize the world food market and will pose serious threat to global food security (Rasul, 2021).

Given importance to agriculture sector-based economies of these countries, this also reveals that South Asia will experience massive economic losses due to extreme climatic changes. A decline in crops productivity due to extreme heat and drought stress is also a serious threat for agriculture sector (Zandalinas et al., 2018). Importantly, high temperature stress during reproductive stage causes huge loss of crop yield. High temperature stress during pre-anthesis mediates floret infertility which translates to decline seed number (Bheemanahalli et al., 2019; Kumar et al., 2017a). This consequence can't be rescued and might result in an irreversible loss of crop productivity (Liu et al., 2019). Furthermore, a recent study suggests that only drought causes nearly 75% reduction of all the globally harvested areas of wheat, soybeans, rice, and maize, between 1983-2009 (Kim et al., 2019). In next section, we will discuss effect of high temperature stress on plants pollination because crop productivity is strongly linked with successful pollination.

3.1. Effect of high temperature stress on plants pollination

Plants are sessile and unable to face harsh effects of high temperature exposure that are increasing in period and rate duration because of recent climate change

conditions. Although heat wave affects all the plants' growth stages, while plants' reproductive stages remain the most susceptible stages of the life cycle. This susceptibility during reproductive stage contributes to huge reduction in both the seed set and crops production (Hein et al., 2021; Jagadish et al., 2021). It has been reported that reproductive stage of various food crops including soybean (Zhao et al., 2017a), wheat (Liu et al., 2016b), maize (Liu et al., 2020), rice (Zhang et al., 2018) and cotton (Masoomi-Aladizgeh et al., 2021) is extremely sensitive to heat stress (Figure 1). Extreme high temperature stress leads to pollen abortion, thereby leading to failed pollination (Lohani et al., 2020a, b). Successful reproduction mainly relies on the interaction between pollen and pistil and as well as viability of the pistil and pollen following extreme heat stress. Both the pollen and pistil are very sensitive to high temperature stress (Masoomi-Aladizgeh et al., 2020; Wang et al., 2021b), however, available studies mainly focus on impact of heat wave on the pollen development. Nonetheless, recent data focuses on the sensitivity of female reproductive organ to heat stress in various crops such as wheat, maize, rice, sorghum, and tomato (Gonzalo et al., 2020; Jagadish, 2020; Lohani et al., 2020b). These novel findings demonstrate a substantial variation in response of pistil against high temperature stress across various crops. The pistil is comprised of stigma, style, and ovary. Both stigma and style are engaged in triggering, promoting, and guiding pollen tube growth toward female gametes within ovule. High temperature stress disrupts interaction between pollen and pistil and fertilization, thereby leading to reduction in both seed set and crop yield. High temperature stress during pollen tetrad and binucleate stages results in severe pollen damage despite of elevated sugar level, suggesting molecular mechanisms beyond carbohydrate supply as major for the pollen sterility (Masoomi-Aladizgeh et al., 2021). Further, high temperature stress during the development of pollen tube shows downregulation of

membrane transporters (Poidevin et al., 2020). Besides membrane transporters, existence of ribosomes on the noncoding RNAs has been proposed a key regulatory aspect of plants fertilization, which points out function of alternative players in both the pollen development and tube growth, apart from sugars (Masoomi-Aladizgeh et al., 2021; Poidevin et al., 2020). Even though sugar furnish is not major mechanism contributing to sterility of pollen grains in cotton (Masoomi-Aladizgeh et al., 2021), however, beans (Santiago et al., 2021) and several other plant species depend on the availability of sugar to sustain viability of pollen grains (Ferguson et al., 2021).

3.2. Impact of high temperature stress on population of pollinators

In this section, we will discuss about effect of high temperature stress on population of pollinators because successful plants pollination depend on the population of the pollinators.

Wild and managed pollinators provide huge benefits to society through contributing to food demand. Currently, climatic changes have been proved a serious threat to pollinators. A well-documented decline has been observed in both the wild and managed pollinators in various regions across the globe (Potts et al., 2016a). Accumulating evidences suggest that climate change extremely affects food production of the flowering crop species through reducing population of the pollinating insects and disturbing their regional distributions (Abrol, 2012; Hegland et al., 2009; Memmott et al., 2007; Potts et al., 2016b). Global warming affects flowering time of plants and causes plant communities to migrate poleward, and this shifting results in mismatches between mutualistic plants-pollinators pairs (Parmesan and Yohe, 2003), thereby disrupting interaction and functionality of the ecosystem. In addition, reduced overlap between plants flowering time and pollinator emergence reduces diet breadth for pollinators, thereby resulting in reduction of pollinators' population and enhanced death of both pollinators and plants.

Finally, elevated CO₂ level also changes nutritional worth of major forages for pollinator species, indecisive outcomes for health of pollinators. Since 1842, one-third reduction has been found in goldenrod pollen protein content, the late-blooming plants that play key nutritional role for the overwintering of pollinators (Ziska et al., 2016). Chamber-based experiments show additional pollinators declines with enhanced atmospheric CO₂ levels (Ziska et al., 2016). A modeling-based study has shown that global declines in pollinators will increase child birth defects and mortality from increased folate and vitamin A deficiency, respectively, and also enhance risk of diabetes, stroke, heart disease, and tumors in adults due to decreased dietary intake vegetables, fruits, seeds, and nuts (Smith et al., 2015).

3.3. Tolerance mechanism of plants during heat stress

To cope with extreme high temperature stress, plants have evolved various and interconnected signaling pathways such as, transcriptional factors (TFs), microRNAs (miRNAs), long noncoding RNAs (lncRNAs) phytohormones,

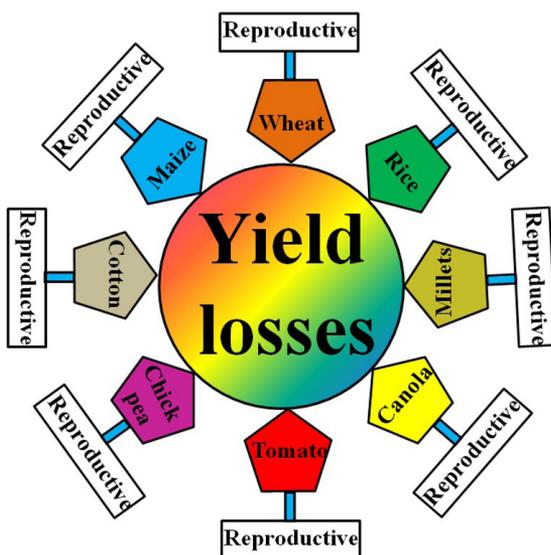


Figure 1. Schematic representation of most sensitive phase of various crops during high temperature stress.

reactive oxygen species (ROS), heat shock proteins (HSPs) and epigenetics etc, resulting in diverse response so as to confer heat tolerance (Figure 2).

3.4. Role of transcriptional factors in response to high temperature stress

Since last decade, huge success has been made in exploring potential role of transcriptional factors (TFs) in response to environmental stresses in various cereal crops. Transcriptional factors (TFs) play critical roles at transcriptional levels either activating or suppressing genes during high temperature stress. Nearly 7% coding knock of the vascular plants genome is associated with transcriptional factors for regulating target genes at transcriptional level (Rushton et al., 2008). To date, scientists have identified thousands of TFs in plants, however, major TF families (AP2/ERF, HSFs, MYB, WRKY, NAC, etc), mediated through signal transduction pathways, recently been utilized to cope with heat stress in various food crops (Guo et al., 2020; Li et al., 2021; Xiang et al., 2021).

In wheat, TaWRKY008, TaWRKY122, and WRKY45 are engaged in drought and high temperature stress responses (Gupta et al., 2019). In wheat, overexpression of TaWRKY2 increases grain yield and drought tolerance. Overexpression of Arabidopsis based AtWRKY2 in transgenic wheat has resulted in increase of relative water content, soluble sugar, and activities of antioxidant enzymes to improve drought stress (Baillio et al., 2019; Wang et al., 2021a). In addition, six MYB TFs associated with high temperature stress have also been identified out of TaMYB80 is more effective during high temperature stress in transgenic Arabidopsis (Zhao et al., 2017b). In rice, overexpression of OsMYB1 gene has been proved effective in enhancing tolerance against high temperature stress (Deeba et al., 2017). In maize, OsMYB55 enhances tolerance against heat stress (Casaretto et al., 2016).

Recently, many novel and smart breeding approaches such as genome editing have been used to develop climate resilient crops by utilizing right TFs. For instance, AtMYB14 and AtMYB15 negatively regulate abiotic stress tolerance in Arabidopsis. This shows that both the AtMYB14 and AtMYB15 participate in the activation of those genes that induce sensitivity in plants against abiotic stress conditions. Hence, if we can manipulate these TFs then they couldn't regulate their respective genes

associated with sensitivity. Finally, plants can develop tolerance against specific abiotic stress because TF which was associated with proliferation of abiotic stress has been manipulated now. Similarly, we can find similar proteins in crop species using system biology and can be targeted via genome editing approach to manipulate their negative function in food crops.

3.5. Role of miRNAs in plants during heat stress

MicroRNAs (miRNAs) are about 20-24 nucleotide long noncoding endogenous regulatory RNAs that regulate expression and accumulation of target mRNAs. They are capable of modulating stress response (Zhao et al., 2016) and regulatory pathways (Curaba et al., 2014). Various evidences have been collected from miRNA-based studies in both cereal and major crops, including wheat, maize, rice, sorghum, cotton, and sunflower during abiotic stress conditions, thereby suggesting their potential role in regulating stress response in different plant species (Basso et al., 2019; Sun et al., 2019; Zhang, 2015). Under extreme heat stress, plants miRNAs have potential of improving its heat tolerance by regulating growth transition, flowering time, and floral organ development (Zhao et al., 2016). For instance, miRNA-156/157 has been emerged as a critical regulator of both flower development and male fertility during high temperature stress (Liu et al., 2017b; Wang et al., 2016; Xing et al., 2010).

In tomato, nearly 69 miRNAs have been reported in small RNA libraries of the stamen following high temperature stress (Pan et al., 2017). In rice, 8 target genes were corresponded to 26 heat-responsive miRNAs from panicle of heat-sensitive and heat-tolerant varieties through integrated sRNA sequencing with QTL mapping. Functional studies demonstrated that miR169r-5p was associated with heat tolerance in rice during flowering stage (Liu et al., 2017b). In cotton, 28 differentially expressed miRNAs have been identified from anthers of heat-sensitive and heat-tolerant varieties under heat stress (Chen et al., 2020; Ding et al., 2017). In cotton, miRNA-157 and miRNA-160 regulate auxin signaling pathway when anther is subjected to high temperature stress, to rescue male fertility (Ding et al., 2017).

To gain insights into identifying targeted miRNAs involved in stress response, we should confirm whether miRNAs abundance is changed during high temperature stress. Pegler et al. (2019) performed RNA-seq to identify miRNAs abundances in Arabidopsis following drought and heat stress. This novel approach have detected numerous miRNAs with elevated expression following drought and heat stress, hence identifying potential miRNAs that can be strong contenders for playing crucial roles under these stress conditions. This study provides a fundamental resource to identify stress-responsive miRNAs in major crops. In another study, López-Galiano et al. (2019) examined change in abundance of miR-159 in tomato under drought stress, where authors identified miR-159 was downregulated under stress, whereas mRNA level of its target gene was derepressed. These novel studies signify foundation of exploration of how miRNAs respond to different stresses and how they can

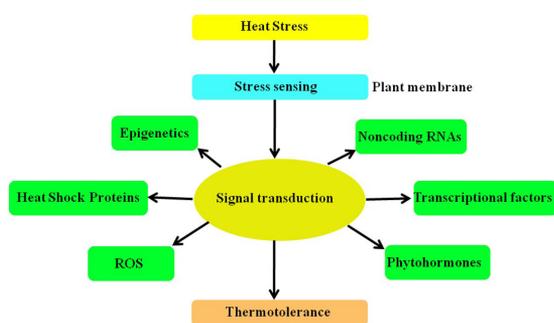


Figure 2. Schematic representation of tolerance mechanism of plants during heat stress.

be used in the development of heat stress tolerant crops. Given significance to central role of miRNAs in plants growth and development by targeting various regulatory genes, and their key role during stress response, their manipulation can alter agronomic traits. Zhang et al. (2019b) has provided overview on several gene silencing pathways and core apparatus in maize, and their roles in maize biology, describing the traits that miRNAs regulate and their use in controlling plant architecture, fertility, and heat stress response. This overview has disclosed the potential application of miRNAs in just maize. Based on deep knowledge on biology of plants miRNAs in the model crop species, future trail of this approach might be applied in major crops, while understanding their potential functions and applying this knowledge can improve various important traits in response to high temperature stress.

3.6. Role of long noncoding RNAs in plants during heat stress

Long noncoding RNAs (lncRNAs) are molecules of > 200 nucleotide and lack discernible coding potential (Palazzo and Koonin, 2020; Rai et al., 2019). In plants, lncRNAs regulate different biological processes, including growth and development, sexual reproduction, and also drought and heat stress responses (Csorba et al., 2014; Liu et al., 2017a; Song et al., 2021). Long noncoding RNAs affect all the elements of the genes such as promoters, untranslated regions, introns, exons, and terminators, regulating gene expression at various levels such as transcription, chromatin remodeling, splicing and translation (Wierzbicki et al., 2021). A growing body of evidences suggests that lncRNAs can modulate drought responses through regulating stress-responsive genes transcription, chromatin remodeling, and antisense transcription-mediated modulation (Jha et al., 2020). Previously, genome-wide transcriptome analysis identified drought and heat stress-responsive lncRNAs in various food crops, including rice (Chung et al., 2016), maize (Pang et al., 2019; Zhang et al., 2014), soybean (Bhatia et al., 2020), wheat (Xin et al., 2011).

Moreover, lncRNAs regulate several drought-responsive regulatory genes participating in ABA and ethylene signaling, calcium signaling, and different metabolic processes in rice (Weidong et al., 2020). In recent years, key role of various abiotic stress-responsive genes and lncRNAs has been widely studied in plants. Huge efforts have been made in designing new bioinformatics tools for the identification of novel genes against abiotic stresses. A wide-ranging and better understanding of mode of actions of the lncRNAs, their diverse regulation patterns, unearthing of the target genes, and lncRNAs-mediated gene regulation is essential for food crops. We must focus on using advanced synthetic biology and genetic engineering tools to develop and effective approach for developing heat stress-tolerant food crops as well as other important crops.

3.7. Role of phytohormones in response to high temperatures stress

Phytohormones regulate different biological events occurred during plants' life cycle. A variety of

phytohormones such as abscisic acid, jasmonic acid, salicylic acid, and ethylene play critical roles in plants growth and heat stress responses (Zhao et al., 2021a). Abscisic acid (ABA) has been reported as a key regulator of plants growth and development and also plants stress responses. Generally, ABA controls plants growth and development to coordinate plants adaption to high temperature stress (Suzuki et al., 2016). Moreover, ABA participates in the developmental process of anther and pollen (Dai et al., 2018; Kovaleva et al., 2018). In rice, exogenous ABA application prevents pollen sterility by mediating sugar metabolism under high temperature stress (Rezaul et al., 2019). Salicylic acid (SA) also plays central role in protecting plants against extreme heat stress. In tomato, SA prevents damage caused by high temperature stress and modulates activities of various antioxidant enzymes such as peroxidase (POD), superoxide dismutase (SOD), and catalase (CAT). In addition, exogenous application of SA increases tolerance of tomato plants against heat stress by enhancing photosynthesis efficiency and scavenging reactive oxygen species (ROS) by inducing antioxidants (Jahan et al., 2019). In rice, SA exogenous application reverses pollen abortion through scavenging of ROS under high temperature stress (Feng et al., 2018). In chickpea, SA and ABA exogenous application activate zeaxanthin pigment cycle prior to flowering, which showed positive response to different physiological processes such photosynthesis and related pigments, thereby leading to less high temperature susceptibility index (Kumar et al., 2020).

Cytokinin also plays crucial role in plants growth and development and also high temperature and drought stress responses (Cortleven et al., 2019; Pavlů et al., 2018). It has great potential for developing more resilient plants for high yields (Berka et al., 2020). Recently, novel transgenic barley lines have been developed by regulating cytokinin content for higher yield and enhanced drought resilience (Holubová et al., 2018; Ramireddy et al., 2018). We foresee that Phytohormones-related mechanisms should be explored in recent crop breeding programs against heat stress tolerance, both from a basic research and application outlook. Certainly, transgenic Phytohormones-modifications are currently being implemented in various crop species due to their strong effect on high yield. A better understanding of the Phytohormones-mediated regulation of metabolic pathways and heat-responsive genes and identification of novel genes under Phytohormones treatment may improve essential knowledge of the plants hormonal biology, permitting both the selection and in planta characterization of novel regulators for plants heat stress adaption.

3.8. Role of ROS signaling in plants heat stress response

The hormonal and ROS signaling are snugly synchronized for regulating growth and development of the plants. In this section, we will discuss about ROS signaling in plants during heat stress conditions. Plants being sessile organisms have equipped with arsenal adaptive strategies to cope with harsh environmental conditions including high temperature stress (Bulgari et al., 2019; He et al., 2018). The key strategy includes induction of the systemic

signals from an area under stress to an unstressed region that consequently activates defense or enhances resilience (Kumar et al., 2017b), arising from signal transducers, including Reactive Oxygen Species (ROS) (Tsaniklidis et al., 2020). The overproduction of ROS than scavenging abilities of antioxidants can result in an oxidative burst within plant cells (Mullineaux and Baker, 2010). For example, overproduction of ROS is accompanied with reduced ROS scavenging capacities of the antioxidants in the pistil of pearl millet as compared to pollen, and led to sensitivity of pistil to high temperature stress (Djanaguiraman et al., 2018). Besides oxidative damage, the critical role of ROS has been well documented during signal transduction that promotes tolerance against high temperature stress (Medina et al., 2021). ROS signaling arbitrates the transcription of various genes which are involved in plant growth and development, as well as protects plants against high temperature stress (Dvorak et al., 2020). ROS act as double-edge sword that stimulates oxidative stress in plants when their production surpasses threshold levels, but low concentration mediates signal transduction that assists retaining cellular homeostasis and improves plants acclimatization abiotic stress conditions. To keep balance between ROS production and their quenching, plants engage antioxidant machinery. However, their capacities diminish during extreme stress conditions. Devising tools that could prevent the damaging aspects of ROS by manipulating genes or signaling pathways involved in ROS overproduction during heat stress conditions improving plants' heat-tolerance mechanisms may unlock avenues for developing new generation high temperature stress-resilient crops.

3.9. Role of heat shock protein

To survive under high temperature stress, plants need to sense a slight increment in temperature to launch an appropriate genetic program. To this end, heat shock proteins (HSPs) play critical role in sensing and initiating heat shock response in plants during high temperature stress. Heat shock response is triggered by HSPs which are accumulated swiftly under temperature increment to reduce expected damage (Serrano et al., 2019). Both the proteome and transcriptome-based studies reported HSPs-mediated regulatory response in plants during high temperature stress (Guihur et al., 2021; Zhao et al., 2021b). With serious concern about high temperature stress, many scientists have utilized HSPs to develop heat-tolerant crops (Chauhan et al., 2012; Song et al., 2014). When plants are exposed to high temperature stress as a result HSPs and heat shock transcription factors (HSFs) genes are induced. The HSFs swiftly induce HSPs, hence, both HSPs and HSFs play crucial role in inducing thermotolerance in plants during high temperature stress (Ohama et al., 2017; Ren et al., 2019). In rice, OsHSP18 plays a key role in improving tolerance against heat stress (Kuang et al., 2017). Similarly, HSP70, HSP90, and HSP100 are upregulated in barley following heat stress exposure during reproduction stage (Chaudhary et al., 2019). Moreover, GhHSP70-26 overexpression in tobacco, while GhHSP70-26 silencing in cotton improves tolerance

against drought stress (Ni et al., 2021). Taken together, these evidences suggest that HSPs play important role in heat stress response and overexpression of novel HSPs in food crops can improve their resistance against heat and drought stress conditions.

3.10. Epigenetic changes in plants to heat stress response

Epigenetics is defined as changes in gene expression owing to DNA methylation and post-translational modifications to histones without changing DNA sequence (Agarwal et al., 2020). Transcriptomic activity of organisms is influenced by epigenetic regulation. Reprogramming by epigenetic changes triggered by several environmental challenges contributes to phenotypic diversity and defense against these challenges. Various environmental stresses are involved in changing genes expression levels by different mechanisms namely histone modification and DNA methylation. Since last two decades, epigenetics branch is continuously progressing. Improvement of crops by using traditional breeding approach is expensive, time consuming, tedious, and unable to meet progressive living standards and global demand, while epigenetics have shown great potential for improvement of crops with respect to nutritional quality and yield by creating novel epialleles (Saraswat et al., 2017). DNA is modified by methylation in response to environmental stresses. However, gene expression can be maintained by keeping balance of methylation and demethylation at the target promoters. Modification in this equilibrium affects stress response either positively (Downen et al., 2012) or negatively (Lee et al., 2014). Environmental stresses induce chromatin remodeling, which controls gene transcription. It is necessary to understand how stress signals activate genes and changes in higher-order organization.

Accumulating evidences suggest that HDACs HD2C, HDA9, and HDA15 are implicated in temperature responses (Mayer et al., 2019; Park et al., 2019). HDA6 regulates various abiotic-stress-responsive genes (ABI1, ABI2, and ERF4) through communicating with HD2C (Luo et al., 2017), while HDA19 with SIN3, SAP18, ERF3, ERF4, and ERF7 are part of the chromatin remodeling complexes in abiotic stress responses. Molecular mechanism of the HDA9 function in signal transduction under abiotic stress responses remains unknown. Recently, a model has been suggested for better understanding key role of HDA9 in ABA-dependent drought stress signaling in plants (Baek et al., 2020). SRTs and HDA15 are played critical role in plants hormone signaling. The HDA15 regulates ABA-dependent signaling by interacting with MYB96. Under high ABA level, MYB96 induces transcription of the ABA-responsive genes, but requires HDA15 to inhibit transcription of ABA-suppressed RHO OF PLANTS genes by promoting H3 and H4 deacetylation at their promoters (Lee and Seo, 2019). Here, we recommend that epigenetics changes and chromatin remodeling are integral parts of plants signaling pathways during heat or drought stress that bridge gap between downstream gene regulation, transcriptional factors, and transcription machinery for signaling output. In addition, we should also decipher nature of plants signals that trigger target epigenetic

modification, accurate mechanisms of how chromatin remodeling and gene regulation dictate responses to diverse signaling pathways, and specific routes by which abiotic stresses feed back to the epigenome landscapes.

4. Novel Approaches for Developing Stress Tolerance Crops

To warrant the fear of global food security in coming years and achieve target of “zero hunger” anticipated by the FAO, crops yield should be increased to meet the food demand of 9.7 billion people by 2050. However, owing to extreme heat stress and other environmental factors responsible for climate change, agricultural production is significantly decreasing and counteracting objective of “zero hunger.” Climate change contributes to various abiotic stresses, among which high temperature is considered critical yield-limiting factor across the globe. Extreme heat stress could disrupt metabolic homeostasis; hence, plants require wide modifications to cope with extreme stress conditions (Raza et al., 2021). To this end, biotechnological tools provide prodigious possibility to increase crops yield to feed worldwide population.

4.1. Genome editing for heat stress resistance

Now a days, genome editing has been emerged as an effective tool for improving crops tolerance mechanism either by gain of gene function, loss of gene function, or multiplex genome editing strategy (Sedeek et al., 2019). There is dire need to use genome editing technology to tackle detrimental climatic changes without affecting global food production. In this line, CRISPR technology may play a key role in food crops improvement. To date, three novel CRISPR systems (Cas9, Cas12a, and Cas12b) for the editing of plants genome have been effectively demonstrated (Ming et al., 2020; Zhang et al., 2019a). These novel tools can make CRISPR technology more effective not only for improving traditional plant breeding but also fundamental research (Chen et al., 2019; Pramanik et al., 2020; Veillet et al., 2020). Growing evidences suggest that CRISPR technology has been emerged as a promising genome editing tool for plants against high temperature stress (Li et al., 2019; Wang et al., 2017).

Recently, scientist have investigated the potential role of OsSAPK2 (osmotic stress/ABA activated protein kinase 2) by using loss-of-function mutants through CRISPR/Cas. They have designed sgRNA to target third exon of gene. Their findings show that *sapk2* mutants display an ABA-insensitive phenotype and show more sensitivity to drought stress than wild type, thereby suggesting that OsSAPK2 plays crucial role against drought stress in rice (Lou et al., 2017). In maize, CRISPR-Cas9 enhances expression level of ARGOS8 to develop drought tolerance; ARGOS8 promoter has been changed into GOS2. These mutants led to increased grain yield during drought stress (Shi et al., 2017). More recently, CRISPR-Cas9 approach has been applied to knockout RVE7 and 4CL genes in the protoplast of chickpeas to better understand molecular mechanism of drought stress. This study has been designed to conduct CRISPR-Cas9 for drought tolerance

and propose effective method for use of free gene editing in the recalcitrant species (Badhan et al., 2021).

In cotton, CRISPR-Cas9 mediated pooled sgRNAs assembly has been optimized to target multiple genes associated with male sterility. Results show that pooled sgRNAs assembly provides a new road map for designing sgRNAs to target both the desired and multiple genes. CRISPR-Cas9 mediated pooled sgRNAs assembly not only applied in cotton, and also be used for all the plant species, particularly those have complex genomes. This study will rescue to cotton male sterility and also provide more genetic resources to improve several traits on field level (Ramadan et al., 2021). Taken together, CRISPR approach offers opportunity to modernized crops genome engineering for improving crops yield and resilience to climate change. In addition, we should take lesson from the past experience and make new efforts to improve technology to avoid regulatory obstacles and make sure that its fruits are within reach for the poor and for survival of the farmers. Genome editing tools are poised to remodel agriculture and global food security to feed burgeoning population worldwide.

4.2. Role of synthetic biology for developing resilient crops against high temperature stress

In recent years, plant synthetic biology has been emerged as a key approach and provides a platform to combine plant biology with engineering principles (Kassaw et al., 2018). It has ability for developing drought tolerant transgenic (Borland et al., 2014; DePaoli et al., 2014; Llorente et al., 2018). Initially, it has been used for bacterial systems, but now also applied to plants. Synthetic regulatory systems have been proved promising tools for developing plant varieties with desired traits. For the development of sentinel plants demonstrating novel traits, effective genetic circuits must be goal of the designing team. Effective genetic circuits can be designed by using Bio-CAD for designing (Nielsen et al., 2016) and Cell Modeller (Dupuy et al., 2008) for assembling genetic parts. The orthogonal genetic components possess the capability to work independently of endogenous regulatory mechanisms of plants (Chen et al., 2013; Morey et al., 2012). Moreover, potential to manage activation of the genetic circuits can facilitate us switch on/off the desired traits as when needed.

In addition, incorporation of the regulatory components including terminators and insulators can also help in controlling synthetic genetic circuit (Y.-J. Chen et al., 2013). However, plants genetic functions are very complex and regulated a series of environmental cues such as temperature, light, and photoperiod, which in turn affect synthetic gene circuit control. These factors, along with gene regulatory information available from various omic studies, must be incorporated during development of sentinel plants. Plants biosensors have been designed for sensing 2,4,6-trinitrotoluene (TNT) through two-component synthetic gene circuit (Antunes et al., 2011). First component serves as transmembrane signal activator following TNT exposure. Then it triggers second component via activation of synthetic promoter. The promoter controls genes activity

which suppresses chlorophyll synthesis and induces its degradation. Lettuce and Arabidopsis have been modified to signal for bacterial contamination effectively through a gene circuit controlled by a positive autoregulatory transcriptional feedback loop (Czarnecka et al., 2012). This emerging approach has great potential to be used broadly, for developing sentinel plant that detects abiotic stresses including high temperature in field and activates gene regulation machinery for imparting heat stress tolerance.

5. Future Perspectives for Application of Modern tools for Improving Crops Genetics

Global elevations in climate have increased severity and unpredictability of extreme high temperature stress, threatening crop production sustainability and food security (Valliyodan et al., 2017). In order to produce an ideotype in terms of quantity, quality, and resistant is a challenging task in traditional breeding. Although utilizing novel biological tools, this task can't be achieved to meet the increased demand of global food. Conventional breeding in developed countries has been declined whereas in developing countries latest technology and strategies are lacking due to less funds. However, sharing information, germplasm resources and technology can help for solving several issues in developing countries (Zahid et al., 2016). Growing evidences show that reproductive phase is the most vulnerable stage to extreme heat stress in most of the crops. There is dire need to find out heat-resistant germplasm for the tailored breeding, for better understanding of pollen development and fertilization and to illustrate reaction of reproductive tissues under high temperature stress (Grover et al., 2016). Various heat-tolerant plant species have been evolved via process of natural selection through attaining acclimation and adjustment mechanism. Wild species and exotic can grow in stressful conditions and possess stress-tolerant features as compared to cultivars (Mickelbart et al., 2015).

Introduction of heat-tolerant traits into the crop germplasm will enhance the diversity to improve crop production sustainability under extreme pattern of climatic change. To achieve this task, we have to discover heat-resistant genetic resources and then incorporate them into the elite germplasm (Foyer et al., 2016). Utilization of natural variation might be a cornerstone approach in plant breeding to increase performance of field crops. There is need to identify stress-tolerance genes for multiple signaling pathways such transcriptional factors signaling, calcium signaling, Sugar signaling, hormone signaling, gene expression signaling, noncoding RNAs and epigenetic regulation from natural genetic variation sources and transformed into current germplasm (Figure 3). Recently, dCas and CRISPR/Cas9 technologies have provided new roadmap in epigenetic field. These novel tools can enable manipulation of the desired epigenetic traits and can be used to modify various crops phenotypes or to investigate relationship between epigenome and transcriptional control under extreme heat stress (Moradpour and Abdulah, 2020). In addition, stress-tolerant genes can be discovered by conducting genome-wide association studies (GWAS)

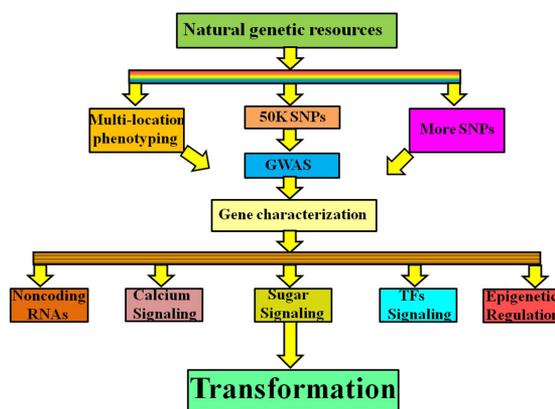


Figure 3. Process of development of heat-resistant cultivars. Identify heat-resistant genes from natural genetic resources through genome wide association mapping and then study the study how these genes are operated. Select those genes which are associated with various signaling pathways and then transform them into current germplasm.

(Varshney et al., 2016). Among stress-tolerant genes, we should identify pioneer transcriptional factors which possess the ability of directly binding to nucleosomes of the closed chromatin and play critical role in the opening of closed chromatin through depositing active histone modification mark. More recent study has shown that active marks and repressive marks coordinate with each other to build a novel chromatin landscape which supports coregulation of bidirectional gene pairs (Fang et al., 2010).

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