Journal of Applied and Natural Science
15(4), 1741 - 1749 (2023)
ISSN : 0974-9411 (Print), 2231-5209 (Online)
journals.ansfoundation.org

Review Article

Physiological impact of heat stress and their alleviation measures in agriculture: A review

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Article Info
https://doi.org/10.31018/jans.v15i4.4532
Received: March 18, 2023
Revised: December 13, 2023
Accepted: December 17, 2023

How to Cite

Jayara, A.S. *et al.* (2023). Physiological impact of heat stress and their alleviation measures in agriculture: A review. *Journal of Applied and Natural Science*, 15(4), 1741 - 1749. https://doi.org/10.31018/jans.v15i4.4532

Abstract

Abiotic stresses are becoming more prevalent in modern agriculture as a result of shifting climate scenarios. Elevated temperature stress is one of the most important abiotic stresses to address since it has detrimental consequences for plant physiology, molecular structure, and phenology. The morphological impact occurs in the form of reduced germination, poor emergence, poor seedling vigor, abnormal seedling. Heat stress also results in the closure of stomata, reduced leaf size and consequent increase in stomatal density. One of the major physiological impacts of heat stress is on the fluidity of the membrane structure of the plant cell. Heat stress leads to increased fluidity of the thylakoid membrane and disruption of metabolic functions, which either deliver or accept electrons from PSII and, thus, cause dislodging of PSII from thylakoid membrane. The respiration generally increases in the temperature range of 0-35/ 40°C, reaches plateau at 40-50°C and decreases beyond 50°C due to damage to the respiratory mechanism. Elevated temperature directly impacts the cellular water content and indirectly through the increased water depletion rate from the soil. In order to design the appropriate corrective actions, it is crucial to research all the factors leading to heat stress thoroughly. The traditional agronomic and breeding interventions are crucial, but the rising food demand and the intensifying heat stress call for some cutting-edge biotechnological interventions, such as transgenics, genome editing, and CRISPR/cas9, to induce genome-level heat tolerance. The present review deals in detail with each of the previously listed aspects.

Keywords: Abiotic stress, Agronomy, Breeding, Eelevated temperature, Plant physiology

INTRODUCTION

Global food security is a major concern for agriculture scientists and policymakers worldwide. Increasing atmospheric temperature is evident in the various reports presented by the Global and national institutions, which directly impact crop yields and production and, thus, ultimately, food security. According to WMO (2020), the global mean temperature for 2020 (January- October) had been 1.2 ± 0.1°C above the pre-industrial baseline (1850-1900), making it one of the three warmest years, and the last five years (2016-2020) and previous decade (2011-2020) averages are warmest on the record. Similarly, 2001-2010/2010-2019 for India had been the warmest decades on record (MOEFCC, 2021). According to FAO (2021), the temperature over the past five decades has been rising progressively compared to the baseline period of 1961-1980. In India, the annual mean temperature during the period of 1901-2019 has seen an increasing trend of 0.61ºC per 100 years with a higher increasing trend of the maximum temperature of 1ºC per 100 years and a minimum temperature of 0.22ºC per 100 years, with higher trend in post-monsoon season (0.88ºC per 100 years) followed by winter season (0.68ºC per 100 years) (MOEFCC, 2021). Among the weather and climate-related disasters, the frequency of drought, storms and extreme temperature has nearly quadrupled from 40 events per year in 1970s to 150 in 2010s. Out of the total losses caused to all the sectors, agriculture shares 26 per cent (FAO, 2021). Heat stress has varied implications on the crop level. Heat stress has varied physiological, biochemical and reproductive growth implications for crop plants. In general, the impact of heat stress varies with the growth stages of the plant. At physiological level, it can impact photosynthesis, respiration, water relations, and changes in the balance of growth regulators, whereas at the molecular level, there is a production of heat shock proteins, which are essential for heat stress mitigation. All these have a cumulative impact on the final grain size, filling rate and yields. Therefore, it is essential to understand all these phenomena to design suitable heat-tolerant cultivars and agronomic management under a heat-stressed environment.

IMPACT OF HEAT STRESS

Morpho-anatomical impacts

Morphological impacts

The morphological impact occurs in the form of reduced germ nation, poor emergence, poor seedling vigor, abnormal seedling (Hemantaranjan *et al*., 2020), poor stand establishment, and visual symptoms of sunburn, scorching of leaves & twigs, senescence (Kondamudi *et al*., 2012), growth inhibition and discoloration of fruits and leaves (Fahad *et al*., 2017). All 10 cultivars of faba bean under observation have shown significant reduction in the plant height, dry weight, fresh weight and leaf area when temperature increased from 25ºC to 37ºC (Siddiqui *et al*., 2015). The ambient temperature above 45ºC led to a reduction in the germination & emergence of seedlings in wheat (Poudel and Poudel, 2020), and it also ceases coleoptile growth in maize (Wahid *et al*., 2007). Heat stress increases the number of leaves, particularly during the arrested reproductive stage, however, it reduces the root number, length and diameter (Iqbal *et al*., 2017). Pollen viability is considered as a single characteristic particularly susceptible to heat stress and determines reproductive success (Van Es, 2020). Pollen sterility is induced due to the high-temperature stress on account of changes in the ultra-structural changes in the pollen grains and irregularities during the microsporogenesis (Barnabas *et al*., 2007). Terminal heat stress for one week (108-114 DAS) resulted in a significant wheat grain yield decline (Kaur *et al*., 2017).

Anatomical impacts

Heat stress results in the closure of stomata, reduced leaf size and consequent increase in stomatal density. The heat stress also results in the alteration of the xylem vessel. In a study on Rhododendron, Shen *et al*. (2017) reported reduced stomata size to adapt to higher water loss under high-temperature conditions and increased stomatal density. Wang *et al*. (2016), in a comparative study on C3 (*Solidago canadensis*) & C4 (*Andropogon gerardii*) plants observed that the former tended to close stomata in response to heat stress to reduce evapotranspiration losses and thus, later has lower foliage temperature due to evapotranspiration (ET) losses. Higher temperature reduces the stomatal conductance (Haworth *et al*., 2018).

Physiological impacts

Membrane stability

The major physiological impact of heat stress is on the fluidity of the membrane structure of the plant cell. The cell membrane is the first physiologically sensitive structure to heat stress(El Sabagh *et al*., 2020). Heat stress leads to severe changes in cell membrane stability, which also serves as stress signaling. Sharma *et al.* (2017) reported that electrical conductivity (due to electrolyte leakage in response to change in membrane stability under heat stress) increased in all the twelve genotypes of wheat at 45ºC when compared to control and further increased at 100ºC. Similar findings are reported by Kumar *et al*. (2012), where cell membrane stability decreased at grain hardening of the wheat crop, followed by the milky dough stage and pollination when compared to the vegetative stage owing to increased temperature with successive stages. Under heat stress, the inward flux of Ca^{2+} in the cytoplasm from extracellular spaces and respiratory burst oxidase homolog D (RBOHD) protein located on the membrane is activated by an increase in cytoplasmic Ca^{2+} and/or phosphorylation of Ca-dependent protein kinase (CDPK) which is involved in the generation of hydrogen peroxide (H_2O_2) and this H_2O_2 serve as crucial heat stress messenger (Niuand Xiang, 2018).

Photosynthesis

The physiological impacts of heat stress are on photosynthesis and respiration in plants. Photosynthesis is among the most thermosensitive functions in plants (Li *et al*., 2018); however, photosynthesis in C4 plants is comparatively thermotolerant than C3 plants due to its higher water use efficiency and lower photorespiration (Wang *et al*., 2016). Photosynthetic process is tolerant to the temperature range of 30-35ºC. However, starts decreasing above 40ºC (Kaushal *et al*., 2016).The reduction in photosynthesis occurs due to the deactivation of RUBISCO by inhibition of the Rubisco activase enzyme and damage to PSII (Naz*et al*., 2018). Heat stress leads to increased fluidity of the thylakoid membrane and disruption of metabolic functions, which either deliver or accept electrons from PSII and, thus, cause dislodging of PSII from thylakoid membrane (Prasad *et al*., 2008). Fig. 1 clearly indicates the adverse effect of heat stress on photosynthesis as a result of the dissociation of PS II from the thylakoid membrane. The resultant lipid peroxidation due to the heat stress can facilitate the destabilisation and denaturation ofPsbO (PsbP and PsbQ in spinach PSII) protein binding to the PSII core complex and promoting manganese ion release from the Mn_4O_5Ca cluster, causing inactivation of electron transport on the donor side of PSII and heat stress also suppress the electron transport from Q_A to Q_B on electron acceptor side (Niuand Xiang, 2018).

Respiration

The respiration generally increases in the temperature range of 0-35/ 40ºC, reaches plateau at 40-50ºC and decreases beyond 50ºC due to damage to the respiratory mechanism (Prasad *et al*., 2008). Increased respiration causes the depletion of photosynthates. Mohammad and Tarpley (2009) reported that lower yield in rice is correlated with increased respiration rate with an increase in night temperature. The increased rate of mitochondrial respiration is related to the activation of parp1 (Poly ADP Ribose polymerase) and parp2 enzymes in the plant cell nucleus, which activates polymerization of ADP-ribose. This polymerization is at the expense of NAD+ as substrate, which ultimately uses ATP for its synthesis. Thus, mitochondrial respiration increases and negatively impacts the energy homeostasis in plants (Fig. 2). The correlation between parp activity and oxidative stress was established when *Brassica napus* callus regrowth was hardly impacted with acetylsalicylic acid treatment when parp inhibitor 3-methoxybenzamide (3-MB) was used (DeBlock *et al*., 2005).

Plant water relationship

Another major physiological impact on the plant system is on the platn water relationship. Temperature directly impacts the cellular water content and indirectly through the increased water depletion rate from the soil. Wahid and Close (2007) observed a sharp decline in the relative water content and osmotic potential under heat stress in the initial 12 hours, irrespective of the water supply to sugarcane seedling. Tissue water was found to be sufficient irrespective of temperature when the moisture supply was adequate; however, it was influenced negatively by higher temperature and reduced water supply (Wahid *et al*., 2007) and a similar relationship was reported in sorghum and wheat (Machado and Paulsen, 2001).

Production of secondary metabolites

There are three major groups of secondary metabolites in plants based on biosynthetic pathways nitrogen-containing compounds (cyanogenic glycosides, alkaloids and glucosinolates), phenolic compounds (flavonoids and phenylpropanoids) and terpenes (isoprenoids)and fourth one is S containing compounds

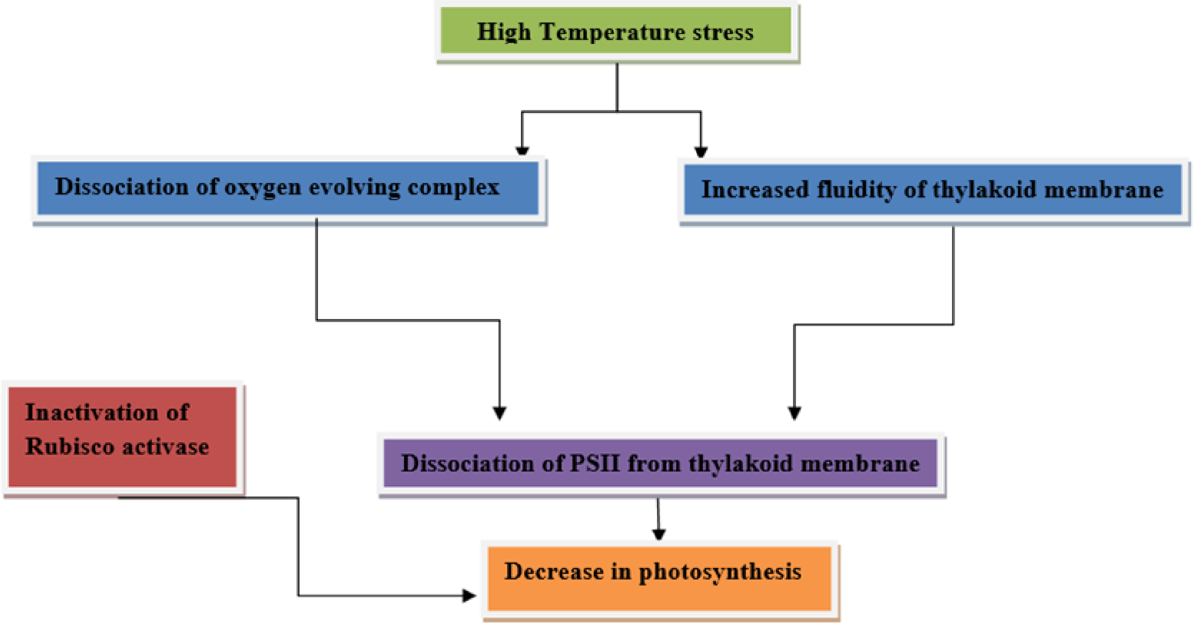


Fig 1. *Showing High-temperature stress impacting the OEC and electron transport to PSII and increasing the fluidity of thylakoid membrane, which ultimately causes the dissociation of PSII from the thylakoid membrane. High temperature also causes inhibition of RuBisCo activase enzyme, which impairs the functioning of RuBisCo. These two physiological effects reduce photosynthesis in plant*

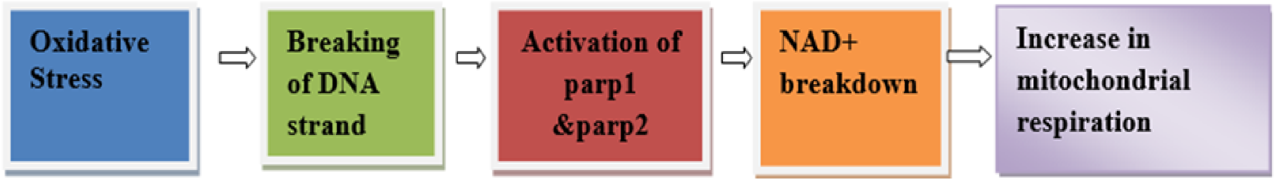


Fig 2. *Oxidative stress in plants leads to DNA strand breakdown, activating parp1 & parp2 enzymes which causes ADP polymerization at the expense of NAD+ breakdown. This NAD+ synthesis requires the ATP for its synthesis. Therefore, ultimately the mitochondrial respiration increases which disrupts the plant energy homeostasis.*

(glutathionds, thionins, defensins) (Akhi *et al*., 2021).Phenylamides, flavnoids, phenolics and polyphenolics play an important role in eliciting plant antioxidant responses and development, pigment and lignin biosynthesis, e.g. production of sesquiterpenes is associated with the defense response system in members of the family Solanaceae. The Brassicaceae members produce glucosinolates-myrosinase, stilbenes with the Vitaceae, isoflavones with Fabaceae, while limonoids are produced by Rutaceae and Meliaceae (Isah, 2019). Terpenes directly react with oxidants or alter ROS signaling and prevent membrane and protein disintegration by enhancing hydrophobic interaction between membrane proteins and lipids under heat stress, whereas phenolic production occurs as suberin and lignin under cold stress to protect against freezing stress(Akhi *et al*., 2021). These secondary metabolites are also exploited for their medicinal, therapeutic, aromatic and culinary purposes (Alhaithloul *et al*., 2019),e.g., Artemisinin (*Artemesia annua*) as antimalarial drug; Camptothecin (*Camptotheca acuminate); Ellipticine (Orchrosia elliptica) as anti-cancerous and Stevioside (Stevia rebaudiana) as sweetener etc. (Isah, 2019).* However, these secondary metabolites have fixed carbon (during photosynthesis) costs in plants and impact their overall growth (Isah, 2019); Isoprene biosynthesis is energetically expensive. However, its antioxidant nature and cell membrane protection outweigh it (Austen *et al*., 2019).

Hormonal imbalance

Heat stress has an impact on the hormonal balance in the plants. Heat stress alters the hormonal homeostasis, stability, content, biosynthesis and compartmentalization in plants and almost all the growth hormones abscisic acid (ABA), cytokinins, salicylic acid, jasmonic acid, brassinosteroids, auxins, gibberellic acids and ethylene play a role in heat stress response in plants (Ahammed*et al*., 2016). In sensitive wheat genotypes, ABA and IAA-conjugate levels increase under heat stress (Van ES, 2020). Heat stress led to the increased leaf trans-zeatin and ABA, and decreased gibberellic acid concentration (Li *et al*., 2020). Zheng *et al*. (2020) reported that under high-temperature concentrations of ABA and GA3 significantly increased, whereas cytokinin and ABA decreased when compared to the normal temperature and humidity in tomato plant. Wu and Yang (2019) reported that rice seedlings treated with a combination of heat stress and 1-aminocyclopropane-1-carboxylic acid (an ethylene precursor), had more chlorophyll content, higher membrane stability, enhanced activity of scavenging enzymes, suggesting ethylene-mediated signaling is involved in the expression of heat stress transcription factors (*HSFs)* and downstream ethylene-signaling-related genes, thereby increasing the seedlings' thermotolerance.

Production of osmolytes

One of the important aspects of the impact of heat stress on physiological functioning in plants is the accumulation of osmolytes, free amino acids and soluble sugars. These are low molecular weight and highly soluble compounds, also known as compatible solutes and some of the major osmolytes are amino acids (proline), polyamines, polyols, mannitols, trehalose, sorbitols, glucose, fructose, sucrose, quarternary ammonium compounds (β-alanine betaine; glycine betaine). These change the cellular redox potential and thus reduce ROS production (Shen *et al*., 2017). This decreases the osmotic potential of the plants and, thus, protects them from stress, causing protein stabilisation and detoxification of ROS. Alhaithloul (2019) reported an increase in proline, mannitol, inositol and sorbitol content in *Artemisia seiberri* under heat stress; however, it was less when compared to drought stress. Proline protects the protein, membranes, sub-cellular structures and cellular functions by scavenging ROS (Singh *et al*., 2017).

Production of heat shock proteins

Induction of heat shock factors (HSF) and heat shock protein (HSP) are considered to be important for tolerance under heat stress (Dinesh *et al*., 2016). Heat shock proteins act as chaperons for the signaling of heat stress. When plants are exposed to heat stress, heat shock factors (HSF) are released from the HSP, then undergo trimerization followed by phosphorylation and enter the nucleus where they bind with Heat Shock Elements (HSE) (which are located on the promoter region of HSP genes) leading to HSP synthesis (Usman *et al*., 2014), thus acts as transcriptional activators for heat shock (Al-Whaibi, 2011). HSP are of the five types based on their molecular weight (Fig 3).

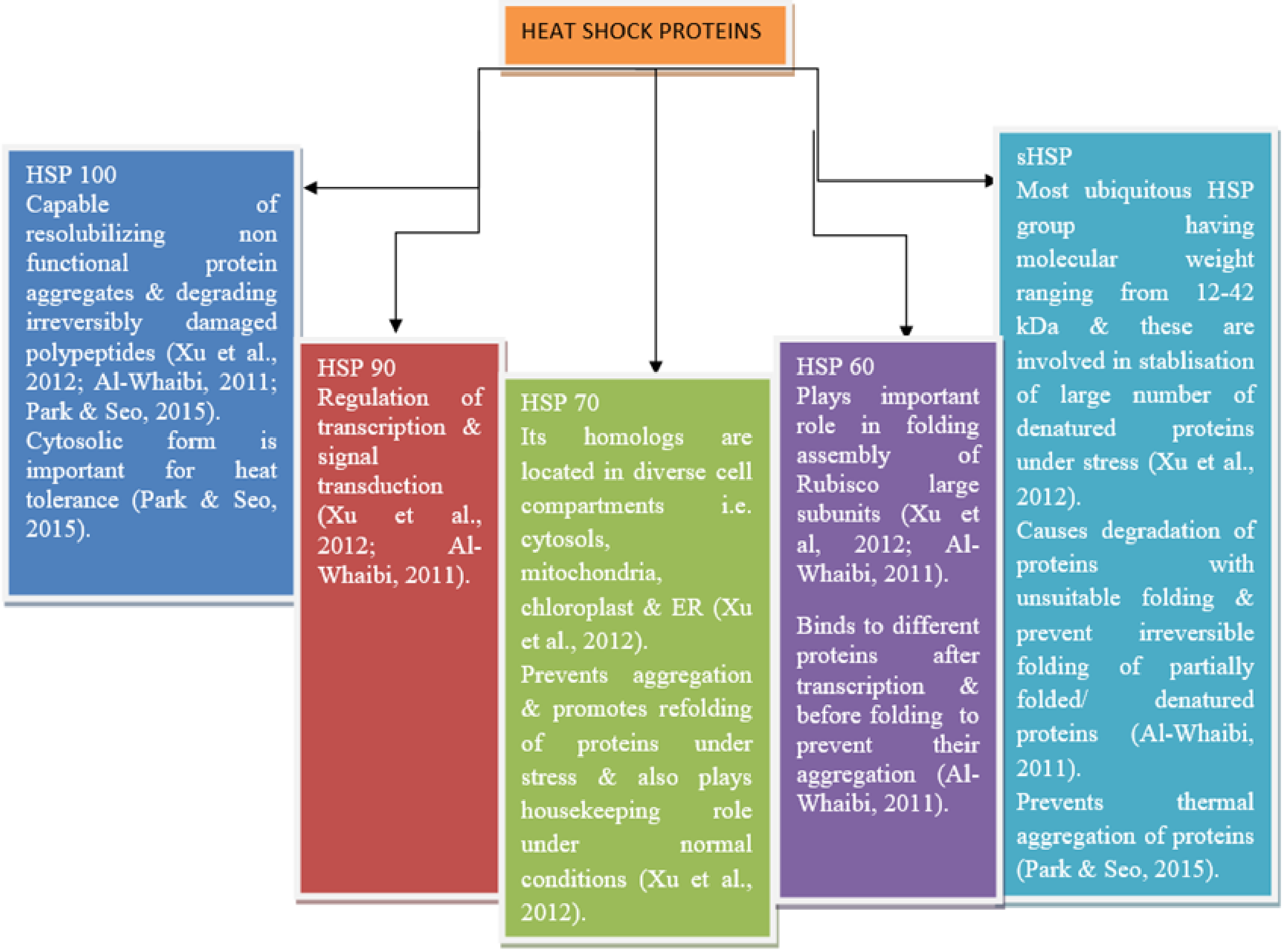
MITIGATION MEASURES

The plant responses to heat stress involve avoidance and tolerance mechanism. The avoidance mechanism works when there is an incidence of heat stress in the form of various morphological and physiological adaptations,e.g., reduced stomatal number and conductance, leaf rolling and folding, etc., whereas tolerance involves cellular and biochemical mechanisms for maintaining tissue hydrostatic pressure through the osmotic adjustments (Lamaoui *et al.*, 2018). High-temperature stress can be alleviated through Agronomy and Breeding approaches.

Agronomic measures

The major non-monetary or less input agronomic measures include selecting crops and varieties, adjusting the sowing date, practicing conservation tillage, and irrigation management. The selection of C4 crops such as millets and sorghum and some tropical C3 crops such as rice, common bean, cassava, and oil palm is suitable under high-temperature environment (Ferrante and Mariani, 2018).Due to their short-duration nature, some varieties can escape heat stress. Varietal selection considers either the shorter duration, which undergo fruiting cycle and maturity before incidence of the heat stress or it possesses heat tolerance (Brown and Zeiher, 2021). Irrigation has a strong mitigating effect on reducing the high-temperature stress in the crops and keeping adequate soil water content can have better thermoregulation under high temperature conditions (Ferrante and Mariani, 2018).

Heat stress tolerance can be induced through nutrient management, crop acclimation, and seed and foliar treatment. Majority of plant nutrients, including nitrogen, potassium, boron and selenium, reduce ROS production under high-temperature stress and increase the anti-oxidant activity. In addition, Mg plays a vital role in energy transfer from PSII to NADP+, which reduces the accumulation of energy and consequent oxidative damage to membranes; boron improves seed germination and seed grain formation through increased sugar transport in plant system; manganese has an indirect role through enhanced photosynthesis and N-metabolism; selenium has a structural role in glutathione peroxidase and thus protects tissues from oxida-



HSP 100
Capable of resolubilizing non functional protein aggregates & degrading irreversibly damaged polypeptides (Xu et al., 2012; Al-Whaibi, 2011; Park & Seo, 2015).
Cytosolic form is important for heat tolerance (Park & Seo, 2015).

HSP 90
Regulation of transcription & signal transduction (Xu et al., 2012; Al-Whaibi, 2011).

HSP 70
Its homologs are located in diverse cell compartments i.e. cytosols, mitochondria, chloroplast & ER (Xu et al., 2012).
Prevents aggregation & promotes refolding of proteins under stress & also plays housekeeping role under normal conditions (Xu et al., 2012).

HSP 60
Plays important role in folding assembly of Rubisco large subunits (Xu et al, 2012; Al-Whaibi, 2011).
Binds to different proteins after transcription & before folding to prevent their aggregation (Al-Whaibi, 2011).

sHSP
Most ubiquitous HSP group having molecular weight ranging from 12-42 kDa & these are involved in stablisation of large number of denatured proteins under stress (Xu et al., 2012).
Causes degradation of proteins with unsuitable folding & prevent irreversible folding of partially folded/ denatured proteins (Al-Whaibi, 2011).
Prevents thermal aggregation of proteins (Park & Seo, 2015).

Fig. 3. *Types of HSPs generated under stressed conditions and their functions in terms of plant response to heat stress (HSPs are classified according to their molecular weights and have the main function as preventing the protein aggregation under heat stress)*

tive damage (Waraich *et al*., 2012). Similarly, Zn- - nutrition in cotton crops under superoptimal temperature stress increased the activity of superoxide dismutase, peroxidase, catalase, ascorbic acid, total phenyl content and reduced malondialdehyde concentration (Sarwar *et al*., 2019). Seed and foliar treatment with several biostimulants have been proven effective in providing heat tolerance to plants such as lignosulphonates-based bio-stimulant KIEM in cucumber seeds, led to increased germination percentage, reduced H2O2 production and upregulation scavenging genes (Campobenedetto *et al*., 2020); inoculation of tomato seeds with PGPR bacterial strain *Bacillus ceres* leads to better growth parameters under heat stress (Mukhtar *et al*, 2020); treatment with*Azospirillumbrasilense* N040 and*Bacillus amyloliquefaciens*5113 led to more than 40 per cent wheat seedling survival after 24 hrs of heat stress treatment (El-Daim *et al*., 2014).

Fahad *et al.* (2016) reported the highest pollen fertility, anther dehiscence and pollen germination in rice cultivars with the application of brassinosteroids, methyl jasmonates along with Vitamin E and C and Sharma *et al.* (2018) reported the mitigating effect of exogenous IAA application on spikelet fertility, pollen viability and yield components in 23 rice genotypes under high-temperature stress. Brassinosteroids (BR) are emerging as a new class of growth regulators which mitigate heat stress through enhancing the photosynthetic rate and anti-oxidative mechanism (Vidhyavardhini, 2019); enhancing chlorophyll content and reducing chlorophyllase activity regulating cell division and cell expansion; accumulating osmolytes; its interaction and cross-talk with other growth regulators in plants (Sharma*et al*., 2017). Exogenous application of BR under heat stress at various concentrations haspositive impacts on several crops, including rice and wheat. However, more studies are needed on the effects of BR treatment and heat stress relative to other abiotic stress and the duration of its impact on crops (Kothari and Lachowiec, 2021). Exogenous application of osmolytes can also mitigate heat stress. Application of Poly ADP Ribose polymerase (PARP) inhibitor can prove effective for maintaining energy balance in plants as it will reduce the mitochondrial respiration rate. The protective action of PARP inhibitors (3-methoxybenzamide and nicotinamide) was evident on *Brassica napus* callus under oxidative stress (DeBlock *et al*., 2005).

Breeding measures

The breeding measures involve two approaches: conventional breeding and modern methods. Conventional breeding involves screening germplasm under heat stress and subsequently identifying better-performing lines (Fahad *et al*., 2017). However, screening of germplasm under field conditions like of chickpea has led to the identification of tolerant genotype ‘ICCV 92944’ (Jha *et al*., 2014) and “Ripper” a drought tolerant variety of wheat developed through conventional breeding (Lamaoui *et al*., 2018). Physiological trait-based breeding is better than the conventional selection approach as the abiotic stress tolerance is related to quantitative genes. The potential physiological traits for genetic improvement for heat tolerance in wheat are rapid ground cover/ early vigor, canopy architecture favoring the higher light interception, stay green, high Rubisco affinity for CO_2, improved Rubisco activase under heat stress, lower respiration, accumulation of photoprotective molecules like cartenoids and flavnoids, presence of glaucosness/ epicuticular wax, membrane thermostability, spike fertility, accumulation of water soluble carbohydrates in stem and starch synthesis (Cossani and Reynolds, 2012). With the help of DNA markers and genotyping assays, the Quantitative Trait Loci (QTLs) can be located on the chromosomes for particular heat-tolerant characteristics. QTLs have been identified for various crops for different physiological traits like lower canopy temperature and high chlorophyll fluorescence in wheat, internal heat necrosis in potatoes, pollen tube growth and quality in maize, spikelet fertility in rice under high temperature (Dreidonks *et al*., 2016).

“Omics” technology is the new approach which includes genomics, transcriptomics and proteomics, considering DNA as the starting point which contains gene for the thermotolerance (genomics) followed by its transcription in mRNA (transcriptomics) and then their translation into functional protein responsible for heat tolerance (proteomics) (Hemantaranjan *et al*., 2014). The important technologies employed are Genome wide association studies (GWAS) for high mapping resolution and identifying the genetic basis for complex phenotypic traits; microarray technology for understanding the expression pattern of gene (transcriptomics) and suppression subtractive hybridization (SSH) for identification of genes with differential expression under heat stress (Singh *et al*., 2019).

Mutation assisted plant breeding provides an opportunity for developing the “designer crop varieties” in the uncertainty in global climate scenario and the various techniques of molecular mutation breeding are ECO-TILLING, high-resolution melt analysis (HRM) and targeting induced limited lesions in genomes (TILLING) (Hallajian, 2016). Now, there are new breeding techniques comprising of genome editing, transgenics and mutation breeding for heat stress tolerance with CRISPR (clustered regularly interspaced palindromic repeats)/ Cas9 (CRISPR associated protein 9) technique, which can have targeted genome modifying capability and has been used in 20 crop species including tomato, maize, rice, cotton and wheat (Janni *et al*., 2020); other genome editing techniques are ZF (zinc finger nucleases) and TALEN (transcriptionactivator–

like effector nucleases) (Lamaoui *et al*., 2018). Transgenic approach has made it possible to introduce abiotic stress tolerance traits into crop varieties and includes over-expression of ABA pathway-related TF; upregulation of glyoxalase pathway (Lamaoui *et al*., 2018) and over-expression of HSPs (Janni *et al*., 2020**).**

Conclusion

The present review concludes that among all abiotic stressors in crop plants, rising temperature is the one that has the most deteriorating effect on the plants, irrespective of the phenological stage. Reproductive stage in plants is most sensitive to rising temperature, especially pollen viability, pollen tube growth, stigma receptivity which ultimately affects the yield of the crops. It is indispensable to study the effect of high temperature, especially the plant's response to heat stress at the molecular level, including signaling mechanism, the role of Ca2+ in signaling and various heat shock proteins that protect proteins' folding and aggregation. Studies are required for growth regulators under high-temperature stress in crop plants. Traditional agronomic or breeding approaches should be seen in tandem with the modern induction of thermotolerance to genomics, transcriptomics and proteomics approach. Various mechanisms of inducing thermo tolerance, especially seed treatment/ foliar spray of osmolytes/ osmoprotectants, zeatin, etc., have given new directions in agronomic management of heat stress. As well as transgenics and genome editing are important for developing heat tolerant cultivars, especially when the abiotic stress-related traits have polygenic nature. These emerging approaches for thermotolerance, along with the response mechanism of crop plants towards heat stress, need to be studied further to refine scientific understanding.

Conflict of interest

The authors declare that they have no conflict of interest.

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