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# Zinc Oxide Nanoparticles in Alleviation of Toxicity Induced by Heat Stress in Plants

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**Abstract**

Climate change-related abiotic pressures have an impact on plant development and yield, which decreases the amount of food produced. High temperature (HT) stress has a large worldwide impact on plant development, metabolism, and productivity. The growth and development of plants involves numerous temperature-sensitive metabolic processes. The widespread practise of producing crops in polluted surroundings is currently environmentalists' top worry. So, in order to maintain high crop yields under HT stress, which is currently a key worry for crop production, it is vital for agriculture to develop various strategies. A current relevant technology for enhancing food production and ensuring sustainability in the pursuit of food safety is highly developed nanotechnology. Nanotechnology boosts agricultural productivity by improving input effectiveness and reducing relevant losses. This review looks at earlier studies that show how zinc oxide nanoparticles (ZnO-NPs) can mitigate the negative effects of heat stress. ZnO-NPs application is the most effective method available globally to greatly boost agricultural output in challenging settings. With the aid of a number of cutting-edge technologies for reversing the symptoms of oxidative stress brought on by heat stress, ZnO-NPs can revolutionize the agricultural and food industries. The impact of ZnO-NPs on the physiological, antioxidative and biochemical activities in different plants has also been thoroughly studied. This review summarizes the current understanding and future perspectives of plant-ZnO-NPs research.

Keywords: Heat stress, nanoparticles, Heat shock proteins, zinc oxide, plants

## 1. Introduction

Nanotechnology is a promising platform, which ensures improved stress adaptation and sustainable agriculture globally (Saxena et al., 2016; Das and Das, 2018). Due to their distinctive physical and chemical characteristics, such as their small size (varying from 1-100 nm), extraordinary cellular durability, vast surface area, and reactive power, nanoparticles have become more important in the study of molecular biology (Nejatzadeh, 2021). Numerous uses in the agricultural and healthcare industries have been made possible by the unique physiochemical characteristics and the innate surface area-to-volume ratio of nanoparticles. Enhancing the production of different crops could completely transform the agronomic industry. Plants use antioxidant enzymes as part of their defense mechanism against reactive oxygen species (ROS). Exposure to nanoparticles improves plant stress tolerance by increasing the capacity of plants to scavenge free radicals and their ability to produce antioxidant enzymes (Jalil and

Ansari, 2019). Nanoparticles penetrate plants via a size-dependent process, are translocated to growing plantlets, and accumulated in all tissues, including developing seeds. In comparison to traditional approaches, the use of nanomaterials can aid in faster plant germination, improved output through the development of resistance to biotic and abiotic stresses, optimum nutrient use, and enhanced plant growth (Mozafari et al., 2018).

Abiotic stresses cause significant crop losses that could get worse as a result of the problems caused by climate change (Yadav et al., 2020). The growth and development of plants are severely impacted by sudden rise in temperature. In dry and semi-arid regions, heat stress is ranked as the second most detrimental abiotic stress to crop development and productivity, after drought (Kareem et al., 2022). It is one of the most serious obstacles to agriculture in the globe, negatively affecting plant physiological and metabolic changes which leads to cell death (Ahuja et al., 2010).

Although it is obvious that high temperatures and other abiotic stresses are limiting factors for crops grown on marginal soils, crop yield worldwide is frequently subjected to arbitrary climatic changes (Jagdish et al., 2012). The majority of agricultural regions would likely face more harsh environmental changes as a result of global climate change (Hemantaranjan et al., 2014). Among different abiotic stresses the most detrimental stress is the heat stress. High temperatures can directly harm plants by denaturing and aggregating proteins and by increasing the fluidity of membrane lipids. The inactivation of mitochondrial and chloroplast enzymes, inhibition of protein synthesis, breakdown of proteins, and loss of membrane integrity are the examples of indirect or delayed heat damage (Howarth, 2005). Heat stress is frequently described as a time when temperatures are high enough for an extended time period to permanently harm plant's development or function. High air or soil temperatures, as well as high daytime or night time temperatures, can also harm plants. Additionally, heat stress alters a variety of physiological processes, including growth, development, and yield, frequently in a negative way (Lippmann et al., 2019). Reactive oxygen species (ROS) are produced in excess as a result of HT stress, and this results in oxidative stress (Nosaka and Nosaka, 2017). A plant may withstand heat stress to some extent by making physical adjustments to its structure and frequently by sending signals to its metabolism. In response to HT, plants change their metabolism in a number of ways, most notably by creating soluble compounds that can organize proteins and cellular structures, maintain cell turgor through osmotic adjustment, and alter the antioxidant system to restore cellular redox balance and homeostasis (Wang et al., 2018).

Zinc (Zn) is considered as a vital micronutrient for sustained growth in humans, animals, and plants. Various studies were emphasized on how zinc affects plant development and metabolism (Auld, 2001). Due to its necessity in numerous enzymatic processes, metabolic functions, and oxidation-reduction reactions, it is essential to crop nutrition. Zinc is a vital element which play essential role in the activation of various enzymes viz., isomerases, dehydrogenases, transphosphorylases, aldolases, and RNA and DNA polymerases, which are necessary for a number of crucial physiologic processes (Lacerda et al., 2018). Additionally, Zn is also helpful in cell division, tryptophan synthesis, membrane structure maintenance, and photosynthesis (Marschner, 2011; Lacerda et al., 2018).

Zinc oxide (ZnO), an amphoteric oxide, is soluble in most of the acids but is insoluble in water (Spero et al., 2000). Zinc oxide nanoparticles (ZnO-NPs) are widely used in a variety of products and materials, including medicine, cosmetics, solar cells, rubber and concrete, and foods, because of its unique characteristics, such as high thermal conductivity, refractive index, binding energy, UV protection, and antibacterial properties (Uikey and Vishwakarma, 2016). The ZnO-NPs, which are utilized in rubber manufacturing, biosensors, electronics, coatings and paints, and UV protection (Brayner et al., 2010; Kool et al., 2011). ZnO-NPs have a wide variety of industrial uses, which can be utilized to forecast their production in future. Nowadays, the cost-effective application of ZnO-NPs as Zn fertilizers all over the world become practical on a large-scale agriculture. In plants, ZnO-NPs play crucial role in minimizing the toxic effects of ROS in cell organelles. Additionally, ROS are also known to activate a number of defense mechanisms by triggering the cell signaling cascade as well as by inducing or suppressing the expression of various genes (Hancock et al., 2001). However, plants have enzymatic and nonenzymatic systems which are helpful in scavenging harmful ROS. Zinc oxide nanoparticles helps to protect plants from a variety of abiotic stresses by stimulating antioxidant enzyme activity, osmolytes accumulation, free amino acids, as well as nutrients (Taran et al., 2017; Venkatachalam et al., 2017; Wang et al., 2018). Recently, Kareem and his co-workers, (2022) demonstrated that ZnO-NPs at low levels have a positive effect in alleviating high temperature stress and also promote plant growth and development. Zinc oxide nanoparticles have tremendous potential for enhancing the quality of crop plants as well as productivity under heat stress in plants (Kareem et al., 2022).

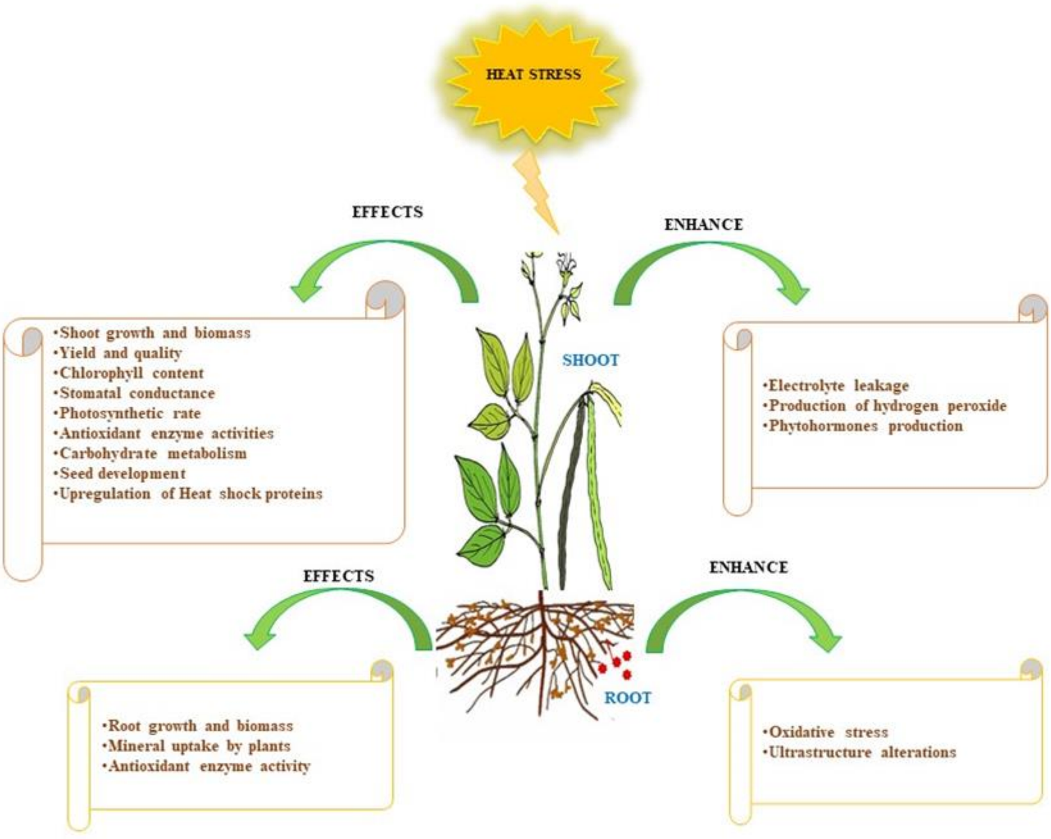


**Figure 1:** High Temperature effects on plants

In this review, we focus on the new strategies and different responses seen in plants under HT stress along with the positive role of zinc oxide nanoparticles in enhancing HT stress tolerance in plants.

## 2. Various plant responses to heat stress

Plant responses to heat stress differ with the degree of temperature, time, and type of plant. Extreme high temperature may cause cell death within minutes, which could result in a catastrophic collapse of cellular organization (Kumar et al., 2021; Hassan et al., 2022). Heat stress has an impact on every stage of a plant's life, including germination, growth, reproduction, development, and yield (Essemine et al., 2010; Lobell et al., 2011; Hassan et al., 2022). In addition, RNA species, proteins stability, cytoskeleton structures, membranes, and enzymatic reactions in the cell are also affected by heat stress, which impairs the efficiency of enzymatic reactions in cell and ultimately leads to metabolic imbalance (Johkan et al., 2011; Parrotta et al., 2016; Pan et al., 2018; Hassan et al., 2022).

### 2.1 Growth

Among the different stages of plant growth, the germination is highly affected by HT. The germination stage of a plant's growth is the stage that is highly affected. Although the temperature range vary significantly, depending upon the crop species. Heat stress has detrimental effects on many crops during seed germination (Hossain et al., 2013). Major effects of heat stress have been seen in a variety of cultivated plant species, including decreased germination percentage, aberrant seedlings, reduced radicle and plumule growth, plant emergence, low seedling vigor of geminated seedlings (Essemine et al., 2010). It is widely known that HT can inhibit seed germination, which is frequently accomplished via inducing abscisic acid (ABA) (Huang et al., 2016).

High temperature stress also effects wheat seedling growth, reduce seedling establishment rate, seed germination and caused cell death (Akter and Islam, 2017). Additionally, high temperature decrease water content of cells, which reduces cell size and ultimately effect growth (Farooq et al., 2011; Akter and Islam, 2017). The morpho-physiological symptoms of heat stress include branches, abscission, twigs and stems, stunted growth of shoots and roots, leaf senescence, sunburn of leaves, as well as discoloration of fruit (Rodríguez et al., 2005). Further, Kohila and Gomathi, (2018) demonstrated that oxidative stress induced by HT, effect yield, productivity and sustainability in sugarcane plants. Similarly, HT severely affects common bean (*Phaseolus vulgaris*) morpho-physiological traits such as germination, phenology, and seedling development (Hernandez and Cortes, 2019). Additionally, growth at HTs causes elongated stems and hyponasty of leaves in several plant species, as well as a decrease total biomass (Jayawardena et al., 2019). Similarly, wheat plants under HT, reduce tiller numbers, seedling growth, plant water efficiency as well as cell turgidity (Rahman et al., 2009; Akter and Islam, 2017). Due to shortening of the life span, high temperature can change the total phenological duration. Extreme HTs in plants leads to programmed cell death of cells or tissues due to denaturation and aggregation of proteins. In contrast, moderate heat stress over an extended period causes gradual death. Both types of injuries or deaths can result in leaves shedding, the abortion of flowers and fruits, or even death of the entire plant (Hasanuzzaman et al., 2010; HanumanthaRao et al., 2016).

### 2.2 Photosynthesis

Photosynthesis, one of the most heat sensitive physiological process in plants (Feng et al., 2014). The photosynthetic capacity of both C3 and C4 plants is highly affected by high temperature stress (Kumar et al., 2017). The primary sites of damage under HTs in chloroplast are carbon metabolism in the stroma and photochemical reactions in thylakoid lamellae (Akter and Islam, 2017). The thylakoid membrane is quite vulnerable to HT. Chloroplasts undergo significant changes, including altered thylakoids structural organization, and loss of grana stacking, during heat stress (Djanaguiraman et al., 2011; Wang et al., 2018). In addition, under HTs, photosystem II (PSII) activity is also decreased or even ceases (Akter and Islam, 2017). The amount of photosynthetic pigments is decreased by heat shock. Heat tolerance is directly correlated with plant's capacity to sustain the rates of $CO_2$ uptake and leaf gas exchange under heat stress (Kohila and Gomathi, 2018). Further, heat stress significantly affects leaf water efficiency, stomatal conductance, and intercellular $CO_2$ concentration. Stomatal closure under heat stress is another factor that leads to reduced photosynthesis and can affect intercellular $CO_2$ (Farooq et al., 2011; Akter and Islam, 2017; Zhang et al., 2018). Heat stress in sorghum plants results in lipid peroxidation of chloroplast and thylakoid membranes (Mohammed et al., 2010; Nadeem et al., 2018). Under the same stress condition, the photochemistry of photosystem II was also decreased. Similarly, in soybean plants, heat stress significantly decreases the amount of total chlorophyll (chl), chl a, chl a/b ratio, Fv/Fm ratio, and Pn (Herritt and Fritschi, 2020). Moreover, in tobacco plants, Tan and his co-workers, (2011) revealed that under high temperature stress, the sucrose content dropped by 9%, while the reducing sugar and leaf soluble sugar contents increased by 47% and 36%, respectively. When the temperature increased from 25 to 45 °C, in *Vitis vinifera*, the photosynthetic rate reduced by 60%, along with anthocyanin and sugar content (Martinez-Luscher et al., 2017). Mathur and Jajoo, (2014) demonstrated that wheat plants grown under heat stressed conditions effect soluble proteins, Rubisco binding proteins (RBP), large-subunits (LS), and small-subunits (SS) of Rubisco in darkness, and photosynthesis. Moreover, high temperature also has a significant impact on the synthesis of starch and sucrose due to decreased activity of sucrose phosphate synthase, ADP-glucose pyro phosphorylase, and invertase (Asthir and Bhatia, 2014; Zhang et al., 2019). Additionally, heat has detrimental effects on plant leaves, leaf water potential, decreased leaf area, and premature leaf senescence, which leads to decrease in the plant's overall ability to synthesize food (Daryl et al., 2016).

2.3 Reproductive development

The reproductive tissues of plants are most sensitive to heat stress, and even a small increase in temperature during the flowering period can cause the loss of entire grain crop cycles (Kaushal et al., 2016). This is true even though all plant tissues are susceptible to heat stress at almost all growth and developmental stages. A short period of heat stress, affects floral buds and ovule abortion during reproduction (Gupta et al., 2015). Under extreme HTs, during reproductive developmental stages, plant may not produce flowers or flowers that are formed may not yield fruit or seeds (Kaushal et al., 2016). HT impaired meiosis in both the male and female organs, impaired pollen germination and pollen tube growth, leads to the reduction in number of pollen grains retained by the stigma, growth of the endosperm, proembryo and effect unfertilized embryo which cause increased sterility under abiotic stress conditions (Boyer and McLaughlin, 2007; Bita and Gerats, 2013). In rice, HT treatment at heading stage significantly decreases anther dehiscence and pollen fertility rate, results in a decrease in the number of pollens on the stigma. Sensitive rice varieties were more susceptible to this occurrence than tolerant varieties. High night time temperatures (32 °C) led to an increase in rice spikelet sterility (by 61% compared to control), which was caused by lower pollen germination (36%) (Madan et al., 2012). Similarly, in the wheat ear length, number of spikelets, and number of fertile floret main stems were all significantly reduced as a result of heat stress and ultimately leads to late seeding, which decrease grain output (Hossain et al., 2013). Wheeler and von

Braun (2013) reported that HTs in soybean plants leads to abscission and abortion of flowers, as well as decrease in young pods, and developing seeds. It is well known that soybean pollen viability declines at flowering stage under high temperatures.

2.4 Yield

Concerns about crop yield and food security are increasing due to the high temperatures (Savin et al., 1997). Due to its terrible affect, crop yields are significantly impacted by even a minor temperature increase (1.5 °C) (Warland et al., 2006). Increased temperature has an impact on phenological development processes, which mostly affect grain yield. Many cultivated crops, such as cereals (rice, wheat, barley, sorghum, maize), pulses (chickpea, mungbean), oil-producing plants (soybean, canola), and more, have been shown to suffer from heat-induced yield reduction (Kumar et al., 2013; Bindumadhava et al., 2016; Wang et al., 2018; Ahmad et al., 2021). It has been Illustrated that even 1 °C increase in seasonal average temperature reduces cereal grain yield by 4.1% to 10.0% (Hasanuzzaman et al., 2013). Compared to tolerant crop varieties, the sensitive crop varieties are more severely affected by heat stress. Sensitive Shuanggui 1 and tolerant Huanghuazhan varieties of rice experienced grain weight reductions of 7.0%–7.9% and 3.4%–4.4%, respectively, during heat stress of 35–40 °C. Shuanggui 1, a heat-sensitive rice cultivar, showed a larger yield reduction (35.3% to 39.5%) than heat-tolerant Huanghuazhan (21.7% to 24.5%) cultivar (Ahamed et al., 2010). In O. sativa plants grown under high night temperatures, spikelet sterility was increased by 61% and as a result yield was reduced upto 90% (Suwa et al., 2010; Aghamolki et al., 2014). Similarly, wheat grain yield loss is caused by heat stress, which alters the grain weight and grain dry matter yield (Vignjevic et al., 2014). Further, due to heat stress, the yield of sorghum was decreased by 53% and 51%, respectively, in terms of filled seed weight and seed size (Djanaguiraman et al., 2010). High temperature of more than 30 °C, effect grain yield and its components, 50% flowering stage to mid podding stage as well as decrease oil quality in canola (*Brassica* spp.) plants (Uppal et al., 2019). Under heat stress, in wheat plants, productivity is primarily affected by reduced assimilatory capacity which is due to decreased photosynthesis and altered membrane permeability (Akter and Islam, 2017). Likewise, Waqas and his co-workers, (2021) demonstrated that high temperatures in maize severely affect light capture, biomass output, and harvest index, whereas heat at the flowering stage results in greater yield loss than at the grain filling period. Additionally, increased temperature has an impact on crop quality and performance. Under heat stress, barley grain quality parameters are substantially changed while the concentrations of total non-structural carbohydrates, fructose, starch, and raffinose, as well as lipids, were reduced in barley grain, but numerous proteinogenic amino acid concentrations and maltose content was enhanced (Högy et al., 2013).

2.5 Oxidative stress

Various metabolic processes are dependent upon enzymes that are heat-sensitive with varying degrees of HT. It has been proposed that heat stress, like other forms of abiotic stress, may uncouple enzymes and metabolic pathways that results in the undesired and harmful ROS accumulation. The most frequent causes of oxidative stress are singlet oxygen ($1O_2$), superoxide radical ($O_2$), hydroxyl radical (OH) and hydrogen peroxide ($H_2O_2$) (Das and Roychoudhury, 2014). Though ROS are produced in different organelles, such as peroxisomes and mitochondria, as well as in the reaction centres of PSI and PSII in chloroplasts. There is a linear relationship exists between the PSII's maximum efficiency and the total ROS accumulation

(Asada, 2006; Das and Roychoudhury, 2014). If PSI and PSII absorb photon intensity under these stress conditions, then the excess photons needed for $CO_2$ assimilation are considered as surplus electrons, those act as the source of ROS (Asada, 2006). In chloroplasts, singlet oxygen is produced during photoinhibition and PS II electron transport processes (Takagi et al., 2016). Cells effectively avoid OH by sequestering the catalytic metals to metallochaperones. Plants exposed to varied degrees of heat stress suffer from a variety of physiological damages (Taratima et al., 2022). All biomolecules, including pigments, proteins, lipids, and DNA, as well as almost all cellular components, are potentially reactive with hydroxyl radicals (Sharma et al., 2012; Das and Roychoudhury, 2014). Protein, polyunsaturated fatty acids, and DNA can all be directly oxidized by singlet oxygen (Wagner et al., 2004). Through the peroxidation of membrane lipids and the disturbance in the integrity of cell membrane caused by protein denaturation, leads to oxidative stress. Even with mild HTs, functional decline in the photosynthetic light reaction has been shown to cause oxidative stress by increasing the production of ROS through enhanced electron leakage from the thylakoid membrane (Hasanuzzaman et al., 2013; Das and Roychoudhury, 2014). The HT enhance leaf temperature, which in turn decrease antioxidant enzyme activity and increase malondialdehyde (MDA) levels in the leaves of rice plant (Kumar et al., 2016). Further, in wheat plants, oxidative stress caused by heat stress was found to significantly diminish cell viability by causing damage to membrane characteristics, protein breakdown, and enzyme deactivation. In addition, due to increase in membrane peroxidation and by decreasing membrane thermostability there is an enhancement in heat stress-induced oxidative stress in wheat (Poudel and Poudel, 2020). Cotton, canola, and soybeans were also found to be affected by high temperature stress, leads to membrane lipid peroxidation and worsened membrane injury (Ahmad et al., 2021). Heat stress (above 28°C) in canola leads to membrane damage, decrease root length, photosynthetic rate, biomass accumulation and enhanced level of MDA, in comparison to the control plant (Waraich et al., 2022). Additionally, the ROS generated by HT stress are involved in protein proteolysis or the breakdown of polymeric protein into simple soluble forms, both of which contribute to early senescence of cotton leaves (Saleem et al., 2021). Inhibition of root growth in wheat after 2 days in the heat was linked to strong oxidative stress, with a considerable rise (68%) in $O_2$ generation in root cells. In the early stages of seedling development, the MDA concentration also increased by 27% in the first leaf, two days after exposure, and this tendency also persisted during the later stages of development (Savicka and Skute, 2010).

## 3. Plant adaptations to heat stress

Depending on their optimal growing temperature, plants can be divided into three classes (Figure 2). There are three types of plants: (a) Psychrophiles, which grow best at low temperatures between 0 and 10 °C; (b) Mesophyles, which prefer moderate temperatures and thrive between 10 and 30 °C; and (c) Thermophyles, which thrive at high temperatures between 30 and 65 °C or more (Źróbek-Sokolnik, 2012). Among different plant species there is a great variation in terms of tolerance and response to HTs.

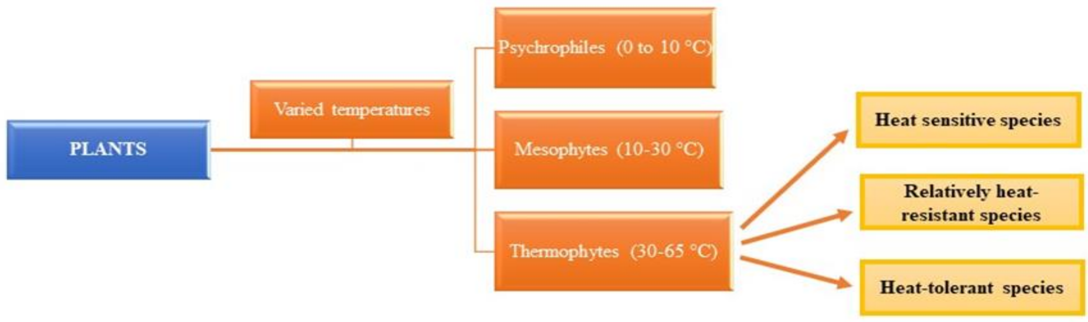


**Figure 2:** Plants classification on the basis of their varied optimal growing temperatures

3.1 Mechanism of avoidance by plants

Under HT conditions, plants exhibit a variety of survival strategies, including long-term evolutionary, phenological and morphological adaptations as well as short-term avoidance or acclimation strategies like changing the orientation of the leaves, transpirational cooling, or altering the lipid composition of membranes. Common heat-induced plant characteristics include stomata closing, decreased water loss, higher stomatal and trichomatous densities, and bigger xylem vessels (Caine et al., 2019). By lowering the absorption of solar radiation, plants living in hot climates avoid heat stress. This is due to the presence of a thick coat of small hairs (tomentose) on the leaf and cuticle (a protective waxy covering) surface. These plants have leaf blades that frequently turn away from the sun and align themselves parallel to sun rays. Additionally, moving leaf blades can lessen solar exposure. As a result of the smaller resistance of air boundary layer compared to large leaves, plants with small leaves are also more likely to survive under heat stress as they can quickly release heat to the ambient environment. (Fitter and Hay, 2002; Nievola et al., 2017). When there is a water shortage, plants use the same morphological and physiological adaptation processes to reduce transpiration. Intensive transpiration reduces heat stress in well-hydrated plants, and the temperature of the leaves can be 6 or even 10-15 degree Celsius lower than the surrounding air. Although C3 plants are also prevalent in desert floras, such morphological and phenological adaptations are frequently linked to biochemical adaptations that promote net photosynthesis at HT (particularly C4 and CAM photosynthetic pathways) (Fitter and Hay, 2002; Mathur and Jajoo, 2014). In many plants, leaf rolling can be affected by high temperatures. By improving the effectiveness of water metabolism in the flag leaves of wheat under HT, leaf rolling had a physiological role in maintaining adaption potential (Akter and Islam, 2017). All plants are extremely susceptible to temperature stress when they are actively growing. While some terrestrial plant species only show an increase in heat tolerance during the summer, others exhibit the highest level of tolerance during the winter season (Fitter and Hay, 2002).

Crop management techniques, such as choosing the best sowing techniques, sowing date, cultivars, irrigation techniques, etc., can also help prevent high temperature stress (Khan et al., 2019). For instance, cool-season annuals like lettuce may exhibit incomplete germination and emergence in subtropical zones when sown in the late summer due to high soil temperature (Hall, 2011). By irrigating the beds in the late afternoon after the lettuce seed has been sown into dry beds during the day, the incomplete emergence problem can be solved. Another remedy to this issue is seed priming, which involves soaking of the seeds in an osmotic solution for several days at room temperature before drying them. In contrast, due to the extremely hot soil surface, tropical crops may experience poor plant emergence and establishment, which can reduce the yield of various warm-season annual crops. So, this deep placement can solve the issue in certain situations. The sowing date can be changed in temperate or subtropical climate zones with seasonal temperature changes to maximize the likelihood that annual crop species will not be stressed out by HTs during later, sensitive stages of development. Fruit can occasionally be harmed by HT and due to direct sun light (Hall, 2011, Hasanuzzaman et al., 2013).

### 3.2 Tolerance mechanisms

Heat tolerance is the plant's ability to grow and generate an economic yield while exposed to HT. Plants developed a variety of mechanisms to survive in hotter climates. They can be long-term evolutionary adaptations or short-term avoidance and acclimatization mechanisms. In order to offset the effects of stress, some important tolerance mechanisms, such as ion transporters, late embryogenesis abundant (LEA) proteins, osmoprotectants, antioxidant defense, and factors involved in signaling cascades and transcriptional regulation, are crucial (Hemantaranjan et al., 2014). Short-term responses, such as leaf orientation, transpirational cooling, and changes in membrane lipid composition, are more crucial for survival in case of acute heat stress (Rodríguez et al., 2005). Plant tissues differ in terms of developmental complexity, exposure, and reactions to various types of applied or ubiquitous stresses (Queitsch et al., 2000; dos Santos et al., 2022). The initial stress signal, in the form of an ionic or osmotic effect or changes in membrane fluidity, establishes the stress response system in plants. In addition, this helps in the restoration of homeostasis and is also involved in protecting and repairing damaged proteins and membranes (Vinocur and Altman, 2005; Zhu, 2016).

### 3.3 Antioxidant defense mechanisms

For plants to thrive under HT, oxidative damage induced by heat must be prevented. Crop plants' ability to withstand HT stress has been linked to an increase in antioxidant capacity (Zandalinas et al., 2017). Studies based on the comparison of heat-acclimated cold season turfgrass species to non-acclimated ones, revealed that the former produce fewer reactive oxygen species (ROS) due to increased ascorbate (AsA) and glutathione synthesis (GSH) which suggests that particular signaling molecules might enhance cell's antioxidant capability. As a result of the production of different enzymatic and non-enzymatic ROS scavenging and detoxifying mechanisms, ROS-tolerant plants tend to protect themselves from their detrimental effects (Xu et al., 2006; Huang et al., 2019). The activities of several antioxidant enzymes, are temperature sensitive which occurs at varied temperatures. However, these enzyme activities increase with increasing temperature. According to Rajput et al. (2021) the activities of the enzymes, catalase (CAT), ascorbate peroxidase (APX), and superoxide dismutase (SOD) increased initially before declining at 50 °C, while the activities of the enzymes peroxidase (POX) and glutathione reductase (GR) decreased at the temperature ranges between 20 and 50 °C. Additionally, the overall antioxidant activity increased at 30 °C for susceptible cultivars and 35-40 °C for tolerant ones. Their activities also vary according to their tolerance mechanism and also due to susceptibility of different crop varieties, their growing season and different growth stages (Almeselmani et al., 2006). Plants are also protected from oxidative stress by different antioxidant metabolites such as AsA, GSH, tocopherol, and carotene (Harsh et al., 2016).

### 3.4 Heat shock proteins (HSPs) in mitigating heat induced oxidative stress

Several heat inducible genes, also known as "heat shock genes" (HSGs), which encode HSPs, are often up-regulated in response to heat stress. These active products are crucial for plant survival in fatal heat stress conditions (Chang et al., 2007; Hemantaranjan et al., 2014). Most of these proteins are constitutively expressed at high temperatures, which serves as a chaperone by preventing denaturation of intracellular proteins and maintaining their stability and function through protein folding (Baniwal et al., 2004). The HSPs are highly varied in nature, and current research indicates that this dynamic protein family is continuously growing. It has been reported that for certain plant developmental stages, such as embryogenesis, seed germination, microsporogenesis, and fruit maturation, the expression of HSPs has been restricted (Wang et al., 2014; Koo et al., 2015). The well-characterized HSPs in plants can be divided into five families: HSP100 (also known as ClpB), HSP90, HSP70 (also known as DnaK), HSP60 (also known as GroE), and HSP 20 (also known as small HSP, sHSP) (Swindell et al., 2007; Kumar et al., 2020). The fact that HSP90 proteins are among the most highly conserved in nature, as they play a crucial role under heat stress conditions. Additionally, sHSPs, which have extremely low molecular masses of 12–43 kDa, are most diverse in plants (Hu et al., 2022). HSPs because of their thermotolerance, have conserved heat shock elements (HSEs) in their promoter regions, which cause transcription to be triggered in response to heat. This allows heat treatment to activate the expression of HSP. The palindromic nucleotide sequence (5-AGAANNTTCT-3) in these cis-acting elements (HSE) serves as a binding site for heat shock transcription factors, also known as heat shock factors (HSFs) (Scharf et al., 2012). Plants that have been transplanted with heat shock regulatory proteins have achieved thermotolerance against heat stress. The majority of plant species have constitutive expression of HSFs, which normally exist in the cytoplasm as a monomer linked to an HSP70. As soon as the plant sense heat stress, HSP70 separates from cytoplasmic monomeric HSFs and enters the nucleus, where it forms a trimer that can bind with the HSEs (Lee et al., 1995). Heat shock factor binding recruits the additional transcriptional elements, which trigger the expression of genes in response to an increased temperature within minutes. Since, all HSGs have the conserved HSE sequence, overexpression of the HSF gene inturn activates almost all HSGs, providing protection from heat stress. Despite this, the fundamental system is present in all eukaryotic cells, and it is extremely complex in plants. Plants have been proven to have several copies of these genes, in contrast to animals and yeasts, which may have only four or fewer HSFs. For instance, the *Arabidopsis* has 21 different HSF genes and tomato plant has at least 24 HSFs. These genes have been divided into three classes A, B, and C, which can be distinguished on the basis of flexible linkers and oligomerization domains (Nover et al., 2001; Scharf et al., 2012). Since many HSFs are heat-inducible, the precise HSF responsible for a gene's transcription may change depending upon time and severity of the stress. Plant HSFs can generally be overexpressed to enhance their thermotolerance. Heat induces the upregulation of a variety of non-HSP genes in plants (Morrow and Tanguay, 2012). In particular, it has been demonstrated that the *Arabidopsis* cytosolic ascorbate peroxidase gene (*APX1*) not only responds to heat but also has a functional heat shock element (HSE) in its 5'-promoter region. Other HSFs, possibly including heat-inducible HSFs, are apparently responsible for the induction of genes expressed later in *Arabidopsis*. In the absence of normal HSP synthesis, the plant becomes very sensitive to HTs (Mishra et al., 2002; Charng et al., 2007). Thus, through the HSF system, plants appear to possess a remarkable capacity to precisely regulate the expression of heat-induced genes. According to several studies, the HSP level in the cell and corresponding stress tolerance are correlated positively (Wang et al., 2005). Heat shock proteins, either individually or in the form of chaperones, have been implicated in plant cell defense mechanisms in response to heat stress; they play crucial role in protein synthesis, maturation, targeting, and degradation as well as in maintaining the stability of protein and membrane under heat stressed conditions (Haq et al., 2019). Heat shock proteins maintain and maintain the structure of companion proteins as well as it targets foreign proteins for degradation and cell removal. These proteins primarily function to control the proper folding and conformation of both structural (*i.e.*, cell membrane) and functional (*i.e.*, enzyme) proteins, ensuring the correct function of many cellular proteins under high temperature. One such protein, NtHSP70-1, was constitutively overexpressed in tobacco to ascertain its role in plant stress response and tolerance (Cho and Hong, 2006).

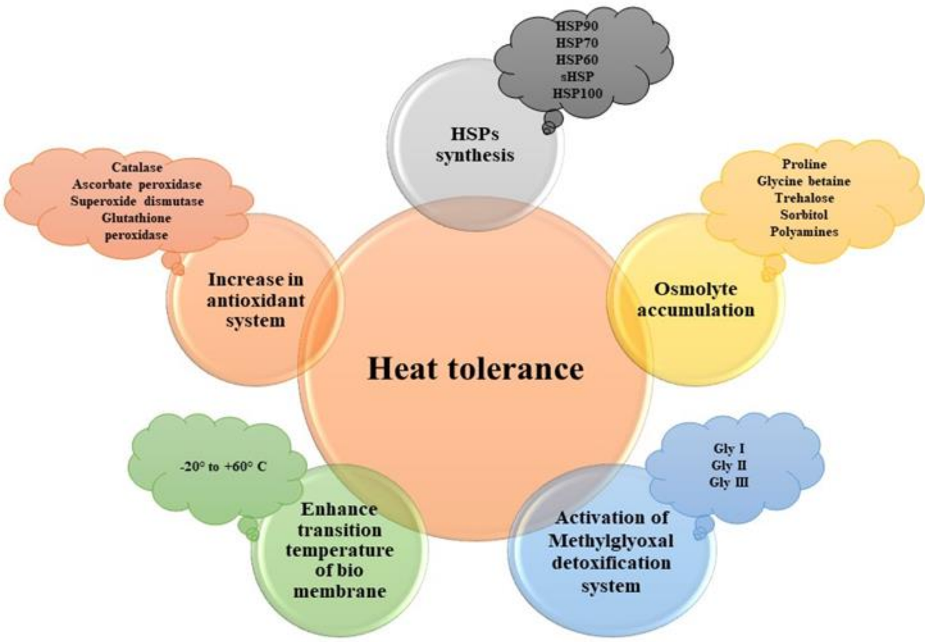


**Figure 3:** Heat tolerance mechanisms in plant

**6. Zinc oxide nanoparticles in alleviating heat stress in plants**

Zinc oxide nanoparticles rank third on the list of metal-containing nanoparticles, with an expected global annual output between 550 and 33,400 tons (Peng et al., 2017; Adeel et al., 2021). Zinc is an essential metal that is more effective in alleviating abiotic stresses. It plays a crucial role as a structural, regulatory and functional cofactor of various enzymes (Kareem et al., 2022). Additionally, zinc is beneficial in lowering ROS production and protecting cells from ROS toxicity. In contrast, Zn deficiency leads to a higher accumulation of ROS that can cause damage to plants (Sturikova et al., 2018). Zinc oxide nanoparticles due to their distinct physical and chemical characteristics, are most frequently used in various industries. Due to their wide range of advantageous effects on plants, n-ZnO are considered safe and highly efficient for many environmental stresses (Caldelas and Weiss, 2017). n-ZnO is particularly effective in absorbing UV light, enhancing antioxidant enzyme activity and increasing plant development and provide resistance to high-temperature stress (Kareem et., 2022) (Figure: 4). Additionally, plant morphology and physiological characteristics may be improved by Zn-based nanoparticle treatment under normal and stressed conditions (Mahmoud et al., 2020). In various plants under salt, drought, heat and heavy metal stress, it has been demonstrated that n-ZnO-mediate enhancement of enzyme activities, uptake of mineral nutrients and photosynthesis (Rizwan et al., 2019; Kareem et al., 2022).

Several studies support that zinc oxide nanoparticles ameliorate the effect of heat stress in plant tissues. Hassan and his co-workers, (2018) examined the role of zinc oxide nanoparticles to enhance tolerance against toxicity induced by heat stress in wheat plants. As a result, they revealed that the ZnONPs promote plant growth, grain yield, maintain stability of the plasma membrane and proteins, and enhance glutathione and antioxidant (SOD, POD, CAT) enzyme activity and ultimately limits $H_2O_2$ and MDA level in both wheat {Sids1 (heat tolerant) and Gimmeza7 (heat sensitive)} cultivars grown under high temperature stress. Similarly, heat stress tolerance was observed *Arabidopsis thaliana* when treated with ZnONPs, enhance GUS (β-glucuronidase) gene alleviation, maintain enzymatic reactions efficiency as well as stability of various cellular components. It also helps in the upregulation of heat stress related genes in *Arabidopsis* plants grown under high temperature stress (Wu and Wang, 2020). Further, Thakur and his colleagues, (2022) demonstrated the positive role of zinc oxide nanoparticles in wheat plants under high temperature stress. They explored that ZnONPs when applied at low concentrations have growth promoting effects. It also increases antioxidant enzyme (SOD, GPX, CAT) activity, phenolic content and maintain membrane stability and ultimately decrease MDA and $H_2O_2$ content in both wheat (Unnat PBW 343 and HD 296) cultivars grown under heat stressed conditions. Further, the combined effect of zinc oxide and titanium oxide nanoparticles on the aforementioned physiological processes was more than that when applied individually. Recently, the study was conducted on nanosized zinc oxide particles in alleviating heat stress induced damage in alfalfa seedlings. As a result, ZnONPs stimulate osmolyte content, antioxidant enzyme and prevent heat stress induce membrane damage and oxidative stress in alfalfa plants (Kareem et al., 2022).

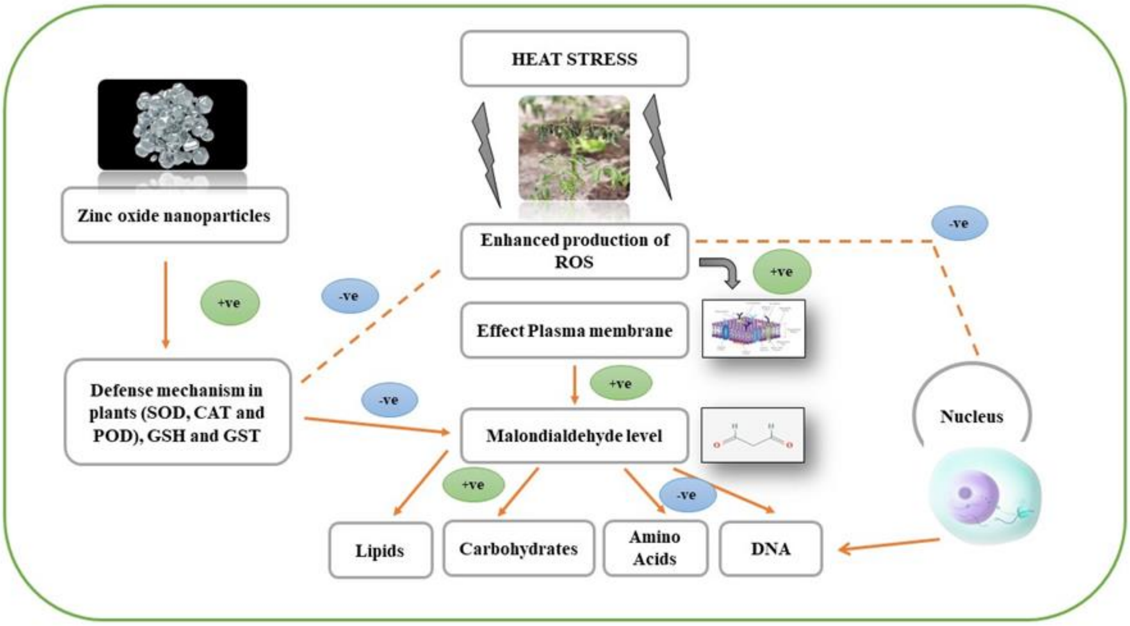


**Figure 4:** Alleviation of oxidative stress induced by high temperatures by zinc oxide nanoparticles (ZnO NPs)

**Table 1:** Effect of ZnO nanoparticles under heat stressed plants

| S.No. | Plants | ZnO NPs concentration | Method of exogenous application | Heat stress level | Effects of ZnONPs | References |
|---|---|---|---|---|---|---|
| 1. | *Triticum aestivum* L. var. Sids1 and Gimmeza7 | 0.25, 0.50, 0.75, 1.0 and 10 ppm | Foliar spray of ZnONPs | - | Enhance antioxidant enzyme (SOD, CAT, POD) activities and maintain bio-membrane and protein stability and alleviate oxidative stress induced by high temperatures | Hassan et al., 2018 |
| 2. | *Arabidopsis thaliana* (L.) Heynh. | 0.1, 0.5 and 1µg/mL | Culture seedlings in a medium containing ZnONPs | 37°C | Enhance efficiency of membrane reactions and upregulate heat stress related genes and inhibit lipid peroxidation | Wu and Wang, 2019 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 3. | *Triticum aestivum* L. var. Unnat PBW 343 and HD 296) | 1.5 ppm and 10 ppm | Seed priming with ZnONPs | 25°C and 32°C | Enhance seedling growth, germination, phenolic content and decrease MDA and $H_2O_2$ level | Thakur et al., 2021 |
| 4. | *Medicago sativa* L. | 90 mg/L | Foliar spray with ZnONPs | - | Stimulate antioxidant enzyme activity, maintain membrane stability and also inhibit ROS-induce oxidative stress | Kareem et al., 2022 |

## 7. Conclusion

Heat stress is a serious stress that has a negative impact on plant's morphological growth by interfering with its photosynthetic processes, which are caused by an increased amount of oxidative stress. The mechanisms of heat stress absorption, translocation, and accumulation in plants are still not fully understood. Nanotechnology has recently emerged as an evolutionary science that has given rise to a plethora of cutting-edge applications in the fields of energy, electronics, life science, and medicine. According to the studies, NPs have a favorable impact on the growth and development of plants. However, according to several research findings, treatment with ZnONPs protect plants against heat stress. Therefore, morphological features (such as root number, root shoot length, leaf area and number, and plant fresh and dry weight) may be improved in various plants at varying ZnONPs levels. Additionally, the use of zinc oxide nanoparticles enhance the enzymatic activity of plants under extreme temperatures, especially the activity of GPX, CAT, APX, and SOD. As a result, ZnONPs' exposure reduces the harmful effects of heat stress by enhancing photosynthesis as well as by lowering lipid peroxidation and cell wall degradation. Therefore, the primary focus should be on the mode of action of ZnONPs, their interference with biomolecules, and their effect on gene expression regulation in plants under heat stress. However, many unclear grey areas still exist that require explanation in order to use zinc oxide nanoparticles that can be beneficial for the plant's response mechanisms and tolerance to high temperature stress.

## References

1. Adeel, M., Ma, C., Ullah, S., Rizwan, M., Hao, Y., Chen, C., et al. (2019). Exposure to nickel oxide nanoparticles insinuates physiological, ultrastructural and oxidative damage: A life cycle study on Eisenia fetida. *Environmental Pollution*, *254*, 113032.
2. Aghamolki, M. T. K., Yusop, M. K., Oad, F. C., Zakikhani, H., Jaafar, H. Z., Kharidah, S., & Musa, M. H. (2014). Heat stress effects on yield parameters of selected rice cultivars at reproductive growth stages. *Journal of Food, Agriculture and Environment*, *12*(2), 741-746.
3. Ahamed, K. U., Nahar, K., Fujita, M., & Hasanuzzaman, M. (2010). Variation in plant growth, tiller dynamics and yield components of wheat (Triticum aestivum L.) due to high temperature stress. *Advances in Agriculture and Botanics*, *2*(3), 213-224.

4. Ahmad, M., Waraich, E. A., Skalicky, M., Hussain, S., Zulfiqar, U., Anjum, M. Z., et al. (2021). Adaptation strategies to improve the resistance of oilseed crops to heat stress under a changing climate: An overview. *Frontiers in plant science*, *12*, 767150.
5. Ahuja, I., de Vos, R. C., Bones, A. M., & Hall, R. D. (2010). Plant molecular stress responses face climate change. *Trends in plant science*, *15*(12), 664-674.
6. Akter, N., & Rafiqul Islam, M. (2017). Heat stress effects and management in wheat. A review. *Agronomy for sustainable development*, *37*(5), 1-17.
7. Almeselmani, M., Deshmukh, P. S., Sairam, R. K., Kushwaha, S. R., & Singh, T. P. (2006). Protective role of antioxidant enzymes under high temperature stress. *Plant science*, *171*(3), 382-388.
8. Asada, K. (2006). Production and scavenging of reactive oxygen species in chloroplasts and their functions. *Plant physiology*, *141*(2), 391-396.
9. Asthir, B., & Bhatia, S. (2014). In vivo studies on artificial induction of thermotolerance to detached panicles of wheat (Triticum aestivum L) cultivars under heat stress. *Journal of Food Science and Technology*, *51*(1), 118-123.
10. Auld, D. S. (2001). Zinc coordination sphere in biochemical zinc sites. *Zinc biochemistry, physiology, and homeostasis*, 85-127.
11. Baniwal, S. K., Bharti, K., Chan, K. Y., Fauth, M., Ganguli, A., Kotak, S., et al. (2004). Heat stress response in plants: a complex game with chaperones and more than twenty heat stress transcription factors. *Journal of biosciences*, *29*(4), 471-487.
12. Bita, C. E., & Gerats, T. (2013). Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. *Frontiers in plant science*, *4*, 273.
13. Boyer, J. S., & McLaughlin, J. E. (2007). Functional reversion to identify controlling genes in multigenic responses: analysis of floral abortion. *Journal of experimental botany*, *58*(2), 267-277.
14. Brayner, R., Dahoumane, S. A., Yéprémian, C., Djediat, C., Meyer, M., Couté, A., & Fiévet, F. (2010). ZnO nanoparticles: synthesis, characterization, and ecotoxicological studies. *Langmuir*, *26*(9), 6522-6528.
15. Caine, R. S., Yin, X., Sloan, J., Harrison, E. L., Mohammed, U., Fulton, T., et al. (2019). Rice with reduced stomatal density conserves water and has improved drought tolerance under future climate conditions. *New Phytologist*, *221*(1), 371-384.
16. Caldelas, C., & Weiss, D. J. (2017). Zinc homeostasis and isotopic fractionation in plants: a review. *Plant and Soil*, *411*(1), 17-46.
17. Chang, H. C., Tang, Y. C., Hayer-Hartl, M., & Hartl, F. U. (2007). SnapShot: molecular chaperones, Part I. *Cell*, *128*(1).
18. Charng, Y. Y., Liu, H. C., Liu, N. Y., Chi, W. T., Wang, C. N., Chang, S. H., & Wang, T. T. (2007). A heat-inducible transcription factor, HsfA2, is required for extension of acquired thermotolerance in Arabidopsis. *Plant physiology*, *143*(1), 251-262.
19. Chastain, D. R., Snider, J. L., Choinski, J. S., Collins, G. D., Perry, C. D., Whitaker, J., et al. (2016). Leaf ontogeny strongly influences photosynthetic tolerance to drought and high temperature in Gossypium hirsutum. *Journal of plant physiology*, *199*, 18-28.

20. Cho, E. K., & Hong, C. B. (2006). Over-expression of tobacco NtHSP70-1 contributes to drought-stress tolerance in plants. *Plant cell reports*, *25*(4), 349-358.
21. Das, A., & Das, B. (2019). Nanotechnology a potential tool to mitigate abiotic stress in crop plants. *Abiotic and biotic stress in plants*.
22. Das, K., & Roychoudhury, A. (2014). Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants. *Frontiers in environmental science*, *2*, 53.
23. Djanaguiraman, M., Prasad, P. V. V., & Al-Khatib, K. (2011). Ethylene perception inhibitor 1-MCP decreases oxidative damage of leaves through enhanced antioxidant defense mechanisms in soybean plants grown under high temperature stress. *Environmental and experimental botany*, *71*(2), 215-223.
24. Djanaguiraman, M., Prasad, P. V., & Seppanen, M. (2010). Selenium protects sorghum leaves from oxidative damage under high temperature stress by enhancing antioxidant defense system. *Plant Physiology and Biochemistry*, *48*(12), 999-1007.
25. dos Santos, T. B., Ribas, A. F., de Souza, S. G. H., Budzinski, I. G. F., & Domingues, D. S. (2022). Physiological Responses to Drought, Salinity, and Heat Stress in Plants: A Review. *Stresses*, *2*(1), 113-135.
26. Essemine, J., Ammar, S., & Bouzid, S. (2010). Impact of heat stress on germination and growth in higher plants: physiological, biochemical and molecular repercussions and mechanisms of defence. *Journal of Biological Sciences*, *10*(6), 565-572.
27. Farooq, M., Bramley, H., Palta, J. A., & Siddique, K. H. (2011). Heat stress in wheat during reproductive and grain-filling phases. *Critical Reviews in Plant Sciences*, *30*(6), 491-507.
28. Feng, B., Liu, P., Li, G., Dong, S. T., Wang, F. H., Kong, L. A., & Zhang, J. W. (2014). Effect of heat stress on the photosynthetic characteristics in flag leaves at the grain-filling stage of different heat-resistant winter wheat varieties. *Journal of Agronomy and Crop Science*, *200*(2), 143-155.
29. Fitter, A. H., & Hay, R. K. (2012). *Environmental physiology of plants*. Academic press.
30. Gupta, S. K., Rai, K. N., Singh, P., Ameta, V. L., Gupta, S. K., Jayalekha, A. K., et al. (2015). Seed set variability under high temperatures during flowering period in pearl millet (Pennisetum glaucum L. (R.) Br.). *Field Crops Research*, *171*, 41-53.
31. Hall, A. E. (2011). Accessed on 3rd June. *The mitigation of heat stress. Available online: http://www. planstress. com*.
32. Hancock, J. T., Desikan, R., & Neill, S. J. (2001). Role of reactive oxygen species in cell signalling pathways. *Biochemical Society Transactions*, *29*(2), 345-349.
33. HanumanthaRao, B., Nair, R. M., & Nayyar, H. (2016). Salinity and high temperature tolerance in mungbean [Vigna radiata (L.) Wilczek] from a physiological perspective. *Frontiers in Plant Science*, *7*, 957.
34. Harsh, A., Sharma, Y. K., Joshi, U., Rampuria, S., Singh, G., Kumar, S., & Sharma, R. (2016). Effect of short-term heat stress on total sugars, proline and some antioxidant enzymes in moth bean (Vigna aconitifolia). *Annals of Agricultural Sciences*, *61*(1), 57-64.
35. Hasanuzzaman, M., Nahar, K., & Fujita, M. (2013). Extreme temperature responses, oxidative stress and antioxidant defense in plants. *Abiotic stress-plant responses and applications in agriculture*, *13*, 169-205.

36. Hasanuzzaman, M., Nahar, K., Alam, M. M., Roychowdhury, R., & Fujita, M. (2013). Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. *International journal of molecular sciences*, *14*(5), 9643-9684.
37. Hassan, N. S., Salah El Din, T. A., Hendawey, M. H., Borai, I. H., & Mahdi, A. A. (2018). Magnetite and zinc oxide nanoparticles alleviated heat stress in wheat plants. *Current nanomaterials*, *3*(1), 32-43.
38. Hemantaranjan, A., Bhanu, A. N., Singh, M. N., Yadav, D. K., Patel, P. K., Singh, R., & Katiyar, D. (2014). Heat stress responses and thermotolerance. *Adv. Plants Agric. Res*, *1*(3), 1-10.
39. Högy, P., Poll, C., Marhan, S., Kandeler, E., & Fangmeier, A. (2013). Impacts of temperature increase and change in precipitation pattern on crop yield and yield quality of barley. *Food chemistry*, *136*(3-4), 1470-1477.
40. Hossain, A., Sarker, M. A. Z., Saifuzzaman, M., Teixeira da Silva, J. A., Lozovskaya, M. V., & Akhter, M. M. (2013). Evaluation of growth, yield, relative performance and heat susceptibility of eight wheat (Triticum aestivum L.) genotypes grown under heat stress. *International Journal of Plant Production*, *7*(3), 615-636.
41. Howarth, C. J. (2005). Genetic improvements of tolerance to high temperature. In M. Ashraf & P.J.C. Harris (Eds.), *Abiotic stresses–plant resistance through breeding and molecular approaches* (pp. 277–300).
42. Hu, C., Yang, J., Qi, Z., Wu, H., Wang, B., Zou, F., et al. (2022). Heat shock proteins: Biological functions, pathological roles, and therapeutic opportunities. *MedComm*, *3*(3).
43. Huang, L. J., Cheng, G. X., Khan, A., Wei, A. M., Yu, Q. H., Yang, S. B., et al. (2019). CaHSP16. 4, a small heat shock protein gene in pepper, is involved in heat and drought tolerance. *Protoplasma*, *256*(1), 39-51.
44. Huang, Y. C., Niu, C. Y., Yang, C. R., & Jinn, T. L. (2016). The heat stress factor HSFA6b connects ABA signaling and ABA-mediated heat responses. *Plant physiology*, *172*(2), 1182-1199.
45. Jagadish, S. V. K., Septiningsih, E. M., Kohli, A., Thomson, M. J., Ye, C., Redona, E., et al. (2012). Genetic advances in adapting rice to a rapidly changing climate. *Journal of Agronomy and Crop Science*, *198*(5), 360-373.
46. Jalil, S. U., & Ansari, M. I. (2019). Nanoparticles and abiotic stress tolerance in plants: synthesis, action, and signaling mechanisms. *Plant signaling molecules*, 549-561.
47. Jayawardena, D. M., Heckathorn, S. A., Bista, D. R., & Boldt, J. K. (2019). Elevated carbon dioxide plus chronic warming causes dramatic increases in leaf angle in tomato, which correlates with reduced plant growth. *Plant, Cell & Environment*, *42*(4), 1247-1256.
48. Johkan, M., Oda, M., Maruo, T., & Shinohara, Y. (2011). Crop production and global warming. *Global warming impacts-case studies on the economy, human health, and on urban and natural environments*, 139-152.
49. Kareem, H. A., Hassan, M. U., Zain, M., Irshad, A., Shakoor, N., Saleem, S., et al. (2022). Nanosized zinc oxide (n-ZnO) particles pretreatment to alfalfa seedlings alleviate heat-induced morpho-physiological and ultrastructural damages. *Environmental Pollution*, *303*, 119069.
50. Kaushal, N., Bhandari, K., Siddique, K. H., & Nayyar, H. (2016). Food crops face rising temperatures: an overview of responses, adaptive mechanisms, and approaches to improve heat tolerance. *Cogent food & agriculture*, *2*(1), 1134380.

51. Khan, S., Anwar, S., Ashraf, M. Y., Khaliq, B., Sun, M., Hussain, S., et al. (2019). Mechanisms and adaptation strategies to improve heat tolerance in rice. A review. *Plants*, *8*(11), 508.
52. Kohila, S., & Gomathi, R. (2018). Adaptive physiological and biochemical response of sugarcane genotypes to high-temperature stress. *Indian journal of plant physiology*, *23*(2), 245-260.
53. Koo, H. J., Park, S. M., Kim, K. P., Suh, M. C., Lee, M. O., Lee, S. K., et al. (2015). Small heat shock proteins can release light dependence of tobacco seed during germination. *Plant Physiology*, *167*(3), 1030-1038.
54. Kool, P. L., Ortiz, M. D., & van Gestel, C. A. (2011). Chronic toxicity of ZnO nanoparticles, non-nano ZnO and ZnCl2 to Folsomia candida (Collembola) in relation to bioavailability in soil. *Environmental Pollution*, *159*(10), 2713-2719.
55. Kumar, A., Sharma, S., Chunduri, V., Kaur, A., Kaur, S., Malhotra, N., et al. (2020). Genome-wide identification and characterization of Heat Shock Protein Family reveal's role in development and stress conditions in Triticum aestivum L. *Scientific reports*, *10*(1), 1-12.
56. Kumar, N., Shankhdhar, S. C., & Shankhdhar, D. (2016). Impact of elevated temperature on antioxidant activity and membrane stability in different genotypes of rice (Oryza sativa L.). *Indian Journal of Plant Physiology*, *21*(1), 37-43.
57. Kumar, R. R., Goswami, S., Shamim, M., Dubey, K., Singh, K., Singh, S., et al. (2017). Exploring the heat-responsive chaperones and microsatellite markers associated with terminal heat stress tolerance in developing wheat. *Functional & integrative genomics*, *17*(6), 621-640.
58. Kumar, S., Thakur, P., Kaushal, N., Malik, J. A., Gaur, P., & Nayyar, H. (2013). Effect of varying high temperatures during reproductive growth on reproductive function, oxidative stress and seed yield in chickpea genotypes differing in heat sensitivity. *Archives of Agronomy and Soil Science*, *59*(6), 823-843.
59. Kumar, V., Dwivedi, P., Kumar, P., Singh, B. N., Pandey, D. K., Kumar, V., & Bose, B. (2021). Mitigation of heat stress responses in crops using nitrate primed seeds. *South African Journal of Botany*, *140*, 25-36.
60. Lacerda, J. S., Martinez, H. E., Pedrosa, A. W., Clemente, J. M., Santos, R. H., Oliveira, G. L., & Jifon, J. L. (2018). Importance of zinc for arabica coffee and its effects on the chemical composition of raw grain and beverage quality. *Crop Science*, *58*(3), 1360-1370.
61. Lee, J. H., Hübel, A., & Schöffl, F. (1995). Derepression of the activity of genetically engineered heat shock factor causes constitutive synthesis of heat shock proteins and increased thermotolerance in transgenic Arabidopsis. *The Plant Journal*, *8*(4), 603-612.
62. Lippmann, R., Babben, S., Menger, A., Delker, C., & Quint, M. (2019). Development of wild and cultivated plants under global warming conditions. *Current Biology*, *29*(24), R1326-R1338.
63. Lobell, D. B., Schlenker, W., & Costa-Roberts, J. (2011). Climate trends and global crop production since 1980. *Science*, *333*(6042), 616-620.
64. López-Hernández, F., & Cortés, A. J. (2019). Last-generation genome–environment associations reveal the genetic basis of heat tolerance in common bean (Phaseolus vulgaris L.). *Frontiers in genetics*, *10*, 954.
65. Madan, P., Jagadish, S. V. K., Craufurd, P. Q., Fitzgerald, M., Lafarge, T., & Wheeler, T. R. (2012). Effect of elevated CO2 and high temperature on seed-set and grain quality of rice. *Journal of experimental botany*, *63*(10), 3843-3852.

66. Marschner, H. (Ed.). (2011). *Marschner's mineral nutrition of higher plants*. Academic press.
67. Martinez-Luscher, J., Chen, C. C. L., Brillante, L., & Kurtural, S. K. (2017). Partial solar radiation exclusion with color shade nets reduces the degradation of organic acids and flavonoids of grape berry (Vitis vinifera L.). *Journal of agricultural and food chemistry*, *65*(49), 10693-10702.
68. Mathur, S., & Jajoo, A. (2014). Effects of heat stress on growth and crop yield of wheat (Triticum aestivum). In P. Ahmad & M.R. Wani (Eds.), *Physiological mechanisms and adaptation strategies in plants under changing environment* (pp. 163-191). Springer: New York, NY.
69. Mishra, S. K., Tripp, J., Winkelhaus, S., Tschiersch, B., Theres, K., Nover, L., & Scharf, K. D. (2002). In the complex family of heat stress transcription factors, HsfA1 has a unique role as master regulator of thermotolerance in tomato. *Genes & development*, *16*(12), 1555-1567.
70. Mohammed, A. R., & Tarpley, L. (2010). Effects of high night temperature and spikelet position on yield-related parameters of rice (Oryza sativa L.) plants. *European journal of agronomy*, *33*(2), 117-123.
71. Morrow, G., & Tanguay, R. M. (2012). Small heat shock protein expression and functions during development. *The international journal of biochemistry & cell biology*, *44*(10), 1613-1621.
72. Mozafari, A. A., & Ghaderi, N. (2018). Grape response to salinity stress and role of iron nanoparticle and potassium silicate to mitigate salt induced damage under in vitro conditions. *Physiology and molecular biology of plants*, *24*(1), 25-35.
73. Nadeem, M., Li, J., Wang, M., Shah, L., Lu, S., Wang, X., & Ma, C. (2018). Unraveling field crops sensitivity to heat stress: Mechanisms, approaches, and future prospects. *Agronomy*, *8*(7), 128.
74. Nejatzadeh, F. (2021). Effect of silver nanoparticles on salt tolerance of Satureja hortensis l. during in vitro and in vivo germination tests. *Heliyon*, *7*(2).
75. Nievola, C. C., Carvalho, C. P., Carvalho, V., & Rodrigues, E. (2017). Rapid responses of plants to temperature changes. *Temperature*, *4*(4), 371-405.
76. Nosaka, Y., & Nosaka, A. Y. (2017). Generation and detection of reactive oxygen species in photocatalysis. *Chemical reviews*, *117*(17), 11302-11336.
77. Nover, L., Bharti, K., Döring, P., Mishra, S. K., Ganguli, A., & Scharf, K. D. (2001). Arabidopsis and the heat stress transcription factor world: how many heat stress transcription factors do we need? *Cell stress & chaperones*, *6*(3), 177.
78. Pan, T., Sun, X., Liu, Y., Li, H., Deng, G., Lin, H., & Wang, S. (2018). Heat stress alters genome-wide profiles of circular RNAs in Arabidopsis. *Plant molecular biology*, *96*(3), 217-229.
79. Parrotta, L., Faleri, C., Cresti, M., & Cai, G. (2016). Heat stress affects the cytoskeleton and the delivery of sucrose synthase in tobacco pollen tubes. *Planta*, *243*(1), 43-63.
80. Peng, Y. H., Tsai, Y. C., Hsiung, C. E., Lin, Y. H., & Shih, Y. H. (2017). Influence of water chemistry on the environmental behaviors of commercial ZnO nanoparticles in various water and wastewater samples. *Journal of hazardous materials*, *322*, 348-356.
81. Poudel, P. B., & Poudel, M. R. (2020). Heat stress effects and tolerance in wheat: A review. *Journal of Biology and Today's World*, *9*(3), 1-6.
82. Queitsch, C., Hong, S. W., Vierling, E., & Lindquist, S. (2000). Heat shock protein 101 plays a crucial role in thermotolerance in Arabidopsis. *The Plant Cell*, *12*(4), 479-492.

83. Rahman, M. A., Chikushi, J., Yoshida, S., & Karim, A. J. M. S. (2009). Growth and yield components of wheat genotypes exposed to high temperature stress under control environment. *Bangladesh Journal of Agricultural Research*, *34*(3), 360-372.
84. Rajput, V. D., Singh, R. K., Verma, K. K., Sharma, L., Quiroz-Figueroa, F. R., Meena, M., et al. (2021). Recent developments in enzymatic antioxidant defence mechanism in plants with special reference to abiotic stress. *Biology*, *10*(4), 267.
85. Rizwan, M., Ali, S., Ali, B., Adrees, M., Arshad, M., Hussain, A., et al. (2019). Zinc and iron oxide nanoparticles improved the plant growth and reduced the oxidative stress and cadmium concentration in wheat. *Chemosphere*, *214*, 269-277.
86. Rodríguez, M., Canales, E., & Borrás-Hidalgo, O. (2005). Molecular aspects of abiotic stress in plants. *Biotecnología Aplicada*, *22*(1), 1-10.
87. Saleem, M. A., Malik, W., Qayyum, A., Ul-Allah, S., Ahmad, M. Q., Afzal, H., et al. (2021). Impact of heat stress responsive factors on growth and physiology of cotton (Gossypium hirsutum L.). *Molecular Biology Reports*, *48*(2), 1069-1079.
88. Savicka, M., & Škute, N. (2010). Effects of high temperature on malondialdehyde content, superoxide production and growth changes in wheat seedlings (Triticum aestivum L.). *Ekologija*, *56*(1), 26-33.
89. Savin, R., Stone, P. J., Nicolas, M. E., & Wardlaw, I. F. (1997). Effects of heat stress and moderately high temperature on grain growth and malting quality of barley. *Australian Journal of Agricultural Research*, *48*, 615-624.
90. Saxena, R., Tomar, R. S., & Kumar, M. (2016). Exploring nanobiotechnology to mitigate abiotic stress in crop plants. *Journal of Pharmaceutical Sciences and Research*, *8*(9), 974.
91. Scharf, K. D., Berberich, T., Ebersberger, I., & Nover, L. (2012). The plant heat stress transcription factor (Hsf) family: structure, function and evolution. *Biochimica et Biophysica Acta (BBA)-Gene Regulatory Mechanisms*, *1819*(2), 104-119.
92. Sharma, P., Jha, A. B., Dubey, R. S., & Pessarakli, M. (2012). Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. *Journal of botany*, *2012*.
93. Spero, J. M., Devito, B., & Theodore, L. (2000). *Regulatory chemicals handbook*. CRC press.
94. Sturikova, H., Krystofova, O., Huska, D., & Adam, V. (2018). Zinc, zinc nanoparticles and plants. *Journal of hazardous materials*, *349*, 101-110.
95. Suwa, R., Hakata, H., Hara, H., El-Shemy, H. A., Adu-Gyamfi, J. J., Nguyen, N. T., et al. (2010). High temperature effects on photosynthate partitioning and sugar metabolism during ear expansion in maize (Zea mays L.) genotypes. *Plant Physiology and Biochemistry*, *48*(2-3), 124-130.
96. Swindell, W. R., Huebner, M., & Weber, A. P. (2007). Transcriptional profiling of Arabidopsis heat shock proteins and transcription factors reveals extensive overlap between heat and non-heat stress response pathways. *BMC genomics*, *8*(1), 1-15.
97. Takagi, D., Takumi, S., Hashiguchi, M., Sejima, T., & Miyake, C. (2016). Superoxide and singlet oxygen produced within the thylakoid membranes both cause photosystem I photoinhibition. *Plant Physiology*, *171*(3), 1626-1634.

98. Tan, W., wei Meng, Q., Brestic, M., Olsovska, K., & Yang, X. (2011). Photosynthesis is improved by exogenous calcium in heat-stressed tobacco plants. *Journal of plant physiology*, *168*(17), 2063-2071.
99. Taran, N., Storozhenko, V., Svietlova, N., Batsmanova, L., Shvartau, V., & Kovalenko, M. (2017). Effect of zinc and copper nanoparticles on drought resistance of wheat seedlings. *Nanoscale Research Letters*, *12*(1), 1-6.
100. Taratima, W., Chuanchumkan, C., Maneerattanarungroj, P., Trunjaruen, A., Theerakulpisut, P., & Dongsansuk, A. (2022). Effect of Heat Stress on Some Physiological and Anatomical Characteristics of Rice (Oryza sativa L.) cv. KDML105 Callus and Seedling. *Biology*, *11*(11), 1587.
101. Thakur, S., Asthir, B., Kaur, G., Kalia, A., & Sharma, A. (2022). Zinc oxide and titanium dioxide nanoparticles influence heat stress tolerance mediated by antioxidant defense system in wheat. *Cereal Research Communications*, *50*(3), 385-396.
102. Uikey, P., & Vishwakarma, K. (2016). Review of zinc oxide (ZnO) nanoparticles applications and properties. *International Journal of Emerging Technology in Computer Science & Electronics*, *21*(2), 239-42.
103. ul Haq, S., Khan, A., Ali, M., Khattak, A. M., Gai, W. X., Zhang, H. X., et al. (2019). Heat shock proteins: dynamic biomolecules to counter plant biotic and abiotic stresses. *International journal of molecular sciences*, *20*(21), 5321.
104. Ul Hassan, M., Rasool, T., Iqbal, C., Arshad, A., Abrar, M., Abrar, M. M., et al. (2022). Linking plants functioning to adaptive responses under heat stress conditions: a mechanistic review. *Journal of Plant Growth Regulation*, *41*(7), 2596-2613.
105. Uppal, R. K., Brill, R., & Bromfield, J. (2019). Effect of heat stress on canola grain yield and quality. *Barton: Grains Research and Development Corporation*.
106. Venkatachalam, P., Jayaraj, M., Manikandan, R., Geetha, N., Rene, E. R., Sharma, N. C., & Sahi, S. V. (2017). Zinc oxide nanoparticles (ZnONPs) alleviate heavy metal-induced toxicity in Leucaena leucocephala seedlings: a physiochemical analysis. *Plant Physiology and Biochemistry*, *110*, 59-69.
107. Vignjevic, M., Wang, X., Olesen, J. E., & Wollenweber, B. (2015). Traits in spring wheat cultivars associated with yield loss caused by a heat stress episode after anthesis. *Journal of Agronomy and Crop Science*, *201*(1), 32-48.
108. Vinocur, B., & Altman, A. (2005). Recent advances in engineering plant tolerance to abiotic stress: achievements and limitations. *Current opinion in biotechnology*, *16*(2), 123-132.
109. Wagner, D., Przybyla, D., op den Camp, R., Kim, C., Landgraf, F., Lee, K. P., et al. (2004). The genetic basis of singlet oxygen induced stress responses of Arabidopsis thaliana. *Science*, *306*(5699), 1183-1185.
110. Wang, F., Jing, X., Adams, C. A., Shi, Z., & Sun, Y. (2018). Decreased ZnO nanoparticle phytotoxicity to maize by arbuscular mycorrhizal fungus and organic phosphorus. *Environmental Science and Pollution Research*, *25*(24), 23736-23747.
111. Wang, K., Zhang, X., Goatley, M., & Ervin, E. (2014). Heat shock proteins in relation to heat stress tolerance of creeping bentgrass at different N levels. *PLoS One*, *9*(7).
112. Wang, Q. L., Chen, J. H., He, N. Y., & Guo, F. Q. (2018). Metabolic reprogramming in chloroplasts under heat stress in plants. *International journal of molecular sciences*, *19*(3), 849.

113. Wang, Y., Ying, J., Kuzma, M., Chalifoux, M., Sample, A., McArthur, C., et al. (2005). Molecular tailoring of farnesylation for plant drought tolerance and yield protection. *The Plant Journal*, *43*(3), 413-424.
114. Waqas, M. A., Wang, X., Zafar, S. A., Noor, M. A., Hussain, H. A., Azher Nawaz, M., & Farooq, M. (2021). Thermal stresses in maize: effects and management strategies. *Plants*, *10*(2), 293.
115. Waraich, E. A., Hussain, A., Ahmad, Z., Ahmad, M., & Barutçular, C. (2022). Foliar application of sulfur improved growth, yield and physiological attributes of canola (Brassica napus L.) under heat stress conditions. *Journal of Plant Nutrition*, *45*(3), 369-379.
116. Warland, J. S., McDonald, M. R., & McKeown, A. M. (2006). Annual yields of five crops in the family Brassicacae in southern Ontario in relation to weather and climate. *Can. J. Plant Sci*, *86*, 1209-1215.
117. Wheeler, T., & Von Braun, J. (2013). Climate change impacts on global food security. *Science*, *341*(6145), 508-513.
118. Wu, J., & Wang, T. (2020). Synergistic effect of zinc oxide nanoparticles and heat stress on the alleviation of transcriptional gene silencing in Arabidopsis thaliana. *Bulletin of environmental contamination and toxicology*, *104*(1), 49-56.
119. Xu, S., Li, J., Zhang, X., Wei, H., & Cui, L. (2006). Effects of heat acclimation pretreatment on changes of membrane lipid peroxidation, antioxidant metabolites, and ultrastructure of chloroplasts in two cool-season turfgrass species under heat stress. *Environmental and Experimental Botany*, *56*(3), 274-285.
120. Yadav, S., Modi, P., Dave, A., Vijapura, A., Patel, D., & Patel, M. (2020). Effect of abiotic stress on crops. In M. Hasanuzzaman, M. Fujita, M.C.M.T. Filho & T.A.R. Nogueira (Eds.), *Sustainable crop production*. IntechOpen.
121. Zandalinas, S. I., Balfagón, D., Arbona, V., & Gómez-Cadenas, A. (2017). Modulation of antioxidant defense system is associated with combined drought and heat stress tolerance in citrus. *Frontiers in Plant Science*, *8*, 953.
122. Zhang, C. X., Feng, B. H., Chen, T. T., Fu, W. M., Li, H. B., Li, G. Y., et al. (2018). Heat stress-reduced kernel weight in rice at anthesis is associated with impaired source-sink relationship and sugars allocation. *Environmental and experimental botany*, *155*, 718-733.
123. Zhang, W., Wang, J., Huang, Z., Mi, L., Xu, K., Wu, J., et al. (2019). Effects of low temperature at booting stage on sucrose metabolism and endogenous hormone contents in winter wheat spikelet. *Frontiers in Plant Science*, *10*, 498.
124. Zhu, J. K. (2016). Abiotic stress signaling and responses in plants. *Cell*, *167*(2), 313-324.
125. Źróbek-Sokolnik, A. (2012). Temperature stress and responses of plants. In *Environmental adaptations and stress tolerance of plants in the era of climate change* (pp. 113-134). Springer, New York, NY.