Chapter

Effects of High Temperature on Crops

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Abstract

The effect of high-temperature situations leads to a significant reduction in yield. The elevated temperature on crops is expected to have a widespread negative effect as a consequence of global warming. Meanwhile, the global population is rapidly increasing and is predicted to be 11 billion in 2100. An increase in 70% of global food production is a challenging task to feed the increasing population. Increasing the food crop yield is crucial to meet the global food demand and ensuring food security. An increase in high temperature every year due to global warming and an increase in greenhouse gases leads to a rise in temperature. The rise in temperature significantly affects the yield; so, it is important to understand the mechanism and how to counteract high temperature on food crops. It is also important to neutralize the effect of high temperature on food crops and to increase the yield by minimizing the effect of high temperature and developing heat resistant or tolerant variety. It is essential to develop heat-tolerant crops or transgenic food crops that can assure great yield and food security for future generations. It is essential to examine the metabolic, physiological, and molecular mechanisms of food crops to have an enhanced understanding of high temperature and their effects on crops.

Keywords: heat stress, high temperature, photosynthesis, pollen and root

1. Introduction

Agricultural productivity is prone to change in temperatures. Knowledge of climate change, specifically high temperatures, is essential for agronomists, decision-makers, and crop producers to ensure food security across the globe [1]. Crops thrive at their optimum growth temperatures. However, elevation in temperature level predominantly influences plants' physiological processes, especially photosynthesis, transpiration, respiration, and yield. High temperature causes declining yields in major food crops, which is a major concern for depreciating agricultural productivity [2, 3]. Temperature is classified as minimum, optimum and maximum, and it has been predicted that the temperature will rise 2–5°C in the future climate in 2100 (IPCC, 2014) [4–6]. Agnolucci et al. [7] have demonstrated the significance and impact of climate change with different statistical patterns in 18 crops that contribute

70% of the land and 65% of calorific value. In conclusion, we emphasize the yield disparity in the primary crop is associated with high temperature [8].

The maximum threshold temperature for various crops differs. However, high temperatures above 35°C can cause damage to rice crops. Evident injuries were observed due to high temperatures in different developmental stages. Recent studies exposed that sorghum pistils and pearl millet both are similarly sensitive to high temperatures [9]. Moreover, Zhao et al. [1] have investigated and concluded that the rise in global temperature leads to global yield loss in four significant food crops. In addition, it also raises concern about the increasing temperature, and reduced yield should be neutralized with modern and sustainable modern agricultural techniques to fend off global hunger and to meet the prospective food requirement. Global warming due to greenhouse gas (GHG) emissions, is considered a significant threat to global agriculture productivity [10]. It is evaluated that without the use of CO_2 fertilization, efficient solution, genetic transformation, each 1°C rise in the global

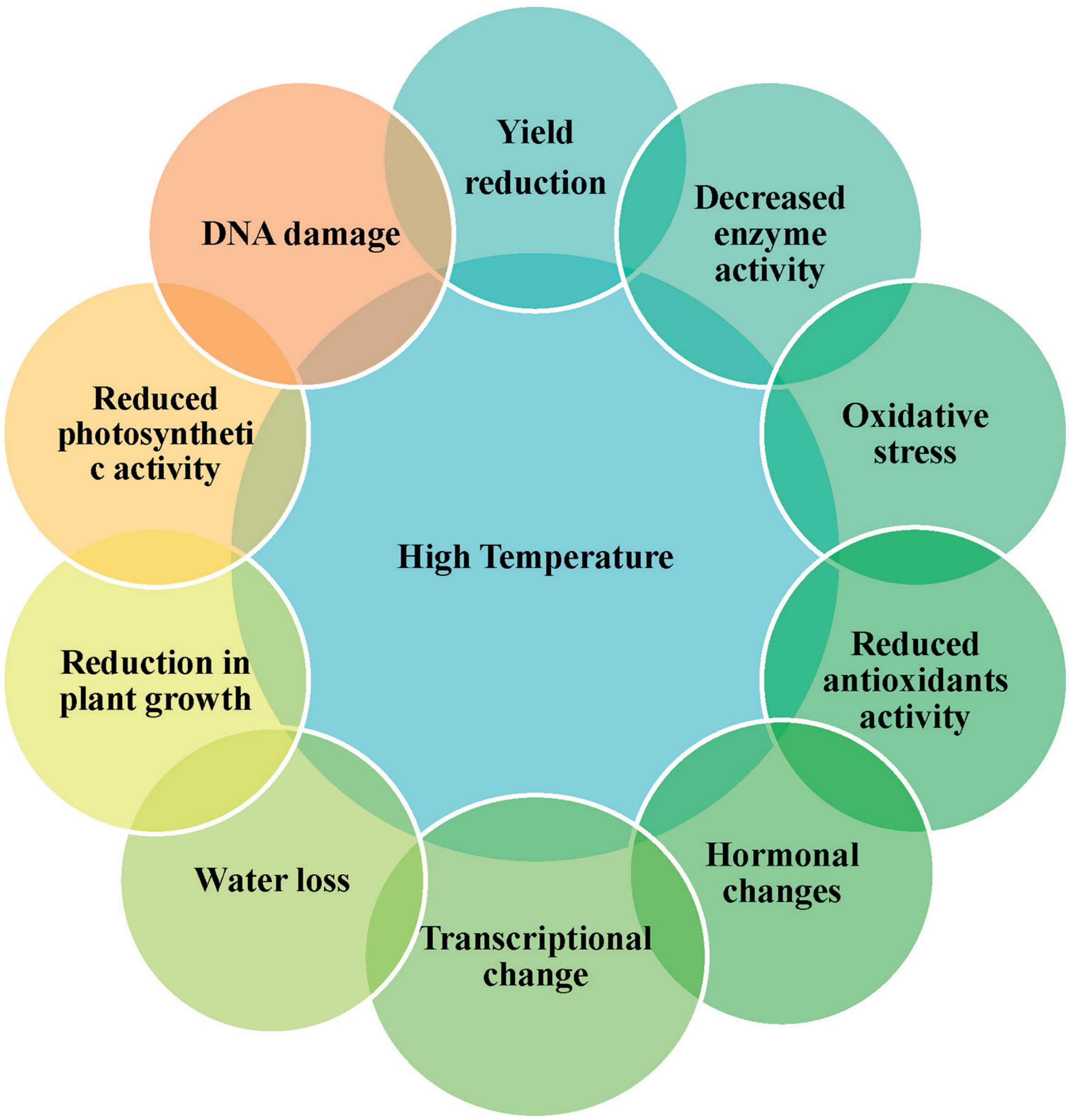

Figure 1.
High-temperature influences on crops.

mean temperature reduces global maize yield by 7.4%, wheat yield by 6.0%, rice yield by 6.2%, overall milled rice by 7.1–8.0%, head rice by 9.0–13.8% and overall milling profit by 8.1–11.0% and soybean yield by 3.1% [1, 11]. According to Food and Agriculture Organization (FAO) data, the relative rates of increase in yield for major cereal crops are reducing. However, crop productivity must be increased as the population is projected to reach 11 billion in 2100 (UN Population Division report) [12] and about a 70% increase in global agricultural productivity is essential; increase in 2°C or increase in the average temperature could lead to 20–40% reductions in cereal grain output, notably in Asia and Africa [13]. The increasing global warming provokes the weather pattern, leading to an increase in global temperature by 2.0–3.5°C in all regions as reported in the fifth assessment report (AR5) by the Intergovernmental Panel of Climatic Change (IPCC, 2018) it will reach 2.5–5.8°C before the 2100 s [6, 14]. High temperature during grain-filling has a significant effect on sunflower seeds and oil constituents [15]. In addition, it also reduces the linoleic acid content in numerous oilseed oils [16]. It also reduces the oil content, seed yield, and speeds up seed maturity as a consequence, erucic acid over seed development was influenced **Figure 1** [17].

2. Stage and intensity

High temperature limits the yield and affects various growth stages in plants. The reproductive stage is the most vulnerable phase of the crop's entire lifespan; this vulnerability during the reproductive stage leads to significant depletion in seed set and crop yield [9, 18]. Numerous food crops such as rice, wheat, soybean, maize, cotton, sorghum, and tomato are tremendously vulnerable to high temperatures [19]. Intense high temperature causes pollen abortion resulting in incomplete pollination. The interactions and stability between pollen and pistil during high temperatures lead to successful reproduction. But pollen and pistil both are extremely susceptible to high-temperature [20]. Crops have a variety of alternatives for resisting, minimizing, and surviving high temperatures during flowering. Plants can survive in high temperatures by keeping a cooler canopy through enhanced transpiration [9]. An elevated temperature could disturb numerous metabolic processes that take place in guard cells, as a result of high temperature; the stomatal response is frequently influenced by transpiration rate, photosynthetic rate, plant water status, and vapor pressure deficit [21]. High temperature considerably influences the crops by affecting several physiological injuries like leaf abscission, leaf scorching, senescence, and root and shoot growth limitation that subsequently leads to a reduction in yield. Moreover, the impact of high temperature affects photosynthetic membranes followed by ion leakage, enlargement of grana stacks, and aberrant stacking. By downregulating particular genes in carbohydrate metabolism, high temperature alters the activities of carbon metabolic enzymes, starch accumulation, and sucrose production. High temperature increases certain essential phytohormones such as abscisic acid, ethylene, and salicylic acid and reduces a few like gibberellic acid, cytokinin, and auxin; it furthermore leads to the fabrication of reactive oxygen species [4]. In addition, the high temperature throughout the day is properly not reported. However, the progressive rise in night temperature needs to be scrutinized considering that it causes prior to time of day of anthesis in cereal grains like rice crop.

3. Changes in mechanism under temperature stress

3.1 Effects of high-temperature stress

Plants endure various factors during growth and development, and high-temperature stress is one of the major abiotic factors that adversely affect crop production. High-temperature stress causes risk at different growth stages and ultimately reduce the yield by affecting the physiological mechanism [22]. The seedling stage of crops is susceptible to high-temperature stress in rice, mungbean, wheat [23, 24] and the reproductive stage in rice, wheat, and other cereals [25, 26]. High temperature modifies cells' morphogenetic structure, leading to a decrease in cell size, enhancing stomatal density and cell membrane permeability, inflating xylem vessels, and impairing mesophyll cells [27].

High-temperature stress causes various physiological changes in crops during the different growth stages and germination is affected at the initial stage. The impact of temperature on seeds has decreased seed germination percentage, plant emergence, poor seedlings vigor, abnormal seedlings, and decrease radicle and plumule growth [4]. Seed germination is inhibited under high temperatures through the stimulation of abscisic acid biosynthesis. Exposure to high temperatures reduces plant height, total biomass, and the number of tillers. In wheat, the germination rate was completely inhibited and caused cell death and the embryo for seedlings establishment rate was additionally decreased. The morphophysiological characteristics such as phenology, plant water relations, dry matter partitioning, and shoot growth were restricted by heat stress in bean plants [28]. In some plants, it reduces total phenological duration, shorter grain filling period, and diminishes the germination period. The loss of cell water content due to high temperature eventually decreases the cell size and growth. In response to high temperature, the net assimilation rate was reduced, and it was directly associated with plant growth. Elevated temperature causes programmed cell death in specific cells or tissues as long as the denaturation of proteins. In addition, the high temperature for a prolonged period might cause gradual death; these injuries may lead to the shedding of leaves, abortion of flowers, or even death of the whole plant [29]. Furthermore, high temperature enhances the evapotranspiration during vegetative and reproductive stages ration which limits plant's water availability and uptake, which influences dehydration that reduces growth at the organ level as well as the whole plant level [30].

3.2 Root physiology

Root size and morphology play a vital role in plant water, and nutrient uptake, whereas the plant root system requires the optimal temperature to grow, if it exceeds the normal temperature it may change the uptake [31]. The temperature of the root system is lower when compared to the shoot. In addition, the optimum root temperature may vary across plant species [32]. Exposure to high temperatures (>29°C) leads to a decrease in primary root length, lateral root density, and root growth in sunflower crops [32, 33]. Even though species share the same environment, their root system architecture (RSA) may differ from species to species by the changes in soil temperatures [34, 35]. In some plants, the increased temperature may produce an expanded root system, whereas, in adult maize plants, it suppresses the lateral root growth by developing the long axial root to take up water from deep soil layers. Similarly, at increased temperature, the initiation and elongation of adventitious and lateral roots were inhibited [36] in potatoes. Swelling of root cap meristem and blends in root tip were found on potatoes [37] with the rise in soil temperature. Root zone temperature in Sorghums causes a decreased rate of cell production and root elongation. Overall, these changes by the high temperature hinder the root growth with a decreased rate of cell division [38]. The impact of elevated temperature on the formation of root growth in lupine species was studied at the initial and lateral stages. Temperature modifies the growth through altering the root architecture [39]. On the other hand, root respiration could vary based on the temperature range. During this root respiration process, cells uptake the oxygen which is surrounded in the spaces among the soil particles at the root zone, increasing with every 10°C on soil temperature, where the solubility of oxygen is in contrast to temperature. This increased requirement for oxygen leads to root hypoxia [32]. Reactive oxygen species (ROS) produced in excess under high-temperature stress results in oxidative stress [40]. The increase in ROS production includes hydrogen peroxide (H_2O_2), superoxide free radicals (O_2^-), and lipid peroxidation, which leads to the enhancement of cell membrane damage [41, 42]. To prevent the effect of ROS, plants produce antioxidant enzymes, such as catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), glutathione reductase (GR), dehydroascorbate reductase (DHAR), and glutathione S transferase (GST), and nonenzymatic antioxidants such as anthocyanin, flavonoids, carotenoids, and ascorbic acid (AA) that protect crop growth from various other stresses also. Overall, the high temperature on root growth of plants either be promotive, inhibitory, or first stimulatory and then inhibitive once the optimum temperature is crossed [14].

3.3 Leaf physiology

High-temperature stress showed various morphological symptoms in shoots such as sunburns of leaves and twigs, scorching of leaves and stems, leaf senescence, root and shoot inhibition, fruit damage, and discolorization, which finally caused a decrease in crop productivity. In some cases, high temperature causes drying and rolling of leaves, scorching of leaf tips and margins, and necrosis was found in sugarcane. Leaf photosynthesis is considerably affected by extreme temperatures. The components of photosynthetic metabolism processes are sensitive to temperature [43]. Chloroplast is substantially affected by high temperature during the photosynthesis process including swelling of grana stacks and abnormal stacking [44]. However, chloroplast plays an important role to activate the adaptive process to these extreme conditions [45]. Studies reported that high temperature is associated with the upregulation of two hundred chloroplast-related genes in model rice plants [46]. To evaluate the heat-resistant crops, stay-green physiological traits were used to affirm the mechanism of heat damage interacting with Chl adaptability, antioxidant and photosynthetic capacity. Stay-green genotypes are highly associated with chlorophyll metabolism, these genes encode magnesium dechelatase, which is involved in the degradation of chlorophyll. A chloroplast targeted DnaJ protein (SlCDJ2) which is located in the thylakoids and stroma, protects the Rubisco activity and regulates the CO_2 assimilation in tomato plants to cope with heat stress [47, 48]. In lettuce seedlings, the application of exogenous spermidine regulates the stability of mitochondrial and chloroplast structure. The stomatal opening and density are inhibited by exogenous spermidine, thus leading to an increase in the photosynthetic rate and biomass of lettuce. It significantly alleviates the high-temperature stress and protects the leaves from damage [49].

3.4 Reproductive physiology

The reproductive tissues of plants are more susceptible to elevated temperatures among the other plant tissues, which result in a yield penalty. At the time of reproduction in crops, a short period of extreme temperature could significantly increase flower abortion. Similarly, heat spells at reproductive stages may not produce flowers, or flowers do not produce fruit or seed [29]. Reproductive development in various species is reported to be sensitive under high-temperature stress that disrupts/affects meiosis in male and female gametes, pollen germination and pollen tube growth, pollen/pistil interactions, ovule viability, number of pollen grains, formation of endosperm and embryo development, fertilization, and post-fertilization processes. The effect of high-temperature day/night causes an impact on pollen viability in crops including sorghum, wheat, rice, canola, groundnut, common bean, and soybean [50]. Due to high-temperature stress ROS accumulation, membrane integrity, changes in protein, carbohydrate, and lipid mechanism, and alters in phospholipids profiles in the mature pollen causes loss of pollen viability [41, 51, 52]. High temperature (33°C) subsequently reduces anther dehiscence and pollen fertility rate; it causes a decrease in the number of pollen on stigma which leads to decreased fertilization, spikelet fertility, and sterile seed in rice [53]. The process of anther dehiscence prompts to dispense mature pollen grains from the locules of the anther is responsible for pollination. During this process, the anther wall is opened by degeneration of anther tissues called septum and stomium [54]. The proper release of pollen from the anther needs expanding of endothecial cells and also strengthening and thickening of cell walls. In common bean and rice plants, the anther indehiscence happens due to high temperature, thus disrupting the pollen release. In addition, the inhibition of thickening in the endothecium cell and dissolution of interlocular septa in common bean and tomato were observed, which lead to failure in anther dehiscence and pollination [55, 56]. Heat treatment during panicle initiation significantly reduced the yield through a decreased number of spikelets per panicle and seed setting percent in rice. However, the heat susceptible variety showed poor seed setting percent mainly associated with spikelet fertility which is induced by a decrease in anther dehiscence, reduced pollen viability, and poor shedding of anthers [57]. Exposure to heat stress for a short period alters pollen development during meiosis. Increased spikelet sterility might decrease pollen germination due to high night temperature in rice. Other intrinsic factors of pollen development are carbohydrate metabolism and partitioning [50]. Reduced pollen viability is directly associated with sugar level accumulation in developing anther and pollen walls.

Plant female reproductive organ pistil/carpel includes stigma, style, and ovary. Female gametophyte occurs in the ovary, and the nutritional support and shelter were provided by sporophytic maternal tissue. The development of female gametophytes occurs in two phases: megasporogenesis and megagametogenesis. Generally, it consists of three antipodal cells, two synergid cells, one egg cell, and one central cell. Male reproductive development is susceptible to high-temperature stress when compared to female reproductive development. However, heat stress affects female reproductive development it causes degenerated eggs and synergids, embryo sac malformations, less number of ovules, increase ovule abnormalities and abortion, decrease in the size of transmitting tissue present in the style, and dried and drooping stigma, style and ovary [41, 51]. Heat stress interrupts the pollen-pistil interactions by changing the structural positioning of anthers and stigma. In response to high temperature, the maturation of stigma/style changes it leading to modification in cell division and elongation [58]. Heat stress affects reproductive function and has been reported in many studies. For example, in *Brassica* it decreases the fertility of microgametophytes, in tomato, it impaired meiosis in the male gametophyte which causes pollen germination and pollen tube growth. To counteract this problem, variations in genotypes of various pollen traits were selected to study the heat-tolerant genotypes. In recent study, 12 cultivars of *Brassica napus* L. were used to study heat tolerance based on pollen traits such as pollen germination, pollen viability, and pollen tube growth [59]. Abortion of flowers, young pods, and loss of seed numbers in soybean was observed under high-temperature stress [60]. Even mild heat stress (30°C/25°C) for 5 days, as long as the loss of tapetum differentiation and injuries to the microsporogenesis process was observed in Barley. The tapetum cells consist of enough mitochondria and a high metabolic activity under optimum growing temperature which in turn production of reactive oxygen species (ROS). But the plants exposed to high temperature provokes ROS homeostasis in the tapetum and microspores which cause accumulation of ROS initiation to lead to unplanned programmed cell death in tapetal cells through stimulating the membrane damage, lipid peroxidation, decreased transcription, and translation [61]. Extreme temperatures shortened the plant growing days, which resulted in early maturity, a lower life cycle, and accumulation of lesser biosynthetic products which eventually decreased grain development. The duration of grain filling decides the grain development which is related to grain yield. Crop yield is associated with temperature because even a 1.5°C increase in temperature might cause drastic yield loss in crops. The grain yield was mostly affected via the phenological development process. Many reports show that high temperatures cause a reduction in yield in various crops including pulses, cereals, and oil-yielding crops [29, 62]. Filled seed weight and size were ultimately reduced due to heat stress which directly affects grain yield in sorghum was reported. In addition, heat stress not only affects the yield, but it also correlates to reduce the quality of grain in barley. The concentration of non-structural carbohydrates, starch, raffinose, fructose, and lipids was reduced in barley grain, whereas in okra, the fiber content was decreased [63].

4. Physiological traits associated with high temperature stress

4.1 Cell membrane integrity

In response to heat stress, various physiological modifications might cause cell membrane damage. Exposure to heat stress causes cell membrane damage resulting from denaturing membrane protein, and inactivating enzyme, which leads to cell membrane permeability and integrity causing reduced ion flux, leakage of electrolytes, changes in relative water content, production of toxic compounds, and interruption in homeostasis that result in decreased cell viability. Reduced cell viability ceased plant growth and prompted leaf wilting, leaf abscission, and leaf area reduction [64]. Among the other physiological factors, membrane permeability and relative cell injury were affected at different growth stages under heat stress. Cell membrane stability differs with plant tissue, age, growing season, growth stage, plant species, and severity of heat stress. To measure electrolyte leakage from the cell membrane in an aqueous medium is used to determine the cell membrane malfunction in response to heat stress [65]. Leaf membrane stability index (MSI) was estimated in leaf tissues (100 mg) heated at 40°C for 30 min (C1) and 100°C for 10 min (C2) in water bath.

The conductivity of samples is measured by the using conductivity bridge and MSI was calculated using the following formula (MSI = [1 – (C1/C2)] × 100) [66].

4.2 Leaf gas exchange parameters

Transpiration is the physiological process that occurs in crops where the net radiation energy is converted into heat, underneath physiological control through alters in the stomatal aperture. In plants, photosynthesis and stomatal conductance play a vital role in all aspects. The leaf gas exchange parameters are commonly measured using a portable photosynthesis system including LI-6400 and LI-6800 (LI-COR®, Lincoln, USA), the CIRAS-3 (PP systems, Amesbury, USA), the GFS-3000 (Walz Gmbh, Effeltrich, Germany), and the iFL (Opti-sciences, Hudson, USA) [21]. However, decrease root hydraulic conductance in response to soil drying is an important control mechanism of stomatal closure. Low leaf water potential induced by high transpiration rates results in decreased stomatal conductance. The potential of crops to maintain CO_2 assimilation rate and leaf gas exchange under high temperatures is accompanied by heat tolerance. The water status in the leaf, stomatal conductance, and intercellular CO_2 concentration are affected by high temperatures [67]. Stomatal closure under high temperature is a distinct reason for impaired photosynthesis which disturbs the intercellular CO_2. In many plant species, the stomatal conductance (g_s) and net photosynthetic rate decline due to mild heat stress; it was caused due to reduced activation of Rubisco. High temperature affects vapor pressure density (VPD) but it may change hydraulic conductance and water supply to the leaf area [68]. Higher stomatal conductance accelerates transpirational cooling and canopy temperature depression (CTD). Increased stomatal conductance and related leaf cooling contribute to heat tolerance against high temperature; these conclude a positive interaction between stomatal conductance and the yield of wheat under extreme temperatures [69].

4.3 Chlorophyll pigments

Chlorophyll biosynthesis in plastids plays an important role in light-harvesting was high impact due to high-temperature stress. In addition, the high-temperature stress causes impairment and degradation of chlorophyll pigments in plastids. Chlorophyll biosynthesis was inhibited due to high temperature stress through the eradication of enzymes involved in the mechanism of chlorophyll biosynthesis. The enzymatic activity of 5-aminolevulinate dehydratase (ALAD), the first enzyme of pyrrole biosynthesis was decreased under high-temperature stress [70]. In some cases, the barley seedlings pre-treated with temperature for 4 h or 8 h prohibited the chl biosynthesis which result in reduced protochlorophyllide. Similarly in wheat, the protochlorophyllide (Pchlide) synthesis, Pchlide oxidoreductase, and porphobilinogen deaminase are eventually affected. These conclude that high temperature causes reduction in chlorophyll a, total chlorophyll content, sucrose content, and in contrast, it increases the reducing sugar content and leaf soluble sugar was observed in soybean [29]. However, in celery leaves, chlorophyll biosynthesis was inhibited under extreme temperatures due to the down-regulation of mRNA genes associated with biosynthesis [71]. Chlorophyll content was measured in the leaf using acetone by spectrophotometrically measuring the absorption at 663, 652, and 645 nm [72]. Non-destructively chlorophyll can be measured using the handheld devices such as SPAD chlorophyll meter (SPAD 502 Plus Chlorophyll Meter, Konica Minolta, Japan)

[73], CCM Chlorophyll content meter (CCM-200plus *Chlorophyll Content Meter,* Opti-Sciences, Inc., USA), CL-01 Chlorophyll Meter (Hansatech Instruments Ltd., United Kingdom). The NIR reflectance spectroscopy can be a promising methodology to measure/predict chlorophyll and other pigments under field conditions [74].

4.4 Heat shock proteins (HSPs)

Production of heat shock proteins in plants to protect the cell from various stress factors. These types of proteins were not found in non-stressed plants [75]. These proteins are categorized into high molecular (68kD to 110kD) and low molecular weight proteins (15kD to 27kD). Low molecular weight HSPs are found in higher plants which are plant-specific proteins whereas high molecular weight is found in all types of plants. Some heat shock proteins are known as molecular chaperones but not all HSPs are molecular chaperones [76]. Molecular chaperones are proteins that generate during high-temperature stress. Chaperones bind to denature proteins or unfolded proteins to make them stabilize and protect from thermal aggregation. Heat shock proteins regulate cellular homeostasis by eliminating harmful proteins which rise from aggregation and misfolding [69]. Some classical HSPs show chaperone activity to protect the protein denaturation from thermo-aggregation. The non-classical heat shock proteins consist of plastid protein synthesis elongation factor (EF-Tu) and peptidyl-prolyl cis/trans isomerases that produce low molecular weight proteins and provide heat resistance. Under heat stress, the EF-Tu gene in transgenic wheat exhibits reduced thermo-aggregation and decreased thylakoid membrane damage moreover increasing the photosynthetic system [77]. The chloroplast localized HSPs provide heat resistance to the photosynthetic electron transport chain in isolated chloroplast. Some studies revealed that small heat shock proteins pertain with thylakoid and protect O_2 evolution and oxygen-evolving complex proteins of PSII from heat stress. The heat treatment in tomato leaves protects PSII from temperature-dependent oxidative stress by chloroplast heat shock protein HSP21 present in chloroplast. In addition, the chloroplast HSPs may not repair the stress-induced damage but they avoid damage [78].

4.5 Optimal light and dark reaction

High-temperature stress is directly associated with light intensity which damages the photosystem. Heat stress alters cell respiration and photosynthesis, which shortens the life cycle and reduces crop production [79]. Thermal stress modified the structural changes of chloroplast protein complexes and decreased the activity of enzymes. Light-dependent chemical reactions occur in the thylakoid membrane and carbon metabolism takes place in the stroma, which is an important portion, that is damaged in response to high temperature. Increased temperature of the leaf and photon flux density impacts the thermo-tolerance adjustment of photosystem (PS) II. For measuring the quantum yield of PSII mostly modulated fluorimeters are used such as the Mini-PAM II by Walz, FMS2 by Hansatech instruments (King's Lynn, UK), the OS5+ by Opti-Sciences, or the FluorPen FP 100-MAX of Photo Systems Instruments (Drasov, Czech Republic) [21, 80, 81]. PSII is particularly receptive to temperature and its activity is enormously impacted to some extent and terminated under high temperature stress. Oxygen developing complex is exposed to temperature causing damage; it concludes in an imbalance flow of electrons to the acceptor site of PSII. The synthesis of starch and sucrose was eventually affected being a decrease in the activities of some enzymes such as sucrose phosphate synthase, adenosine diphosphate-glucose pyrophosphorylase, and invertase due to high-temperature stress. Net photosynthesis in many plant species is suppressed because of a decrease in the activation state of the CO_2 binding enzyme, Rubisco. Although these negative impacts of adverse conditions on photosynthesis, the optimum temperature prerequisites for photosynthesis are familiar to rise with increased concentration of CO_2 in the atmosphere [30]. The decrease in photosynthesis was due to damage to the chlorophyll pigments, reduced leaf nitrogen content, a hindrance to PSII reaction and electron flow, reduced quantum efficiency (Fv/Fm), and down-regulation of PSII photochemistry.

Many studies reported PSI is more stable than PSII towards heat stress. PSI activity increased the thylakoid proton conductance and cyclic electron flow under high temperatures. When the activity of PSII is reduced due to adverse conditions, the proton conductance and cyclic electron flow around PSI could be the favorable process that produces ATP. Further, heat stress enhances the dark reduction of plastoquinone and stimulates the thylakoid proton gradient which was elucidated to activate the cyclic electron flow around PSI [76]. There is an increase in ATP under mild temperature stress due to Rubisco activase and active photorespiration. The larger requirement of ATP under mild heat stress as long as a higher in NADPH/ATP ratio is helpful for non-photochemical reduction of the plastoquinone pool from stroma donors which is sequential to activate the NADH-mediated cyclic electron pathway. This process could distribute the energy and produce increased ATP to regulate active CO_2 fixation.

5. Future perspectives

High-temperature stress eventually affects germination, vegetative stage, reproductive stage, and yield. Due to increased global warming, the temperature will increase in upcoming years which drastically affects crop production. Subsequently, the decreased yield may lead to food scarcity in the future. Even though many research projects work on abiotic and biotic stress to protect the plants from adverse conditions. We need to improve the crop from the seedling stage to the harvest stage. At each stage, optimum growth conditions need to be provided for the plants. To counteract the problem, researchers found stress-tolerant genotypes. However, these can act on particular metabolic pathways and regulate the mechanism to improve plant growth. Sometimes, the crops endure both biotic and abiotic stress which can significantly affect the yield. In the future, we need to target the multi-stress-tolerant approach to protect the plants from multiple or unprecedented stress conditions.

6. Conclusion

High temperature is a devastating environmental factor that influences crop growth and yield by affecting numerous crop mechanisms. High temperature is an alarming concern that needs to be considered since it directly affects yield in a situation where have to generate high yield to sort out global hunger and meet the demands of global food hunger and ensure food security. High-temperature tolerance is not only important for the current situation, but also for the future since the simulated predictions show the elevating high temperature that enormously affects yield. New possibilities to resist or enhance high-temperature tolerance need to be investigated. Even though there are several studies related to high temperature on crops that reveal various factors that are up-regulated and down-regulated, there are abundant wild types that are not explored. Touching the untouched wild types can reveal amazing outcomes on how high temperatures can be managed with novel tolerant genes. Advancements in molecular techniques provide rapid detection of traits in wild types. It is also important to implement or follow advanced agricultural practices across the globe towards raising the global temperature, by implementing climate-smart practices, high-throughput phenotyping methods, and revealing the traits that are tolerant can protect, safeguard and defend tomorrow.

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