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REVIEW ARTICLE

High temperature stress - Physiological mechanism in crop plants

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Abstract

High temperature stress is one of the abiotic stresses that hinders plant growth, metabolism and productivity. In plants, numerous physiological and biochemical reactions are temperature dependent. Photosynthesis is the key physiological process, which is directly associated with crop yield and this process is highly sensitive to high temperature stress. High temperature stress induces oxidative damage in cellular organelles through the generation of reactive oxygen species (ROS) that causes lipid peroxidation, protein denaturation and disruption of cell structure. Chloroplast is the primary site of ROS production during the light reaction of photosynthesis, that disrupts thylakoid membrane and reduces the efficiency of photosystem II (PS II), electron transport and ATP synthesis. Enzymes are mostly temperature sensitive and RuBisCO, the key enzyme involved in CO_2 fixation process is inactivated due to the destruction of ultrastructure of chloroplast. High temperature stress also reduces the transpiration by inducing partial closure of stomata and thus reduces the uptake of water and nutrients by plants. Respiration rate increases in response to increase in temperature and enhances the utilization of stored carbohydrates leading to an imbalance in energy production and demand. In addition, high temperature stress leads to reduced pollen tube growth and viability, stigma receptivity and fertilization which results in poor seed set. Hence, understanding the physiological and biochemical changes occurs in plants under high temperatures stress conditions is essential for developing heat-tolerant crop varieties and ensuring agricultural sustainability under warm climates. This review is mainly focused on the effects of high temperature stress on photosynthesis, respiration, ROS, plant water relations, nutrient uptake and yield of crops.

Keywords: abiotic stress; high temperature; photosynthesis; physiology; reactive oxygen

Introduction

Climate change causes a drastic effect on agricultural production leads to significant threat to food security. Weather extremities like altered and erratic rainfall pattern, increased temperature and CO_2 concentration in the atmosphere results in climate change. The impact of climate change on plant functionality will be influenced by both its frequency and intensity. In past few decades, National Oceanic and Atmospheric Administration noticed that since 1850 the global air temperature has increased by 0.06 °C (0.11 °F) per decade and 2024 was recorded as the warmest year (1). Rise in the global temperature has also led to frequent drought, pest and disease attack that hinders the plant growth. The Sixth Assessment Report of Intergovernmental Panel on Climate Change reported that global warming increased the world temperature up to 1.1°C in 2020 which affects nearly 3.3 - 3.6 billion people across the world (2). The extreme temperature above the long-term average causes heat stress in plants and alters its physiological functions like photosynthesis, respiration, nutrient uptake, pollination, flowering, fruits formation, grain filling and ultimately the yield (3, 4).

High temperature stress significantly affects the productivity of agricultural crops. Field crops like cereals, millets, pulses and oil seeds behave accordingly to short and long-term exposure to high temperature stress at different phases of its growth and development, particularly during reproductive stages (5). A rise in the average global temperature by 2 °C could lead to a decrease in the grain yield of cereal crops by 20-40 %, particularly affecting regions in Asia and Africa (6). In staple crops like rice, wheat and maize high temperature stress causes a yield loss of 18-43 % (7). In India, a major wheat-producing Indo-Gangetic Plains are vulnerable to high temperature stress, which could result in a yield reduction of 8-27 % over the next few decades (8). Correspondingly, it has been indicated that the yields of rice (3.2 %), maize (7.4 %), wheat (6.0 %) and soybean (3.1 %) may decline with each 1 °C rise in average temperature. Furthermore, when temperature exceedingly above 25 °C can lead to a yield reduction of 20-70 % in Rabi season pulse crops like chickpea, lentils, faba and field peas cultivated in India (9,10).

High day and night time temperature stress significantly influences the plant growth and development in distinct ways. The degree of high temperature stress varies depending on the various climate zone and the pattern of temperature fluctuations experienced during both day and night time (11). High night time temperature (HNT) can reduce crop yield by limiting the distribution of biomass to reproductive sink, which affect fruit and seed development (12). Whereas high daytime temperature primarily affect photosynthesis by inducing oxidative damage through the generation of reactive oxygen species (ROS).

Plants under high-temperature stress undergo a variety of physiological changes that have significant impacts on their growth, development and yield. The processes like photosynthesis, respiration and nutrient uptake are mainly affected during high temperature stress by damaging chloroplasts and lowering the amount of chlorophyll in the plant, which reduces the amount of energy produced during photosynthesis (13). High temperature reduces the efficiency of the nitrogen fixing enzymes and deactivate RuBisCO enzyme (14, 15). Furthermore, high temperatures episodes increase the respiration rates, which causes energy expenditure and decreases biomass accumulation. Plant growth is further inhibited by the reduced nutrient uptake due to poor root system (4). High temperature stress also affects the uptake, movement and utilization of nutrients, that lowers the quality and nutritional value of the crops (16), which slows down the plant growth, metabolism and productivity at different stages of development (17).

High temperature stress poses significant threats during the reproductive stages of field crops, by causing membrane damage and protein dysfunction, which disturb biosynthetic pathways by inactivating key enzymes (18). Grain legumes are sensitive to high temperature stress at the flowering stage, as exposure to temperatures of 30-35 °C can lead to considerable yield loss due to heavy flower drop or pod abortion (19). Similarly, coincide of high daytime temperature stress during reproductive stage can cause damage to reproductive process and observed in cereals (30-38 °C), millets (40 °C), oilseeds (35-36 °C) and pulses (32-40 °C) (5). In addition, an increase in temperature leads to premature senescence and consequently produces fewer grains and reduces the yield (14).

Recovery from high temperature stress depends on the stress severity and its effects on various physiological processes. Alterations in leaf water potential and abscisic acid levels in plants tend to recover quickly, however, the disturbances in the leaf gas exchange process will take longer time particularly under more severe drought or temperatures over 40 °C (20). The adaptive mechanism of plants in response to high temperature, often insufficient to address rapid water depletion under extreme heat, leading to wilting, leaf desiccation and yield losses (21). For developing mitigation strategies against the detrimental impacts of high temperature stress on agricultural yields and food security, it is essential to understand these physiological changes in crops under stress conditions. Still, the effects of high night temperatures as well as combined effect of high day and night temperatures in plants are not clearly elucidated (22). Such efforts will help in breeding for heat-tolerant crop varieties under the changing climate scenario. This review article primarily addresses the physiological and bio-chemical changes that occur in plants in response to high temperature stress (Fig. 1).

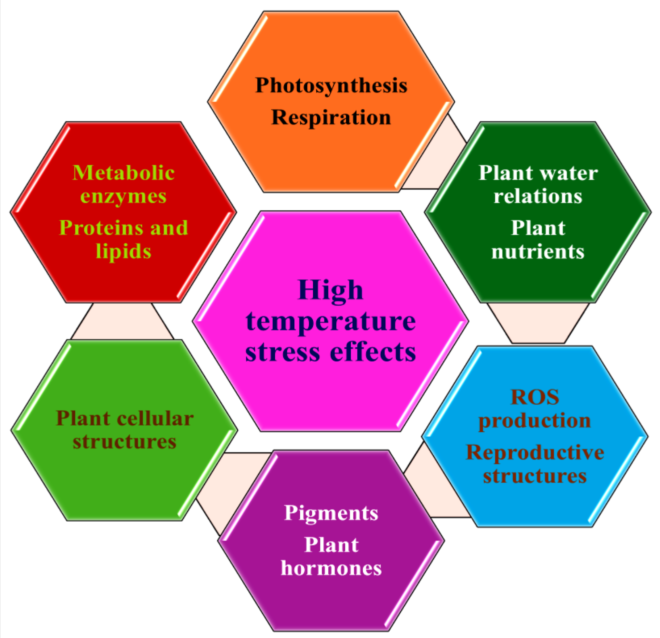

Fig. 1. Key effects of heat stress on plant growth and development.

Effect on plant cellular structures

Plant cellular structure particularly plasma membrane which is made up of phospholipid bilayer was severely affected as high temperature stress alters both the membrane permeability and fluidity. High temperature stress reduced tolerant capacity of the plant by interfering with microdomain remodelling, protein folding, signalling pathway and intracellular responses (23). Pectin, natural polysaccharide has a primary role in cell adhesion and hydration process was reduced under high temperature stress thereby it affects the plant morphogenesis and water content. The enzyme, pectin methylesterases (PMEs) get activated during high temperature stress and this alters the cell wall flexibility by interfering with pectin, thereby plants lose more water under high temperature stress (24). High temperature stress damages the membrane system by changing the composition of cell wall that led to denaturation of proteins and enzyme inactivation, which disrupt cellular functions and significantly affect plant growth, development and yield (25).

The production of ROS in chloroplast was triggered during high temperature stress that affects chloroplast proteins and retrograde signals communication to the nucleus (26). Impact on chlorophyll structure ultimately reduced the photosynthetic process with induced pre-mature leaf senescence and that affects biomass accumulation, grain number, weight and quality in crops (27). High temperature stress also led to mitochondrial swelling, increased lipid peroxidation and the release of cytochrome c which triggers the programmed cell death (28). The endoplasmic reticulum (ER) is essential for protein folding. When plant experiences high temperature stress (50 °C) induces structural changes in endoplasmic reticulum (ER) that transforms the tubular structures into flattened sacs (cisternae) present inside ER. As the duration of stress increases tubular structure nearly disappeared and showed only perforated cisternae, indicated severe disruption in ER organization and function (28). Structural changes in ER happened due to the accumulation of misfolded proteins.

To counteract this, cell triggers the unfolded protein response (UPR) by upregulating molecular chaperones, enhancing ER-associated degradation (ERAD), activating stress-responsive transcription factors, reducing protein synthesis and boosting antioxidant defences to restore protein homeostasis and maintain cellular function. Consequently, exposure to high temperature stress leads to considerable alterations in the cellular structures of plants due to the production of ROS which induced cell membrane damages thereby affecting signalling pathway, energy production, plant growth, development and productivity (28).

Effect on pigments

Plant pigments such as chlorophylls, carotenoids and anthocyanins are essential for absorbing light energy to drive photosynthesis. Pigments play a crucial role in regulating plant growth, development, defence mechanisms and helps the plant to adapt various environmental conditions. Chlorophyll, the primary pigment for photo-synthesis, absorbs blue and red light, while carotenoids function as accessory pigments, transferring energy to chlorophyll and protecting plants from excess light damage. High temperature stress disrupts pigment composition by damaging chloroplast membranes, which is essential for pigment stability and function. High temperature stress accelerated the chlorophyll degra-dation, particularly affected chlorophyll a, leading to reduced light absorption and photosynthetic rates (30). As the temperature rises beyond the optimal levels, chloro-phyll content significantly declined by denaturing the pigments and limits light harvesting and ATP generation, ultimately it reduced carbon assimilation and plant growth of maize. However, chlorophyll b tends to be more heat stable than chlorophyll a, allowing for a partial retention of photosynthetic function.

In contrast, carotenoid content often increases under moderate high temperature stress which helps in stabilization of photosynthetic apparatus by scavenging harmful ROS generated under stress conditions (30). Antioxidant role of carotenoids protects the chlorophyll from photodamage, ensuring enhanced photosynthetic efficiency under stress. Extended exposure to extreme temperatures can lead to the degradation of carotenoids, thereby diminishing their protective function. This may lead to excessive accumulation of ROS, which can damage membranes and proteins involved in photosynthesis. Similarly, anthocyanins function as stress-responsive pigments in plants, increased under moderate heat stress and they neutralize the excess ROS and thus protects the cellular structures. However, severe or prolonged heat stress downregulated the genes involved in anthocyanin biosynthesis, leading to reduced accumulation and decreased effectiveness in protecting plant cells against high temperature stress (31).

Effect on photosynthesis

Photosynthesis is highly sensitive to high temperature stress, since HT denatures the chloroplastic proteins, RuBisCO enzyme, photosynthetic electron transport system (ETS) components such as plastoquinone, plastocyanin, ATP synthesis and pigments associated in photosynthetic process by disturbing the chloroplast membrane (32). Chlorophyll is the major photosynthetic pigment that harvest light energy and drive ETS of photosynthesis. The increased activity of chlorophyllase and chlorophyll degrading peroxide enzymes during high temperature stress affected the chlorophyll biosynthesis which ultimately resulted in reduced chlorophyll content and photosynthetic rate (33). Thylakoid membrane and Photosystem II (PSII) were highly sensitive to high temperature stress (34). High temperature stress reduced the carbon fixation in crops by affecting the thylakoid membrane and PS II activity due to enhanced production of ROS (Fig. 2) (35).

The direct impact of high temperature stress on thylakoid membrane reduced the efficiency of PS II, PS I, D1 protein, cytochrome b6f complex, PS I and RuBisCO enzyme (36). High temperature stress shifts the photo phosphorylation pathway from its non-cyclic mode to cyclic mode, thereby it decreases CO_2 assimilation rate and photosynthetic process. High temperature stress also alters lipid composition and metabolism, particularly in thylakoid membranes, contributing to decreased photosynthetic rates (34). Uptake and assimilation of plant nutrients and photo-assimilates is also related with photosynthesis (37). Therefore, nutrient homeostasis was either directly or indirectly affected by photosynthetic process under high temperature stress.

RuBisCO is an important carboxylation enzyme in carbon fixation reaction of photosynthesis. High temperature stress damages the ultrastructure of chloroplast and inactivates RuBisCO that led to reduced photo-synthetic rate (38). The activity of RuBisCO enzyme was inhibited under

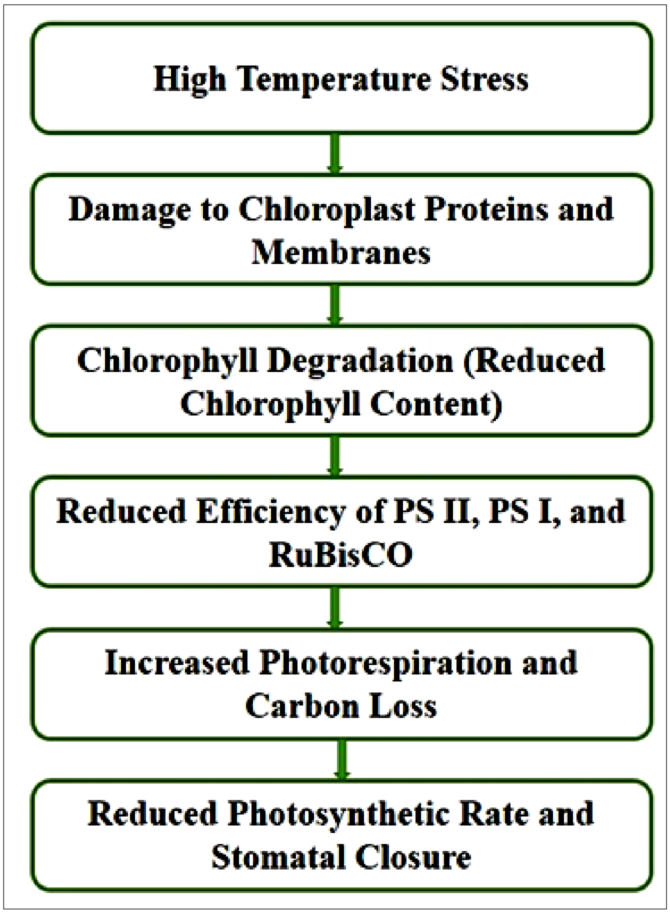

Fig. 2. Impact of high temperature stress on photosynthesis in plants.

moderate and high temperature stress condition that resulted in declined photosynthesis, because the affinity of RuBisCO for CO_2 got decreased under high temperature stress and tend to catalyze its oxygenase reaction which resulted in increased photorespiration process, ultimately the yield was reduced (39, 33). Especially, high daytime temperature upregulated RuBP (Ribulose-1,5-bisphosphate) oxygenase enzyme activity that directly influence the carbon fixation cycle through enhanced production of hydrogen peroxide through side reaction (40). Increased photorespiration process led to 30 % carbon loss under high daytime temperature stress resulted in chlorophyll degradation, reduced photosynthetic efficiency and premature leaf senescence (41). Plant undergoes partial closure of stomata to minimize transpiration loss under high daytime temperature stress. Stomatal closure causes reduced internal CO_2 concentration in mesophyll cells and limited the photosynthetic process (Table 1) (42).

HNT stress damages chlorophyll structure and lowers the net CO_2 assimilation rate in both C_3 and C_4 plants (43). Chlorophyll degradation by high night temperature causes quick senescence of leaves, that directly influences photosynthesis (44). The decrease in leaf photosynthesis were found to be higher at high night-time temperature (45) because of reduced chlorophyll content and increased thylakoid membrane damage (46). High night temperature reduced the photosynthetic efficiency by increased thylakoid membrane permeability causes excessive ion leakage (47) and this decreased chlorophyll content, quantum yield of PSII and overall photosynthetic process (43). In rice and wheat, decreased photosynthetic rates, low Rubisco activity and increased membrane lipid peroxidation under HNT stress altered photo-assimilation process (48).

Effect on respiration

Plant respiration is a crucial process in plant growth and development and can consume nearly 30-70 % of carbon gained through photosynthetic process. Increase in temperature can increase respiration rate that supports and maintain protein turnover and ion flux (27). Respiration rate is more sensitive to environmental changes and linearly related to tissue nitrogen content. Increased respiration rate can lead to enhanced ROS production led to reduced non-structural carbohydrates by consuming more photo-assimilates that ultimately affect the crop yield (49).

Studies on rice, maize and cotton showed that HNT stress increased night respiration rates, potentially consumed up to 40 % more carbon. High respiration rate indirectly reduced the photosynthetic process by depleting reserved carbohydrate, resulted in reduced crop growth rate (50). However, HNT showed several effects on photosynthesis in different crops, positive effect was observed in *Populus spp*., whereas negative effects were noticed in wheat and rice. High night temperature decreased the membrane stability through enhanced ROS production (51). At the cellular level, HNT

Table 1. Impact of high day and nighttime temperature stress in different crops.

S.No	Crop	Temperature (Day/ Night °C)	Stage	Major effects	References
1	Rice	38/30 °C	Booting and grain filling	Reduced spikelet number, seed setting percentage, grain weight and protein content.	(110)
2	Rice	35 °C and 41 °C	Meiosis, flowering and grain filling	Resulted in failure of fertilization process, floret sterility. Reduced grain number per panicle, seed setting rate and 1000 grain weight.	(111)
3	Maize	40/30 °C	Seed setting	Decreased metabolomic enzyme activity, starch accumulation and kernel weight.	(112)
4	Maize	32.5 °C and 33.8 °C	Flowering	Increased water loss led to decreased fertilization process, pollen viability, spikelet opening and seed set percentage.	(113)
5	Sorghum	42 °C/32 °C	Pollen Mother Cell (PMC) and booting	At pollen mother cell stage - damages tapetum and pollen led to pollen sterility and yield loss. At booting stage - reduced seed production.	(114)
6	Foxtail millet	39-41 °C/28-30 °C	Grain filling	Disrupted sugar transport from source organs to grains and reduced grain number, weight and irreversible yield loss.	(115)
7	Finger millet	37 ± 1 °C	Early seedling	Decreased germination percentage, root and shoot growth,	(116)
8	Black gram	> 35 °C	Flowering and maturity	Accelerated phenological development led to early flowering and maturity. Shortened grain filling period causes early maturation and yield reduction.	(117)
9	Chickpea	35 °C and 40 °C	Flowering and pod setting (Maturity)	At flowering stage - reduced photosynthesis and pollen viability, resulted in lower seed set and yield. At maturity stage - decreased nutrient uptake, poor seed development and seed quality.	(118)
10	Groundnut	45 °C	Reproductive	Increased ROS production causes membrane damage and yield	(119)
11	Tomato	37 ±1 °C / 27 ±1 °C	After flowering	Decreased photosynthetic rate and nutrient transport causes enhanced floral abortion, low fruit set percentage, yield and quality.	(120)
12	Lentil	32/14 °C	Flowering	Increased the level of phytic acid and reduced the concentration of protein, iron (Fe) and zinc (Zn).	(121)

causes mitochondrial dysfunction, alters dark respiration and triggers programmed cell death (27). Studies in rice and wheat showed that increased accumulation of TCA cycle intermediates in leaves under high night temperature stress enhanced the respiration rate (52). Night respiration was positively correlated with leaf carbohydrate content and increase in temperature, increases respiration process and the response is less pronounced after acclimation (53).

Effect on plant water relations

High temperature stress has a major impact on plant water relations, leading to a rapid decline in both the water potential and osmotic potential of the leaf (54). Under high temperature stress conditions, plants losses more water through the transpiration process that led to rapid soil moisture depletion (55). To limit the water loss and to conserve moisture, plants may close their stomata thereby limits carbon dioxide uptake and affects photosynthetic process (56). Transpiration occurs during night may benefit the plant growth by allowing respiratory CO_2 to escape and supports leaf expansion (57). High temperature stress affects the integrity of root membrane and hydraulic conductivity resulted in reduced water uptake (58). At cellular level, low water content affects various physiological process such as gas exchange, nutrient assimilation, respiration and sucrose transport (23). The movement of water across the cell membranes is severely affected under high temperature stress due to inactivation of aquaporin in plants (58). Regulation of stomata is the key physiological trait that controls water loss through transpiration and the entry of CO_2, which is essential for photosynthesis during high temperature stress (56).

Effect on plant nutrients

Nutrients are essential and critical in maintaining the normal functions in plants. In plants, different forms of nutrients elements are found to be in association with enzymes for the proper functioning of metabolic processes. Nutrients such as nitrogen (N), potassium (K) and magnesium (Mg) play vital role in various physiological processes like photosynthesis, carbohydrate partitioning and plant stress tolerance (59). Micronutrients such as boron (B), copper (Cu), iron (Fe) and zinc (Zn) are also involved in various metabolic processes and photosynthetic activities which are required in small proportions (60).

High temperature stress significantly effects on plant nutrient relations by interfering with uptake, transport and assimilation processes. The concentration of nutrients in both root and shoot was decreased, especially roots were more sensitive than shoots under high temperature stress (61). The rate of nutrient uptake generally dependent on temperature. High temperature stress alters root cellular machinery which includes complex interactions between genes, phytohormones and ROS (62). When temperature increases above 40 °C there is a substantial reduction in the total protein concentration and levels of nutrient-uptake and its assimilation in roots that potentially decrease yield and nutritional quality of the grain (61). However, the response of nutrients to high temperature stress varies, for instance, boron uptake may be increased at moderately elevated temperatures. In cereal crops, the growth of root was severely affected by high temperature stress, resulting in diminishing nutrient and water uptake (16). Root thermotolerance was highly associated with efficient carbon and protein metabolism and activation of stress defence proteins (63).

Plasma membrane H+-ATPases play a crucial role in nutrient uptake and stress responses by creating proton gradients for secondary active transport (64). The interrelation between nutrient transporters and aqua-porins is important for understanding plant responses to abiotic stresses, including high temperature stress. In tolerant plants, there was an upregulation in the expression of both nutrient transporters and aquaporins in plasma membrane were upregulated during the period of nutrient deficiency caused by high temperature stress conditions (65). Further research is needed to elucidate the complex mechanisms of nutrient uptake under high temperature stress and develop strategies to improve plant nutrition and resilience.

Effect on proteins and lipid metabolism

Proteins are essential for various cellular functions, including photosynthesis, metabolism and signal trans-duction. However, high temperatures can severely affect protein stability and function. High temperature stress causes direct damage to plants by inducing protein denaturation, aggregation and increased membrane fluidity. Indirect effects include enzyme inactivation in both chloroplasts and mitochondria, inhibition of protein synthesis and protein degradation (66). Extreme temperature can affect the nitrogen availability to plants and decreased the protein content of the seed by suppressing the key storage protein genes, such as GmGy1, GmGy2, GmGy4, GmGy5 and Gmβ-conglycinin. In contrast, high temperature stress promotes lipid accumulation by upregulating lipid biosynthesis-related genes like GmBCCP2 and GmKAS1. Additionally, the increased expression of GmWRI1-like1, a key regulator of lipid metabolism, contributes increased lipid content in seeds of soybean under high temperature stress (67).

Lipids play a crucial role in energy storage and serve as structural components of the plasma membrane that maintains cellular integrity and facilitates signalling pathways. High temperature stress triggers excessive production of ROS, leading to lipid peroxidation, membrane damage, electrolyte leakage and eventually causes cell death (68). To mitigate these detrimental effects, plants undergo lipid remodelling, modifies membrane lipid composition and fatty acid saturation levels to ensure the membrane stability under high temperature (69). Certain lipids, such as phosphoinositides, phosphatidic acid, sphingolipids, lysophospholipids, oxylipins and free fatty acids, serve as precursors for signalling molecules that regulates stress responses (70).

Effect on ROS production

In plants, high temperature stress leads to increased production of ROS such as singlet oxygen, superoxide, hydroxyl radical and hydrogen peroxide (71). Under HT conditions, ROS were generated in various cellular components including chloroplasts, mitochondria and peroxisomes (Fig. 3) (72). Under normal situations the production of ROS is minimum and its level is balanced by antioxidant enzymes. However, their production was increased exponentially under stress

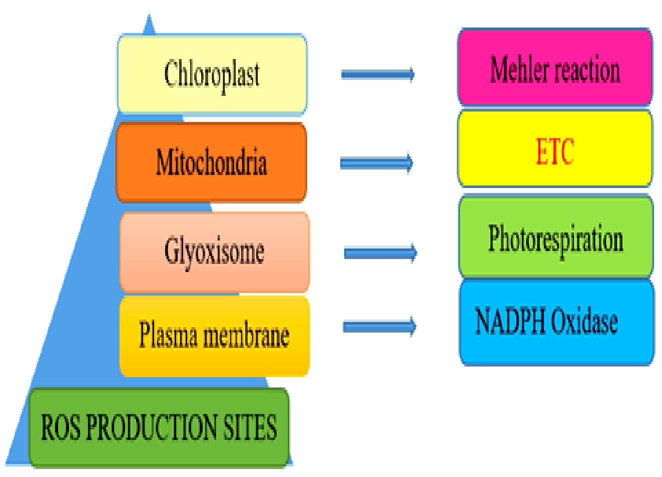

Fig. 3. ROS production sites and process.

conditions, potentially causes oxidative damage to biomolecules and this disrupts the cellular redox homeostasis (73). In photosynthetic process, ROS were produced during energy transfer, electron transport and incomplete water oxidation under high temperature stress situations (74). In addition to oxidative damage, ROS also plays a crucial role as signalling molecules in plant stress responses (71).

Studies on wheat, sorghum and rice have shown that elevated temperatures increase ROS production, leading to membrane damage, reduced chlorophyll content and decreased photosynthetic efficiency (45). These effects were observed in various plant organs, including leaves and pollen grains, resulting in reduced seed set and grain yield (75). The rise in ROS production in plant cells leads to alterations in lipid metabolism, thereby creating the imbalance between ROS and antioxidant defence systems (34). In photosynthetic process, carbon fixation and oxygen evolution rates were reduced by ROS, which damages PS II repair mechanism rather than directly harming the reaction centre (76). ROS production also affects both vegetative and reproductive stages of plants resulted in reduced fruit size and yield (66). Studies found that accumulation of ROS in anther and pollen grain induces oxidative stress and affects pollen viability by altering phospholipid composition (34).

Effect on metabolic enzymes

High temperature stress affects plant metabolic processes by altering metabolic pathways through enzyme inactivation and misfolding of proteins thereby reduced the growth, development and yield of the crops (77). RuBisCO enzyme activity was consistently decreased under high temperature stress which lowers carbon fixation efficiency in plants. In tomato, the declined Rubisco activity during high temperature stress reduced the photosynthetic efficiency and further fruit development (78). Another critical effect of high temperature stress was mitochondrial dysfunction, where the key enzymes of the TCA cycle, such as citrate synthase and malate dehydrogenase were inhibited, led to energy deficiency and decreased ATP production that affects carbon metabolism and limits the plant growth.

High temperature stress also leads to excessive generation of ROS, which causes oxidative damage to metabolic enzymes. The activity of key enzymes involved in carbohydrate metabolism such as sucrose synthase (SS), soluble starch synthase (SSS) and ADP-glucose pyro phosphorylase (AGPase) were reduced under high temperature stress and resulted in reduced accumulation of starch and energy availability for plant growth (79). Besides the metabolism of starch, sugar metabolism was also compromised due to the disruption of enzymes such as invertase and hexokinase. These enzymes are essential for regulating sugar transport and sink strength in developing grains, which further caused yield losses under high temperature (80). The activity of the enzymes such as nitrate reductase (NR) and glutamine synthetase (GS) was also reduced which led to declined amino acid biosynthesis and nitrogen assimilation (81). Additionally, heat stress enhances the protease enzyme activity which accelerates the protein degradation and nitrogen imbalance in plants. In wheat, reduced activity of starch-metabolizing enzymes such as sucrose synthase (SS) and soluble starch synthase (SSS) negatively impacted the grain filling and yield (82). In sugarcane, high temperature stress significantly reduced the activity of sucrose phosphate synthase (SPS) and sucrose synthase (SS) led to decreased sugar metabolism (81). High temperature stress causes severe metabolic disruptions by inactivating key enzymes thereby enhancing the oxidative stress. These effects ultimately reduced the plant growth and yield.

Effect on plant hormones

Plant hormones, plays a key role in regulating plant growth, development in responses to environmental stresses. Plant hormones such as auxin (IAA), gibberellin (GA), cytokinin (CK), ethylene (ET), abscisic acid (ABA), brassinosteroids (BR), salicylic acid (SA) and jasmonic acid (JA) also regulates the plant defence mechanisms against several abiotic stresses like drought, high temperature, salinity, etc. High temperature stress disrupts hormonal balance and thus affects plant metabolism, growth and productivity (Fig. 4) (83).

Auxin, a key signalling molecule in plants, regulates vital processes in plants such as root development, tissue differentiation and organogenesis (84). Increased temperature suppressed the expression of IAA synthesis genes, leading to reduced auxin production. In tobacco, high temperature stress significantly reduced the level of IAA levels in roots that resulted in altered root architecture with shorter primary roots and fewer lateral roots, ultimately it affects the plant growth and nutrient uptake. Expression of IAA-related genes, such as YUCCAs and PINs were downregulated, while auxin response factors (ARF1 and ARF2) were upregulated in roots disrupted auxin biosynthesis, signalling and transport (85). Reduced auxin production showed negative impact on shoot elongation, lateral bud formation and flower development, reproductive success and overall biomass accumulation. Similarly in rice, IAA content was significantly reduced in grains under high temperature stress by upregulating the expression of Aux/IAA gene OsIAA29. Reduction of IAA was associated with adverse effects on grain filling, led to a higher percentage of shrunken and chalky seeds, as well as reduced 1000 grain weight (86).

Gibberellins regulate plant growth processes like seed germination, stem elongation and flowering. High-temperature stress decreased the level of GA which resulted in reduced stem elongation, delayed flowering and seed set percentage.

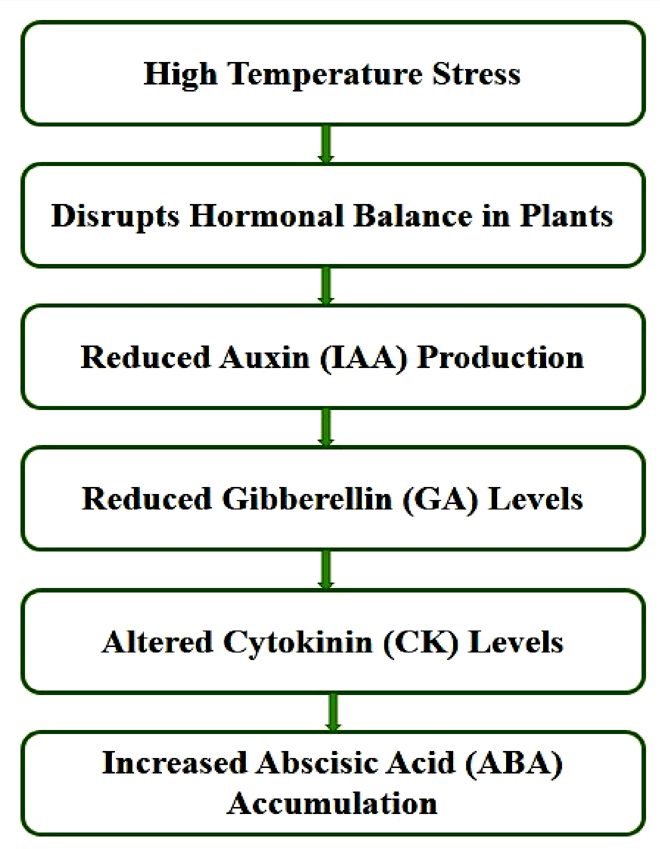

Fig. 4. Effect of high temperature stress on plant hormonal balance and growth.

Downregulation of gibberellin biosynthesis genes, such as GA20ox (gibberellin 20-oxidase), reduced active GA levels and causes stunted growth with shortened internodes. Additionally, reduced GA levels negatively affect the viability and fertility of pollen grains which contributes to lower grain yield (87). Cytokinin regulate cell division, growth and stress response activities in plants. High temperature stress alters the cytokinin levels in different plant tissues. The degradation of chlorophyll accelerates because of cytokinin depletion, which results in yellowing and premature aging of leaves and reduced biomass accumulation. Cytokinin also plays a crucial role in maintaining thermotolerance by promoting stomatal opening and transpiration thereby it regulates leaf temperature. However, prolonged heat stress disrupts cytokinin homeostasis, leading to flower abortion, reduced grain filling and yield loss (88).

Abscisic acid (ABA) plays a critical role in regulating plant responses to high temperature stress by reduced stomatal opening, transpiration and maintains plant water status. Under high temperature stress, ABA gets accumulated rapidly and enhanced absorption of water by roots (89). However, reduced carbon fixation due to ABA accumulation in stomatal guard cells impairs biomass production and lowers grain yield by reduced photosynthetic efficiency. ABA-induced thermotolerance improves the survival of crops like wheat and maize by mitigating heat-induced kernel abortion and maintaining kernel weight (90). ABA activates antioxidant defence mechanisms and protects the plant cells from oxidative stress and membrane damage caused by high temperature stress.

Ethylene regulates fruit ripening, leaf senescence and stress responses. High temperatures altered ethylene biosynthesis and signalling that reduced fruit yield and postharvest quality in apple (91). High temperature stress disrupted ethylene-dependent responses in plants by downregulating ethylene biosynthesis genes which affected fruit colour, firmness and sugar accumulation. In crops such as tomatoes, high temperature stress delays ripening process, resulted in uneven fruit development and reduced shelf life. Increased ethylene production under high temperature stress triggers premature senescence causes early leaf yellowing, shedding and reduced vegetative growth (92). In rice, high temperature stress disrupted the phytohormonal balance, level of active cytokinin (CTKs), gibberellin A1 (GA_1) and indole-3-acetic acid (IAA) were decreased while the level of abscisic acid (ABA) and bound cytokinin in young panicles were increased. These changes negatively affect the spikelet fertility, grain number and its weight, ultimately lowers the grain yield. The decline in growth promoting hormones reduced panicle development and grain filling in rice, while ABA accumulation accelerated stress responses (93).

Effect on reproductive biology

Reproductive development is very crucial in determining both quantitative and qualitative growth and develop-ment of plants. Plant reproduction is severely affected by diverse environmental conditions. Abiotic stresses like high temperature causes numerous effects on reproductive organs such as reduced pollen viability, pollen tube growth, stigma function and receptivity, fertilization and embryogenesis process which results in poor seed set development (94). Reduced pollen function, ovule viability and total number of ovules resulted in reproductive failure by denaturing of proteins under high temperature stress (95). High mean temperature (> 24 °C) occurred during heading and grain filling stages decreased floret fertility and individual grain weight, leading to substantial yield losses (96).

Recent studies on high temperature stress showed that in plants male reproductive organs were found to be more sensitive than female reproductive organs (97). In maize, female tissues exhibited resistance to both cold and high temperature stress, whereas mature pollen was highly susceptible. The effect of heat stress on male reproductive organs in several ways, including meiotic defects, spore abortion and alterations in cytoskeleton, tapetum and sugar metabolism in the pollen grains (98). Some Studies also suggested that female reproductive organs may be more vulnerable to heat stress in certain species. For instance, in *Brassica napus*, female reproductive organs showed greater sensitivity to transient heat stress during early flowering stage (99).

Cereal crops like wheat showed reduced photosynthetic capacity, dry matter accumulation and grain yield under high temperature stress (96). In legumes, it was prominent that high temperature causes flower abortion, pollen and ovule infertility, impaired fertilization and reduced seed filling rate and duration (100). HNT increases ROS accumulation in pollen grains (73). The decreased photosynthetic rate under high temperature stress was attributed to lipid desaturation, oxidation of the cellular organelles (34). These changes resulted in reduced pollen function, lower seed set and decreased crop yield (43). High night temperature during flowering or grain filling stages shortens the grain filling period which in turn alters the flowering schedule (51).

High temperature stress during the anthesis or grain filling stage increases thylakoid membrane damage in plants. The photosynthetic rate and grain yield per plant exhibited a significant positive relation (101). Reduced photosynthesis and inactivation of RuBisCO enzyme affect the photo assimilation production and distribution, which in turn affect flowering, seed filling and finally the crop yield. HNT during flowering and grain-filling stages exhibited negative impact on physiological process and yield of several crops. Reduction of total dry matter production and yield might be related to increased night respiration which utilize carbohydrates stored during day in maize kernel (50). Similarly in wheat, grain number and weight were reduced by affecting the carbon balance (52).

Role of heat shock proteins

Heat shock proteins (HSPs) are the molecular chaperones that help organisms to cope up with various stresses, particularly under high temperature. HSP prevents protein aggregation and aids in proper protein folding, maintenance of cellular homeostasis under stress conditions (102). HSPs were rapidly induced in response to high temperature stress and enhance the plant tolerance. In plants, HSPs play vital role such as maintenance of cell membrane integrity, scavenging of ROS through enhanced production of antioxidant enzymes (103). Accumulation of HSP depends on plasma membrane signalling and activates the families of heat shock transcription factor (HSF). HSP were categorized into different families based on molecular weight, including HSP100, HSP90, HSP70, HSP60 and small HSPs (104).

HSPs were involved in various cellular functions, including signalling, translation, host-defence mechanisms and metabolism (105). HSPs expressions are regulated by interconnected signalling cascades and heat stress transcription factors that enhances the tolerance of plants to various environmental stresses (106). Therefore, HSPs are essential for plant to grow, survive and adapt to numerous abiotic stresses, particularly high temperature stress (105). When plants are exposed to high temperature stress, it receives high temperature stimulus and transmit the signal through physio-biochemical aspects and regulatory genes. HT stress cause oxidative stress in plants through ROS production which affects the macromolecules and nucleic acid synthesis. To overcome this stress, plants depend upon HSPs to protect cell membrane, detoxify ROS production and increase antioxidant enzyme activity (106).

Heat shock proteins (HSPs) serve as molecular chaperones in plants, aiding in protein stabilization, refolding and cellular homeostasis under heat stress. In wheat, 753 HSP genes have been identified, with increased expression observed during heat stress and seed development (107). Similarly, in maize, proteomic analysis has highlighted the upregulation of key HSPs, including HSP26 and HSP16.9, which support protein stability and chloroplast function under high temperatures (108). In cotton, specific HSPs such as HSP101, GHSP26 and HSC701 enhance heat tolerance by maintaining membrane integrity and protecting photosynthetic machinery. Genotypes with higher HSP gene expression, like Cyto-177 and VH-305, exhibit improved photosynthesis, stomatal conductance and heat resilience (109).

Conclusion

High temperature stress poses a critical challenge to plant physiology and biochemistry, impacting water relations, photosynthesis, respiration and ultimately yield and quality of crops (Fig. 5). High temperature induces oxidative damage through generation of ROS which affects physiological process like photosynthesis, respiration and water status of the plant. Additionally, increased night respiration under high temperature stress leads to carbon loss, which has been associated with yield reduction. However, respiration alone does not fully account for yield and quality losses, suggesting that other interconnected factor like carbon balance, starch and protein metabolism and specific enzymatic activities play substantial roles in plants.

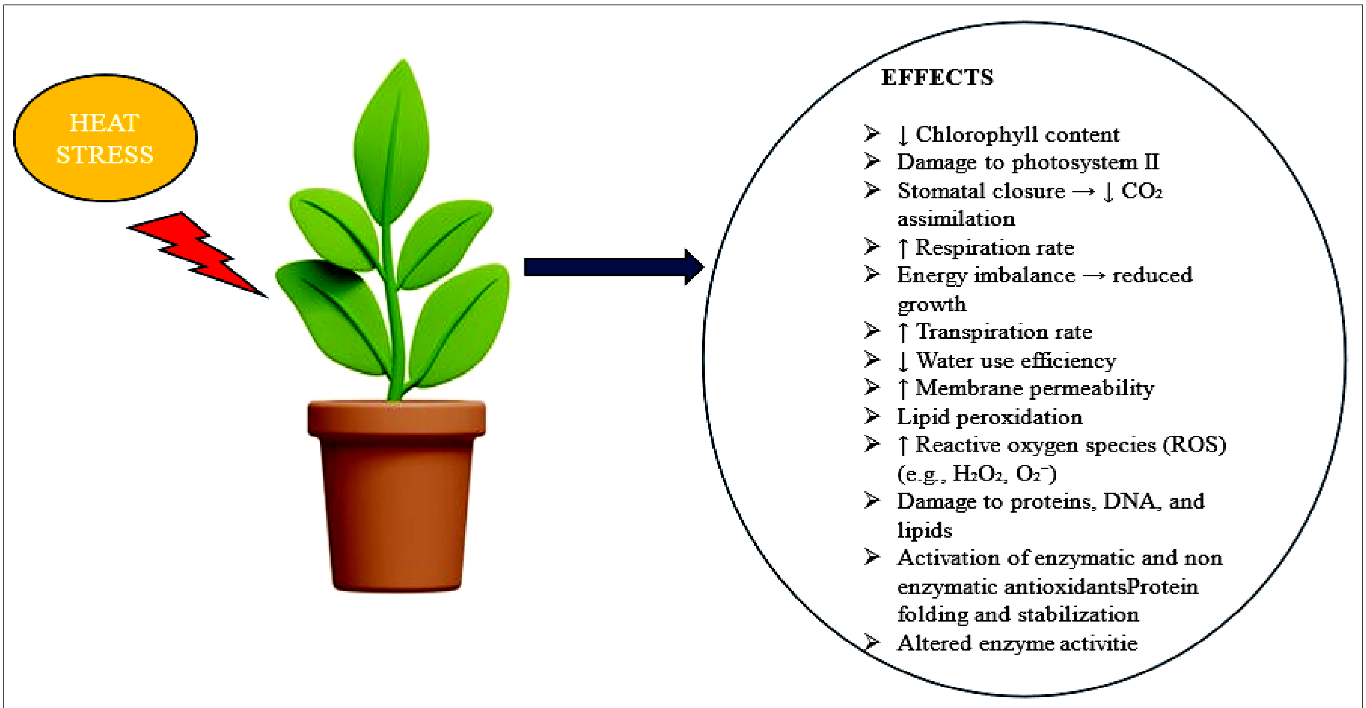

Fig. 5. Schematic representation of high temperature stress effects in plants.

However, future research should focus on elucidating the precise impact of high night temperatures on carbon balance, particularly the interplay between carbon loss (through respiration) and carbon gain (through photosynthesis). Furthermore, understanding starch and protein metabolism under high temperature stress could offer insights into developing crop varieties with improved resilience. Field-based studies, involving large, genetically diverse mapping populations combined with high-throughput phenotyping are essential to accurately assess the genetic and physiological responses to high day and night temperature stress.

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Authors' contributions

MSS conceptualized the review, compiled relevant literature and drafted the manuscript. MR contributed to the literature analysis and assisted in structuring the physiological mechanisms section. KA and MD reviewed and edited the manuscript, ensuring clarity and coherence and contributed to manuscript revision. RK and RS assisted in organizing references and ensuring proper citation formatting. AS supervised the entire review process and approved the final version.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

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