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Consequences and Mitigation Strategies of Heat Stress for Sustainability of Soybean (*Glycine max* L. Merr.) Production under the Changing Climate

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Abstract

Increasing ambient temperature is a major climatic factor that negatively affects plant growth and development, and causes significant losses in soybean crop yield worldwide. Thus, high temperatures (HT) result in less seed germination, which leads to pathogenic infection, and decreases the economic yield of soybean. In addition, the efficiency of photosynthesis and transpiration of plants are affected by high temperatures, which have negative impact on the physio-biochemical process in the plant system, finally deteriorate the yield and quality of the affected crop. However, plants have several mechanisms of specific cellular detection of HT stress that help in the transduction of signals, producing the activation of transcription factors and genes to counteract the harmful effects caused by the stressful condition. Among the contributors to help the plant in re-establishing cellular homeostasis are the applications of organic stimulants (antioxidants, osmoprotectants, and hormones), which enhance the productivity and quality of soybean against HT stress. In this chapter, we summarized the physiological and biochemical mechanisms of soybean plants at various growth stages under HT. Furthermore, it also depicts the mitigation strategies to overcome the adverse effects of HT on soybean using exogenous applications of bioregulators. These studies intend to increase the understanding of exogenous biochemical compounds that could reduce the adverse effects of HT on the growth, yield, and quality of soybean.

Keywords: *Glycine max* L., osmoprotectants, crop productivity, heat stress, mitigation strategies

1. Introduction

Soybean is one of the key source of food energy for humans, it has principal economic value for the high-quality oil and protein, and it is grown about 6% arable lands across the globe [1, 2]. Being the members of the Leguminosae (Fabaceae) family, soybean seeds are predominantly rich in proteins and essential-fatty acids [3]. Presently, it is also dignified as a prospective plant for the production of biodiesel [4].

Adverse environmental conditions such as increasing ambient temperature, water deficit, salinity, among others, are expected as a part of the phenomenon called global climate change and these are the great threat in agriculture. Heat stress is a foremost unfavorable weather factor of climate change, which has a negative impact on crop production [5, 6]. An increase in air temperatures modifies photosynthetic rates by affecting photosystems of plants which decreases the growth and development of plant, resulted in the reduction of crop yield [7]. At the physio-biochemical level, HT tempts to denature protein, increases lipid fluidity in cells membrane, over production of ROS, ultimately inhibits the role of the photosynthetic apparatus [8]. Besides, a variety of mechanisms are developed in plants that allow them to survive with HT stress including fluctuations in leaf positioning, alteration of membrane lipid configuration, stimulation of antioxidant defense, buildup of osmolites, hormonal regulation, and quick ripening [9, 10].

Environmental stress negatively influences the growth, yield, and quality of plants and there have been efforts to improve genotypes for higher stress tolerance [11–13]. However, HT stress limits the growth and yield of soybean by changing the different physiological and biochemical processes of plants. Several antioxidants, such as glycinebetaine (GB) and proline (Pro), act as compatible solutes or osmoprotectants which can be used to mitigate the hostile impacts of HT stress [14–16]. Osmoprotectants can influence plant growth through various ways via the rooting-medium, foliar spray, and pre-sowing seeds treatment. It is reported that the application of Pro alleviates the unfavorable effects of environmental stresses [17]. GB applications enhance plant tolerance under stressful environments [18]. Considering the above discussion, the chapter aims to clarify the physiological and biochemical responses of soybean during various growth stages under HT stress conditions and to evaluate the exogenous application of different compounds for the mitigation of antagonistic effects of HT stress on soybean and exploiting the yield.

2. The consequences of heat stress on the productivity of soybean

High-temperature (HT) stress has been directly linked to a decrease in photosynthetic efficiency and finally decreased crop yield [19]. High temperature induces a limited supply of water and nutrition, which influences the leaf expansion, internodes elongation, motivates the flower bud abortion in plants [20]. Heat-associated damage to the reproductive part of different crops is the major reason for yield loss worldwide [21, 22]. HT stress during flowering has a destructive effect on legume seed yield, mainly due to loss of seed number. A series of biochemical mechanisms comprising the accumulation of HT shock proteins, metabolites, antioxidants, and hormones are proposed to play a key role in regulating legume seed set in response to HT stress [23]. A diverse set of antioxidant metabolites, including tocopherols,

flavonoids, phenylpropanoids, and ascorbate precursors, were found to be enriched in the seed of the heat-tolerant genotype [24]. Studies in soybean plants showed that the stomatal conductance or non-stomatal factors under HT stress are associated with the low photosynthetic rate [25, 26] also concluded that HT stress increased the production of reactive oxygen species (ROS) which results in premature leaf senescence and lower leaf photosynthesis. However, the specific mechanisms causing lower photosynthesis under HT stress in soybeans are still not clearly understood.

2.1 The adverse effect of heat stress on germination and seedling establishment

Complete, rapid, and uniform germination is essential for having a good green area and crop growth rate for better radiation utilization and higher yield. The percentage of germination and other traits related to germination are severely influenced by abiotic stress [3]. Imposing long-term high-temperature stress during crop growth life cycle delays seed emergence, grain vigor, and reduces dry matter accumulation [27]. Germination and early seedling development in soybean is highly sensitive to HT stress. During the early germination process of soybean, high temperature significantly reduces the rate of imbibition, the ability of embryo tissue to expand, and mitochondrial respiration. Thus, temperature stress causes harmful effects to plant metabolism by disrupting their cellular homeostasis. Exposure of plants to high-temperature above the range of optimal levels can cause disturbance to the overall life cycle of the plant. HT stress can generate oxidative stress by accumulating the ROS [28]. Many physiological processes (such as photosynthesis, respiration) in surviving cells are sensitive to temperature stress [29]. Interestingly, exposure to low temperature during the seedling stage substantially extends the vegetative growth rate and increases the number of axillary branches, the rate of dry weight per plant and pod setting. Seed vigor is also reduced due to exposure of plants at the seedling stage. Germination is declined, as the number of days at 33/28°C (day/night temperatures) during seed development increased. Seed vigor determined by measured axis dry weight is also reduced [30]. Previous researches have demonstrated that the high-temperature stress during the seed filling period reduced the germination and vigor in soybean seed [30]. Increased temperatures have a strong negative effect on seed germination potential and result in a decrease in seed viability and poor germination [31].

2.2 The adverse effect of heat stress on growth and development of soybean

The growth performance of crops is adversely affected by high-temperature stress. Unfavorable environmental conditions (temperature and rainfall variability) during the reproductive growth stage can reduce the seed yield of soybean [32]. Disturbance induced by high-temperature stress in various crops reduces crop growth and development and severely reduces the physiological growth attributes [33, 34]. It has been reported that temperature and photoperiod predominantly affect the vegetative growth and development of soybean plants among other environmental variables. Reproductive growth periods of soybean are more sensitive to high temperatures than vegetative growth periods [35]. Environmental conditions, particularly day-time temperature have a direct effect on photosynthesis and transpiration, consequently affecting soybean yield. Therefore, plant reproductive organs are more vulnerable to changes in short episodes of high temperatures prior to and during the early flowering stage [36].

It is known that the roots of plants play an important role in the establishment of symbiotic associations with different microorganisms [37]. Genome-wide transcriptomic and proteomic studies on isolated root hairs of soybean plants (a

single, epidermal cell type) as compared to stripped roots under HT stress showed global changes in their transcriptional and proteomic profiles. A diversity of proteins was determined whose expression changed after 3 h of HT stress application. Most such proteins were supposed to play a significant role in thermo-tolerance, post-transcriptional regulation and in the remodeling of chromatin [5].

The negative effects of HT stress are also observed in photosynthesis, transpiration, stomatal conductance, and yield. Thereby, a significant reduction was observed in dry matter accumulation, crop phenology (grain-filling duration), crop growth rate and relative growth rate as well as yield contributing characters (grains per plant and grain weight) under HT and water stress [38]. Similarly, stress condition causes a reduction in chlorophylls (Chl a and b) and carotenoids contents as well as the Chl 'a/b' and carotenoid/Chl 'a+b' ratios in the leaves that leads to decrease in the final yield [39].

In addition, a decrease in photosynthesis at HT stress can be mediated through anatomical and structural changes in the cell and cell organelles, particularly the chloroplast and mitochondria. For example, leaves of soybean under HT stress are characterized by a higher carbon isotope ratio and increased content of leaf reducing sugars [40]. Furthermore, temperature stress is the main reason for reactive oxygen species (ROS) production, such as hydrogen peroxide and hydroxyl radicals that cause severe damage to cellular membranes, and antioxidant activity resulting in decreased crop growth rate [41]. HT stress destroys the chlorophyll pigments and also declines the photosynthesizing efficiency that may produce ROS and ultimately negatively affects plant growth [42]. Photosynthesis metabolisms like mitochondrial membrane and catabolism of carbon present in the stroma are usually influenced by temperature stress [43]. Thus, reduction in photosynthesizing efficiency during high-temperature stress reduces crop growth which reduces crop yield [44]. Recently, several studies also found that stress conditions resulted in a decrease in relative leaf water content, membrane stability index and an increase in lipid peroxidation level and catalase and peroxidase activities [10]. Taken together, these studies demonstrate that several compounds and processes are contributing to reduce the growth and development of soybean plants under HT stress.

2.3 The adverse effect of heat stress on the yield of soybean

HT stress can significantly modify the seed development and decreases seed yield in legumes [45–47]. HT stress has a negative impact on the process of seed filling and ultimately influences the seed yield. Collectively, these adverse effects eventually decrease assimilate production and mobilization to developing seeds in various crops [48]. Exposure to HT stress during pod and seed filling stages results in a substantial decrease in the economic yield of crop plants by the reduction in seed weight. The decline in seed weight and seed number due to high temperatures has been reported in several crops including legumes [49]. High-temperature stress speeds up the rate of seed filling by reducing the duration of this stage and therefore reduces the yield potential [50–52]. The time of seed filling was reduced in pea, soybean and white lupin, resulting in smaller grains. High temperature during seed filling stimulates leaf senescence and reduces reduction in seed size is related to structural and functional reasons.

The yield and yield attributed traits have been significantly reduced by the photosynthetic capacity, which impacts seed development and reduces growth and yield traits in grain legumes [47, 52]. Accordingly, the environmental stresses [53]. Further, it is observed that water stress for a short period during the grain development stage decreases grain size and grain weight which ultimately affects the final grain yield. The seed yield reduction of soybean due to water deficit stress was

recently reported [12]. Further, reduction of growth, yield, and attributing traits of various crops has been well-documented [54–56].

Flower initiation was reduced by temperature > 32°C and seed formation was delayed at 40–30°C [57]. The yield reduction of about 27% was measured when soybean plants were exposed to temperature at 35°C for 10 h during the day. Hence, it is essential to protect crop yield from higher and more frequent episodes of extremely higher temperatures both in current and future climates [58]. Physiologically, the high-temperature stress during reproductive development may have affected flower abortion, sequent sink site, and later pod abscission resulting in a decreased number of seeds per plant [59]. These results indicate that branch seed yield of determinate soybean is dependent on the vegetative growth of the branch that occurs during the flowering and pod formation stages [59]. Less information is known about the effects of temperature stress on soybean branch growth and branch seed yield or how temperature stress affects the distribution of seed yield between the main stem and branches [60].

Temperature exceeds about 35°C caused high-temperature stress. HT stress declined the plant development and grains in pods that ultimately decreased the biomass accumulation [61–64]. High-temperature stress produces less sterile pollen grains which decreased the grain formation. Temperature range about 29.4°C reduces pods quantity while when temperature range exceeds about 37.2°C strictly stops production of pods that ultimately reduces biomass production of various crops (Figure 1).

2.4 The adverse effect of HT stress on seed quality of soybean

High-quality seed production is a major obstacle to the expansion of soybean production to new areas of the tropic. Tropical conditions with high relative humidity and temperature are not conducive to seed growth and production of soybean. Such conditions do not support harvestable moisture levels for soybean growth with the final aim to get the high-quality seed. Modeling soybean yields based on carbon assimilation alone underestimated yield loss with high-intensity heat-wave and overestimated yield loss with low-intensity heat-wave, thus supporting the influence of direct HT stress on reproductive processes in determining yield [65]. The uniformity of seed development within the crop is a major factor that depends on

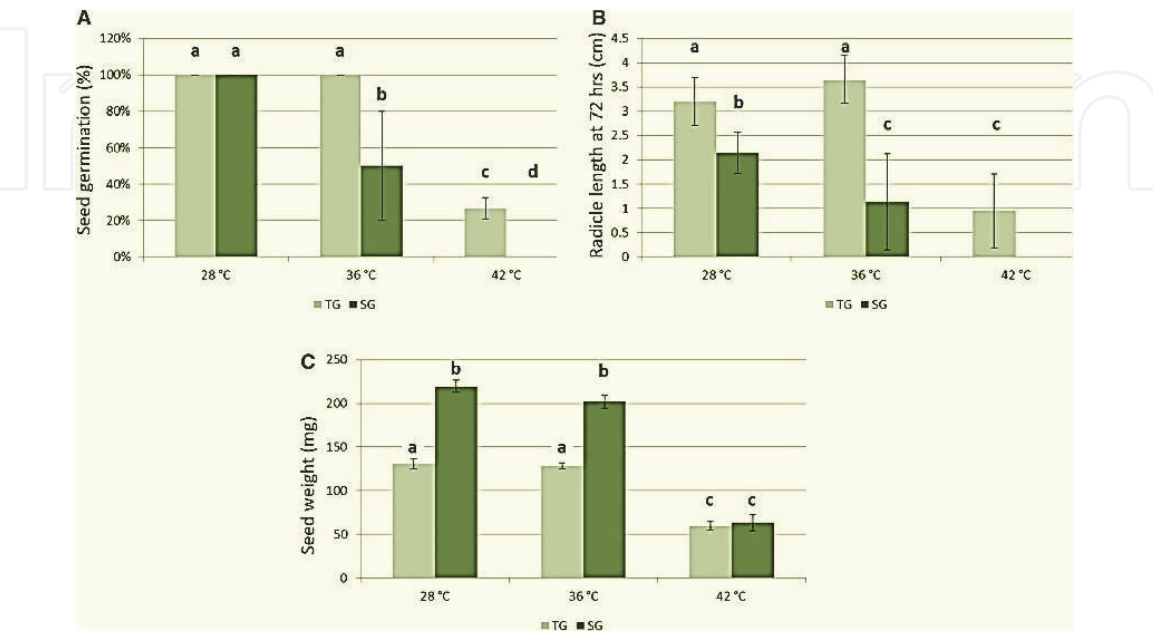


Figure 1. Influence of high temperature during seed development on seed quality parameters. Germination percentage at 25°C after 72 h (A), radicle length (B), and mature seed weight (C) in two soybean genotypes: TG (high-temperature tolerant) and SG (high-temperature sensitive).

production practices and growing conditions. During the growth of field crops, maximum seed quality is generally regarded to be attained at physiological maturity, i.e., at the end of seed filling. Seed quality is, however, sensitive to temperature during the seed-filling period because high temperature differentially affects the various processes involved in seed filling and seed composition. In addition, high-temperature stress reduced the size of seeds and their milling quality [59]. **Figure 1** shows the effect of HT stress imposed during seed development on various seed quality characteristics like germination, radicle length, and mature seed weight.

The composition of soybean seed depends on many factors, including genotype, growing season, geographic location, and agronomic practices. The fatty acid composition of soybean oils is not constant. The fatty acid composition of soybean oils varies depending on mainly temperature and genetic factors. Environmental conditions play a decisive role in oil content and fatty acid development [66]. Temperature is the primary factor that contributes to seed filling which is the most critical growth stage in soybean. Oil content in developing seeds begins to accumulate at 15–20 days after flowering. Jung et al. [67] reported that the composition of oleic acid was positively influenced by increasing temperature, whereas the proportions of linoleic and linolenic acid were reduced. Severe water stress or high temperature resulted in higher C16:0 but lower C18:0. Genotypes differed in their responses to temperature and water stress [68].

HT and drought stress hinders the accumulation of various seed constituents, primarily starch and proteins [52, 69], through inhibiting the enzymatic processes of synthesis of starch [70] and proteins [71]. At a biochemical level, high temperature induces protein denaturation, increases membrane lipid fluidity and ROS production, and inhibits the function of photosynthetic apparatus [8, 72].

During the growth period of plants, seed formation is an important growth stage that includes the assembling of several compounds of leaves into the seed during the chemical formation of several organic compounds like starch, lipid, glucose, etc. [73, 74]. Grain formation is a very sensitive growth phase that is severely affected by high-temperature stress. Plant yield is severely declined when plants are directly exposed to high-temperature stress during seed formation stage and it ultimately reduces the seed weight and biological yield and quality of seeds. The reason for this decrease is that plants are unable to stand their growth under temperature stress circumstances; therefore, minimum photosynthetic efficiency was observed during the whole growth lifecycle. Thus, the assimilation of various seed constituents like protein, lipid, starch and carbohydrates, etc., get affected due to disturbance in enzymatic activity under high-temperature stress conditions [70, 71, 75]. Protein assimilation was decreased due to high-temperature stress in seeds [76], since there was a close relationship was noticed among leaf nitrogen concentration and seed protein contents [77]. HT stress leads to results decrease in gluten protein concentration and lactic acid concentration. Seed protein concentration is totally dependent on sedimenting amino acids while high-temperature stress decreases these sedimenting amino acids due to which seed protein contents were reduced [78].

2.5 Heat stress effects on nitrogen fixation in soybean

The understanding of environmental stress on nitrogen fixation is intensely required for growing soybean under adverse environmental conditions. High root temperatures strongly affect the bacterial infection and N₂ fixation in several legume species, including soybean. Indeed, temperature affects the root hair infection, bacteroid differentiation, nodule structure, and the functioning of the legume root nodule.

Several studies have shown that *Rhizobium*, a Gram negative N-fixing soil bacterium, has a positive impact on legumes.

Several environmental conditions are critical factors which can have detrimental effects on the steps involved in Rhizobium-legume symbiosis as infection process, nodules development and function, resulting in low nitrogen fixation and crop yield [79]. Under stress conditions, the aerobic bacteria have shown their ability to use nitrogen oxides as terminal electron acceptors which can help them to survive and grow during periods of anoxia. This may present a great advantage for the survival of rhizobia in soil [80]. High temperature is one of the main factors influencing symbiotic nitrogen fixation [81].

Nitrogen fixation is often especially inhibited by temperature extremes which have less effect on plant growth. High soil temperature is one of the critical factors that can prevent the development of a nitrogen-fixing association between the two symbiotic partners especially in arid and semi-arid regions [80]. High temperature can induce an inhibiting effect on bacterial adherence to root hairs, on bacteroid differentiation, on nodule structure and on legume root nodule's functioning [80]. High soil temperatures will delay nodulation or restrict it to the subsurface region. A better understanding of nodule activity physiological responses to extrinsic stress factors is very important to improve productivity by harnessing the biological nitrogen fixation process.

3. Strategies to mitigate heat stress on soybean for the sustainability of soybean production

3.1 By using “Stay-Green” genotypes or delay leaf senescence

Delayed senescence or Stay-Green (SG) genotypes constitute an important source of germplasm for the genetic improvement of plants to mitigate HT stress. These genotypes are of agronomic interest because their green leaves and photosynthesis capacity are maintained for a longer time after anthesis as compared to standard genotypes [82]. These plants are tolerant to biotic and abiotic stresses showing delayed leaf senescence under stress and improved yield production [83–85].

It has been reported that HT stress induces the leaf senescence by a decline in the Chl content of leaves, due to accelerated Chl degradation. Proteins encoded by the so-called “Stay-Green Rice” (SGR) genes may function as positive or negative regulators of Chl degradation during senescence [86]. For example, soybean plants have two SGR genes called D1 and D2, which encode GmSGR1 and GmSGR2, respectively [87]. Studies of these genes demonstrated that the leaves of d1 d2 double mutants exhibited a stronger “Stay-Green” phenotype than leaves of d1 mutants. These results indicate that the two GmSGRs have redundant functions and suggesting that SGR and SGRL could act in Chl catabolism during vegetative growth [87].

The utilization of SG trait in breeding programs results in important genetic progress for high grain yield and tolerance to HT stress. Thus, there is a need to increase the knowledge of the SG potentiality to increase grain yield under high-temperature conditions in soybean and to explore genotypes of SG ability in leaves to sustain seed filling in breeding programs.

3.2 By enhancing the production or exogenous application of antioxidants

HT stress triggers sudden and abrupt changes at the time of pollination as well as grain-filling stage which leads to early maturity along with deteriorating appropriate development of grains [88, 89]. Recently, global warming has multiplied the incidence of environmental stress leading to a serious decline in crop yield [90]. One of the ways to deal with adverse effects of HT stress may involve exploring

some molecules that have the potential to protect the plants from the harmful effects of high temperature [91]. Previous studies report that exogenous proline application improves the tolerance against different types of abiotic stresses such as osmotic stress, but not in HT stress. HT stress often leads to excess accumulation of ROS such as superoxide radical (O_2^-) and hydrogen peroxide (H_2O_2), causing oxidative damage to DNA, proteins, and lipids and thus reproductive failure [23, 92]. Different types of antioxidants produced endogenously or applied have the potential to impart HT tolerance to crop plants under varying agro-climatic conditions. Antioxidants may improve HT tolerance through improvement of gaseous exchange and modulating metabolic activities of the plants along with reducing the generation of reactive oxygen species. Antioxidants enable plants to cope with oxidative burst and prevent damage to chloroplast [93].

Crop failure owing to HT stress becomes evident if the temperature gets increased even by 3–6°C during vegetative or reproductive growth stages of field crops. Liang et al. [94] reported that exogenous application of melatonin improved the activity of antioxidants especially catalase (CAT), superoxide dismutase (SOD), and peroxidase (POD) and thus enabling plants to cope with HT stress. It was inferred that glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), ascorbate peroxidase (APX), and dehydroascorbate reductase (DHAR) imparted HT resistance owing to the regulation of AsA-GSH cycle. Plants can accumulate proline to cope with HT stress while antioxidants effectively enhance the production of melatonin in tea, wheat, cherry, tomato, and kiwi leaves by triggering proline biosynthesis pathway [95]. Antioxidants, such as glutathione (GSH), ascorbic acid (AsA), and proline play essential roles in protecting plants from oxidative damage by scavenging ROS and thus enhance HT tolerance of legumes. For example, the application of exogenous GSH enhanced mung bean seedling tolerance of short-term high-temperature stress (42°C) by modulating the antioxidant and glyoxalase systems [8, 23]. Under abiotic stresses, such as heat, drought, and salinity, plants often over-produce different types of compatible organic solutes, among which proline and glycine betaine are important in stress tolerance of plants by acting as osmoprotectants and ROS scavengers [17]. Thus, the exogenous application of antioxidants offers tremendous potential to enable crop plants to cope with HT stress especially at the reproductive growth stage because abrupt changes at the grain-filling stage drastically reduce grain development as well as its quality. However, further in-depth field and in-vitro investigations are direly needed to explore underlying plant mechanisms for the production of antioxidants and their ameliorative effect on plants subjected to HT stress.

3.3 Other compatible solutes as a means of heat stress defensive mechanism

HT stress causes the plant to gradually wilt at the vegetative growth stage while its incidence at reproductive stages severely hampers grain formation. One of the mechanisms to cope with HT stress is the synthesis of compatible solutes for regulating water content. Most of the solutes improve water retention by modulating cellular water potential and thus referred to as compatible solutes or osmoprotectants. The extensively studied osmolytes include betaine, trehalose, glycine, proline, and mannitol. However, proline is one the most effective compatible solute and it may be ranked at the top among osmoprotectants in plants [96, 97].

Several studies reported that proline plays a regulatory role in the activity and function of the enzymes in plant cells and in their participation in the development of metabolic responses to environmental factors [98]. Thus, proline can be a promising signaling molecule to take HT stress in the plant [88]. Similarly, these mechanisms are promoting photosynthesis, maintaining enzymatic activity, and

scavenging ROS. Earlier studies noticed that the exogenous application of proline regulates the uptake of mineral nutrients in plants subjected to water deficit conditions [99] and it is one of the osmotic protection mechanisms in the plant under water [100]. However, the proposed functions of accumulated proline are osmoregulation, maintenance of membrane, and protein stability under water stress conditions [101]. Enhancement of proline concentration in whole plant organs is considered to be correlated with HT and water stress tolerance. The accumulation of proline to mitigate the negative effect on plant growth and development under HT stress was reported in chickpea [102, 103] and sorghum [104]. Much attention has been paid to define the role of proline in stress environment tolerance as a compatible osmolyte. However, little attention has been given to its role in affecting the uptake and accumulation of inorganic nutrients in plants [105].

Proline may enhance HT tolerance of chickpea through alleviating the inhibition of HT stress on key enzymes in carbon and oxidative metabolism in seedlings [106]. Therefore, it is speculated that proline and its transportation might regulate the response of legume reproduction to HT stress, which should be further testified by more direct evidence [23]. There are many defense mechanisms in plants such as osmoregulation, ion homeostasis, antioxidant and hormonal systems which induce HT stress tolerance in plants. Many plants in dry habitats are known to accumulate organic solutes such as GB [107]. GB is known to serve as compatible osmolytes, macromolecules protections, and also as scavengers of ROS under stressful environments [17]. In a stressful environment, plants store multiple groups of compatible solutes such as sugars, free amino acids like GB polyols to survive [108]. GB is a member of quaternary ammonium compounds that are pre-dominant in higher plants subjected to HT and water stress conditions. In [17, 109], the positive effects of exogenous application of GB on plant growth and final crop yield of soybean under water stress are reported. Wang et al. [110] reported that the application of GB increased the osmotic adjustment in plants for water stress tolerance by improving the anti-oxidative defense system including anti-oxidative enzymes in wheat. Although the exact mechanism is still unclear, it has been suggested that GB can mitigate HT stress via a number of different mechanisms. One of them is the protection of photosynthetic machinery [111].

Most studies with GB have focused on its physiological role and biosynthetic pathway, with little interest in its effect on the anti-oxidative defense system. GB, as one of the compatible solutes, which plays an important role in stress environment by osmotic adjustment in plants [112, 113], through protecting the proteins by maintaining the structure of enzymes such as Rubisco [196], protecting the membrane structure, protection of cytoplasm and chloroplasts [114], protection of photosynthetic mechanism [115], and by functioning as oxygen radical sweeper.

3.4 Production of stress defensive phytohormones

Plants have developed a variety of adaptations that allow them to cope with HT stress. Some of these responses include changes in leaf orientation, modification of membrane lipid composition, activation of anti-oxidative mechanisms, accumulation of osmolites, and hormonal regulation [8]. HT stress often leads to excess accumulation of ROS such as superoxide radical (O_2^-) and hydrogen peroxide (H_2O_2), causing oxidative damage to DNA, proteins, and lipids, and thus reproductive failure [23, 92].

Hormones are chemical messengers that control plants growth and development in response to adverse environmental conditions. The application of mineral fertilizers harmfully influences the environment, so eco-friendly agro-technologies are required, to improve crop production [2]. Small fluctuations of hormone contents

alter the cellular dynamics and, hence, they have a central role in regulating plant growth responses to abiotic stress [116]. Moreover, hormones play vital roles in plant reproduction under both normal and HT stress conditions. In general, auxins (AX), gibberellins (GA), and cytokinins (CK) positively regulate plant reproductive tolerance to HT stress [117]. Ethylene (ET) may play a negative role in legume reproduction under HT stress. HT treatments in soybean plants increases the rate of ET production along with induction of oxidative damage, which triggers flower abscission and decreased pod set percentage [40]. A few studies have been conducted on the role of hormones in the HT tolerance of legume reproduction to date [23].

ABA and GA play several roles in the regulation of seed dormancy and germination. The metabolism and signaling by both hormones, ABA and GA, are modified during the development, dormancy and germination of seeds and the establishment of plants [118]. Recently, Shuai and his group, in 2017, demonstrated that applications of AX on soybean seeds represses the germination by increasing of ABA biosynthesis, while impairing the GA biogenesis, and finally decreasing GA1/ABA and GA4/ABA ratios. Accordingly, treatments of fluridone (ABA biosynthesis inhibitor) on seeds reversed the delayed-germination phenotype associated to AX applications, while treatments of Paclobutrazol (GA biosynthesis inhibitor) inhibited the germination of soybean seeds [119]. However, changes in hormones contents and signaling in soybean seed germination under HT stress remain unclear.

Ethylene, a gaseous phytohormone, affects seed germination, plant development and fruit production under abiotic stress [120, 121]. It is well-known that this hormone (provides tolerance to HT stress [122, 123]). It triggers the expression of certain genes essential for stress tolerance adaptation by influencing different osmolytes, which can protect the plants under stressful conditions [124–126]. Further researches are needed to identify the effects of ET and other hormones on seed germination under adverse environmental conditions. Recently, the indoleamine molecule (melatonin) has been proposed as a new plant hormone [127]. Melatonin is involved in several physiological processes in plants playing as an antioxidant molecule and triggers antioxidant responses in plants under abiotic stress [128]. Therefore, applications of this molecule in plants are being evaluated by numerous researchers. Wei et al. [129] studied the effect of melatonin on soybean growth and development. Applications of this molecule in seeds promoted the leaf size and height of soybean plants. In addition, melatonin increased the pod number and seed number, but not 100-seed weight. Under salinity and drought stress, melatonin applications showed an improvement of tolerance in soybean plants [129]. Similarly, melatonin applications could increase the soybean tolerance to HT stress; the evidence indicates that adverse environmental conditions can increase the melatonin content in plants as a protective response [127].

3.5 Biotechnological strategies to improve heat stress tolerance in soybean plants

The development of genotypes with tolerance to HT stress and agronomic practices avoiding the detrimental effects of high temperatures are required to sustain and increase the production of soybean plants. Therefore, scientists are looking for strategies to enhance soybean productivity to manage the necessity of feeding an increasing population. Among the strategies for improving soybean tolerance under challenging environments, numerous technologies are contributing to this purpose. Omics is one of the most emerging technologies which allows for studying the global metabolomic, transcriptomic and/or genomic responses of soybeans to HT stress for developing metabolomic markers, utilizing metabolic pathways, and assisting soybean breeding programs. Recently, Das et al. [130] performed a

soybean metabolomic study of leaves and they determined differential abundances of various primary and secondary metabolites in response to HT stress. Metabolites for several processes, such as glycolysis, the tricarboxylic acid cycle, the pentose phosphate pathway, and amino acid metabolism, peptide metabolism, and purine and pyrimidine biosynthesis, were found to be affected by HT stress. Thus, soybean metabolomic profiling demonstrated that carbohydrate and nitrogen compounds are of prime significance under high-temperature conditions [130]. These results provide useful information for the development of tolerant soybean varieties to HT stress varieties. Similarly, seed metabolites were analyzed in several soybean genotypes with differential tolerance to high temperatures [24]. A total of 275 metabolites were identified. Antioxidant metabolites, such as tocopherols, flavonoids, phenylpropanoids, and ascorbate precursors were found to be enriched in seeds of the heat-tolerant soybean genotype. These metabolites in the tolerant genotype could be responsible, at least in part, for the greater tolerance to high temperatures during seed development. Moreover, studies of transcriptomic in soybean plants grown at high-temperature conditions were performed. For example, Xu and his group, in 2019, used a high-throughput RNA-Seq profiling technique to study the molecular mechanisms in the reproductive stage soybean in response to heat. They demonstrated that a total of 633 annotated genes were differentially expressed in heat-stressed soybeans, in which 417 genes were up-regulated and 216 were down-regulated. These genes encode for compounds related to flowering, oxidative stress, protein and mRNA folding and degradation, protective molecule synthesis, and hormonal biosynthesis and signaling [131]. Besides these, the transcriptomic analysis was performed on soybean seeds in response to abiotic stresses. Gene expression analysis revealed 49, 148, and 1576 differentially expressed genes in the soybean seed coat in response to drought, elevated ozone, and high temperatures, respectively [132]. The expressed genes in the seeds under high temperature were involved in DNA replication and several metabolic processes, suggesting that the timing of events that are important for cell division and development of seed were altered in a stressful growth environment.

Taken together, these studies show that soybeans plants employ diverse pathways and complex mechanisms to cope with high-temperature conditions. However, some of the identified genes and pathways could be used to improve HT tolerance in soybeans via either molecular breeding methods or genetic engineering.

4. Concluding remarks

In conclusion, this review clarified the numerous physiological and biochemical responses of different growth stages of soybean plants under HT stress. Therefore, HT stress has an adverse effect on growth, physiology, yield, and quality of soybean. However, applications of several compounds have a direct role in supporting enzymes, proteins, aminoacids, and lipids involved in protecting systems that participate in reducing HT stress in plants. Application of antioxidants, osmoprotectants, and phytohormones may improve the HT tolerance in soybean plants through different mechanisms. Accordingly, the antioxidant protection activity of several compounds, such as antioxidants, compatible solutes, and hormones against HT stress is powerful and can solve the seasonal HT stress problem to a greater extent and also provide the technical knowledge for sustainable development in agriculture. Emerging “omics” intervention, including genomics, epigenomics, transcriptomics, proteomics, and metabolomics could greatly improve our current understanding of the intricate gene networks and signaling cascades involved in the role of these compounds applied to minimize the harmful effects of HT stress on soybean plants.

Conflicts of interest

The authors declare no conflicts of interest.

Disclosure statement

Authors declare that no conflict of interest could arise.

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