Chapter

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

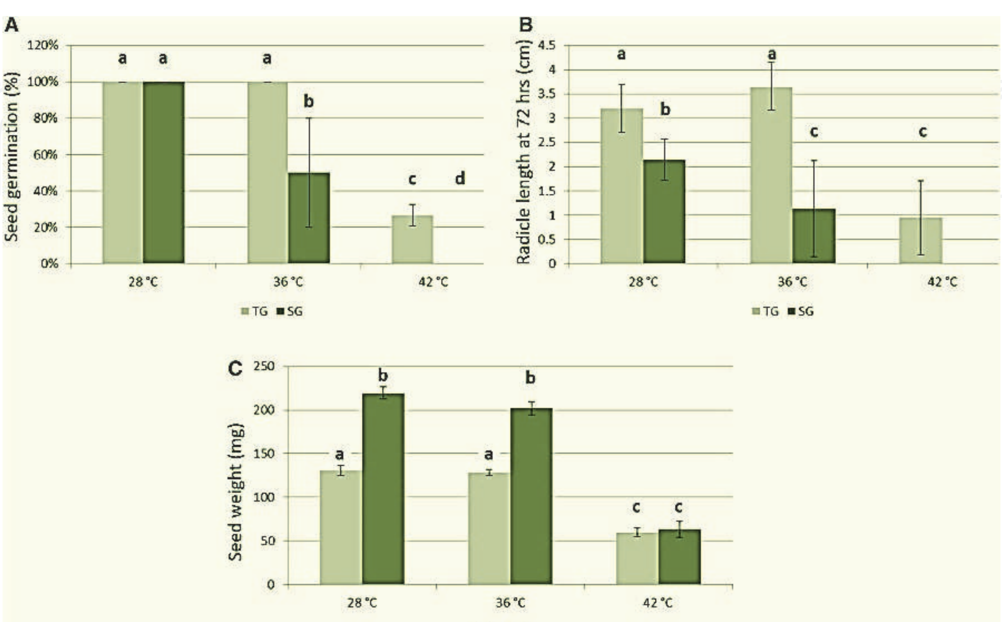

Figure 1.
Influence of high temperature during seed development on seed quality parameters. Germination percentage at 25°C after 72 h (A), radicle length (B), and mature seed weight (C) in two soybean genotypes: TG (high-temperature tolerant) and SG (high-temperature sensitive).

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 N_2 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 Rubisco1996, 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 temperate 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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References

[1] Hartman GL, West ED, Herman TK. Crops that feed the World 2. Soybean-worldwide production, use, and constraints caused by pathogens and pests. Food Security. 2011;**3**:5-17

[2] EL Sabagh A, Hossain A, Islam MS, Barutçular C, Ratnasekera D, Kumar N, et al. Sustainable soybean production and abiotic stress management in saline environments: A critical review. Australian Journal of Crop Science. 2019;**13**:228-236

[3] EL Sabagh A, Omar AE, Saneoka H, Barutçular C. Physiological performance of soybean germination and seedling growth under salinity stress Soyada. Dicle University Journal of Institute of Natural and Applied Science. 2015;**4**: 6-15

[4] Meena RS, Gogaoi N, Kumar S. Alarming issues on agricultural crop production and environmental stresses. Journal of Cleaner Production. 2017;**142**: 3357-3359

[5] Valdés-López O, Batek J, Gomez-Hernandez N, Nguyen CT, Isidra-Arellano MC, Zhang N, et al. Soybean roots grown under heat stress show global changes in their transcriptional and proteomic profiles. Frontiers in Plant Science. 2016;**7**:517. DOI: 10.3389/fpls.2016.00517

[6] Raza A, Razzaq A, Mehmood SS, Zou X, Zhang X, Lv Y, et al. Impact of climate change on crops adaptation and strategies to tackle its outcome: A review. Plants. 2019;**8**:34. DOI: 10.3390/plants8020034

[7] Mathur S, Jajoo A. Effects of heat stress on growth and crop yield of wheat (*Triticum astivum*). In: Physiological Mechanisms and Adaptation Strategies in Plants Under Changing Environment. New York, NY: Springer; 2014. pp. 163-191

[8] Hasanuzzaman M, Nahar K, Fujita M. Extreme temperature responses, oxidative stress and antioxidant defense in plants. Abiotic Stress-Plant Responses and Applications in Agriculture. 2013;**13**:169-205

[9] Fahad S, Ullah A, Ali U, Ali E, Saud S, Rehman K, et al. 7 drought tolerance in plants role of phytohormones and scavenging system of ROS. In: Hasanuzzaman M, Fujita M, Oku H, Islam MT, editors. Plant Tolerance to Environmental Stress: Role of Phytoprotectants. Boca Raton: CRC Press; 2019. p. 10

[10] Saleem MH, Fahad S, Khan SU, Din M, Ullah A, EL Sabagh A, et al. Copper-induced oxidative stress, initiation of antioxidants and phytoremediation potential of flax (*Linum usitatissimum* L.) seedlings grown under the mixing of two different soils of China. Environmental Science and Pollution Research. 2019;**1**:5211-5221. DOI: 10.1007/s11356-019-07264-7

[11] Islam MS, Akhter MM, EL Sabagh A, Liu LY, Nguyen NT, Ueda A, et al. Comparative studies on growth and physiological responses to saline and alkaline stresses of foxtail millet (*Setaria italic* L.) and Proso millet (*Panicum miliaceum* L.). Australian Journal of Crop Science. 2011;**5**:1269

[12] EL Sabagh A, Omara A, Saneokab H, Islamc MS. Roles of compost fertilizer on nitrogen fixation in soybean (*Glycine max* L.) under water deficit conditions. Agricultural Advances. 2016;**5**:340-344. DOI: 10.14196/aa.v5i7.2326

[13] Kovar M, Brestic M, Sytar O, Barek V, Hauptvogel P, Zivcak M. Evaluation of hyperspectral reflectance parameters to assess the leaf water content in soybean. Water. 2019;**11**:443

[14] Hadiarto T, Tran LS. Progress studies of drought-responsive genes in

rice. Plant Cell Reports. 2011;**30**: 297-310. DOI: 10.1007/s00299-010-0956-z

[15] Thapa GD, Dey M, Sahoo L, Panda SK. An insight into the drought stress induced alterations in plants. Biologia Plantarum. 2011;**55**:603-613

[16] Dadhich RK, Reager ML, Kansoti BC, Meena RS. Efficacy of growth substances on mustard (*Brassica juncea* L.) under hyper arid environmental condition of Rajasthan. The Ecoscan. 2014;**8**:269-272

[17] Ashraf MF, Foolad MR. Roles of glycine betaine and proline in improving plant abiotic stress resistance. Environmental and Experimental Botany. 2007;**59**:206-216

[18] Meena H, Meena RS, Rajput BS, Kumar S. Response of bio-regulators to morphology and yield of clusterbean [*Cyamopsis tetragonoloba* (L.) Taub.] under different sowing environments. Journal of Applied and Natural Science. 2016;**8**:715-718

[19] Mathur S, Allakhverdiev SI, Jajoo A. Analysis of high temperature stress on the dynamics of antenna size and reducing side heterogeneity of Photosystem II in wheat leaves (*Triticum aestivum*). Biochimica et Biophysica Acta (BBA)-Bioenergetics. 2011;**1807**:22-29

[20] Young LW, Wilen RW, Bonham-Smith PC. High temperature stress of *Brassica napus* during flowering reduces micro-and megagametophyte fertility, induces fruit abortion, and disrupts seed production. Journal of Experimental Botany. 2004;**55**:485-495

[21] Suzuki N, Miller G, Sejima H, Harper J, Mittler R. Enhanced seed production under prolonged heat stress conditions in *Arabidopsis thaliana* plants deficient in cytosolic ascorbate peroxidase 2. Journal of Experimental Botany. 2013;**64**:253-263

[22] Fahad S, Hussain S, Saud S, Khan F, Hassan S, Nasim W, et al. Exogenously applied plant growth regulators affect heat-stressed rice pollens. Journal of Agronomy and Crop Science. 2016;**202**: 139-150

[23] Liu Y, Li J, Zhu Y, Jones A, Rose RJ, Song Y. Heat stress in legume seed setting: Effects, causes, and future prospects. Frontiers in Plant Science. 2019;**10**:938. DOI: 10.3389/fpls.2019.00938

[24] Chebrolu KK, Fritschi FB, Ye S, Krishnan HB, Smith JR, Gillman JD. Impact of heat stress during seed development on soybean seed metabolome. Metabolomics. 2016;**12**:28. DOI: 10.1007/s11306-015-0941-1

[25] Djanaguiraman M, Boyle DL, Welti R, Jagadish SV, Prasad PV. Decreased photosynthetic rate under high temperature in wheat is due to lipid desaturation, oxidation, acylation, and damage of organelles. BMC Plant Biology. 2018;**18**:55. DOI: 10.1186/s12870-018-1263-z

[26] Djanaguiraman M, Prasad PV. Ethylene production under high temperature stress causes premature leaf senescence in soybean. Functional Plant Biology. 2010;**37**:1071-1084

[27] Wahid A, Gelani S, Ashraf M, Foolad MR. Heat tolerance in plants: An overview. Environmental and Experimental Botany. 2007;**61**:199-223

[28] Essemine J, Ammar S, Bouzid S. Impact of heat stress on germination and growth in higher plants: Physiological, biochemical and molecular repercussions and mechanisms of defence. Journal of Biological Sciences. 2010:565-572

[29] Suzuki N, Mittler R. Reactive oxygen species and temperature stresses: A delicate balance between signaling and destruction. Physiologia

Plantarum. 2006;**126**:45-51. DOI: 10.1111/j.0031-9317.2005.00582.x

[30] Egli DB, TeKrony DM, Heitholt JJ, Rupe J. Air temperature during seed filling and soybean seed germination and vigor. Crop Science. 2005;**45**: 1329-1335

[31] Fahad S, Bajwa AA, Nazir U, Anjum SA, Farooq A, Zohaib A, et al. Crop production under drought and heat stress: Plant responses and management options. Frontiers in Plant Science. 2017;**8**:1147

[32] Thanacharoenchanaphas K, Rugchati O. Simulation of climate variability for assessing impacts on yield and genetic change of Thai soybean. Genetics. 2011;**21**:4-5

[33] Naz N, Durrani F, Shah Z, Khan NA, Ullah I. Influence of heat stress on growth and physiological activities of potato (*Solanum tuberosum* L.). Phyton: International Journal of Experimental Botany. 2018;**87**:225-230

[34] Setiyono TD, Weiss A, Specht J, Bastidas AM, Cassman KG, Dobermann A. Understanding and modeling the effect of temperature and daylength on soybean phenology under high-yield conditions. Field Crops Research. 2007;**100**:257-271. DOI: 10.1016/j.fcr.2006. 07.011

[35] Reddy KR, Kakani VG. Screening capsicum species of different origins for high temperance tolerance by in vitro pollen germination and pollen tube length. Scientia Horticulturae. 2007;**112**: 130-135

[36] Puteh AB, ThuZar M, Mondal MM, Abdullah AP, Halim MR. Soybean [*Glycine max* (L.) Merrill] seed yield response to high temperature stress during reproductive growth stages. Australian Journal of Crop Science. 2013;**7**:1472-1479

[37] Braga RM, Dourado MN, Araújo WL. Microbial interactions: ecology in a molecular perspective. Brazilian Journal of Microbiology. 2016; **47**:86-98

[38] Ghassemi-Golezani K, Ghanehpoor S, Dabbagh M-NA. Effects of water limitation on growth and grain filling of faba bean cultivars. Journal of Food, Agriculture and Environment. 2009;**7**:442-447

[39] El-Tayeb MA. Differential response of two Vicia faba cultivars to drought: Growth, pigments, lipid peroxidation, organic solutes, catalase and peroxidase activity. Acta Agronomica Hungarica. 2006;**54**:25-37

[40] Djanaguiraman M, Prasad PV, Boyle DL, Schapaugh WT. High-temperature stress and soybean leaves: Leaf anatomy and photosynthesis. Crop Science. 2011;**51**:2125-2131

[41] Yin H, Chen Q, Yi M. Effects of short-term heat stress on oxidative damage and responses of antioxidant system in *Lilium longiflorum*. Plant Growth Regulation. 2008;**4**:45-54

[42] Camejo D, Jiménez A, Alarcón JJ, Torres W, Gómez JM, Sevilla F. Changes in photosynthetic parameters and antioxidant activities following heat-shock treatment in tomato plants. Functional Plant Biology. 2006;**33**: 177-187

[43] Wise RR, Olson AJ, Schrader SM, Sharkey TD. Electron transport is the functional limitation of photosynthesis in field-grown Pima cotton plants at high temperature. Plant, Cell & Environment. 2004;**27**:717-724

[44] Xu S, Li J, Zhang X, Wei H, Cui L. Effects of heat acclimation pretreatment on changes of membrane lipid peroxidation, antioxidant metabolites, and ultrastructure of chloroplasts in two cool-season turfgrass species under heat

stress. Environmental and Experimental Botany. 2006;**56**:274-285

[45] Bhandari K, Siddique KH, Turner NC, Kaur J, Singh S, Agrawal SK, et al. Heat stress at reproductive stage disrupts leaf carbohydrate metabolism, impairs reproductive function, and severely reduces seed yield in lentil. Journal of Crop Improvement. 2016; **30**(2):118-151

[46] Sharma L, Priya M, Bindumadhava H, Nair RM, Nayyar H. Influence of high temperature stress on growth, phenology and yield performance of mungbean [*Vigna radiata* (L.) Wilczek] under managed growth conditions. Scientia Horticulturae. 2016;**213**:379-391. DOI: 10.1016/j.scienta.2016.10.033

[47] Sita K, Sehgal A, Kumar J, Kumar S, Singh S, Siddique KH, et al. Identification of high-temperature tolerant lentil (*Lens culinaris* Medik.) genotypes through leaf and pollen traits. Frontiers in Plant Science. 2017;**8**:744. DOI: 10.3389/fpls.2017.00744

[48] Zare M, Nejad MG, Bazrafshan F. Influence of drought stress on some traits in five mung bean (*Vigna radiata* (L.) R. Wilczek) genotypes. International Journal of Agronomy and Plant Production. 2012;**3**:234-240

[49] Devasirvatham V, Tan DK, Trethowan RM, Gaur PM, Mallikarjuna N. Impact of high temperature on the reproductive stage of chickpea. In: Food Security from Sustainable Agriculture Proceedings of the 15th Australian Society of Agronomy Conference; 2010. pp. 15-18

[50] Prasad PV, Pisipati SR, Momčilović I, Ristic Z. Independent and combined effects of high temperature and drought stress during grain filling on plant yield and chloroplast EF-Tu expression in spring wheat. Journal of Agronomy and Crop Science. 2011;**197**: 430-441. DOI: 10.1111/j.1439-037X.2011.00477.x

[51] Kaushal N, Bhandari K, Siddique KH, Nayyar H. Food crops face rising temperatures: An overview of responses, adaptive mechanisms, and approaches to improve heat tolerance. Cogent Food & Agriculture. 2016;**2**: 1134380. DOI: 10.1080/23311932.2015.1134380

[52] Farooq M, Nadeem F, Gogoi N, Ullah A, Alghamdi SS, Nayyar H, et al. Heat stress in grain legumes during reproductive and grain-filling phases. Crop & Pasture Science. 2017;**68**: 985-1005

[53] EL Sabagh A, Islam MS, Ueda A, Saneoka H, Barutçular C. Increasing reproductive stage tolerance to salinity stress in soybean. The International Journal of Agriculture and Crop Sciences. 2015;**8**:738-745

[54] EL Sabagh A, Sorour S, Ueda A, Saneoka H. Evaluation of salinity stress effects on seed yield and quality of three soybean cultivars. Azarian Journal of Agriculture. 2015;**2**:138-141

[55] EL Sabagh A, Sorour S, Ragab A, Saneoka H, Islam MS. The effect of exogenous application of proline and glycine betaineon the nodule activity of soybean under saline condition. Journal of Agriculture Biotechnology. 2017;**2**: 01-05

[56] EL Sabagh A, Abdelaal KA, Barutcular C. Impact of antioxidants supplementation on growth, yield and quality traits of canola (*Brassica napus* L.) under irrigation intervals in North Nile Delta of Egypt. Journal of Experimental Biology and Agricultural Sciences. 2017;**5**:163-172

[57] Thomas JM, Boote KJ, Allen LH, Gallo-Meagher M, Davis JM. Elevated temperature and carbon dioxide effects on soybean seed composition and

transcript abundance. Crop Science. 2003;**43**:1548-1557. DOI: 10.2135/cropsci2003.1548

[58] Salem MA, Kakani VG, Koti S, Reddy KR. Pollen-based screening of soybean genotypes for high temperatures. Crop Science. 2007;**47**: 219-231. DOI: 10.2135/cropsci2006.07.0443

[59] Thuzar M. The effects of temperature stress on the quality and yield of soya bean [(*Glycine max* L.) Merrill.]. The Journal of Agricultural Science. 2010;**2**:172-179

[60] Frederick JR, Camp CR, Bauer PJ. Drought-stress effects on branch and mainstem seed yield and yield components of determinate soybean. Crop Science. 2001;**41**:759-763

[61] Tubiello FN, Soussana JF, Howden SM. Crop and pasture response to climate change. Proceedings of the National Academy of Sciences. 2007; **104**:19686-19690

[62] Canci H, Toker C. Evaluation of yield criteria for drought and heat resistance in chickpea (*Cicer arietinum* L.). Journal of Agronomy and Crop Science. 2009;**195**:47-54

[63] Canci H, Toker C. Evaluation of annual wild *Cicer* species for drought and heat resistance under field conditions. Genetic Resources and Crop Evolution. 2009;**56**:1. DOI: 10.1007/s10722-008-9335-9

[64] Wheeler T, Von Braun J. Climate change impacts on global food security. Science. 2013;**341**:508-513

[65] Thomey ML, Slattery RA, Köhler IH, Bernacchi CJ, Ort DR. Yield response of field-grown soybean exposed to heat waves under current and elevated [CO_2]. Global Change Biology. 2019;**25**:4352-4368

[66] Bellaloui N, Bruns HA, Abbas HK, Mengistu A, Fisher DK, Reddy KN. Agricultural practices altered soybean seed protein, oil, fatty acids, sugars, and minerals in the Midsouth USA. Frontiers in Plant Science. 2015;**6**:31. DOI: 10.3389/fpls.2015.00031

[67] Jung G, Lee J, Kim Y, Kim D, Hwang T, Lee K, et al. Effect of planting date, temperature on plant growth, isoflavone content, and fatty acid composition of soybean. Korean Journal of Crop Science/Hanguk Jakmul Hakhoe Chi. 2012;**57**:373-383

[68] Gulluoglu L, Bakal H, EL Sabagh A, Arioglu H. Soybean managing for maximize production: Plant population density effects on seed yield and some agronomical traits in main cropped soybean production. Journal of Experimental Biology and Agricultural Sciences. 2017;**5**:31-37

[69] Farooq M, Gogoi N, Barthakur S, Baroowa B, Bharadwaj N, Alghamdi SS, et al. Drought stress in grain legumes during reproduction and grain filling. Journal of Agronomy and Crop Science. 2017;**203**:81-102. DOI: 10.1093/jxb/err139

[70] Ahmadi A, Baker DA. The effect of water stress on grain filling processes in wheat. The Journal of Agricultural Science. 2001;**136**:257-269

[71] Triboï E, Martre P, Triboï-Blondel AM. Environmentally-induced changes in protein composition in developing grains of wheat are related to changes in total protein content. Journal of Experimental Botany. 2003;**54**: 1731-1742

[72] Qu AL, Ding YF, Jiang Q, Zhu C. Molecular mechanisms of the plant heat stress response. Biochemical and Biophysical Research Communications. 2013;**432**:203-207. DOI: 10.1016/j.Bbrc.2013.01.104

[73] Barnabás B, Jäger K, Fehér A. The effect of drought and heat stress on reproductive processes in cereals. Plant, Cell & Environment. 2008;**31**:11-38

[74] Awasthi R, Kaushal N, Vadez V, Turner NC, Berger J, Siddique KH, et al. Individual and combined effects of transient drought and heat stress on carbon assimilation and seed filling in chickpea. Functional Plant Biology. 2014;**41**:1148-1167

[75] Behboudian MH, Ma Q, Turner NC, Palta JA. Reactions of chickpea to water stress: Yield and seed composition. Journal of the Science of Food and Agriculture. 2001;**81**:1288-2891

[76] Lizana XC, Calderini DF. Yield and grain quality of wheat in response to increased temperatures at key periods for grain number and grain weight determination: Considerations for the climatic change scenarios of Chile. The Journal of Agricultural Science. 2013; **151**:209-221

[77] Iqbal M, Raja NI, Yasmeen F, Hussain M, Ejaz M, Shah MA. Impacts of heat stress on wheat: A critical review. Advances in Crop Science and Technology. 2017;**5**:251-259

[78] Dias AS, Bagulho AS, Lidon FC. Ultrastructure and biochemical traits of bread and durum wheat grains under heat stress. Brazilian Journal of Plant Physiology. 2008;**20**:323-333

[79] Lebrazi S, Benbrahim KF. Environmental stress conditions affecting the N_2 fixing rhizobium-legume symbiosis and adaptation mechanisms. African Journal of Microbiological Research. 2014;**8**: 4053-4061

[80] Abd-Alla MH, Issa AA, Ohyama T. Impact of harsh environmental conditions on nodule formation and dinitrogen fixation of legumes. Advances in Biology and Ecology of Nitrogen Fixation. 2014;**29**:9

[81] Keerio MI. Nitrogenase activity of soybean root nodules inhibited after heat stress. OnLine Journal of Biological Sciences. 2001;**1**:297-300

[82] Thomas H, Ougham H. The stay-green trait. Journal of Experimental Botany. 2014;**65**:3889-3900

[83] Peleg Z, Blumwald E. Hormone balance and abiotic stress tolerance in crop plants. Current Opinion in Plant Biology. 2011;**14**:290-295

[84] Reguera M, Peleg Z, Abdel-Tawab YM, Tumimbang EB, Delatorre CA, Blumwald E. Stress-induced cytokinin synthesis increases drought tolerance through the coordinated regulation of carbon and nitrogen assimilation in rice. Plant Physiology. 2013;**163**:1609-1622

[85] Luche HD, Silva JA, Maia LC, Oliveira AC. Stay-green: A potentiality in plant breeding. Ciência Rural. 2015; **45**:1755-1760

[86] Sakuraba Y, Piao W, Lim JH, Han SH, Kim YS, An G, et al. Rice ONAC106 inhibits leaf senescence and increases salt tolerance and tiller angle. Plant & Cell Physiology. 2015;**56**(12): 2325-2339

[87] Nakano M, Yamada T, Masuda Y, Sato Y, Kobayashi H, Ueda H, et al. A green-cotyledon/stay-green mutant exemplifies the ancient whole-genome duplications in soybean. Plant & Cell Physiology. 2014;**55**:1763-1771

[88] Iqbal N, Fatma M, Khan NA, Umar S. Regulatory role of proline in heat stress tolerance: Modulation by salicylic acid. In: Plant Signaling Molecules. Kidlington, United Kingdom: Woodhead Publishing; 2019. pp. 437-448. DOI: 10.1016/B978-0-12-816451-8.00027-7

[89] Ahmed JU, Hassan MA. Evaluation of seedling proline content of wheat genotypes in relation to heat tolerance. Bangladesh Journal of Botany. 2011;**40**: 17-22

[90] Kumar S, Meena RS, Lal R, Yadav GS, Mitran T, Meena BL, et al. Role of legumes in soil carbon sequestration. In: Legumes for Soil Health and Sustainable Management. Singapore: Springer; 2018. pp. 109-138

[91] Sharma L, Priya M, Kaushal N, Bhandhari K, Chaudhary S, Dhankher OP, et al. Plant growth-regulating molecules as thermoprotectants: Functional relevance and prospects for improving heat tolerance in food crops. Journal of Experimental Botany. 2020;**71**:569-594

[92] Oktyabrsky ON, Smirnova GV. Redox regulation of cellular functions. Biochemistry (Moscow). 2007;**72**: 132-145

[93] Bonnefont-Rousselot D, Collin F, Jore D, Gardès-Albert M. Reaction mechanism of melatonin oxidation by reactive oxygen species in vitro. Journal of Pineal Research. 2011;**50**:328-335

[94] Liang D, Gao F, Ni Z, Lin L, Deng Q, Tang Y, et al. Melatonin improves heat tolerance in kiwifruit seedlings through promoting antioxidant enzymatic activity and glutathione S-transferase transcription. Molecules. 2018;**23**:584. DOI: 10.3390/molecules23030584

[95] Sarropoulou V, Dimassi-Theriou K, Therios I, Koukourikou-Petridou M. Melatonin enhances root regeneration, photosynthetic pigments, biomass, total carbohydrates and poline content in the cherry rootstock PHL-C (*Prunus avium* × *Prunus cerasus*). Plant Physiology and Biochemistry. 2012;**61**: 162-168

[96] Lehmann S, Funck D, Szabados L, Rentsch D. Proline metabolism and transport in plant development. Amino Acids. 2010;**39**:949-962

[97] Siddique A, Kandpal G, Kumar P. Proline accumulation and its defensive role under diverse stress condition in plants: An overview. Journal of Pure and Applied Microbiology. 2018;**12**: 1655-1659

[98] Öztürk L, Demir Y. In vivo and in vitro protective role of proline. Plant Growth Regulation. 2002;**38**:2592-2564. DOI: 10.1023/A:1021579713832

[99] Jaleel CA, Gopi R, Manivannan P, Panneerselvam R. Responses of antioxidant defense system of *Catharanthus roseus* (L.) G. Don. to paclobutrazol treatment under salinity. Acta Physiologiae Plantarum. 2007;**29**: 205-209

[100] Yamada M, Morishita H, Urano K, Shiozaki N, Yamaguchi-Shinozaki K, Shinozaki K, et al. Effects of free proline accumulation in petunias under drought stress. Journal of Experimental Botany. 2005;**56**:1975-1981. DOI: 10.1093/jxb/eri195

[101] Taiz L, Zeiger E. Plant Physiology. 4th ed. Sunderland, MA, USA: Sinauer Associates, Inc.; 2006

[102] Chakraborty U, Tongden C. Evaluation of heat acclimation and salicylic acid treatments as potent inducers of thermotolerance in *Cicer arietinum* L. Current Science. 2005;**89**: 384-389

[103] Lv WT, Lin B, Zhang M, Hua XJ. Proline accumulation is inhibitory to Arabidopsis seedlings during heat stress. Plant Physiology. 2011;**156**:1921-1933

[104] Gosavi GU, Jadhav AS, Kale AA, Gadakh SR, Pawar BD, Chimote VP. Effect of heat stress on proline, chlorophyll content, heat shock proteins and antioxidant enzyme activity in sorghum (*Sorghum bicolor*) at seedlings

stage. Indian Journal of Biotechnology. 2014;**13**:356-363

[105] Khedr AH, Abbas MA, Wahid AA, Quick WP, Abogadallah GM. Proline induces the expression of salt-stress-responsive proteins and may improve the adaptation of *Pancratium maritimum* L. to salt-stress. Journal of Experimental Botany. 2003;**54**:2553-2562. DOI: 10.1093/ jxb/erg277

[106] Kaushal N, Gupta K, Bhandhari K, Kumar S, Thakur P, Nayyar H. Proline induces heat tolerance in chickpea (*Cicer arietinum* L.) plants by protecting vital enzymes of carbon and antioxidative metabolism. Physiology and Molecular Biology of Plants. 2011;**17**:203-213. DOI: 10.1007/s12298- 011-0078-2

[107] Khan MA, Gul B. Halophyte seed germination. In: Ecophysiology of High Salinity Tolerant Plants. Dordrecht: Springer; 2006. pp. 11-30

[108] Hoque MA, Banu MN, Okuma E, Amako K, Nakamura Y, Shimoishi Y, et al. Exogenous proline and glycinebetaine increase NaCl-induced ascorbate–glutathione cycle enzyme activities, and proline improves salt tolerance more than glycinebetaine in tobacco bright yellow-2 suspension-cultured cells. Journal of Plant Physiology. 2007;**164**:1457-1468

[109] Chaitanya KV, Rasineni GK, Reddy AR. Biochemical responses to drought stress in mulberry (*Morus alba* L.): Evaluation of proline, glycine betaine and abscisic acid accumulation in five cultivars. Acta Physiologiae Plantarum. 2009;**31**:437-443

[110] Wang GP, Hui Z, Li F, Zhao MR, Zhang J, Wang W. Improvement of heat and drought photosynthetic tolerance in wheat by over accumulation of glycinebetaine. Plant Biotechnology Reports. 2010;**4**:213-222. DOI: 10.1007/ s11816-010-0139-y

[111] Chen TH, Murata N. Glycinebetaine protects plants against abiotic stress: Mechanisms and biotechnological applications. Plant, Cell & Environment. 2011;**34**:1-20

[112] Meena RS, Yadav RS. Yield and profitability of groundnut (*Arachis hypogaea* L.) as influenced by sowing dates and nutrient levels with different varieties. Legume Research. 2015;**38**(6): 791-797

[113] Meena RS, Dhakal Y, Bohra JS, Singh SP, Singh MK, Sanodiya P. Influence of bioinorganic combinations on yield, quality and economics of mungbean. American Journal of Experimental Agriculture. 2015;**8**(3): 159-166

[114] Rahman MS, Miyake H, Takeoka Y. Effects of exogenous glycinebetaine on growth and ultrastructure of salt-stressed rice seedlings (*Oryza sativa* L.). Plant Production Science. 2002;**5**:33-44

[115] Sakamoto A, Murata N. The role of glycine betaine in the protection of plants from stress: Clues from transgenic plants. Plant, Cell & Environment. 2002;**25**:163-171

[116] Singh A, Meena RS. Response of bioregulators and irrigation on plant height of Indian mustard (*Brassica juncea* L.). Journal of Oilseed Brassica. 2020;**11**(1):9-14

[117] Ozga JA, Kaur H, Savada RP, Reinecke DM. Hormonal regulation of reproductive growth under normal and heat-stress conditions in legume and other model crop species. Journal of Experimental Botany. 2017;**68**: 1885-1894. DOI: 10.1093/ jxb/erw464

[118] Shu K, Qi Y, Chen F, Meng Y, Luo X, Shuai H, et al. Salt stress represses soybean seed germination by negatively regulating GA biosynthesis while positively mediating ABA biosynthesis. Frontiers in Plant Science. 2017;**8**:1372. DOI: 10.3389/ fpls.2017.01372

[119] Shuai H, Meng Y, Luo X, Chen F, Zhou W, Dai Y, et al. Exogenous auxin represses soybean seed germination through decreasing the gibberellin/abscisic acid (GA/ABA) ratio. Scientific Reports. 2017;**7**:12620. DOI: 10.1038/s41598-017-13093-w

[120] Abeles FB, Morgan PW, Saltveit Jr ME. Ethylene in plant biology. 2nd edition. United States: Elsevier Science Publishing Co. Inc.; 1992. p. 414. Available from: https://doi.org/10.1016/C2009-0-03226-7

[121] Meena RS, Lal R, Yadav GS. Long term impacts of topsoil depth and amendments on soil physical and hydrological properties of an Alfisol in Central Ohio, USA. Geoderma. 2020; **363**:1141164

[122] Meena RS, Kumar S, Datta R, Lal R, Vijayakumar V, Britnicky M, et al. Impact of agrochemicals on soil microbiota and management: A review. Land. 2020;**9**:34. DOI: 10.1016/j.geoderma.2019.114164

[123] Cao WH, Liu J, He XJ, Mu RL, Zhou HL, Chen SY, et al. Modulation of ethylene responses affects plant salt-stress responses. Plant Physiology. 2007; **143**:707-719

[124] Hattori T, Mitsuya S, Fujiwara T, Jagendorf AT, Takabe T. Tissue specificity of glycinebetaine synthesis in barley. Plant Science. 2009;**176**:112-118. DOI: 10.1016/j.plantsci.2008.10.003

[125] Iqbal N, Umar S, Khan NA. Nitrogen availability regulates proline and ethylene production and alleviates salinity stress in mustard (*Brassica juncea*). Journal of Plant Physiology. 2015;**178**:84-91

[126] Cui M, Lin Y, Zu Y, Efferth T, Li D, Tang Z. Ethylene increases accumulation of compatible solutes and decreases oxidative stress to improve plant tolerance to water stress in *Arabidopsis*. Journal of Plant Biology. 2015;**58**:193-201

[127] Arnao MB, Hernández-Ruiz J. Melatonin as a chemical substance or as phytomelatonin rich-extracts for use as plant protector and/or biostimulant in accordance with EC legislation. Agronomy. 2019;**10**:570. DOI: 10.3390/agronomy9100570

[128] Zhang N, Sun Q, Zhang H, Cao Y, Weeda S, Ren S, et al. Roles of melatonin in abiotic stress resistance in plants. Journal of Experimental Botany. 2015;**66**:647-656

[129] Wei W, Li QT, Chu YN, Reiter RJ, Yu XM, Zhu DH, et al. Melatonin enhances plant growth and abiotic stress tolerance in soybean plants. Journal of Experimental Botany. 2015;**66**:695-707

[130] Das A, Rushton PJ, Rohila JS. Metabolomic profiling of soybeans (*Glycine max* L.) reveals the importance of sugar and nitrogen metabolism under drought and heat stress. Plants. 2017;**6**:21. DOI: 10.3390/plants6020021

[131] Xu C, Xia Z, Huang Z, Xia C, Huang J, Zha M, et al. Understanding the physiological and transcriptional mechanism of reproductive stage soybean in response to heat stress. Crop Breeding, Genetics and Genomics. 2019; **27**(1):2. DOI: 10.20900/cbgg20200004

[132] Meena RS, Kumar V, Yadav GS, Mitran T. Response and interaction of *Bradyrhizobium japonicum* and *Arbuscular mycorrhizal* fungi in the soybean rhizosphere: A review. Plant Growth Regulators. 2018;**84**:207-223