

REVIEW

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Review of oxidative stress and antioxidative defense mechanisms in *Gossypium hirsutum* L. in response to extreme abiotic conditions

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Abstract

Oxidative stress occurs when crop plants are exposed to extreme abiotic conditions that lead to the excessive production and accumulation of reactive oxygen species (ROS). Those extreme abiotic conditions or stresses include drought, high temperature, heavy metals, salinity, and ultraviolet radiation, and they cause yield and quality losses in crops. ROS are highly reactive species found in nature that can attack plant organelles, metabolites, and molecules by interrupting various metabolic pathways until cell death occurs. Plants have evolved defense mechanisms for the production of antioxidants to detoxify the ROS and to protect the plant against oxidative damage. Modern researches in crop plants revealed that low levels of ROS act as a signal which induces tolerance to environmental extremes by altering the expression of defensive genes. In this review, we summarized the processes involved in ROS production in response to several types of abiotic stress in cotton plants. Furthermore, we discussed the achievements in the understanding and improving oxidative stress tolerance in cotton in recent years. Researches related to plant oxidative stresses have shown excellent potential for the development of stress-tolerant crops.

Keywords: Abiotic stresses, Anti-oxidative mechanism, Cotton, Oxidative stress, Reactive oxygen species

Background

Stress is an adverse state that inhibits the normal functioning of plants. Stress can be categorized into biotic and abiotic types. Biotic stresses include pathogens, insects, and rodents, while abiotic stresses are heat, salinity, drought, ultraviolet radiation, and metal toxicity (Mahajan and Tuteja 2005). These factors affect plant growth, thus leading to lower yield and harvest quality. The normal balance of defensive mechanisms in plants is disturbed by abiotic stresses (Mullineaux and Baker

2010). Environmental stresses lead to the excess generation and accumulation of reactive oxygen species (ROS) within cells. When ROS production is greater than a plant's ability to scavenge excess ROS, there is rapid leakage of excess ROS (a state known as oxidative stress) into other parts of the plant. Elevated ROS levels are harmful to plants and may alter the cell's physiological, morphological and metabolic processes. The main sites for ROS production in plant cells are mitochondria, chloroplast, and peroxisomes. In addition, ROS are a by-product of metabolic processes. ROS, including hydrogen peroxide (H₂O₂), superoxide anion (O₂⁻), hydroxyl radical (OH[•]), and singlet oxygen (O₂), each has a characteristic half-life and oxidizing potential (Apel and Hirt 2004; Miller et al. 2010). These toxic molecules can

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cause oxidative damage to lipids by lipid peroxidation, to DNA by affecting nucleic acids, and to enzyme inhibition by protein oxidation that promotes programmed cell death (PCD) (Apel and Hirt 2004). Excess of ROS is deleterious to plants; therefore, plants have evolved a complex array of enzymatic and non-enzymatic detoxification mechanisms to combat oxidative damage due to ROS. Anti-oxidative enzymes of plants include glutathione peroxidase (GPX), superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione S-transferase (GST), dehydroascorbate reductase (DHAR), glutathione reductase (GR), peroxide reduction (PRX), mono-hydroascorbate reductase (MDAR), and catalase (CAT). Non-enzymatic antioxidants include glutathione, carotenoids, tocopherols, and flavonoids. Both types of antioxidants are pivotal for ROS homeostasis (Fig.1) (Mahmood et al. 2020). Studies have shown that high anti-oxidative activity is linked with increased stress tolerance in plants (Apel and Hirt 2004). The present review discusses the increase in ROS in cotton plants during abiotic stress events and the resulting biochemical and morphophysiological changes that occur within the plant. We provide an overview of anti-oxidative defense enzymes involved in the cotton plant for ROS detoxification under various stresses. Further, we focus on recent advancements in the production of resistant cotton varieties by conventional and transgenic incorporation of defense genes against several abiotic stresses.

Abiotic stresses in crop plants

Crop plants are often exposed to multiple abiotic stresses during the growing season. Abiotic stresses are serious threats that can collectively lead to major losses in all field crops, including cotton (Saranga et al. 2009). Adverse climatic conditions with unpredictable rainfall have negatively affected the growth of crop plants (Mittler and Blumwald 2010). If the level of stress becomes extremely high or is extended for prolonged periods, it may disturb metabolic processes of cells, thus hindering

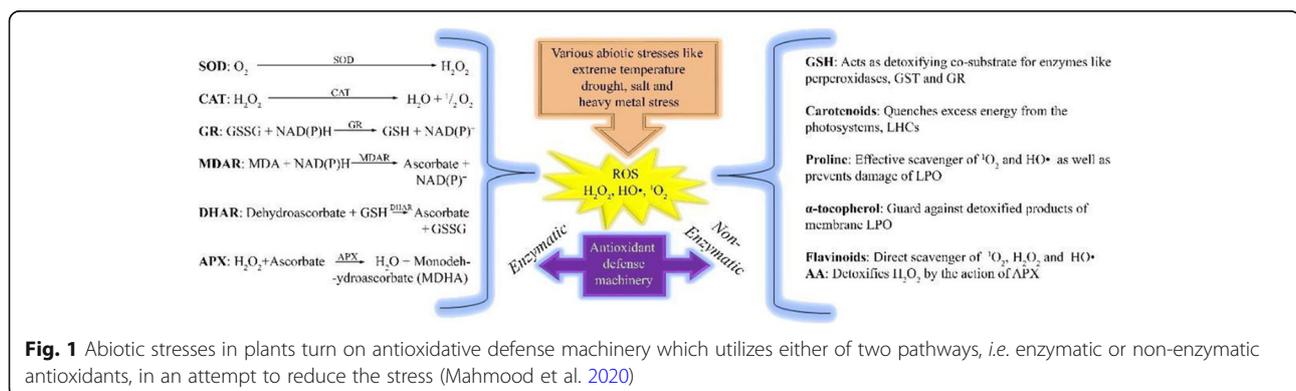
crop growth, and in extreme conditions may result in plant death (Taiz and Zeiger 2006).

Drought stress

Drought refers to low water availability to plants for an extended period that influences crop productivity (Abdelraheem et al. 2019). Under drought conditions, ROS concentrations are elevated in several ways. First, the plant closes its stomata to avoid losses of water from the leaf surface. This closure of stomata leads to a decrease in photosynthetic activity in plants, causing a reduction in NADP^+ . Second, under drought conditions, there is an increase in the transfer of electrons to oxygen (O_2) during photosynthesis (Carvalho 2008). The Mehler reaction reduces the O_2 to O_2^- by donating an electron to photosystem 1 (PS1). Moreover, O_2^- can be converted into H_2O_2 via the SOD antioxidant enzyme, and then transformed into H_2O via ascorbate peroxidase (Heber et al. 2005). Drought stress also enhances photorespiratory activity, especially when the oxygenation of ribulose 1,5-bisphosphate (RuBP) is high due to limited CO_2 fixation reduction. Approximately 70% of the total H_2O_2 produced during drought stress comes from the photorespiration process (Heber et al. 2005).

Tolerance to drought conditions is a complex phenomenon due to the interaction of more than one gene in cellular signaling pathways that improves the physiological, biochemical and molecular responses to drought stress. The sessile nature of plants has led to the evolution of sophisticated molecular mechanisms to sense and respond to various abiotic stresses, which can result in stress tolerance or stress avoidance. Adaptations in antioxidant enzyme metabolism influence drought response in cotton. A detailed discussion about the ROS defense pathway has been studied by Das and Roychoudhury (2014). The antioxidant machinery in cotton plants against oxidative stress has two defensive mechanisms, i.e., enzymatic and non-enzymatic.

SOD, CAT, GPX, APX, GR, NADH, and MDHAR are enzymatic antioxidants. While flavonoids, carotenoids,



ascorbic acid (AA), reduced glutathione (GSH), and osmolyte proline are non-enzymatic antioxidants. To scavenge ROS, both enzymatic and non-enzymatic defense mechanisms work jointly (Das and Roychoudhury 2014; Heiber et al. 2007). The Halliwell-Asada pathway involves the reduction of MDHAR, GR, APX, and NADH into H_2O_2 in cotton (Uzilday et al. 2012). In the ascorbate-glutathione cycle, APX causes the reduction of H_2O_2 into H_2O via oxidation of ascorbate to MDHA (de Azevedo et al. 2006). In this cycle, GSH is reduced via GR oxidation to oxidized glutathione at the expense of NADPH. Of particular importance, the activity of GR was enhanced in cotton under drought stress to bring the ratios of glutathione to normal (Chan et al. 2013).

The equilibrium between ROS production and activation of scavenging enzymes determines whether signaling or damage will occur (Zhang et al. 2014). The amount of anti-oxidative activity in cotton when exposed to drought governs the plant's stress tolerance level. Cotton drought-tolerant variety M-503 has active anti-oxidative proteins to defend the plant from oxidative damage caused by lipid peroxidation (Sekmen et al. 2014). Similarly, there is an increased production of APX and GR in response to ROS to protect plants from prevailing drought conditions (Ratnayaka et al. 2003). Zhang et al. (2014) directed a field experiment for the evaluation of drought-tolerant and susceptible cotton lines. Of the lines studied, CIM-546 was the best line for drought conditions due to its high vigor, heightened antioxidant activity and increased GR (glutathione reductase) contents as well as its longer root length. A second line, CCRI-60, can scavenge ROS and gives better protection against drought stress when compared with other lines. In *G. barbadense*, there is a down-regulation of the drought-tolerant gene 'gbMYB5', thus enhancing oxidative damage under drought stress due to reduction in antioxidant activities, i.e., GST, CAT, POD, and SOD (Chen et al. 2015). Further, zinc is considered a supplemental element that increases anti-oxidative activity in cotton (Wu et al. 2015). The cotton plant contains several drought-resistant genes that help in the activation of multiple antioxidant enzymatic pathways. Additionally, exogenous application of zinc in the presence of oxidative stress is also an effective method to enhance antioxidant levels in crop plants (Wu et al. 2015).

Drought coping strategies in cotton

Due to the increasing demand for cotton, improvements are needed to enhance production in low annual rainfall areas. In this situation, varieties that require less water and give better yield are desirable. Along with traditional breeding, there are advancements in biotechnology to

produce transgenic cotton that can perform better under drought stress. However, foliar application of supplements, growth enhancers, and minerals can also be used to improve resistance against drought stress. As part of the process for improving cotton production, genes or traits that are responsible for drought tolerance are identified using techniques like quantitative trait locus (QTL) analysis and transgenic approaches.

High-temperature stress

The cotton plant is perennial with an indeterminate growth habit and a complex set of fruiting patterns. Temperature stress on the cotton crop causes deleterious effects during germination, early-season growth, flowering, and gossypol formation. Essential physiological processes including carbon assimilation and leaf chlorophyll content are very sensitive to high-temperature extremes. High-temperature stress occurs when morphophysiological and biochemical attributes of plant development are altered. Air temperatures above 30 °C reduce photosynthesis in plants. Temperature beyond 35 °C restricts the elongation of sympodial branches in cotton (Ekinci et al. 2017). Signal transduction networks form a large proportion of the complex machinery that provokes several self-activated and hormone-dependent mechanisms in plants under temperature stress (Fig. 2) (Awasthi et al. 2015; Pandey et al. 2016). Heat stress affects cell biochemistry by enhancing ROS production. Heat stress causes an alteration in mitochondrial function, leading to the induction of oxidative damage by lipid peroxidation (Davidson and Schiestl 2001; Vacca et al. 2004). Numerous studies revealed enhanced lipid peroxidation under heat stress (Wu et al. 2010). Temperature extremes lead to ROS production, including OH^- , H_2O_2 , and O^{2-} , thus causing oxidative stress (Yin et al. 2008). During heat stress, rubisco speeds up the production of H_2O_2 due to its oxygenase activity (Kim and Portis 2004). ROS provokes autocatalytic peroxidation of lipids in cell membranes and pigments, thus affecting the permeability of the membrane and its function (Xu et al. 2006).

Tolerance to oxidative damage is directly correlated with antioxidant production in crop plants (Almeselmani et al. 2009). Elevated protein levels from ROS scavenging enzymes are observed under high temperatures (Rainwater et al. 1996; Rizhsky et al. 2002). Moreover, plants can evolve heat tolerance defense mechanisms to prevent oxidative damage under high-temperature stress (Bergmüller et al. 2003). Zhang et al. (2016) reported increased ROS production in cotton during reproductive stages, i.e., an increase in the lipid peroxidation by-product malondialdehyde (MDA) that affects all cellular organelles. The cotton plant was unable to scavenge ROS under high-temperature stress. The antioxidant

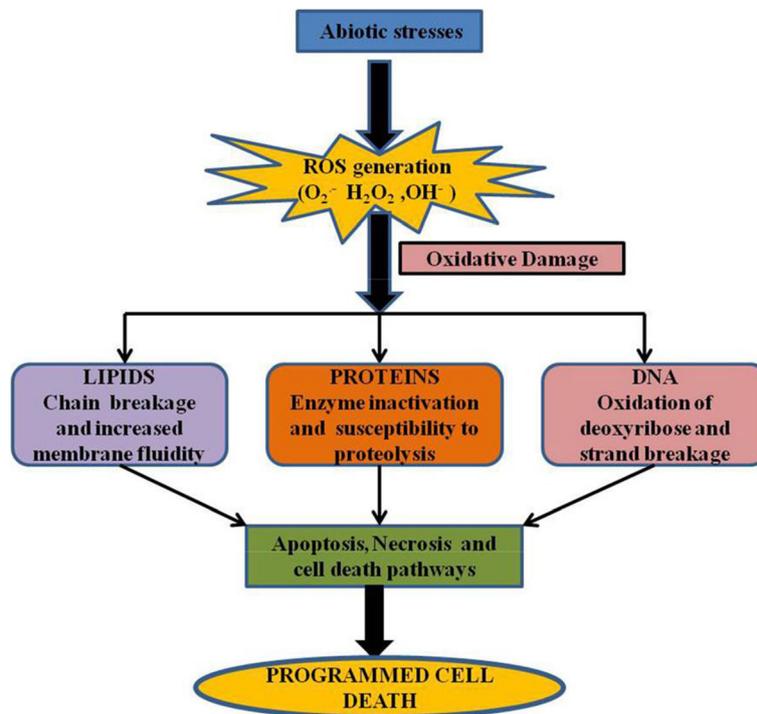


Fig. 2 Systemic diagram showing correlation of high-temperature stress with signal transduction pathways and activation of defense pathway in response to ROS (Awasthi et al. 2015)

enzymes SOD and CAT were up-regulated in cotton leaves but were unable to protect cells from oxidative damage (Snider et al. 2009). Temperature stress reduced the number of sympodial branches and boll weight in cotton as reported by Singh et al. (2007) that might be due to hindrance in the supply of assimilates to developing bolls. In summary, antioxidant enzymes in cotton are elevated but failed to scavenge ROS due to more pressure on organelles under heat stress (Snider et al. 2009). Recent studies demonstrated the effect of a foliar spray of H_2O_2 to induce thermo-tolerance (Gao et al. 2010; Hossain et al. 2015). Exogenous application of H_2O_2 improved plant growth and reduced oxidative stress by protecting DNA structures from damage. *Moringa* leaf extract (MLE) and AA are also considered to be essential for the enhancement of antioxidative activity (Fahad et al. 2016). H_2O_2 acts as a signaling molecule that increases chlorophyll content under high-temperature stress. Similarly, *moringa* leaf extract is rich in zeatin which protects the cell from oxidative stress. Studies have shown that these growth regulators (H_2O_2 , ASA and MLE) increased cotton fiber length. H_2O_2 played an essential role in cell expansion and differentiation of cotton fibers (Li et al. 2007). *Moringa* leaf extract was abundant in cytokinins that enhanced fiber quality components (Ali et al. 2011).

Cotton plant heat tolerance strategies

The ROS produced under heat stress poses a serious threat to plant cells by damaging proteins and lipids (Fahad et al. 2017). Osmoprotectants are compounds that help organisms survive extreme osmotic stresses. Several osmoprotectants including salicylic acid (SA), proline, and AA have been applied exogenously for thermal stability. Under heat stress, cotton plants regulate the osmotic adjustments by maintaining the turgor pressure and enhanced the production of antioxidants against ROS (Anjum et al. 2011). SA is a hormone that induces thermo-tolerance in the cotton plant (Hayat et al. 2009). SA sprayed on cotton plants under heat stress reduced the membrane oxidative stress (Sarwar et al. 2019). Therefore, SA helped reduce ROS by increasing antioxidants and decreasing photosynthetic damage (El Sabagh et al. 2020). AA has significant effects on crop plants under stress conditions. It has an antioxidative system that scavenges ROS thus enhancing crop productivity (Kamal et al. 2017). It is also involved in ROS detoxification (Dolatabadian et al. 2009).

High salt (salinity) stress

Salinity is a global issue where excess salt from irrigation limits crop yield. Almost 20 % of irrigated land is impacted by excess salt (Flowers and Yeo 1995). Therefore,

to fully utilize this land for sustainable agriculture and food security, salt-tolerant crop varieties need to be developed. In crop plants, salinity induces ionic as well as osmotic stress. Plants are prone to oxidative damage due to excessive ROS production. Excess ROS damages membrane proteins, lipids, and nucleic acids (Gomez et al. 1999; Hernández et al. 2001). There is a need to know how crop plants respond and adjust themselves against oxidative stress in the presence of excess salt.

Salt stress may alter any of several biochemical and physiological processes, depending upon the duration and severity of the stress (James et al. 2011; Rozema and Flowers 2008). During the initial stages of increasing salt accumulation, plants have reduced the ability for water uptake and increased the losses due to transpiration (Munns 2005). Osmotic stress leads to physiological changes in plants, including nutrient imbalance, reduced photosynthetic activity and differences in the production of antioxidant enzymes because of stomatal closure (Rahnama et al. 2010). Salt stress is also called hyper ionic concentration stress. When excess Na^+ and Cl^- ions are in the soil, these ions can transport into plant tissues and cells, leading to ionic imbalance and cell membrane damage. Excessive uptake of salts may cause physiological disorders in crop plants. High levels of Na^+ ions in a cell can disturb the process of potassium (K^+) uptake. Potassium is a vital element for plant physiology and the metabolic cycle and reductions in potassium can lead to lower plant dry matter content and, in some cases, plant death (James et al. 2011). In salt-stress conditions, it was observed that the levels of ROS including hydrogen peroxide, singlet oxygen, superoxide, and hydroxyl radicals were enhanced (Apel and Hirt 2004). These ROS severely disturb the metabolic machinery of cells.

Under salt stress in the electron transport chain, electrons react with molecular oxygen (O_2) to form activated oxygen species. ROS like single oxygen (O_2), hydroxyl radical (OH^-), H_2O_2 and superoxide radical (O_2^-) are all capable of oxidation and, therefore, cause oxidative damage to the cell (Groß et al. 2013; Halliwell and Gutteridge 1985). Antioxidants play a key role in the detoxification of ROS induced by salinity stress. The superoxide radical is very dangerous as it reduces the Fe^{3+} and Cu^{2+} ions present within the cells. Therefore, the plant uses superoxide dismutase (SOD) against superoxide to convert superoxide's dismutation into oxygen and hydrogen peroxide. The reduction of metal ions by superoxide uses H_2O_2 to form hydroxyl radicals. Due to their high oxidizing ability, hydroxyl radicals cause damage to proteins and lipids in the cell membrane. There have been no reports of protective enzymes against hydroxyl radicals. Therefore, SOD plays an important role in eliminating the superoxide ion so that hydroxyl radicals are not formed.

Salt tolerance strategies

Although cotton is known as a moderately salt-tolerant crop with a salinity threshold level of $7.7 \text{ dS}\cdot\text{m}^{-1}$, its growth stages are adversely affected by high salt concentrations. The species of cotton have different responses to salt stress, therefore breeding strategies using appropriate inter- and intraspecific crosses and selection methods may be used to improve salt tolerance in cotton. Many researchers noted that salinity affected crop plants by altering morphological, physiological and biochemical traits at different growth and development stages. However, some varieties have increased tolerance to excess salt and can withstand prolonged periods of salt stress.

Salinity stress affects the rate of photosynthesis. Salinity increases Na^+ and Cl^- , which, in turn, decreases the level of Mg^{2+} , K^+ and Ca^{2+} in cotton leaves. Slight increases in K^+ and modest accumulation of Na^+ under salt stress have also been identified in the literature. Therefore, the K^+/Na^+ ratio has been used as a successful selection criterion for salt-tolerance in field crops. Generally, salt tolerance in cotton has been associated with the exclusion of Na^+ ions. High salt stress reduces N and P uptake in cotton, whereas low salinity does not significantly affect the absorption of either of the ions. To mitigate the oxidative damage by ROS, the cotton plant possesses a complex antioxidant system, i.e., non-enzymatic antioxidants such as AA, GSH, tocopherols, and carotenoids as well as enzymatic antioxidants such as SOD, CAT, POD, APX, and GR. This antioxidant system is interlinked and can repair the cellular damage due to oxidative stress imposed by salt in the cotton crop (Arif et al. 2020; Chaudhary et al. 2020).

The studies on the role of an anti-oxidant system under salt stress are comparatively new and this emerging field of research has gained importance during the last decades. However, in the literature, few reports are available for the antioxidant response of cotton under salinity linked with an effective antioxidant system. More advanced studies are required to bring about the authenticity of this phenomenon in cotton plants. Furthermore, transgenic and marker-assisted approaches towards better production in cotton are still needed (Chaudhary et al. 2020).

Heavy metal toxicity and mitigation strategies

Heavy metals (HMs) refer to metals that have relatively high density and that are toxic or poisonous even when present at low concentrations, e.g. mercury (Hg), cadmium (Cd), arsenic (As), chromium (Cr), and lead (Pb). Several physio-biochemical processes in a plant cell are affected by HM, depending upon concentration, type of HM, duration of exposure, toxicity, targeted plant organs, etc. Direct interaction of HM with essential

molecules produces phytotoxic symptoms, *i.e.*, inhibits the functioning of enzymes by substituting essential cations from their respective binding sites (Sharma and Dubey 2007). The presence of toxic metals within plant tissues causes ROS formation, leading to oxidative damage in different parts of the cell. First, HMs interact with ionic compounds available at the entrance of the plant root system. Later, they can interact with proteins, metabolites, and other essential molecules present within the cytoplasm. This influences homeostatic events, including water uptake, food transportation, and transpiration (Fodor 2002). HMs also cause necrosis, rolling of leaves, stunted plant growth, decreased water potential, root growth inhibition, inactivation of several enzymes, and reduced photosynthesis (Sharma and Dubey 2007).

The vulnerability of HMs evokes central anti-oxidative systems, yet the direction of its response entirely depends upon plant species, the HM used, and its severity (Schutzendubel and Polle 2002). During HM stress, glutathione and its corresponding metabolizing enzymes, proteins and peptides play a bio-reductive role and act as main defensive agents against ROS to shield the cell from injury either by the elimination of metals or by chelation of metal ions in cells to reduce metal stress (Xu et al. 2006). Glutathione can directly scavenge metal-induced ROS (Gill and Tuteja 2010). Cai et al. (2011) examined the effect of GSH application on rice seedling against Cd stress and observed that foliar GSH application substantially increased Cd-induced growth inhibition and noticeably decreased uptake of cadmium.

The tolerance against oxidative stress is accompanied by enzymatic antioxidants including CAT, SOD, enzymes of ASA-GSH cycle, GPX, and GST. Collectively, these biochemical traits act as an indicator of HM reactivity and tolerance in several plant species (Hossain and Fujita 2010). Gill and Tuteja (2011) noticed that there was high tolerance against Cd due to the direct association between the antioxidant enzymes which protect the plants. Recent studies reported that plant characteristics, *i.e.*, plant biomass, growth, and photosynthetic activity are reduced under Cd stress in cotton. Further, it was found that the reduced plant growth was due to the reduced cell expansion (Daud et al. 2013; Dias et al. 2013).

The plant has developed methodologies to cope with this stress and to maintain metal homeostasis to prevent further metal ions uptake and accumulation (Saidi et al. 2013). Numerous researchers recommended that a higher level of organic matter in root zones might be a reasonable strategy to deal with HM stress (Arshad et al. 2016; Hédiji et al. 2015; Rizwan et al. 2016). It has been reported in cotton that the presence of glycine betaine (GB) remarkably reduced Cd concentrations in the stem, roots, and leaves. It has been reported in many species

that GB decreased HM concentrations. (Islam et al. 2009). There was a reduction of cadmium in several plant stages due to its defensive role in the cell membrane, thus resulting in reduced cadmium concentrations in cotton plants (Giri 2011). From this research, it was concluded that GB was effective against Cd stress in cotton by regulating an anti-oxidative system. In this way, GB was considered an essential osmolyte that empowered the cotton plant to cope with certain environmental factors.

Ultraviolet radiation stress and anti-oxidative defense response

When certain harmful gases are emitted into the environment, they destroy ozone in the stratosphere layer of the earth's atmosphere. If enough ozone was depleted, this led to an increased amount of ultraviolet-B (UV-B) radiation reaching the earth's surface (Mpoloka 2008). This increase in radiation is anticipated to continue, and it may adversely influence plants directly or indirectly through other natural processes. Prolonged exposure to UV-B radiation is destructive to all photosynthetic organisms (Sinha et al. 2003). Plants are autotrophic and utilize sun-oriented radiation for nourishment, therefore, they are continuously exposed to UV-B radiation. Published reports indicated that exposure of cotton plants to UV-B radiation resulted in reduced plant height and internodal length, decreased branch length, stunted leaf area, and the presence of chlorotic and necrotic patches on the leaf surface. Necrotic and chlorotic patches on leaf surfaces have been widely observed as a result of UV-B exposure in crop plants (Strid and Porra 1992).

In addition to morphological changes, the reproductive behavior of cotton was also altered after exposure to UV-B radiation. Studies revealed that cotton's floral morphology was very susceptible to higher exposure to UV-B radiation. If the exposure persists for a longer period, it causes deformed boll shape and growth, ineffective pollination, and reduced lint yield. It has been observed in several studies that the exposure of cotton flowers to UV-B radiation led to a smaller size and number of flowers, as well as a reduced number of anthers (Cao et al. 2013; Ali et al. 2015). The reduction in the number of anthers indirectly caused an overall reduction in the amount of pollen available for fertilization. Further studies are needed to evaluate the direct effects of UV-B radiation on pollen production, pollen tube growth and germination.

Vulnerability to UV-B produces ROS such as O_2^- , O_2 and OH (Moldau 1999). It has been reported in many plant species that ROS production was increased by UV-B (Agrawal and Rathore 2007; Anjum et al. 2011)

causing oxidative destruction of cell organelles via oxidative damage to lipids, proteins and nucleic acids (Roleda et al. 2006). Unlimited ROS generation within plant cells due to UV-B also caused harmful effects on gene expression and enzymatic activities, driving cellular damage and programmed cell death (Mackerness et al. 2001).

Plants contain complex biochemical defense systems to protect them against UV-B damage (Liang et al. 2006). The activation of antioxidant enzymes including CAT, POX, SOD, APX, and GR has been reported when various species of plants are experiencing UV-B stress. However, at increased levels of UV-B, the antioxidant production decreased. Variation in light intensity affects the cotton plant growth rate, transpiration rate, and photosynthetic rate as these traits are highly sensitive to light. Both low and very high light intensity levels negatively affect cotton growth. Under low light conditions, the rate of photosynthesis is slow but under very intense light conditions, the photosynthesis rate also slows dramatically as the intense light starts to damage the plant.

Concluding remarks and future prospective

Abiotic stresses are major limiting factors to crop productivity. Thus, it is important to take steps towards the understanding of physiological and molecular aspects of abiotic stress tolerance and find appropriate ways to enhance stress tolerance in cotton plants. ROS production, metabolism, and detoxification are key parts of a plant's life cycle. ROS also acts as a signaling molecule in various plant processes. To better understand why and how abiotic stresses cause unfavorable effects, we need to study the plant's mechanisms for defense and tolerance. Advancements in genetic techniques have led to substantial progress in developing conventional lines with improved oxidative stress tolerance or by developing transgenic lines with modified antioxidant levels. Further, it has been reported that foliar application of protectants on plants also helps to improve defense and reduce oxidative stress by stimulating the anti-oxidative system. Over-expression of antioxidant enzymes in transgenic plants has shown an enhanced effect improving stress-tolerance. To build on this result, special consideration should be given to producing transgenic cotton with stacked genes associated with overexpression of more than one antioxidant. This objective may lead to the development of a cotton line with tolerance against multiple abiotic stresses.

Abbreviations

AA: Ascorbic acid; APX: Ascorbate peroxidase; ASA: Ascorbic acid; CAT: Catalase; CO₂: Carbon Dioxide; Cu²⁺: Copper ion; Cd: Cadmium; DHAR: Dehydroascorbate reductase; HM: High metal; Fe³⁺: Ferric ion; GPX: Glutathione peroxidase; GST: Glutathione S-transferase; GSH: Reduced glutathione; K⁺: Potassium ion; H₂O₂: Hydrogen peroxide; OH⁻: Hydroxyl ion; O₂⁻: Superoxide ion; MDAR: Mono-hydro ascorbate reductase; MLE: *Moringa* leaf extract; MDA: Malondialdehyde; NADPH: Nicotinamide adenine

dinucleotide; NaCl: Sodium chloride; Na⁺: Sodium-ion; PS1: Photosystem 1; PRX: Peroxide reduction; ROS: Reactive Oxygen Species; RuBP: Rubulose1, 5 Bisphosphate; RuBisCo: Ribulose-1,5-bisphosphate carboxylase-oxygenase; SOD: Superoxide dismutase; SA: Salicylic acid; UV-B: Ultraviolet light

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References

- Abdelraheem A, Esmaili N, Connell M, et al. Progress and perspective on drought and salt stress tolerance in cotton. *Ind Crop Prod*. 2019;130:118–29. <https://doi.org/10.1016/j.indcrop.2018.12.070>.
- Agrawal S, Rathore D. Changes in oxidative stress defense system in wheat (*Triticum aestivum* L.) and mung bean (*Vigna radiata* L.) cultivars grown with and without mineral nutrients and irradiated by supplemental ultraviolet-B. *Environ Exp Bot*. 2007;59(1):21–33. <https://doi.org/10.1016/j.envenxpbot.2005.09.009>.
- Ali S, Chaudhary A, Rizwan M, et al. Alleviation of chromium toxicity by glycinebetaine is related to elevated antioxidant enzymes and suppressed chromium uptake and oxidative stress in wheat (*Triticum aestivum* L.). *Environ Sci Pollut Res*. 2015;22(14):10669–78. <https://doi.org/10.1007/s11356-015-4193-4>.
- Ali Z, Basra SMA, Munir H, et al. Mitigation of drought stress in maize by natural and synthetic growth promoters. *J Agric Soc Sci*. 2011;7(2):56–62.
- Almeselmani M, Deshmukh P, Sairam R. High temperature stress tolerance in wheat genotypes: role of antioxidant defence enzymes. *Acta Agron Hung*. 2009;57(1):1–14. <https://doi.org/10.1556/AAgr.57.2009.1.1>.
- Anjum S, Wang L, Farooq M, et al. Brassinolide application improves the drought tolerance in maize through modulation of enzymatic antioxidants and leaf gas exchange. *J Agron Crop Sci*. 2011;197(3):177–85. <https://doi.org/10.1111/j.1439-037X.2010.00459.x>.
- Apel K, Hirt H. Reactive oxygen species: metabolism, oxidative stress, and signal transduction. *Annu Rev Plant Biol*. 2004;55(1):373–99. <https://doi.org/10.1146/annurev.arplant.55.031903.141701>.

- Arif Y, Singh P, Siddiqui H, et al. Salinity induced physiological and biochemical changes in plants: an omic approach towards salt stress tolerance. *Plant Physiol Biochem.* 2020;156:64–77. <https://doi.org/10.1016/j.plaphy.2020.08.042>.
- Arshad M, Ali S, Noman A, et al. Phosphorus amendment decreased cadmium (Cd) uptake and ameliorates chlorophyll contents, gas exchange attributes, antioxidants, and mineral nutrients in wheat (*Triticum aestivum* L.) under Cd stress. *Arch Agron Soil Sci.* 2016;62(4):533–46. <https://doi.org/10.1080/03650340.2015.1064903>.
- Awasthi R, Bhandari K, Nayyar H. Temperature stress and redox homeostasis in agricultural crops. *Front Environ Sci.* 2015;3:11. <https://doi.org/10.3389/fenvs.2015.00011>.
- Bergmüller E, Porfirova S, Dörmann P. Characterization of an *Arabidopsis* mutant deficient in γ -tocopherol methyltransferase. *Plant Mol Biol.* 2003;52(6):1181–90. <https://doi.org/10.1023/B:PLAN.000004307.62398.91>.
- Cai Y, Cao F, Cheng W, et al. Modulation of exogenous glutathione in phytochelatin and photosynthetic performance against Cd stress in the two rice genotypes differing in Cd tolerance. *Biol Trace Elem Res.* 2011;143(2):1159–73. <https://doi.org/10.1007/s12011-010-8929-1>.
- Cao F, Liu L, Ibrahim W, et al. Alleviating effects of exogenous glutathione, glycinebetaine, brassinosteroids and salicylic acid on cadmium toxicity in rice seedlings (*Oryza sativa*). *Agrotechnology.* 2013;2(1):107–12. <https://doi.org/10.4172/2168-9881.1000107>.
- Carvalho MD. Drought stress and reactive oxygen species. *Plant Signal Behav.* 2008;3:156–65. <https://doi.org/10.4161/psb.3.3.5536>.
- Chan KX, Wirtz M, Phua S, et al. Balancing metabolites in drought: the sulfur assimilation conundrum. *Trends Plant Sci.* 2013;18(1):18–29. <https://doi.org/10.1016/j.tplants.2012.07.005>.
- Chaudhary MT, Shakeel A, Rana IA, et al. Evaluation of morpho-physiological and biochemical attributes of cotton under salt stress. *Int J Agric Biol.* 2020;24:1061–9. <https://doi.org/10.17957/IJAB/15.1533>.
- Chen T, Li W, Hu X, et al. A cotton MYB transcription factor, GbMYB5, is positively involved in plant adaptive response to drought stress. *Plant Cell Physiol.* 2015;56(5):917–29. <https://doi.org/10.1093/pcp/pcv019>.
- Das K, Roychoudhury A. Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants. *Front Environ Sci.* 2014;2:53. <https://doi.org/10.3389/fenvs.2014.00053>.
- Daud M, Ali S, Variath M, et al. Differential physiological, ultramorphological and metabolic responses of cotton cultivars under cadmium stress. *Chemosphere.* 2013;93(10):2593–602. <https://doi.org/10.1016/j.chemosphere.2013.09.082>.
- Davidson JF, Schiestl RH. Mitochondrial respiratory electron carriers are involved in oxidative stress during heat stress in *Saccharomyces cerevisiae*. *Mol Cell Biol.* 2001;21(24):8483–9. <https://doi.org/10.1128/MCB.21.24.8483-8489.2001>.
- de Azevedo N, Prisco AD, Enéas-Filho JT, et al. Effect of salt stress on antioxidative enzymes and lipid peroxidation in leaves and roots of salt-tolerant and salt-sensitive maize genotypes. *Environ Exp Bot.* 2006;56(1):87–94. <https://doi.org/10.1016/j.envexpbot.2005.01.008>.
- Dias MC, Monteiro C, Moutinho-Pereira J, et al. Cadmium toxicity affects photosynthesis and plant growth at different levels. *Acta Physiol Plant.* 2013;35(4):1281–9. <https://doi.org/10.1007/s11738-012-1167-8>.
- Dolatabadani A, Sanavy SM, Sharifi M. Effect of ascorbic acid (vitamin C) leaf feeding on antioxidant enzymes activity, proline accumulation and lipid peroxidation of canola (*Brassica napus* L.) under salt stress condition. *J Sci Technol Agric Nat Res.* 2009;13(47(B)):611–21.
- Ekinci R, Basbag S, Karademir E, et al. The effects of high temperature stress on some agronomic characters in cotton. *Pak J Bot.* 2017;49(2):503–8. <https://hdl.handle.net/20.500.12604/469>.
- El Sabagh A, Hossain A, Islam MS, et al. Drought and heat stress in cotton (*Gossypium hirsutum* L.): consequences and their possible mitigation strategies. In: Hasanuzzaman M, editor. *Agronomic Crops*. Singapore: Springer; 2020. https://doi.org/10.1007/978-981-15-0025-1_30.
- Fahad S, Bajwa AA, Nazir U, et al. Crop production under drought and heat stress: plant responses and management options. *Front Plant Sci.* 2017;8:1147. <https://doi.org/10.3389/fpls.2017.01147>.
- Fahad S, Hussain S, Saud S, et al. Exogenously applied plant growth regulators affect heat-stressed rice pollens. *J Agron Crop Sci.* 2016;202(2):139–50. <https://doi.org/10.1111/jac.12148>.
- Flowers T, Yeo A. Breeding for salinity resistance in crop plants: where next? *Funct Plant Biol.* 1995;22(6):875–84. <https://doi.org/10.1071/PP9950875>.
- Fodor F. Physiological responses of vascular plants to heavy metals. In: Prasad MNV, Strzalka K, editors. *Physiology and biochemistry of metal toxicity and tolerance in plants*. Dordrecht, Netherlands: Springer; 2002. p. 149–77. https://doi.org/10.1007/978-94-017-2660-3_6.
- Gao Y, Guo YK, Lin SH, et al. Hydrogen peroxide pretreatment alters the activity of antioxidant enzymes and protects chloroplast ultrastructure in heat-stressed cucumber leaves. *Sci Hortic.* 2010;126(1):20–6. <https://doi.org/10.1016/j.scienta.2010.06.006>.
- Gill SS, Tuteja N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiol Biochem.* 2010;48(12):909–30. <https://doi.org/10.1016/j.plaphy.2010.08.016>.
- Gill SS, Tuteja N. Cadmium stress tolerance in crop plants: probing the role of sulfur. *Plant Signal Behav.* 2011;6(2):215–22. <https://doi.org/10.4161/psb.6.2.14880>.
- Giri J. Glycinebetaine and abiotic stress tolerance in plants. *Plant Signal Behav.* 2011;6(11):1746–51. <https://doi.org/10.4161/psb.6.11.17801>.
- Gomez J, Hernandez J, Jimenez A, et al. Differential response of antioxidative enzymes of chloroplasts and mitochondria to long-term NaCl stress of pea plants. *Free Radic Res.* 1999;31(sup1):11–8. <https://doi.org/10.1080/10715769900301261>.
- Groß F, Durner J, Gaupels F. Nitric oxide, antioxidants and prooxidants in plant defence responses. *Front Plant Sci.* 2013;4:419. <https://doi.org/10.3389/fpls.2013.00419>.
- Halliwel B, Gutteridge JM. The importance of free radicals and catalytic metal ions in human diseases. *Mol Asp Med.* 1985;8(2):89–193. [https://doi.org/10.1016/0098-2997\(85\)90001-9](https://doi.org/10.1016/0098-2997(85)90001-9).
- Hayat S, Masood A, Yusuf M, et al. Growth of Indian mustard (*Brassica juncea* L.) in response to salicylic acid under high-temperature stress. *Braz J Plant Physiol.* 2009;21(3):187–95. <https://doi.org/10.1590/S1677-04202009000300003>.
- Heber U, Irrungen Y, Wurrungen JM. The Mehler reaction in relation to cyclic electron transport in C3 plants. In: Govindjee BJT, Gest H, Allen JF, editors. *Discoveries in photosynthesis. Advances in photosynthesis and respiration*, vol 20. Dordrecht, Netherlands: Springer; 2005. p. 551–9. https://doi.org/10.1007/1-4020-3324-9_51.
- Hédiji H, Djebali W, Belkadi A, et al. Impact of long-term cadmium exposure on mineral content of *Solanum lycopersicum* plants: consequences on fruit production. *S Afr J Bot.* 2015;97:176–81. <https://doi.org/10.1016/j.sajb.2015.01.010>.
- Heiber I, Ströher E, Raatz B, et al. The redox imbalanced mutants of *Arabidopsis* differentiate signaling pathways for redox regulation of chloroplast antioxidant enzymes. *Plant Physiol.* 2007;143(4):1774–88. <https://doi.org/10.1104/pp.106.093328>.
- Hernández JA, Ferrer MA, Jiménez A, et al. Antioxidant systems and O₂⁻/H₂O₂ production in the apoplast of pea leaves. Its relation with salt-induced necrotic lesions in minor veins. *Plant Physiol.* 2001;127(3):817–31. <https://doi.org/10.1104/pp.010188>.
- Hossain MA, Bhattacharjee S, Armin SM, et al. Hydrogen peroxide priming modulates abiotic oxidative stress tolerance: insights from ROS detoxification and scavenging. *Front Plant Sci.* 2015;6:420. <https://doi.org/10.3389/fpls.2015.00420>.
- Hossain MA, Fujita M. Evidence for a role of exogenous glycinebetaine and proline in antioxidant defense and methylglyoxal detoxification systems in mung bean seedlings under salt stress. *Physiol Mol Biol Plants.* 2010;16(1):19–29. <https://doi.org/10.1007/s12298-010-0003-0>.
- Islam MM, Hoque MA, Okuma E, et al. Exogenous proline and glycinebetaine increase antioxidant enzyme activities and confer tolerance to cadmium stress in cultured tobacco cells. *J Plant Physiol.* 2009;166(15):1587–97. <https://doi.org/10.1016/j.jplph.2009.04.002>.
- James RA, Blake C, Byrt CS, Munns R. Major genes for Na⁺ exclusion, Nax1 and Nax2 (wheat HKT1;4 and HKT1;5), decrease Na⁺ accumulation in bread wheat leaves under saline and waterlogged conditions. *J Exp Bot.* 2011;62(8):2939–47. <https://doi.org/10.1093/jxb/err003>.
- Kamal M, Saleem M, Wahid M, et al. Effects of ascorbic acid on membrane stability and yield of heat-stressed Bt cotton. *J Anim Plant Sci.* 2017;27(1):192–9.
- Kim K, Portis AR. Oxygen-dependent H₂O₂ production by Rubisco. *FEBS Lett.* 2004;571(1–3):124–8. <https://doi.org/10.1016/j.febslet.2004.06.064>.
- Li HB, Qin YM, Pang Y, et al. A cotton ascorbate peroxidase is involved in hydrogen peroxide homeostasis during fibre cell development. *New Phytol.* 2007;175(3):462–71. <https://doi.org/10.1111/j.1469-8137.2007.02120.x>.
- Liang B, Huang X, Zhang G, et al. Effect of lanthanum on plants under supplementary ultraviolet-B radiation: effect of lanthanum on flavonoid

- contents in soybean seedlings exposed to supplementary ultraviolet-B radiation. *J Rare Earths*. 2006;24(5):613–6. [https://doi.org/10.1016/S1002-0721\(06\)60174-9](https://doi.org/10.1016/S1002-0721(06)60174-9).
- Mackerness AH, John S, Jordan CF, et al. Early signaling components in ultraviolet-B responses: distinct roles for different reactive oxygen species and nitric oxide. *FEBS Lett*. 2001;489(2–3):237–42. [https://doi.org/10.1016/S0014-5793\(01\)02103-2](https://doi.org/10.1016/S0014-5793(01)02103-2).
- Mahajan S, Tuteja N. Cold, salinity and drought stresses: an overview. *Arch Biochem Biophys*. 2005;444(2):139–58. <https://doi.org/10.1016/j.abb.2005.10.018>.
- Mahmood T, Khalid S, Abdullah M, et al. Insights into drought stress signaling in plants and the molecular genetic basis of cotton drought tolerance. *Cells*. 2020;9(1):105. <https://doi.org/10.3390/cells9010105>.
- Miller G, Suzuki N, Ciftci-Yilmaz S, et al. Reactive oxygen species homeostasis and signalling during drought and salinity stresses. *Plant Cell Environ*. 2010;33(4):453–67. <https://doi.org/10.1111/j.1365-3040.2009.02041.x>.
- Mittler R, Blumwald E. Genetic engineering for modern agriculture: challenges and perspectives. *Annu Rev Plant Biol*. 2010;61(1):443–62. <https://doi.org/10.1146/annurev-arplant-042809-112116>.
- Moldau H. Ozone detoxification in the mesophyll cell wall during a simulated oxidative burst. *Free Radic Res*. 1999;31(sup1):19–24. <https://doi.org/10.1080/0715769900301271>.
- Mpoloka SW. Effects of prolonged UV-B exposure in plants. *Afr J Biotechnol*. 2008;7(12):25–38. <http://www.academicjournals.org/AJB>.
- Mullineaux PM, Baker NR. Oxidative stress: antagonistic signaling for acclimation or cell death? *Plant Physiol*. 2010;154(2):521–5. <https://doi.org/10.1104/pp.110.161406>.
- Munns R. Genes and salt tolerance: bringing them together. *New Phytol*. 2005;167(3):645–63. <https://doi.org/10.1111/j.1469-8137.2005.01487.x>.
- Pandey GK, Pandey A, Prasad M, Böhmer M. Editorial: abiotic stress signaling in plants: functional genomic intervention. *Front Plant Sci*. 2016;7(4):289–312. <https://doi.org/10.3389/fpls.2016.00681>.
- Rahnama A, James RA, Poustini K, Munns R. Stomatal conductance as a screen for osmotic stress tolerance in durum wheat growing in saline soil. *Funct Plant Biol*. 2010;37(3):255–63. <https://doi.org/10.1071/FP09148>.
- Rainwater DT, Gossett DR, Millhollon EP, et al. The relationship between yield and the antioxidant defense system in tomatoes grown under heat stress. *Free Radic Res*. 1996;25(5):421–35. <https://doi.org/10.3109/10715769609149065>.
- Ratnayaka HH, Molin WT, Sterling TM. Physiological and antioxidant responses of cotton and spurred anoda under interference and mild drought. *J Exp Bot*. 2003;54(391):2293–305. <https://doi.org/10.1093/jxb/erg251>.
- Rizhsky L, Liang H, Mittler R. The combined effect of drought stress and heat shock on gene expression in tobacco. *Plant Physiol*. 2002;130(3):1143–51. <https://doi.org/10.1104/pp.006858>.
- Rizwan M, Meunier JD, Davidian JC, Pokrovsky OS, Bovet N, Keller C. Silicon alleviates Cd stress of wheat seedlings (*Triticum turgidum* L. cv. Claudio) grown in hydroponics. *Environ Sci Pollut Res*. 2016;23(2):1414–27. <https://doi.org/10.1007/s11356-015-5351-4>.
- Roleda MY, Wiencke C, Lüder UH. Impact of ultraviolet radiation on cell structure, UV-absorbing compounds, photosynthesis, DNA damage, and germination in zoospores of Arctic *Saccorhiza dermatodea*. *J Exp Bot*. 2006;57(14):3847–56. <https://doi.org/10.1093/jxb/erl154>.
- Rozema J, Flowers T. Crops for a salinized world. *Science*. 2008;322(4):1478–80. <https://www.jstor.org/stable/20176943>.
- Saidi I, Ayouni M, Dhieb A, et al. Oxidative damages induced by short-term exposure to cadmium in bean plants: protective role of salicylic acid. *S Afr J Bot*. 2013;85:32–8. <https://doi.org/10.1016/j.sajb.2012.12.002>.
- Saranga Y, Paterson AH, Levi A. Bridging classical and molecular genetics of abiotic stress resistance in cotton. In: Paterson AH, editor. *Genetics and genomics of cotton. Plant genetics and genomics: crops and models*, vol 3. New York, NY: Springer; 2009. https://doi.org/10.1007/978-0-387-70810-2_14.
- Sarwar M, Saleem MF, Ullah N, et al. Role of mineral nutrition in alleviation of heat stress in cotton plants grown in glasshouse and field conditions. *Sci Rep*. 2019;9(4):22–6. <https://doi.org/10.1038/s41598-019-49404-6>.
- Schutzendubel A, Polle A. Plant responses to abiotic stresses: heavy metal-induced oxidative stress and protection by mycorrhization. *J Exp Bot*. 2002;53(372):1351–65. <https://doi.org/10.1093/jexbot/53.372.1351>.
- Sekmen A, Ozgur R, Uzilday B, et al. Reactive oxygen species scavenging capacities of cotton (*Gossypium hirsutum*) cultivars under combined drought and heat induced oxidative stress. *Environ Exp Bot*. 2014;99(11):141–9. <https://doi.org/10.1016/j.envexpbot.2013.11.010>.
- Sharma P, Dubey R. Involvement of oxidative stress and role of antioxidative defense system in growing rice seedlings exposed to toxic concentrations of aluminum. *Plant Cell Rep*. 2007;26(11):2027–38. <https://doi.org/10.1007/s00299-007-0416-6>.
- Singh RP, Prasad PV, Sunita K, et al. Influence of high temperature and breeding for heat tolerance in cotton: a review. *Adv Agron*. 2007;93:313–85. [https://doi.org/10.1016/S0065-2113\(06\)93006-5](https://doi.org/10.1016/S0065-2113(06)93006-5).
- Sinha RP, Ambasth NK, Sinha JP, et al. UV-B-induced synthesis of mycosporine-like amino acids in three strains of *Nodularia* (cyanobacteria). *J Photochem Photobiol B Biol*. 2003;71(1–3):51–8. <https://doi.org/10.1016/j.jphotobiol.2003.07.003>.
- Snider JL, Oosterhuis DM, Skulman BW, Kawakami EM. Heat stress-induced limitations to reproductive success in *Gossypium hirsutum*. *Physiol Plant*. 2009;137(2):125–38. <https://doi.org/10.1111/j.1399-3054.2009.01266.x>.
- Strid Å, Porra RJ. Alterations in pigment content in leaves of *Pisum sativum* after exposure to supplementary UV-B. *Plant Cell Physiol*. 1992;33(7):1015–23. <https://doi.org/10.1093/oxfordjournals.pcp.a078325>.
- Taiz L, Zeiger E. *Plant physiology*. 4th ed. Oxford, UK: Sinauer Associates; 2006.
- Uzilday B, Turkan I, Sekmen AH, et al. Comparison of ROS formation and antioxidant enzymes in *Cleome gynandra* (C4) and *Cleome spinosa* (C3) under drought stress. *Plant Sci*. 2012;182:59–70. <https://doi.org/10.1016/j.plantsci.2011.03.015>.
- Vacca RA, de Pinto MC, Valenti D, et al. Production of reactive oxygen species, alteration of cytosolic ascorbate peroxidase, and impairment of mitochondrial metabolism are early events in heat shock-induced programmed cell death in tobacco bright-yellow 2 cells. *Plant Physiol*. 2004;134(3):1100–12. <https://doi.org/10.1104/pp.103.035956>.
- Wu B, Jiang Q, Gu T, et al. Physiological response to high temperature stress in radish seedlings with different heat tolerance. *China Veg*. 2010(10):25–8.
- Wu S, Hu C, Tan Q, et al. Drought stress tolerance mediated by zinc-induced antioxidative defense and osmotic adjustment in cotton (*Gossypium hirsutum*). *Acta Physiol Plant*. 2015;37(8):167. <https://doi.org/10.1007/s11738-015-1919-3>.
- Xu S, Li J, Zhang X, et al. 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. *Environ Exp Bot*. 2006;56(3):274–85. <https://doi.org/10.1016/j.envexpbot.2005.03.002>.
- 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 Regul*. 2008;54(1):45–54. <https://doi.org/10.1007/s10725-007-9227-6>.
- Zhang L, Ma H, Chen T, et al. Morphological and physiological responses of cotton (*Gossypium hirsutum* L.) plants to salinity. *PLoS One*. 2014;9(11):28–36. <https://doi.org/10.1371/journal.pone.0112807>.
- Zhang J, Chen H, Wang H, et al. Constitutive expression of a tomato small heat shock protein gene *LeHSP21* improves tolerance to high-temperature stress by enhancing antioxidation capacity in tobacco. *Plant Mol Biol Report*. 2016;34(2):399–409. <https://doi.org/10.1007/s11015-015-0925-3>.

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