



Review

Morphological and physio-biochemical responses under heat stress in cotton: Overview

Aamir Ali Abro^{a,1}, Muhammad Anwar^{b,1}, Muhammad Umer Jawwad^a, Mjie Zhang^c, Fang Liu^{a,c,*}, Raimundo Jiménez-Ballesta^{d,*}, Ehab A. A. Salama^{e,f}, Mohamed A. A. Ahmed^{g,h}

^a State Key Laboratory of Cotton Research, Chinese Academy of Agricultural Sciences, Anyang 455000, China

^b Institute of Tropical Agriculture and Forestry, Hainan University, Haikou, China

^c Hainan Yazhou Bay Seed Laboratory, China/National Nanfan, Research Institute of Chinese Academy of Agricultural Sciences, Sanya 572025, China

^d Department of Geology & Geochemistry, Autonoma University of Madrid, 28049 Madrid, Spain

^e Department of Plant Biotechnology, Centre for Plant Molecular Biology and Biotechnology, Tamil Nadu Agricultural University, Coimbatore- 641003, India

^f Agricultural Botany Department (Genetics), Faculty of Agriculture Saba Basha, Alexandria University, Alexandria, 21531, Egypt

^g Plant Production Department (Horticulture - Medicinal and Aromatic Plants), Faculty of Agriculture (Saba Basha), Alexandria University, Alexandria 21531, Egypt

^h School of Agriculture, Yunnan University, Chenggong District, Kunming, 650091, Yunnan, China

ARTICLE INFO

Keywords:

Cash crop
Climatic changes
Morphological
Physio-biochemical
Genetics
Fiber quality
Heat tolerance

ABSTRACT

Cotton is an important cash crop in addition to being a fiber commodity, and it plays an essential part in the economies of numerous nations. High temperature is the most critical element affecting its yield from fertilization to harvest. The optimal temperature for root formation is 30 °C–35 °C; however, root development ends around 40 °C. Increased temperature, in particular, influences different biochemical and physiological processes associated with cotton plant, resulting in low seed cotton production. Many studies in various agroecological zones used various agronomic strategies and contemporary breeding techniques to reduce heat stress and improve cotton productivity. To attain desired traits, cotton breeders should investigate all potential possibilities, such as generating superior cultivars by traditional breeding, employing molecular techniques and transgenic methods, such as using genome editing techniques. The main objective of this review is to provide the recent information on the environmental factors, such as temperature, heat and drought, influence the growth and development, morphology and physio-chemical alteration associated with cotton. Furthermore, recent advancement in cotton breeding to combat the serious threat of drought and heat stress.

1. Introduction

Gossypium species, namely *Gossypium hirsutum* L., *Gossypium barbadense* L., *Gossypium arboreum* L., and *Gossypium herbaceum* L. have been growing worldwide to create textile fabric [1]. Most cotton is cultivated in tropical and subtropical regions with temperature changes between 40 °C and 45 °C [2]. The temperature throughout a plant's growth season affects physiological and morphological growth and biomass production (S. [3]) [4]. Cotton loses its blooms and squares when the temperature exceeds up to 36 °C (S. A. [5]). High-temperature stress has a negative impact on cotton vegetative propagation, metabolism, and output [6]. The sensitivity of plants to climate variability and change is determined by the length and severity of the heat stress [7].

Additionally, the stress level is directly associated with water deficiency, which could be aggravated even more by restricted and unpredictable water supplies in cotton-growing areas [8]. The availability of genetic heterogeneity inside a genus is required for a breeding effort to generate cultivars resistant to heat stress (M. M. [9]). All abiotic and biotic stress reactions in plants necessitate an optimal temperature difference, known as the temperature kinetic window (TKW). The temperature of such a plant ought to be in the TKW range. Heat stress occurs when the plant's temperature falls below or rises over TKW. A TKW of 23.5 °C–32 °C is essential for healthy plant development [10]. Cotton breeders are constantly evaluating cotton cultivars against heat sensitivity as a consequence of changing the climate. Seed cotton yield (SCY), like some of the other morphological characteristics, is regarded as a beneficial

* Corresponding author.

E-mail addresses: liufcri@163.com (F. Liu), raimundo.jimenez@um.es (R. Jiménez-Ballesta).

¹ These authors contributed equally to this work.

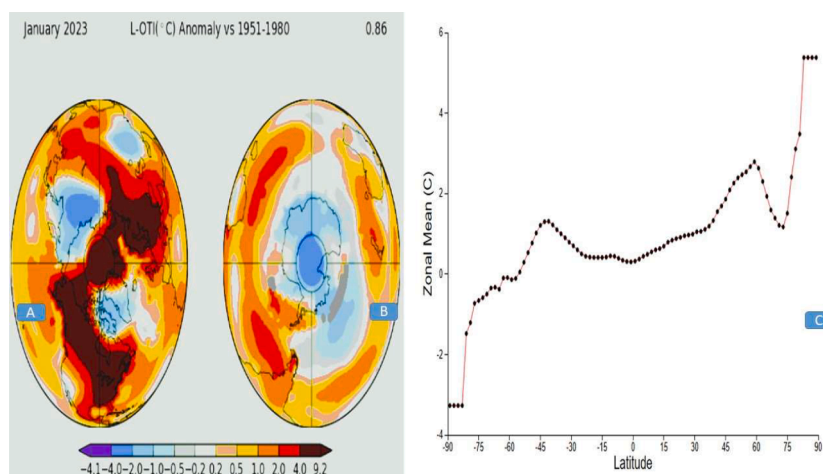


Fig. 1. Trends in global temperature change. (A) Map of the annual mean temperature change (°C) during 2000–2010 relative to 1951–1980. (B) Map of the annual mean temperature change (°C) during 2011–2022 relative to 1951–1980. The data for land surface air temperature are from GHCNv4 (GISS analysis based on global historical climatology network v4), and the data of sea surface temperature are from ERSST_v5 (NOAA/NCEI's extended reconstructed sea surface temperature v5). The number at the top right-hand corner of the map plot is an estimate (°C) of the global mean of the calculated area. Gray areas signify missing data. Ocean data are not used over land nor within 100 km of a reporting land station. The maps were made using the website of GISS Surface Temperature Analysis (<https://data.giss.nasa.gov/gistemp/maps/index.html>). Site reference.

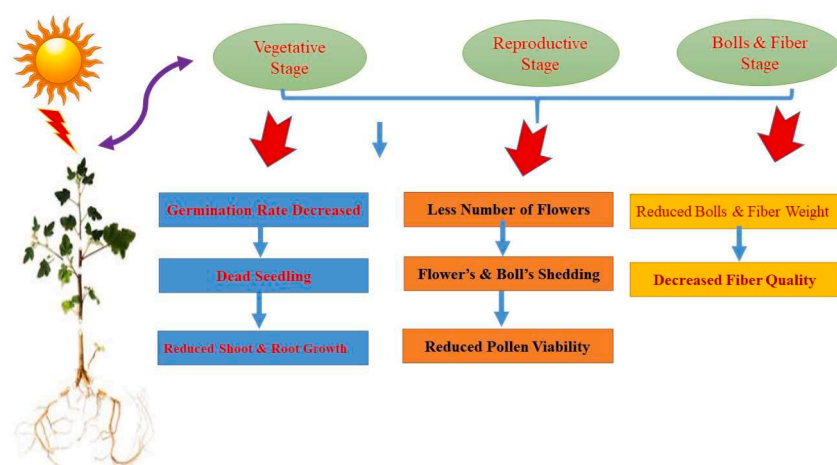


Fig. 2. Morphological Attributes of cotton at Heat tolerance.

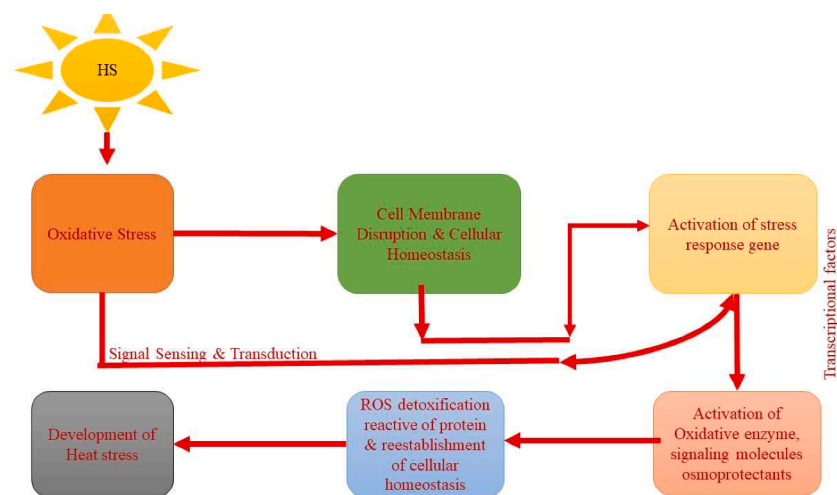


Fig. 3. Application of Phyto-hormones in Heat Tolerance Management.

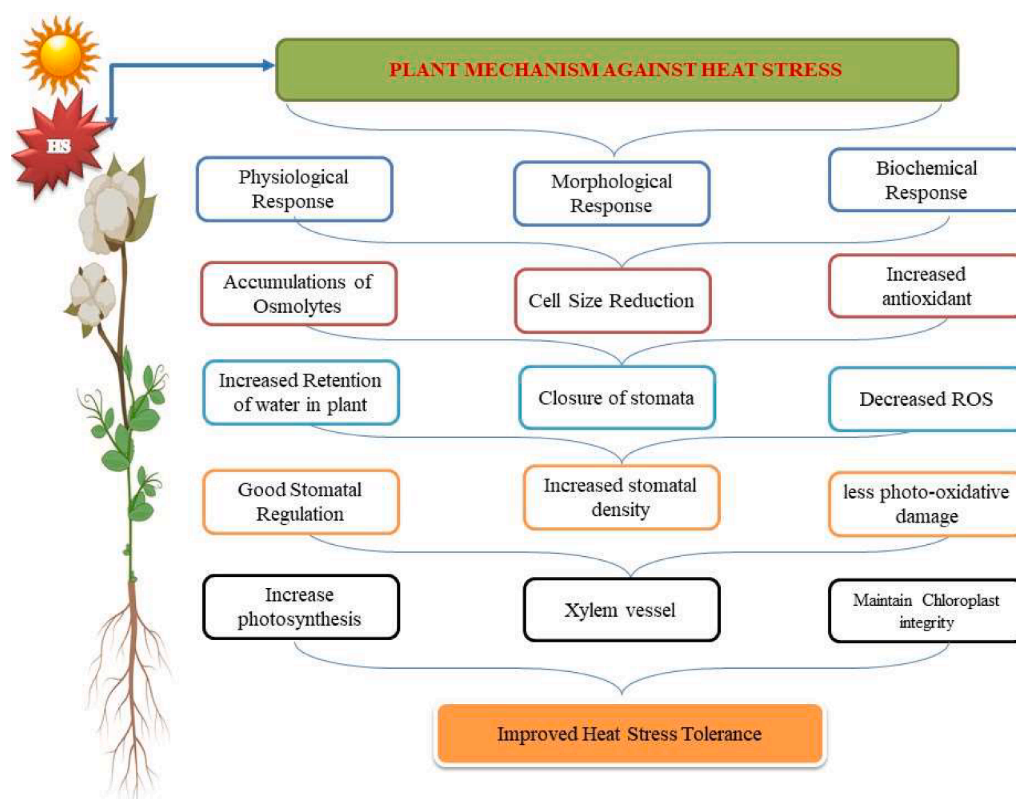


Fig. 4. Response of morphological, physiological and biochemical with heat stress.

Table 1

Optimum temperature required for cotton crop.

Growth stage	Average daily temperature (mm)	Daily water requirement's (mm)	Daily water requirement's (in)
Planting Soil	Minimum 18 °C	0	0
Planting Air	More than 21 °C		
Vegetative growth	21–27 °C	1–2	0.04–0.08
Frist Square leave		2–4	0.08–0.16
Reproduction growth	27–32 °C	3–8	0.12–0.31
Peak bloom		8	0.31
Frist Boll opening		8–4	0.31–0.16
Maturation	21–31 °C	4	0.16

[82].

trait for the growth of cotton genetic variability against high temperature, but it is complex as well as influenced by environmental conditions, necessitating particular breeding programs, and additionally, climate variations cannot be avoided [11]. Heat waves will occur more frequently and persist longer than anticipated due to global warming (Fig.1). Increased temperatures have a detrimental influence because they hinder photosynthetic activity (Y. Y. [12]). Excessive temperatures may bring about explicit changes in physiological processes or cause indirect alterations by affecting behavior processes. High temperatures, for instance, can cause reproduction delays or vigor loss in growing seedlings. It will eventually decrease blooming and vegetative growth [13]. When subjected to elevated temperatures, cotton sheds 35% of its early flowers and 50–75% of its bolls in varying environmental situations.

2. Cotton under heat stress

In numerous regions of the globe, heat exhaustion is usually accompanied by water scarcity. Despite being researched separately, the combined consequences of drought and elevated temperatures on cotton have not been extensively found. Despite the fact that combined impacts

Table 2

Potential antioxidant for heat tolerance in different crops.

Crops	Antioxidant	Response	References
Chines Cabbage	CAT & SOD	There was no consistent link between these enzymes and heat tolerance.	[83]
wheat	Different antioxidant enzymes	A detrimental connection was discovered among enzyme levels of antioxidants and heat tolerance.	[84]
Tomato	APX, SOD and POD	These digestive enzymes were shown to be more active in thermally resistant cultivars.	[85]
Brascia	POD and CAT	A favorable connection with heat resistance	(Hasanuzzaman & Responses, n. d.)
Wheat	CAT and APX	A favorable connection with heat resistance	[86]
Cotton	ROS and Proline	The feared ROS-driven damage accumulated higher proline and protein soluble molecules overall.	[87,60]

Table 3
Yield losses of different crops due to high temperature.

Crops Species	High temperature caused yield loss	References
Cotton	In Nanjing, China, a temperature increase of 2–3 °Celsius over the ideal temperature (32 °Celsius) resulted in a 10% loss in biomass and a 40% decrease in yield.	[11]
Wheat	A 0.5 °C rise in the typical temperature is expected to diminish rainfed crops in China by 4–7% by 2050.	[88]
Wheat	Drought and heat stress high temperature and water deficit stress have the potential to minimize yield losses by 9–10%.	[89]
rice	Heat stress episodes throughout the reproductive season endanger more than 120 million hectares of rice production.	[90]
Maize	Each 1 °Celsius increase above 30 °Celsius decreases production by 1%, with 45% worldwide yield losses estimated by the 2080s.	[91]
Barley	During 1981 to 2002, rising air temperatures lowered yields by eight million metric tons every year, cost around \$1.0 billion.	[92]
Soybean	Around 2100, yield losses in the United States will be 46%.	[93]
Different crops	In India, every 1 °C increase might result in yield losses of \$20 billion each year.	[94]

Yousaf, M. I., Q. Hussain, M. S. Alwahibi, M. Z. Aslam, M. Z. Khalid, S. Hussain, A. Zafar, S. A. S. Shah, A. M. Abbasi and A. Mehboob (2023). "Impact of heat stress on agro-morphological, physio-chemical and fiber related parameters in upland cotton (*Gossypium hirsutum* L.) genotypes." *Journal of King Saud University-Science* 35(1): 102,379.

were recently examined in a variety of crops, such as Tomato, [14], Maize (E. [3]), *Arabidopsis thaliana* [15], Tobacco [16], wheat (*Triticum aestivum* L.) [17], rice (M. [18]) and sorghum (Rajendra [19]). Plants are being exposed to an increased variety of abiotic and biotic stressors due to climate change and potentially associated climatic variances, all of which will have significant adverse impacts on their development and production (H. [20]). Subsequently came to light that high temperatures and a water shortage have additive impacts on individual stressors. In essence, combining both stressors exacerbates individual stress's impacts. If HSPs, reactive oxygen species, mediator reduction enzymes, and many other transcripts were studied using transcriptome analysis, they were found to be more effectively expressed under extreme temperatures and drought stress than under separate stressors [21]. Similar processes that are activated in response to a solitary stress are activated in response to the combined stress. The most hopeful outcome of *Arabidopsis* research [22]. The genomic variant that makes it highly resistant to consolidated stress [23]. A research on cotton (*Gossypium barbadense* L.) found that a combination of drought and high temperatures had a negative impact on physiological processes such as development and advancement if compared to a single stress [24,4]. Cotton breeding initiatives should concentrate on selecting during combined drought and heat tolerance rather than just one of these conditions [25]. The main objectives of this review are to focus on the environmental factors, such as temperature, heat and drought, influences the growth and development, morphology and physio-chemical alteration of cotton. Furthermore, recent advancement on cotton breeding to combat the serious threat of drought and heat.

3. Influence of heat stress on morphological traits of cotton

3.1. Germination and seedling growth

Developing or identifying heat-resistant varieties remains one of the most cost-effective and practical approaches to alleviate the negative consequences of heat stress. Crops display numerous heat and drought

resistance systems, agronomic variations such as varying leaf angle, transpiration rate mechanisms, alterations in phospholipid extracellular matrix components, and morphometric changes under different heat stress regimes [7]. Despite various heat stress conditions (Fig.2), the plant's stomata closure process, reduced water loss, higher stomatal and trachomatous frequencies, and expanding xylem arteries are the most prevalent responses [6]. The development and growth of agricultural plant seedlings depend on maintaining the ideal temperature range of 28 to 30 °C. The starting temperature for seed germination is around 12 °C and 15.5 °C for the germination rate [26]. Cold temperatures among both two and four degrees Celsius are a severe issue in many regions of the country, particularly in the Delta area of Mississippi, particularly seedling germination as well as early development. In cold soil temperatures, genomic variations in fertilization and root growth have been found (X. [27]). Meshram and his colleagues discovered that soil with only a temperature range of 20 to 32 °Celsius is ideal for optimal root development and development [28]. Roots temperatures stress occurs between 35 and 40 °C and negatively impacts the plant's permeability and infiltration capabilities, as well as poor hormone production and delivery [29]. Among the most delicate procedures is the production of cytokinins that arise mostly in roots [30]. Several root processes, including nutrition and water intake, enzyme absorption and biosynthesis, and translocation, are sensitive to temperature. Root temperatures could prove more vital to plant development than shoot heat because roots endure a narrower temperature range and are less responsive to significant fluctuations [28].

3.2. Influence of heat stress on flowering and boll-filling stage

Surprising repeated occurrences of extreme heat stress in cotton-growing areas worldwide, which frequently coincide with distinct reproductive periods such as blossoming and boll-filling, result in poorer boll set and lint output [31]. Increased nighttime temperature as a result of the square stage caused cotton to lose growth and production and rapidly lose inflorescences. Cotton has also shown responsiveness to heat tolerance in flowering growth. At the flowering stage, pollen vitality and germination were reduced [32]. This same size of something like the pollen grain decreased at 29 °C, while the vitality of cotton pollen decreased above 32 °C in adjacent air [13]. Cotton visibility to HT reduced seedlings as well as a number of pods per plant and lint produced. This research found a significant unfavorable link between cotton yield and high temperatures during embryogenesis (N. [27]). Extreme heat can boost transpiration rate while decreasing photosynthetic and carbohydrate synthesis, but high temperatures at nighttime can enhance oxygen consumption while decreasing energy (ATP) levels [33]. Research revealed a 50% decrease in total productivity and a lower number of tillers than plants cultivated within the optimal range [34]. Heat stress reduces carbohydrates and flower bud length by lowering the number of seeds & fibers in each boll. The shortening of the growing season causes high temperatures to have a detrimental impact on growth and yield features. [35]. Crops planted around 36/28 °C day/night heat kept around 70% more bolls than crops cultivated at 30/22 °C temperature [36]. Considering fiber layer formation, fiber cross-sectional development and micronaire influenced by heat [37]. Heat units produced in the first 50 days after planting significantly influenced micronaire at harvest. The rate of structural protein expansion and fiber extension were both influenced by temperatures. Qi and his colleagues revealed in trials with continuous growth conditions, the shortest gap between blooming and boll opening (41 days) occurred at 29.5 °C [38].

3.3. Influence of heat stress on cotton fiber quality

In addition, various considerations, including the texture of fiber may be manipulated as a result of temperature-induced interference with the growth and harvesting of the cotton plant. Cotton fiber quality parameters, including width, resilience, elongation, and micronaire

suffer when temperatures rise [39]. Fiber quality & lint parameters strongly predict atmospheric temperature and agricultural activities [37]. Because the development of photosynthetic activity, which is actually affected by high temperature, determines fiber strength and characteristics [4]. Higher temperature impedes cellulose synthesis, thus compromising the fiber length and strength [40]. The temperature required for overall fiber consistency and micronaire is about 16 °C, whereas the average temp for fiber strength is 18–22 °C [41]. High heat can also have an impact on the yield and quality of fiber (K. [42]). Phosphorus, soluble proteins, and lactate account for 80% of total fiber juice, but temperature increases have a significant impact on these components [43]. Extreme heat can induce fiber roughness, enhancing the micronaire of lint [44]. High temperature during fiber formation can change fiber wall condensation and micronaire cross-sectional development, and fiber production can be lowered by up to 110 kg ha⁻¹ [45].

3.4. Influence of heat stress on cotton yield

Additionally, it has been shown that the temperature significantly affects cotton yield. Due to heat stress's negative impacts on plant development, maturation, DM separation, and reproductive development, crop yield will eventually suffer greatly. It may also lessen the creation of carbohydrates and photosynthesis [46]. The ideal temperature varies from 2 to 28 °C for the leaf area and is also quite vulnerable to extremely high temperatures. The temperature has a significant effect on flowering branches. However, as the daytime temperature rises above 30 °C, severe heat stress throughout blooming results in the loss of leaves and blooms. A rise in fruit production sites of 50% is observed as a result of temperature increases of 10 °C, or from 30 to 40 °C [25]. According to reports, freshly developed bolls begin to shed when the daytime average temperature is 32 °C or even higher. Elevated temperatures during the night will also boost respiration and further limit the amount of carbohydrates that can be accessed, reducing seed set, boll size, the number of seeds per boll, and the length of fibers per seed [47]. Over eighty percent of the entire yield diversity in cotton could be attributed to the quantity of seeds sown per acre. Crop outputs are primarily impacted by morphological processes of growth, which are affected by elevated temperatures [48]. Several crops grown for food, including cereals, are being demonstrated to be impacted by temperature-induced yield reduces, including tomato [14], maize [49], *Arabidopsis thaliana* [50], tobacco [16], wheat (*Triticum aestivum* L.) (R. [51]), rice (Q. [52]). Heat stress largely impacts productivity because of decreased warm capacity, which is produced by decreased photosynthesis due to changed membrane stability, which increases sustained respiratory costs and decreases radiation usage efficiency. (RUE, biomass production per unit of light intercepted by the canopy [53].

4. Influence of heat stress on physio-biochemical response of cotton

4.1. Influence of heat stress on stomata conductance

Because of HS, which additionally affects a number of vital metabolic processes, plants live shorter lifetimes and produce less. In order to decrease evaporation, stomatal openings also decrease photosynthesis. Increased stomatal permeability facilitates evaporative cooling of plants, which lowers temperature stress. In order to decrease evaporation, stomatal openings also decrease photosynthesis. Additional stomatal permeability facilitates evaporative cooling of plants, which lowers temperature stress [54]. Numerous species of plants experience mild heat stress, which inhibits stomatal permeability and net photosynthesis due to drops in the activated state of rubisco [55]. Since stomata control evaporation and the amount of cooling that can be achieved by water evaporation, they may be investigated in the evolution of heat tolerance in agricultural plants. Since CO₂ and water vapors must pass through the stomata, transpiration may be raised and

photosynthetic rates may be better if stomata open broader in higher-yielding lines. In addition, (X. [3]) found that all species under study displayed partial cellular membranes reduction in reaction to a greater transpiration rate to reduce water loss. Photosynthetic capacity and chlorophyll were employed in numerous research investigations to assess the genotypes of wheat and cotton in order to identify cultivars that are heat-tolerant [56].

4.2. Chlorophyll content

The chlorophyll content is among the most extensively used and effective simulations in growing crops, a non-destructive approach for quantifying heat plant stress. Kitajima and Butler invented the Chlorophyll content approach developed by ([57]). Sunlight re-emitted by photosynthetic pigments when transitioning between stimulated to non-stimulated states is employed to measure photosynthesis efficiency among higher plants. A thorough analysis of the Chlorophyll concentration method is provided by [58]. The procedure of photosynthesis is a procedure in cells of plants that are particularly vulnerable to temperature stress [59]. The photosynthesis complicated is the first complex in the electron transport chain used by photosynthesis, and it acts as the catalyst for the oxidative degradation of water and the production of molecular oxygen [60]. The effect of heat stress alters the temperature-oxidation characteristics of PSII acceptors, lowering the transport of electrons effectiveness in photosynthesis systems [61].

4.3. Effects on reactive oxygen species

As a defensive strategy, high-temperature stress causes a range of metabolic changes in plants, including the development of antioxidant and heat shock proteins (Fig. 3). Singlet oxygen, superoxide radicals, peroxides, hydroxyl radicals, and alpha oxygen are all chemically active and unstable molecules known as ROS. ROS, a natural consequence of regular oxygen metabolism, is involved in intercellular communication in addition to homeostasis. In environmentally disturbed situations such as heat stress, ROS are created in excess in chloroplasts and mitochondria, destroying cell components; this is called osmotic damage [62]. Excess ROS interferes with normal cell processes owing to oxidative damage, which can lead to cell death if stress circumstances persist. Plants manufacture various antioxidants as a defensive mechanism to defend cells from damage that is caused by excess ROS production. [63]. Yet, understanding the molecular pathways for selecting crops that are resistant to heat and drought stress is critical (A. [64]). Consequently, the characterization of enzymatic and non-enzymatic and enzymatic systems may be related to stress and might be used to identify plant stress tolerance. Knowing about the connection between antioxidant activities and yield qualities, on the other hand, might be helpful to in developing a practical screening approach for selecting large volumes of plant materials in the least period of time [65]. As a result, combining traditional breeding with antioxidants as screening criteria opens up new avenues for enhancing stress tolerance in cotton.

4.4. Antioxidants

A balance between the production and disintegration of ROS by oxidants is required for appropriate cell functioning and development (Fig. 3). Antioxidants prevent other molecules from oxidizing and neutralizing free radicals, creating less reactive molecules (W. [66]). Plant defense mechanisms include several enzymatic components such as superoxide dismutase (SOD), ascorbate peroxidase (APX), ascorbate (ASC), and glutathione (GSH). Antibodies in cell membranes are heat sensitive and easily denatured by oxidative stress [67]. As a result, the identification of nonenzymatic and enzymatic systems may be associated with stress conditions and utilized as an indication of stress tolerance. Nonenzymatic (proline) and enzymatic antioxidants are produced to reduce cellular damage caused by reactive oxygen species (ROS), such

as superoxide, per hydroxy radicals, hydrogen peroxide, and hydroxyl radicals [68].

4.5. Heat shock proteins (HSPs)

Protein induced by heat shock HSPs is a non-identical collection of non-linear and non-proteins that function as chaperones in nature and are anticipated mainly to aid in organism survival when exposed to stress. [69]. HSPs function as chaperones, preventing cell destabilization and promoting refolding of protein molecules and other stress response systems [70]. The production of HSPs increases as the temperature gradually rises. Cotton has been demonstrated to produce and accumulate HSPs at regulated temperatures ranging from 38 to 41 °C [67]. HSPs are an evolutionarily conserved category of proteins found in both prokaryotes and eukaryotes. These proteins are divided by molecular weight into five primary families: HSP100, HSP90, HSP70, HSP60/40, and HSP20 [71]. The members of these groups contribute to the maintenance of tissue homeostasis and perform distinct non-redundant functions in various developmental stages.

5. Molecular mechanisms and breeding approaches against heat stress

5.1. Screening of heat tolerance cultivars

Widely planted cultivars frequently confront exceptionally high temperatures of up to 50 °C between months (May and June), which would be over 20 °C above the ideal temperature necessary for proper development, severely reducing crop production. A major problem is cultivating high-temperature economic cotton cultivars [22]. When faced with heat stress, seedlings' dynamic responses make identifying and confirming characteristics that confer resistance to high temperatures difficult [25]. Researchers are indeed investigating how plants may be handled in high-temperature environments. Pharmacological, metabolic, and genomic adaptations to highly stressful conditions have been explored to screen recently developed cotton cultivars [72]. Discovery and development of prospective genotypes with higher resistance to heat stress might result in improved yield and quality in heat-prone locations. Various approaches for selecting heat tolerance in actual field ecological systems are commonly used. Field research is more beneficial for studying behavior than controlled circumstances, yet, it has limits in regulating the atmosphere under field conditions [73].

5.2. Conventional breeding method

Conventional heat-resistant crop breeding has relied chiefly on selection, with the most common technique for choosing crops with stress tolerance being to produce genetic resources in a hot targeted testing environment and identify individuals/lines with a greater yield [74]. Because of temperature stress, cotton line improvement using traditional breeding procedures lowers yield loss. At key phases of agricultural plants, genetic lines with high enough temperatures are always selected in hot locations [75]. According to scientists, the best temperature for nitrogen fixation throughout respiration is 23 °C, and heat just above that might influence the photometric mechanisms of cotton plants, reducing seed cotton output and fiber qualities [22]. [76] show that high temperatures slow seedlings and flower bud formation. After exposing their pollens to 35 °C for 15 min, several prospective high-temperature cotton genotypes were discovered to have healthy pollen grains. During population segregation, the same test was used to identify heat-tolerant families.

Moreover, high-temperature cultivars were found based on each cultivar's absolute cell injury percentage (RCI%), heat sensitivity index (HSI) value, and boll retaining percentage. These are easy, dependable, and economical heat tolerance screening procedures. In compared to

other abiotic stressors, heat resistance requires more significant consideration. In the literature, there is little knowledge of stress tolerance in cotton [25].

5.3. Molecular breeding techniques against heat stress

Compared to molecular markers, specifically marker-assisted screening, which is very efficient and accurate, traditional breeding is laborious, time-consuming, and environment-dependent. Biotechnology has made important contributions to comprehending and increasing agricultural plants' high heat tolerance [77]. Many techniques were employed to understand the neuron's nerve cells of stress tolerance, including genetic techniques, correlations, co-segregation, and genetic variability [78]. In *A. thaliana*, for instance, four quantitative trait loci (QTLs) regulating heat tolerance were discovered [79]. The bulked segregate analysis was used to identify RAPD markers linked with heat-resistant properties in cotton under heat stress. Special HSPs have been identified in diverse crop species in response to high temperatures [80]. Similarly, 11 QTLs relevant for pollen tube expansion and pollen germination under heat-stress conditions were found in maize using the DNA markers RFLP (restriction fragment length polymorphism) [81]. Many strategies are already accessible to plant scientists to generate novel germplasm that can deal with harsh situations and provide food and nutrition security, since so many modifications have been previously made to the character of agricultural plants, leading to diminished food security.

6. Conclusion and future perspective

Heat stress has become a serious threat widespread for agronomic crops. The intensity of abiotic stresses varies significantly between climatic regions and is influenced by the likelihood and duration of high temperatures as well as the time of circadian crops under high temperatures. Globally temperature arising due to alarming increasing of carbon dioxide and other greenhouse gasses, such as NO₂ and CO₂, from industry and another various sources. Since seedling, root growth, photosynthesis responsiveness, boll and fiber production are all regulated by ambient temperature changes, maximum and minimum temperature extremes are significant. The optimum growth temperature for tillering is between 30 and 35 °C, while the root process gradually retarded at 40 °C. The fluctuation in temperature adversely impact on vegetative, reproductive phases and metabolic activity. It was determined that 30 °C was optimal for boll formation and preservation. The roots, fiber, and seed development, pollen viability, anther indehiscence are subjected to halted at above 40 °C. Significant crop commodities require a thorough understanding of plant reactions to higher temperatures and the mechanisms involved in identifying or creating heat tolerant cultivars. The way that plants react to extreme heat varies depending on the species, the period of growth, and the species itself. The impacts of extreme heat on various agricultural seasons and their crop, production, and cotton fiber quality are thus illustrated in this review paper. In order to combat the challenges of heat stress in cotton, heat stress tolerance cultivars should be developed by exploiting the recent advanced technology and breeding techniques (Fig. 4, Table 1, Table 2, Table 3).

Funding

This research was funded by The National Key R&D Program of China (2021YFE0101200), and the National Natural Science Foundation of China (32171994, 32072023, 32272090).

Declaration of Competing Interest

All authors declare no conflict of interest.

Data availability

Data will be made available on request.

References

- [1] C.R. Viot, J.F. Wendel, Evolution of the cotton genus, *Gossypium*, and its domestication in the Americas, *CRC Crit. Rev. Plant Sci.* 42 (1) (2023) 1–33, <https://doi.org/10.1080/07352689.2022.2156061>.
- [2] A.U. Rehman, I.A. Rana, S. Majeed, M.T. Chaudhary, M. Zulfiqar, S.H. Yang, G. Chung, Y. Jia, X. Du, L. Hinze, M.T. Azhar, Intra-plant variability for heat tolerance related attributes in upland cotton, *Agronomy* 11 (12) (2021) 1–14, <https://doi.org/10.3390/agronomy11122375>.
- [3] E. Li, J. Zhao, J.W.M. Pullens, X. Yang, The compound effects of drought and high temperature stresses will be the main constraints on maize yield in Northeast China, *Sci. Total Environ.* 812 (2022), <https://doi.org/10.1016/j.scitotenv.2021.152461>.
- [4] M.I. Yousaf, Q. Hussain, M.S. Alwahibi, M.Z. Aslam, M.Z. Khalid, S. Hussain, N.R. Abdelsalam, A.S. Shah, A.M. Abbasi, A. Mehboob, M.W. Riaz, M.S. Elshikh, Impact of heat stress on agro-morphological, physio-chemical and fiber related parameters in upland cotton (*Gossypium hirsutum* L.) genotypes, *J. King Saud University - Sci.* 35 (1) (2023), 102379, <https://doi.org/10.1016/j.jksus.2022.102379>.
- [5] S.A. Zafar, M.A. Noor, M.A. Waqas, X. Wang, T. Shaheen, M. Raza, Mehboob-Ur-Rahman, Temperature extremes in cotton production and mitigation strategies, *Past, Present and Future Trends in Cotton Breeding* (2018), <https://doi.org/10.5772/intechopen.74648>.
- [6] M.U. Hassan, R.Y. Ghareeb, M. Nawaz, A. Mahmood, A.N. Shah, A. Abdel-Megeed, N.R. Abdelsalam, M. Hashem, S.H. Qari, Melatonin: a vital pro-tectant for crops against heat stress: mechanisms and prospects, *Agronomy* (5) (2022) 12, <https://doi.org/10.3390/agronomy12051116>.
- [7] T.B. dos Santos, A.F. Ribas, S.G.H. de Souza, I.G.F. Budzinski, D.S. Domingues, Physiological responses to drought, salinity, and heat stress in plants: a review, *Stresses* 2 (1) (2022) 113–135, <https://doi.org/10.3390/stresses2010009>.
- [8] K. Shahzad, I. Mubeen, M. Zhang, X. Zhang, J. Wu, C. Xing, Progress and perspective on cotton breeding in Pakistan, *J. Cotton Res.* 5 (1) (2022), <https://doi.org/10.1186/s42397-022-00137-4>.
- [9] M.M. Zafar, Y. Zhang, M.A. Farooq, A. Ali, H. Firdous, M. Haseeb, S. Fiaz, A. Shakeel, A. Razaq, M. Ren, Biochemical and associated agronomic traits in *Gossypium hirsutum* L. under high temperature stress, *Agronomy* 12 (6) (2022) 1–19, <https://doi.org/10.3390/agronomy12061310>.
- [10] A. Hussien, Review On Effect of Increased Temperature On Respiratory Costs : Focus on Crops Review on Effect of Increased Temperature On Respiratory Costs : Focus on Crops, 2021. January 2020.
- [11] S. Majeed, I.A. Rana, M.S. Mubarik, R.M. Atif, S.H. Yang, G. Chung, Y. Jia, X. Du, L. Hinze, M.T. Azhar, Heat stress in cotton: a review on predicted and unpredicted growth-yield anomalies and mitigating breeding strategies, *Agronomy* 11 (9) (2021) 1–20, <https://doi.org/10.3390/agronomy11091825>.
- [12] Y.Y. Sun, J.Q. Wang, R.H. Xiang, Z.G. Li, Key role of reactive oxygen species-scavenging system in nitric oxide and hydrogen sulfide crosstalk-evoked thermotolerance in maize seedlings, *Front. Plant Sci.* 13 (November) (2022) 1–15, <https://doi.org/10.3389/fpls.2022.967968>.
- [13] N. Lohani, M.B. Singh, P.L. Bhalla, High temperature susceptibility of sexual reproduction in crop plants, *J. Exp. Bot.* 71 (2) (2020) 555–568, <https://doi.org/10.1093/jxb/erz426>.
- [14] A.A. Aldubai, A.A. Alsadon, H.H. Migdadi, S.S. Alghamdi, S.A. Al-Faifi, M. Afzal, Response of tomato (*Solanum lycopersicum* L.) genotypes to heat stress using morphological and expression study, *Plants* 11 (5) (2022) 1–14, <https://doi.org/10.3390/plants11050615>.
- [15] A. Lambolze, A. Kawamura, T. Takahashi, B. Rymen, A. Iwase, D.S. Favero, M. Ikeuchi, T. Suzuki, S. Cortijo, K.E. Jaeger, F.A. Wigge, K. Sugimoto, Warm temperature promotes shoot regeneration in *Arabidopsis thaliana*, *Plant and Cell Physiol.* 63 (5) (2022) 618–634, <https://doi.org/10.1093/pcp/pcac017>.
- [16] K. Gu, S. Hou, J. Chen, J. Guo, F. Wang, C. He, C. Zou, X. Xie, The physiological response of different tobacco varieties to chilling stress during the vigorous growing period, *Sci. Rep.* 11 (1) (2021) 1–16, <https://doi.org/10.1038/s41598-021-01703-7>.
- [17] A. EL Sabagh, M.S. Islam, M. Skaliky, M. Ali Raza, K. Singh, M. Anwar Hossain, A. Hossain, W. Mahboob, M.A. Iqbal, D. Ratnasakera, R.K. Singhal, S. Ahmed, A. Kumari, A. Wasaya, O. Sytar, M. Brestic, F. ÇİG, M. Erman, M. Habib Ur Rahman, A. Arshad, Salinity stress in wheat (*Triticum aestivum* L.) in the changing climate: adaptation and management strategies, *Front. Agronomy* 3 (2021) 1–20, <https://doi.org/10.3389/fagro.2021.661932>.
- [18] M. Zhang, Z. Li, K. Feng, Y. Ji, Y. Xu, D. Tu, B. Teng, Q. Liu, J. Liu, Y. Zhou, W. Wu, Strategies for indica rice adapted to high-temperature stress in the middle and lower reaches of the Yangtze River, *Front. Plant Sci.* 13 (January) (2023) 1–13, <https://doi.org/10.3389/fpls.2022.1081807>.
- [19] V.B. Rajendra Prasad, M. Govindaraj, M. Djanaguiraman, I. Djalovic, A. Shailani, N. Rawat, S.L. Singla-Pareek, A. Pareek, P.V. Vara Prasad, Drought and high temperature stress in sorghum: physiological, genetic, and molecular insights and breeding approaches, *Int. J. Mol. Sci.* (18) (2021) 22, <https://doi.org/10.3390/ijms22189826>.
- [20] H. Zhang, J. Zhu, Z. Gong, J.K. Zhu, Abiotic stress responses in plants, *Nat. Rev. Genetics* 23 (2) (2022) 104–119, <https://doi.org/10.1038/s41576-021-00413-0>.
- [21] H. Sies, D.P. Jones, Reactive oxygen species (ROS) as pleiotropic physiological signalling agents, *Nat. Rev. Mol. Cell Biol.* 21 (7) (2020) 363–383, <https://doi.org/10.1038/s41580-020-0230-3>.
- [22] S. Saud, L. Wang, Mechanism of cotton resistance to abiotic stress, and recent research advances in the osmoregulation related genes, *Front. Plant Sci.* 13 (August) (2022) 1–17, <https://doi.org/10.3389/fpls.2022.972635>.
- [23] Z. Ma, Y. Zhang, L. Wu, G. Zhang, Z. Sun, Z. Li, Y. Jiang, H. Ke, B. Chen, Z. Liu, Q. Gu, Z. Wang, G. Wang, J. Yang, J. Wu, Y. Yan, C. Meng, L. Li, X. Li, X. Wang, High-quality genome assembly and resequencing of modern cotton cultivars provide resources for crop improvement, *Nat. Genet.* 53 (9) (2021) 1385–1391, <https://doi.org/10.1038/s41588-021-00910-2>.
- [24] H. Zhao, Y. Chen, J. Liu, Z. Wang, F. Li, X. Ge, Recent advances and future perspectives in early-maturing cotton research, *N. Phytologist* (2022), <https://doi.org/10.1111/nph.18611>.
- [25] S. Abro, M. Rizwan, Z.A. Deho, S.A. Abro, M.A. Sial, Identification of heat tolerant cotton lines showing genetic variation in cell membrane thermostability, stomata, and trichome size and its effect on yield and fiber quality traits, *Front. Plant Sci.* 12 (January) (2022) 1–15, <https://doi.org/10.3389/fpls.2021.804315>.
- [26] A. Hamid, M. Neogi, M. Marma, J. Biswas, A. S. Marma, M. Mollah, M. Uddin, M. Islam, Determining planting window for growing upland cotton (*Gossypium hirsutum* L.) during dry season in Bandarban, Bangladesh, *Ann. Bangladesh Agriculture* 24 (2) (2021) 1–14, <https://doi.org/10.3329/aba.v24i2.55780>.
- [27] N. Li, H. Lin, T. Wang, Y. Li, Y. Liu, X. Chen, X. Hu, Impact of climate change on cotton growth and yields in Xinjiang, China, *Field Crops Res.* 247 (August 2019) (2020), <https://doi.org/10.1016/j.fcr.2019.107590>.
- [28] J.H. Meshram, D. Nagrale, *We Are IntechOpen, the World's Leading Publisher of Open Access Books Built by scientists, For Scientists*, 2021, <https://doi.org/10.5772/intechopen.95547>.
- [29] A. Arshad, M.A. Raza, Y. Zhang, L. Zhang, X. Wang, M. Ahmed, M. Habib-ur-rehman, Impact of Climate Warming On Cotton Growth and Yields in China and Pakistan : A Regional Perspective, 2021.
- [30] J. Xu, L. Chen, H. Sun, N. Wusiman, W. Sun, B. Li, Y. Gao, J. Kong, Crosstalk Between Cytokinin and Ethylene Signaling Pathways Regulates Leaf Abscission in Cotton in Response to Chemical Defoliants, 70, 2019, pp. 1525–1538, <https://doi.org/10.1093/jxb/erz036>.
- [31] C. Schaefer, B. Nichols, G. Collins, J. Whitaker, C. Bednarz, C. Main, G. Ritchie, Cotton Maturity Determination Through Vertical Mapping, 70, 2017, pp. 62–70, <https://doi.org/10.12135/cropsci.2016.03.0168>.
- [32] K.R. Reddy, R. Bheemanahalli, S. Saha, K. Singh, S.B. Lokhande, B. Gajanayake, J. J. Read, J.N. Jenkins, D.A. Raska, L.M. De Santiago, A.M. Hulse-Kemp, R. N. Vaughn, D.M. Stelly, High-temperature and drought-resilience traits among interspecific chromosome substitution lines for genetic improvement of upland cotton, *Plants* 9 (12) (2020) 1–22, <https://doi.org/10.3390/plants9121747>.
- [33] N. Sharma, M. Thakur, P. Suryakumar, P. Mukherjee, A. Raza, C.S. Prakash, A. Anand, Breathing out' under heat stress—respiratory control of crop yield under high temperature, *Agronomy* (4) (2022) 12, <https://doi.org/10.3390/agronomy12040806>.
- [34] S.A. Tung, Y. Huang, A. Hafeez, S. Ali, A. Liu, M.S. Chattha, S. Ahmad, G. Yang, Morpho-physiological effects and molecular mode of action of mepiquat chloride application in cotton: a review, *J. Soil Sci. Plant Nutr.* 20 (4) (2020) 2073–2086, <https://doi.org/10.1007/s42729-020-00276-0>.
- [35] M.R. Yadav, M. Choudhary, J. Singh, M.K. Lal, P.K. Jha, P. Udawat, N.K. Gupta, V. D. Rajput, N.K. Garg, C. Maheshwari, M. Hasan, S. Gupta, T.K. Jatwa, R. Kumar, A. K. Yadav, P.V. Vara Prasad, Impacts, Tolerance, Adaptation, and Mitigation of Heat Stress on Wheat under Changing Climates, *Int. J. Mol. Sci.* (5) (2022) 23, <https://doi.org/10.3390/ijms23052838>.
- [36] A. Vijayakumar, R. Beena, Impact of temperature difference on the physicochemical properties and yield of tomato: a review, *Chem. Sci. Rev. Lett.* 9 (35) (2020) 665–681, <https://doi.org/10.37273/chesci.CS205107159>.
- [37] S. Ul-Allah, A. Rehman, M. Hussain, M. Farooq, Fiber yield and quality in cotton under drought: effects and management, *Agricultural Water Manag.* 255 (January) (2021), 106994, <https://doi.org/10.1016/j.agwat.2021.106994>.
- [38] H.kun QI, M.wei DU, L. MENG, L.wei XIE, A.E. ENEJI, D.yong XU, X.li TIAN, Z. hu LI, Cotton maturity and responses to harvest aids following chemical topping with mepiquat chloride during bloom period, *J. Integr. Agric.* 21 (9) (2022) 2577–2587, <https://doi.org/10.1016/j.jia.2022.07.008>.
- [39] A. Manan, M.M. Zafar, M. Ren, M. Khurshid, A. Sahar, A. Rehman, H. Firdous, Y. Youlu, A. Razaq, A. Shakeel, Genetic analysis of biochemical, fiber yield and quality traits of upland cotton under high-temperature, *Plant Prod. Sci.* 25 (1) (2022) 105–119, <https://doi.org/10.1080/1343943X.2021.1972013>.
- [40] A. Jamil, S.J. Khan, K. Ullah, Genetic diversity for cell membrane thermostability, yield and quality attributes in cotton (*Gossypium hirsutum* L.), *Genet. Resour. Crop Evol.* 67 (6) (2020) 1405–1414, <https://doi.org/10.1007/s10722-020-00911-w>.
- [41] Y. Yu, Q. Bian, Y. Lu, X. Zhang, J. Yang, L. Liang, High sensitivity all optical fiber conductivity-temperature-depth (CTD) sensing based on an optical microfiber coupler (OMC), *J. Lightwave Technol.* 37 (11) (2019) 2739–2747, <https://doi.org/10.1109/JLT.2018.2878475>.
- [42] K. Ullah, N. Khan, Z. Usman, R. Ullah, F.Y. Saleem, S.A.I. Shah, M. Salman, Impact of temperature on yield and related traits in cotton genotypes, *J. Integr. Agric.* 15 (3) (2016) 678–683, [https://doi.org/10.1016/S2095-3119\(15\)61088-7](https://doi.org/10.1016/S2095-3119(15)61088-7).
- [43] O.O. Aluko, C. Li, Q. Wang, H. Liu, Sucrose utilization for improved crop yields: a review article, *Int. J. Mol. Sci.* 22 (9) (2021), <https://doi.org/10.3390/ijms22094704>.
- [44] M.H.J. van der Sluijs, G.W. Roth, Comparing dryland cotton upland fibre quality from on-board spindle and stripper harvesting systems, *J. Textile Institute* 112 (2) (2021) 192–199, <https://doi.org/10.1080/00405000.2020.1731288>.

- [45] J. Correia, K.T. Rainert, F.R. Oliveira, R. de Cássia Siqueira Curto Valle, J.A. B Valle, Cationization of cotton fiber: an integrated view of cationic agents, processes variables, properties, market and future prospects, *Cellulose* 27 (15) (2020) 8527–8550, <https://doi.org/10.1007/s10570-020-03361-w>.
- [46] S. Noreen, H.U.R. Athar, M. Ashraf, Interactive effects of watering regimes and exogenously applied osmoprotectants on earliness indices and leaf area index in cotton (*Gossypium hirsutum* L.) crop, *Pak. J. Bot.* 45 (6) (2013) 1873–1881.
- [47] P. Chaturvedi, A.J. Wiese, A. Ghatak, L. Závěská Drábková, W. Weckwerth, D. Honys, Heat stress response mechanisms in pollen development, *N. Phytologist* 231 (2) (2021) 571–585, <https://doi.org/10.1111/nph.17380>.
- [48] J. Calleja-Cabrera, M. Boter, L. Oñate-Sánchez, M. Pernas, Root growth adaptation to climate change in crops, *Front. Plant Sci.* (May) (2020) 11, <https://doi.org/10.3389/fpls.2020.00544>.
- [49] A.H. El-Sappah, S.A. Rather, S.H. Wani, A.S. Elrys, M. Bilal, Q. Huang, Z.A. Dar, M. M.A. Elashtokhy, N. Soaud, M. Koul, R.R. Mir, K. Yan, J. Li, K.A. El-Tarabily, M. Abbas, Heat stress-mediated constraints in maize (*Zea mays*) production: challenges and solutions, *Front. Plant Sci.* (April) (2022) 13, <https://doi.org/10.3389/fpls.2022.879366>.
- [50] X. Lei, Y. Ning, I. Eid Elesawi, K. Yang, C. Chen, C. Wang, B. Liu, Heat stress interferes with chromosome segregation and cytokinesis during male meiosis in *Arabidopsis thaliana*, *Plant Signaling and Behav.* (5) (2020) 15, <https://doi.org/10.1080/15592324.2020.1746985>.
- [51] R. Zhang, G. Liu, H. Xu, H. Lou, S. Zhai, A. Chen, S. Hao, J. Xing, J. Liu, M. You, Y. Zhang, C. Xie, J. Ma, R. Liang, Q. Sun, H. Zhai, Z. Ni, B. Li, Heat Stress Tolerance 2 confers basal heat stress tolerance in allohexaploid wheat (*Triticum aestivum* L.), *J. Exp. Bot.* 73 (19) (2022) 6600–6614, <https://doi.org/10.1093/jxb/erac297>.
- [52] Q. Sun, Y. Zhao, Y. Zhang, S. Chen, Q. Ying, Z. Lv, X. Che, D. Wang, Heat stress may cause a significant reduction of rice yield in China under future climate scenarios, *Sci. Total Environ.* 818 (2022), 151746, <https://doi.org/10.1016/j.scitotenv.2021.151746>.
- [53] N. Zahra, M.B. Hafeez, A. Ghaffar, A. Kausar, M.A. Zeidi, K.H.M. Siddique, M. Farooq, Plant photosynthesis under heat stress: effects and management, *Environ. Exp. Bot.* 206 (December 2022) (2023), 105178, <https://doi.org/10.1016/j.envexpbot.2022.105178>.
- [54] Y. Wang, Y. Wang, Y. Tang, X.G. Zhu, Stomata conductance as a goalkeeper for increased photosynthetic efficiency, *Curr. Opin. Plant Biol.* 70 (2022), 102310, <https://doi.org/10.1016/j.cop.2022.102310>.
- [55] R.M. Marchin, D. Backes, A. Ossola, M.R. Leishman, M.G. Tjoelker, D.S. Ellsworth, Extreme heat increases stomatal conductance and drought-induced mortality risk in vulnerable plant species, *Glob. Chang. Biol.* 28 (3) (2022) 1133–1146, <https://doi.org/10.1111/gcb.15976>.
- [56] P. Peng, R. Li, Z.H. Chen, Y. Wang, Stomata at the crossroad of molecular interaction between biotic and abiotic stress responses in plants, *Front. Plant Sci.* 13 (October) (2022) 1–14, <https://doi.org/10.3389/fpls.2022.1031891>.
- [57] W.L. Butler, M. Kitajima, Fluorescence quenching in photosystem II of chloroplasts, *BBA - Bioenergetics* 376 (1) (1975) 116–125, [https://doi.org/10.1016/0005-2728\(75\)90210-8](https://doi.org/10.1016/0005-2728(75)90210-8).
- [58] M.M. van der Westhuizen, D.M. Oosterhuis, J.M. Berner, N. Boogaers, Chlorophyll a fluorescence as an indicator of heat stress in cotton (*Gossypium hirsutum* L.), *South Afr. J. Plant and Soil* 37 (2) (2020) 116–119, <https://doi.org/10.1080/02571862.2019.1665721>.
- [59] J. Singh, M. Kumar, A. Sharma, G. Pandey, K. Chae, S. Lee, We Are IntechOpen, the World's Leading Publisher of Open Access Books Built by scientists, For Scientists TOP 1%, 11, Intech, 2016, p. 13. <https://www.intechopen.com/books/advanced-biometric-technologies/liveness-detection-in-biometrics>.
- [60] M. Sarwar, M.F. Saleem, N. Ullah, S. Ali, M. Rizwan, M.R. Shahid, M.N. Alyemeni, S.A. Alamri, P. Ahmad, Role of mineral nutrition in alleviation of heat stress in cotton plants grown in glasshouse and field conditions, *Sci. Rep.* 9 (1) (2019) 1–17, <https://doi.org/10.1038/s41598-019-49404-6>.
- [61] D. Jespersen, J. Zhang, B. Huang, Chlorophyll loss associated with heat-induced senescence in bentgrass, *Plant Sci.* 249 (2016) 1–12, <https://doi.org/10.1016/j.plantsci.2016.04.016>.
- [62] R. Babbar, B. Karpinska, A. Grover, C.H. Foyer, Heat-induced oxidation of the nuclei and cytosol, *Front. Plant Sci.* 11 (January) (2021) 1–16, <https://doi.org/10.3389/fpls.2020.617779>.
- [63] H.L. Liu, Z.X. Lee, T.W. Chuang, H.C. Wu, Effect of heat stress on oxidative damage and antioxidant defense system in white clover (*Trifolium repens* L.), *Planta* 254 (5) (2021) 1–17, <https://doi.org/10.1007/s00425-021-03751-9>.
- [64] A. Ullah, H. Sun, X. Yang, X. Zhang, Drought coping strategies in cotton: increased crop per drop, *Plant Biotechnol. J.* 15 (3) (2017) 271–284, <https://doi.org/10.1111/pbi.12688>.
- [65] R. Ekinici, S. Basbağ, E. Karademir, Ç. Karademir, The effects of high temperature stress on some agronomic characters in cotton, *Pak. J. Bot.* 49 (2) (2017) 503–508.
- [66] W. Zhang, Q.M. Zeng, R.C. Tang, Gallic acid functionalized polylysine for endowing cotton fiber with antibacterial, antioxidant, and drug delivery properties, *Int. J. Biol. Macromol.* 216 (June) (2022) 65–74, <https://doi.org/10.1016/j.ijbiomac.2022.06.186>.
- [67] M.A. Farooq, W.S. Chattha, M. Sohaib, U. Karamat, Transgenerational impact of climatic changes on cotton production, *March* (2023), <https://doi.org/10.3389/fpls.2023.987514>.
- [68] M.L. Racchi, Antioxidant defenses in plants with attention to prunus and citrus spp, *Antioxidants* 2 (4) (2013) 340–369, <https://doi.org/10.3390/antiox2040340>.
- [69] A. Sable, K.M. Rai, A. Choudhary, V.K. Yadav, S.K. Agarwal, S.V. Sawant, Inhibition of Heat Shock proteins HSP90 and HSP70 induce oxidative stress, suppressing cotton fiber development, *Sci. Rep.* 8 (1) (2018) 1–17, <https://doi.org/10.1038/s41598-018-21866-0>.
- [70] C. Hu, J. Yang, Z. Qi, H. Wu, B. Wang, F. Zou, H. Mei, J. Liu, W. Wang, Q. Liu, Heat shock proteins: biological functions, pathological roles, and therapeutic opportunities, *MedComm* 3 (3) (2022) 1–39, <https://doi.org/10.1002/mco2.161>.
- [71] E.R. Waters, E. Vierling, Plant small heat shock proteins – evolutionary and functional diversity, *N. Phytologist* 227 (1) (2020) 24–37, <https://doi.org/10.1111/nph.16536>.
- [72] S. Abro, M.T. Rajput, M.A. Khan, M.A. Sial, S.S. Tahir, Screening of cotton (*Gossypium hirsutum* L.) genotypes for heat tolerance, *Pak. J. Bot.* 47 (6) (2015) 2085–2091.
- [73] Mohamed, H., & Abdel-hamid, A.M.E. (2016). Molecular and biochemical studies for heat tolerance on four cotton genotypes Molecular and biochemical studies for heat tolerance on four cotton genotypes High temperature is considered one of the most important environmental factors that affect growth a. November 2013.
- [74] S. Majeed, I.A. Rana, M.S. Mubarak, R.M. Atif, S.H. Yang, G. Chung, Y. Jia, X. Du, L. Hinze, M.T. Azhar, Heat stress in cotton: a review on predicted and unpredicted growth-yield anomalies and mitigating breeding strategies, *Agronomy* (9) (2021) 11, <https://doi.org/10.3390/agronomy11091825>.
- [75] A. Raza, J. Tabassum, H. Kudapa, R.K. Varshney, Can omics deliver temperature resilient ready-to-grow crops? *Crit. Rev. Biotechnol.* 41 (8) (2021) 1209–1232, <https://doi.org/10.1080/07388551.2021.1898332>.
- [76] M. Sajid, M.A.B. Saddique, M.H.N. Tahir, A. Matloob, Z. Ali, F. Ahmad, Q. Shakil, Z.U. Nisa, M. Kifayat, Physiological and molecular response of cotton (*Gossypium hirsutum* L.) to heat stress at the seedling stage, *Sabao J. Breeding and Genetics* 54 (1) (2022) 44–52, <https://doi.org/10.54910/SABAO2022.54.1.5>.
- [77] Z. Khan, Z. Ali, A.A. Khan, Cotton breeding and biotechnology: challenges and opportunities, *Cotton Breeding and Biotechnol. Challenges and Opportunities* (2022), <https://doi.org/10.1201/9781003096856>.
- [78] S. Ahmar, R.A. Gill, K.H. Jung, A. Faheem, M.U. Qasim, M. Mubeen, W. Zhou, Conventional and molecular techniques from simple breeding to speed breeding in crop plants: recent advances and future outlook, *Int. J. Mol. Sci.* 21 (7) (2020) 1–24, <https://doi.org/10.3390/ijms21072590>.
- [79] M. El-Soda, W. Kruijer, M. Malosetti, M. Koornneef, M.G.M. Aarts, Quantitative trait loci and candidate genes underlying genotype by environment interaction in the response of *Arabidopsis thaliana* to drought, *Plant Cell and Environ.* 38 (3) (2015) 585–599, <https://doi.org/10.1111/pce.12418>.
- [80] T. Kim, S. Samraj, J. Jiménez, C. Gómez, T. Liu, K. Begcy, Genome-wide identification of heat shock factors and heat shock proteins in response to UV and high intensity light stress in lettuce, *BMC Plant Biol.* 21 (1) (2021) 1–20, <https://doi.org/10.1186/s12870-021-02959-x>.
- [81] D. Van Inghelandt, F.P. Frey, D. Ries, B. Stich, QTL mapping and genome-wide prediction of heat tolerance in multiple connected populations of temperate maize, *Sci. Rep.* 9 (1) (2019) 1–16, <https://doi.org/10.1038/s41598-019-50853-2>.
- [82] L.J. Erie, O.F. French, K. Harris, Consumptive use of water by crops in Arizona, in: *Technical Bulletin*, 169, The University of Arizona, 1965, p. 46.
- [83] K.L.H. Huang, C. Lin, *Cloning, Expression and Physiological Analysis of Broccoli Catalase Gene and Chinese Cabbage Ascorbate Peroxidase Gene Under Heat Stress*, 2010, pp. 575–593, <https://doi.org/10.1007/s00299-010-0846-4>.
- [84] A. Hameed, M. Goher, N. Iqbal, *Heat Stress-Induced Cell Death, Changes in Antioxidants, Lipid Peroxidation, and Protease Activity in Wheat Leaves*, 2012, pp. 283–291, <https://doi.org/10.1007/s00344-011-9238-4>.
- [85] R. Zhou, L. Kong, X. Yu, C. Otto, O. Tongmin, Z. Fangling, J. Zhen, Oxidative damage and antioxidant mechanism in tomatoes responding to drought and heat stress, *Acta Physiologiae Plantarum* 41 (2) (2019) 1–11, <https://doi.org/10.1007/s11738-019-2805-1>.
- [86] F. Verlag, S. Dash, N. Mohanty, *Response of Seedlings to Heat-Stress in Cultivars of Wheat : Growth temperature-Dependent Differential Modulation of Photosystem 1 and 2 Activity, and Foliar Antioxidant Defense Capacity*, 2002, p. 59.
- [87] S. Galani, S. Hameed, M.K. Ali, Exogenous Application of Salicylic Acid : Inducing Thermotolerance In Cotton Exogenous Application of Salicylic Acid : Inducing Thermo- tolerance In Cotton (*Gossypium hirsutum* L.) Seedlings, 2016, <https://doi.org/10.24102/ijaf.v5i4.691>. October.
- [88] P.K. Aggarwal, P. Batima, K.M. Brander, L. Erda, S.M. Howden, A. Kirilenko, J. Morton, J. Schmidhuber, F.N. Tubiello, M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. Van Der Linden, C.E. Hanson, *Food, Fibre and Forest Prod.* (2007) 273–313.
- [89] C. Lesk, P. Rowhani, N. Ramankutty, Letter, *Nature* 20 (2016), <https://doi.org/10.1038/nature16467>.
- [90] E.I. Teixeira, G. Fischer, H. Van Velthuis, C. Walter, F. Ewert, Agricultural and forest meteorology global hot-spots of heat stress on agricultural crops due to climate change, *Agric. For. Meteorol.* 170 (2013) 206–215, <https://doi.org/10.1016/j.agrformet.2011.09.002>.
- [91] D.B. Lobell, M. Bänziger, C. Magorokosho, B. Vivek, Nonlinear heat effects on African maize as evidenced by historical yield trials, *Nat. Clim. Chang.* (March) (2011) 1, <https://doi.org/10.1038/nclimate1043>.
- [92] D.B. Lobell, C.B. Field, Global Scale Climate – Crop Yield Relationships and the Impacts of Recent Warming, 2007, <https://doi.org/10.1088/1748-9326/2/1/014002>.
- [93] W. Schlenker, M.J. Roberts, Nonlinear Temperature Effects Indicate Severe Damages to U.S. Crop Yields Under Climate Change, 106, 2009, pp. 15594–15598.
- [94] FAO Report, 2009. http://en.wikipedia.org/wiki/Climate_change_and_agriculture. Accessed 18 June 2020.

Further Reading

- [1] M. Hasanuzzaman, P. Responses, The Plant Family Brassicaceae.

- [2] S. Li, S. Dong, Y. Fu, B. Zhou, S. Liu, H. Shen, Y. Xu, X. Gao, J. Xiao, S. Wu, F. Li, Air or soil temperature matters the responses of alpine plants in biomass accumulation to climate warming, *Sci. Total Environ.* 844 (2022), <https://doi.org/10.1016/j.scitotenv.2022.157141>.
- [3] X. Li, J.A. Palta, F. Liu, Editorial: modulation of stomatal response by elevated CO₂ in plants under drought and heat stress, *Front. Plant Sci.* 13 (2022) 1–3, <https://doi.org/10.3389/fpls.2022.843999>.
- [4] X. Li, W. Shi, K. Broughton, R. Smith, R. Sharwood, P. Payton, M. Bange, D.T. Tissue, Impacts of growth temperature, water deficit and heatwaves on carbon assimilation and growth of cotton plants (*Gossypium hirsutum* L.), *Environ. Exp. Bot.* 179 (July (2020) 104204, doi:[10.1016/j.envexpbot.2020.104204](https://doi.org/10.1016/j.envexpbot.2020.104204).