

REVIEW

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High day and night temperatures impact on cotton yield and quality—current status and future research direction

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Abstract

Heat waves, and an increased number of warm days and nights, have become more prevalent in major agricultural regions of the world. Although well adapted to semi-arid regions, cotton is vulnerable to high temperatures, particularly during flowering and boll development. To maintain lint yield potential without compromising its quality under high-temperature stress, it is essential to understand the effects of heat stress on various stages of plant growth and development, and associated tolerance mechanisms. Despite ongoing efforts to gather data on the effects of heat stress on cotton growth and development, there remains a critical gap in understanding the distinct influence of high temperatures during the day and night on cotton yield and quality. Also, identifying mechanisms and target traits that induce greater high day and night temperature tolerance is essential for breeding climate-resilient cotton for future uncertain climates. To bridge these knowledge gaps, we embarked on a rigorous and comprehensive review of published literature, delving into the impact of heat stress on cotton yields and the consequential losses in fiber quality. This review encompasses information on the effects of heat stress on growth, physiological, and biochemical responses, fertilization, cotton yield, and quality. Additionally, we discuss management options for minimizing heat stress-induced damage, and the benefits of integrating conventional and genomics-assisted breeding for developing heat-tolerant cotton cultivars. Finally, future research areas that need to be addressed to develop heat-resilient cotton are proposed.

Keywords Controlled environment, Cotton, Fiber yield and quality, Heat stress, Heat tents, Reproductive failure

Background

Cotton is exceptionally well-suited to meet the growing demands of our global population as a valuable source of fiber generating income and sustaining over 100 million households (Fairtrade Foundation 2022). It is the most produced and utilized natural fiber world-wide, with an annual economic impact valued at approximately \$600 billion (Khan et al. 2020). Cotton is also recognized as a food source, with about 65% of conventional cotton products entering the food chain. This occurs either directly through food oils or indirectly via consumption of meat and milk from animals nourished with cottonseed meal and ginning by-products (Rogers et al. 2002;

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Sekhar and Rao 2011; Meyer 2014). Upland cotton (*Gossypium hirsutum*) and cultivars derived from this species are the most widely cultivated cotton in the world. Cotton is cultivated in more than 35 countries, covering approximately 34.1 million hectares, and produces around 120 million bales per annum (AOF 2022). India is the leading producer of cotton in the world, followed by China and the United States (USDA-ERS 2022). China is the world's largest consumer of cotton, with an estimated annual consumption of around 7.60 million tons (Khan et al. 2020). Being the third largest cotton producer and the leading cotton exporter in the world, the US plays a key role in the global cotton market (USDA-ERS 2022). Many cotton-growing regions, including the US, are likely to experience warming above the global average, causing a potential decline in cotton yields by up to 40% by 2100 (Schlenker and Roberts 2009). Historical analysis indicates that heat stress in the southwest US reduced cotton yields by 26% (Elias et al. 2018). In Arizona's low desert, cotton seed yields are projected to reduce by 40% and 51% by mid- (2036 to 2065) and late-century (2066 to 2095), respectively, compared with the baseline (1980–2005) (Ayankojo et al. 2020). The projected rate of decline in cotton seed yield with increasing temperature provides a compelling rationale for exploring key traits and mechanisms that will help breed heat stress resilient cotton for the future.

Temperature plays a vital role in the growth of cotton, with a critical threshold of 32 °C beyond which yields are adversely impacted (Schlenker and Roberts 2009). Studies indicate that with the current rate of increase in temperature (Supplementary Tables 1 and 2), the average global temperature is expected to increase by 1.5 °C by the mid-twenty-first century. This increase in mean temperature is attributed to an asymmetric increase in both maximum day and minimum night temperatures (Karl et al., 1993). Historical evidence indicates a much faster rate of increase in minimum night temperatures than maximum day temperatures, thus narrowing the diurnal temperature range (Alexander et al. 2006; Sillmann et al. 2013; IPCC 2023). A faster rate of increase and frequent occurrence of warmer nights significantly reduced crop yields, including cotton (Loka and Oosterhuis 2010; Khan et al. 2020). C₃ crops like rice and wheat exhibited differential physiological responses to high day and night temperatures (Jagadish et al. 2015; Shi et al. 2013; Bahuguna et al. 2015; Aiqing et al. 2018; Impa et al. 2019). Similarly, in cotton, high day temperature (HDT) mainly affected reproductive development, resulting in reduced seed number and increased flower abscission leading to reduced fruit retention (Reddy et al. 1992a, b; Brown and Zeiher 1998). Whereas high night temperature (HNT) induced an increase in respiration that

restricted carbohydrate supply into the sink resulting in lower fiber per seed (Soliz et al. 2008). This differential mode of action under high day and night temperatures warrants the need to understand cotton responses under high day and night temperatures independently. In this review, heat/high-temperature stress refers to high day temperature unless explicitly stated as HNT or combined high day and night stress.

Researchers have attempted to comprehend the impacts of heat stress on cotton production (Reddy et al. 1991; Hodges et al. 1993; Brown and Zeiher 1998; Zhao et al. 2005; Pettigrew 2008; Cottee et al. 2010), and to decipher the genetic architecture of key traits conferring heat stress tolerance (Dabbert 2014; Pauli et al. 2016; Rani et al. 2022). However, the majority of studies aimed at evaluating the impact of heat stress on cotton have been conducted in controlled environments limiting their translational relevance to real-world agricultural conditions (Reddy et al. 1992a; Brown and Oosterhuis 2010; Snider et al. 2009). Alternatively, field-based heat stress studies have been conducted using natural hot summers by altering the planting dates, which significantly alters the agronomy of the crop (Thompson et al. 2022). Cotton's response to different levels of heat stress has been studied across scales, including the impact of heat stress on cotton growth and yield (Majeed et al. 2021), adaptive mechanisms (Azhar et al. 2020; Ahmad et al. 2020), and breeding for heat stress tolerance (Singh et al. 2007; Salman et al. 2019a). However, there has not been a systematic synthesis of published research to determine the current status and identify hypothesis-based research questions that need to be addressed to safeguard cotton under future warmer scenarios.

Hence, the overarching objective of this review is to comprehensively synthesize the existing literature on the effects of high day, high night, and combined heat stress on cotton yield, fiber quality, and related traits. In addition, potential management strategies that can effectively mitigate heat stress-induced damage are discussed. The review will cover the current status, progress, and future prospects of breeding heat-tolerant cultivars, leveraging both conventional and genomics-assisted approaches.

Growth, physiological, and biochemical responses of cotton to heat stress

Cotton growth is negatively impacted at temperatures ≥ 35 °C (Reddy et al. 1991). The thermal kinetic window for optimum metabolic activity in cotton is 23–32 °C and maximum photosynthesis is recorded at 28 °C (Burke et al. 1985). High-temperature stress significantly limits seedling emergence and results in the development of suboptimal seedlings (Nabi and Mullins 2008; Raphael et al. 2017). Cotton seedlings

exhibited maximum emergence with vigorous growth at 30 °C, genotypes with larger seed size and weight showed better growth, even at 40 °C, and no seedling emergence was observed at 50 °C (Raphael et al. 2017). Advanced cotton breeding lines exposed to combined high day and night temperature regimes (20/15, 30/20, 35/25, and 40/30 °C), showed a stronger growth at 35/25 °C and the growth was significantly limited at 40/30 °C (Virik et al. 2021). Heat stress accelerates growth and promotes early maturation, but at the same time, it limits plants from achieving their full genetic potential (Reddy and Zhao 2005). With a 5 °C global temperature increase, the crop duration was reduced by up to 35 days from germination to maturity (Reddy et al. 1992a; Ahmad et al. 2020). Leaves are highly sensitive to temperature variations during the early stage of seedling development, with leaves on three-week-old seedlings expanding six to eight times more at temperatures of 28–30 °C compared with those at 20–21 °C (Reddy et al. 1992b). High temperatures significantly reduce plant height, as well as the number of nodes per plant and sympodial branches per plant (Yousaf et al. 2023). This is likely due to a decrease in the internodal distance, chlorophyll content, and net photosynthesis, leading to a reduction in photosynthate availability (Abro et al. 2022).

High-temperature stress stimulates the generation of reactive oxygen species (ROS), including hydroxyl radical ($\cdot\text{OH}$), singlet oxygen ($^1\text{O}_2$), and hydrogen peroxide (H_2O_2), which can interfere with the normal functioning of metabolic and enzymatic pathways (Qamer et al. 2021). Increased accumulation of H_2O_2 in cotton genotypes exposed to heat stress was negatively correlated with cotton seed yield, especially in a heat-sensitive genotype (BH-306) (Majeed et al. 2019; Yousaf et al. 2023). To mitigate the detrimental effects of ROS, cotton plants produce various enzymatic [such as superoxide dismutase (SOD), peroxidases (POD), catalase (CAT)] and non-enzymatic antioxidants [such as carotenoids, flavonoids, ascorbate, and tocopherols] under heat stress that act as scavengers or detoxifying agents (Gür et al. 2010; Sekmen et al. 2014; Qamer et al. 2021). In cotton plants exposed to high-temperature stress, SOD activity was reduced at 45 °C, CAT activity increased at 45 °C, while POD activity increased at 38 °C and ascorbate peroxidase (APX) activity increased at 38 and 45 °C (Gür et al. 2010). In another study, Sekmen et al. (2014) observed that the heat stress sensitivity of the cultivar, 84-S, was associated with decreased activities of CAT and POD, leading to increased H_2O_2 accumulation and oxidative stress-induced lipid peroxidation. On the other hand, the higher heat stress tolerance of the cultivars, M-503 and BH-302, was linked to their ability to maintain constitutive

activities of SOD and APX and induce CAT and POD leading to lower accumulation of H_2O_2 and higher cotton seed yield (Yousaf et al. 2023).

High-temperature stress-induced reduction in photosynthesis has been observed in several crops, including cotton (Aiqing et al. 2018; Mercado Álvarez et al. 2022; Saleem et al. 2021; Yousaf et al. 2023). Optimal net photosynthesis in cotton is observed at 28 °C and a significant decline in photosynthesis and photosynthetic pigments are observed beyond 35 °C (Crafts-Brandner and Salvucci 2000; Van der Westhuizen et al. 2020; Yousaf et al. 2023). Compared with the optimum temperature, a heat stress of 42 °C reduced photosynthesis in some cotton genotypes by 30%, electron transport by 12%, and membrane integrity by 23% (Cottee et al. 2012). High temperatures during the vegetative stage damage leaf photosynthesis components, thereby limiting CO_2 uptake and translocation of assimilates to developing organs (Pettigrew and Gerik 2007). Subtending leaves are the primary source of carbohydrate for boll development, and under heat stress, lower quantum yield and chlorophyll content in these leaves were closely associated with lower fertilization efficiency (Snider et al. 2009). Photosynthesis in subtending leaves of the thermotolerant genotype, VH260, was unaltered under heat stress whereas, the thermosensitive genotype (ST4554) exhibited a 39.5% reduction (Snider et al. 2010). Photosystem II is a highly heat-sensitive component in the photosynthetic apparatus and heat-induced damage to PSII disrupts electron transport and increases chlorophyll fluorescence, thereby leading to photoinhibition (Salvucci and Crafts-Brandner 2004; Pettigrew and Gerik 2007).

The balance between assimilate production and partitioning for seed filling (source strength) and the efficient use of these assimilates for reproductive organ growth and seed development (sink strength) known as the source-sink balance is a crucial factor that determines cotton yield and fiber quality (Nie et al. 2020; Qin et al. 2023). Environmental stresses disrupt the source-sink balance by affecting source capacity and restricting assimilate transport to fruiting branches in cotton (Loka et al. 2020). The conversion of starch to sucrose and its transport into the sink is especially important as cotton fibers are made up of cellulose, a polysaccharide formed by the interlocking of thousands of β -(1, 4)-D-glucose units, whose main carbon source is sucrose (FitzSimons and Oosterhuis 2016). Enhanced respiration under HNT significantly reduces ATP levels indicating greater use of energy pools (Frantz et al. 2004). Sucrose and hexose levels remained unaltered in cotton plants exposed to acute HNT, whereas sucrose levels were significantly reduced under chronic HNT stress (Loka and Oosterhuis 2010). To improve cotton seed yields under heat stress,

it is essential to optimize source-sink relationships by improving photo assimilate production and transport to sink tissues and enhancing the use of these assimilates by sink tissues (Qin et al. 2023). Figure 1 provides an overview of the impacts of elevated day and night temperatures on key traits in cotton.

Reproductive failure—the major cause of heat induced yield loss

The reproductive success of cotton is negatively affected with temperatures above 28–30 °C (Oosterhuis and Snider 2011; Fig. 1). Cotton is highly sensitive to heat stress during the first five weeks of flowering and boll development (Oosterhuis 1990). Heat stress hastens reproductive development process and thereby reduces the time required for formation of square, flower, and boll maturity (Reddy et al. 1997). Heat stress induces several abnormalities in cotton flower development including partial/unopened small flowers, asynchronous development of female and male reproductive organs (anther and pistil tissues), poor anther dehiscence, shorter filaments, improper pollen germination, reduced pollen tube growth, and improper fertilization (Brown 2008;

Burke et al. 2004; Snider et al. 2009 & 2011; Song et al. 2015; Loka and Oosterhuis 2016a, b; Masoomi-Aladizgeh et al. 2021). Microgametophyte development immediately after meiosis (i.e., tetrad formation from microspore mother cells) is highly sensitive to heat stress (Meyer 1966). Similarly, transient exposure of developing male gametophytes to 40 °C during tetrad or binucleate stage significantly damaged male gametophyte development and had pronounced negative effect on pollen viability in cotton (Masoomi-Aladizgeh et al. 2021). HNT stress (29 - 31 °C) had a greater impact on pollen development, leading to male sterility, compared with high day temperature stress (39 - 41 °C) (Khan et al. 2020). Pollen development relies on tightly regulated storage lipids, fatty acids, and jasmonic acid metabolism, which are highly sensitive to HNT.

Intra-plant variability is noticed for pollen germination and viability under heat stress conditions with pollens in flowers at the lower branches exhibiting lesser sensitivity to high temperature stress compared with flowers in the top branches (Rehman et al. 2021b). In cotton, maximum pollen germination was recorded at 28 °C with a reduction noticed as temperatures increased over 28 °C (Burke

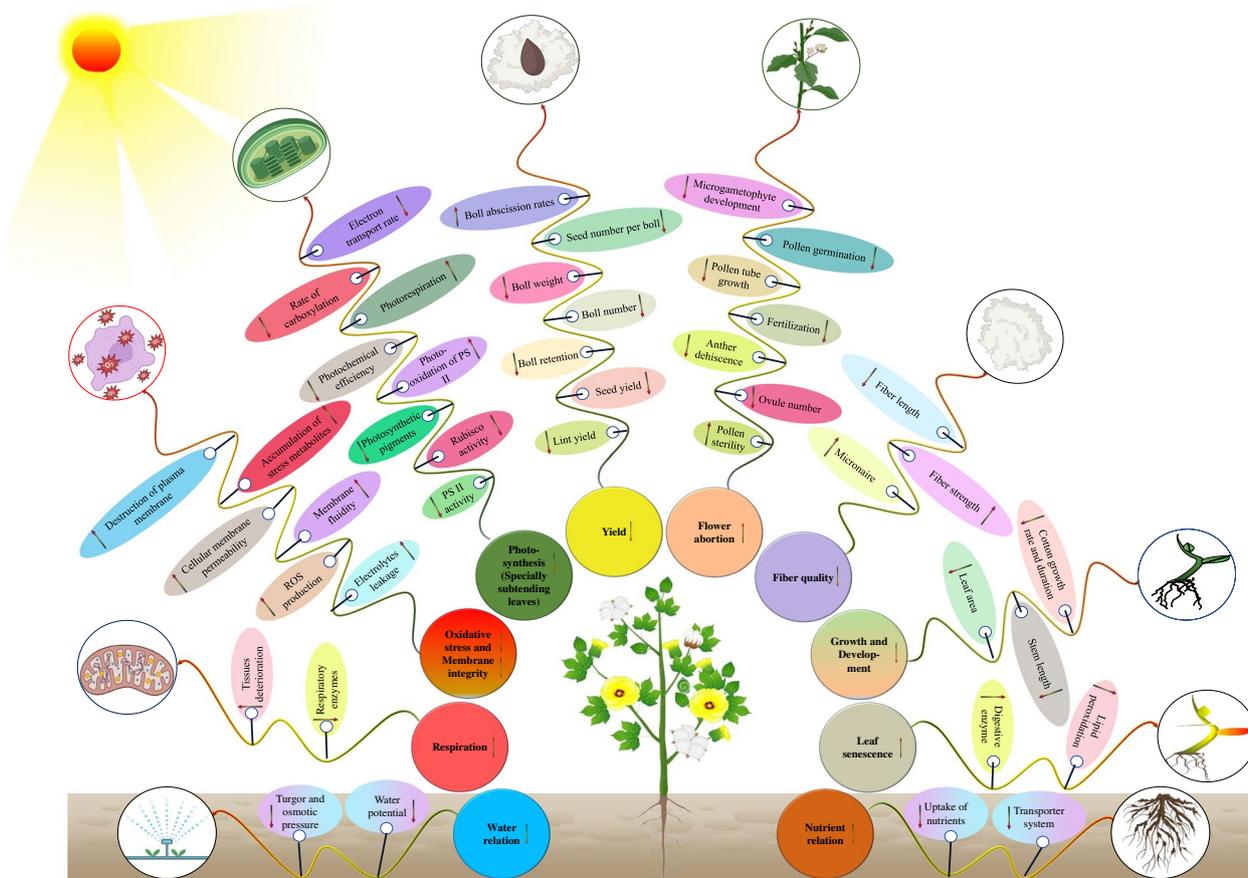


Fig. 1 High day and night temperature impacts on key traits in cotton

2011) and pollen completely failed to germinate at 37 °C (Burke et al. 2004). Similarly, the optimum temperature range for maximum pollen tube growth was 28 - 32 °C, the tube lengths declined significantly at 34 °C and ceased completely at 43 °C (Burke et al. 2004; Kakani et al. 2005). Pollen tube growth is also known to have a strong correlation with boll retention (Liu et al. 2006). Of all the reproductive traits, pollen tube growth was more sensitive to moderately high temperatures (34.6 °C) under field conditions than other reproductive processes like pollen germination and fertilization (Snider et al. 2011). Song et al. (2015) reported that temperatures exceeding 35 °C during microsporogenesis in upland cotton had significant effects on the developmental stages from the sporogenous cell to tetrad. Considerably less information has been documented on the heat stress impacts on female gametophyte development compared with male reproductive organ development. In addition to pollen germination and tube growth, pollen-pistil interaction is an important process that is greatly affected under high temperatures (Snider and Oosterhuis 2012). A decline in ovule number and fertilization efficiency was noticed in cotton plants exposed to 38/20 °C prior to flowering and was significantly associated with enhanced oxidative stress and reduced soluble carbohydrate and ATP content in the pistil (Snider et al. 2009). One of the main causes of abnormal pollen germination and fertilization is the decline in energy reserves such as carbohydrates and ATP concentrations essential for reproductive growth (Snider et al. 2009). Heat stress induced reduction in carbohydrate supply in pistil profoundly hindered pollen tube growth through style even under moderately high temperatures (Snider et al. 2011). Pistils of thermotolerant cotton genotype with higher antioxidant enzyme activity also had higher levels of total and water-soluble calcium and ATP content than the sensitive genotype (Snider et al. 2011). Conversely, in a study by Loka and Oosterhuis (2016a), the pistil antioxidant metabolism was observed to be largely unresponsive to the elevated night temperature stress, indicating a differential response of cotton plants to HDT and HNT stresses. Under elevated night temperatures cotton pistils exhibited an increase in the accumulation of glucose, sucrose, and starch concentrations than control, which was mainly attributed to disruptions in sucrose and starch degradation (Dinar and Rudich 1985). On the contrary cotton pistils exposed to high day temperature stress recorded a reduction in sucrose concentration (Snider et al. 2009).

Flower and square abscission under high temperatures above 30 °C is one of the primary causes of yield reduction in cotton (Reddy et al. 1991). Square abscission increases significantly beyond 35 °C leading to nearly zero boll retention at 40 °C (Hodges et al. 1993). Severe

square loss, and flower abortion 3–5 days after bloom were the main causes of significant yield losses in cotton (Reddy et al. 1992c; Brown 2008). Both HDT and HNT stresses restricted photo-assimilate supply to developing fruits resulting in a lower accumulation of total soluble carbohydrate in reproductive tissues and young bolls leading to improper fertilization and boll abortion (Zhao et al. 2005; Snider et al. 2009; Najeeb et al. 2017).

However, the physiological mechanisms of increased square abscission under high-temperature stress in cotton remain largely unclear. Loka and Oosterhuis (2016b) found that HNT negatively affects cotton flower bud production by disrupting carbohydrate metabolism in flower buds due to insufficient glutathione reductase response. HNT stress showed more pronounced impact on fatty acid and jasmonic acid metabolism within the cotton anthers, thereby inducing higher male sterility than HDT (Khan et al. 2020).

Heat stress-induced reduction in yield and yield components

Though cotton is a tropical crop adapted to be productive under a wide range of environments, high temperatures at critical growth stages significantly reduce its yield and productivity (Fig. 1). Cotton is less sensitive to heat stress at the vegetative stage but flowering and boll-development are the most sensitive stages (Reddy et al. 1997, 1999; Snider and Oosterhuis 2012). A projected 4 °C increase in average growing season temperatures is predicted to reduce cotton yields by 9% in the Mississippi Delta (Reddy et al. 2002). The year-to-year variability in cotton yield is attributed to modern cultivars being more sensitive to environmental stresses including high temperatures, than obsolete cultivars (Brown and Oosterhuis 2010). Heat stress significantly reduced yield and yield-related parameters including lint yield, boll weight, boll number, boll retention, seed yield, seed number per boll, and ginning percentage in cotton (Supplementary Table 3; Reddy et al. 1991; Hodges et al. 1993; Brown and Zeiher 1998; Zhao et al. 2005; Pettigrew 2008; Cottee et al. 2010; Salman et al. 2019a, 2019b; Xu et al. 2020; Abro et al. 2022; Yousaf et al. 2023). Cotton exposed to HDT stress exhibited intra-plant variability with bottom branches recording better physiological, morphological, and yield traits except for boll weight (Rehman et al. 2021b). Combined HDT and HNT increased the severity of damage compared with HDT or HNT stress independently (Supplementary Table 3). A controlled environment study resulted in “0” boll retention under combined HDT and HNT stress (40/32 °C) indicating a complete abscission of all the squares compared with control (30/22 °C) (Reddy et al. 1992c, 1999; Supplementary Table 3). Under field conditions, combined stress

induced up to 50% reduction in cotton seed yield (Cottee et al. 2010; Supplementary Table 3). A mild temperature increase of only 1 °C resulted in a significant (10%) decrease in lint yield which was primarily attributed to a 6% reduction in boll mass, with a concomitant 7% reduction in the number of seeds per boll (Pettigrew 2008). Studies on the impact of heat stress on yield and yield components in cotton either looked at the effect of HDT or combined HDT and HNT, whereas the effect of HNT stress is seldom studied with only one study reporting a 2%~12% reduction in lint yield under HNT stress (27 - 33 °C) compared with the control (21 - 24 °C) (Soliz et al. 2008; Supplementary Table 3).

Heat stress-induced alteration in cotton fiber quality traits

Cotton is primarily cultivated for its fiber which is utilized in textile production. A single seed can generate anywhere from 10 000 to 20 000 fibers under ideal temperature conditions (Seagull and Alspaugh 2001). An average daily temperature of 26 °C is crucial for proper fiber development and temperatures above 35 °C can have significant negative impact on fiber quality traits such as length, strength (especially during cell wall thickening), uniformity, elongation, maturity, micronaire, and lint percent (Manan et al. 2022; Rahman et al. 2006; Pettigrew 2001, 2008; Reddy et al. 1991; Fig. 1). Cotton fiber majorly consists of cellulose (85% of fiber composition) and cellulose synthesis is optimally achieved within a temperature range from 25 to 30 °C, with a reduction in synthesis observed beyond this range (Roberts et al. 1992). Under stress conditions the reduction in cellulose synthesis is believed to occur through a combination of decreased activities of sucrose metabolism enzymes, as well as a preferential conversion of UDP-glucose to callose rather to cellulose (Chen et al. 2017a). Sucrose is not only the main substrate for cellulose synthesis, but also contributes to fiber elongation through turgor pressure (Ding et al. 2021; Tian et al. 2013). Hence, any modification in sucrose concentration directly impacts cellulose synthesis. Excessive temperatures exceeding 35 °C or 40 °C diminish cotton's photosynthetic capacity, reducing sucrose production (Crafts-Brandner and Salvucci 2000). Under unfavourable conditions, such as high temperatures, carbohydrate assimilation is inhibited, leading to a reduction in seed number, size, the number of fibers per seed, and ultimately, yield (Arevalo et al. 2004). Under elevated temperatures, fiber sucrose content was reduced mainly due to decreased source strength and lower expression of the sucrose transporter gene, *GhSUT-1* (Chen et al. 2017a). On the other hand, cotton varieties with high sugar content in fibers often exhibit shorter fiber lengths, as an increase in

sugar content stimulates the generation of ROS, which promotes fiber initiation resulting in the production of more fibers. In addition, an elevated level of ROS also stimulates the biosynthesis of the secondary cell wall, which arrests the fiber elongation process and results in the production of thinner and shorter fibers (Ding et al. 2021).

The fiber elongation stage begins with flowering and continues for up to 25 days, while the secondary cell wall thickening stage extends from 20 - 60 days after flowering and varies based on varieties and temperature conditions or cumulative heat units (Bradov and Davidonis 2010). Fiber elongation requires a lower temperature than that is needed for boll development (Pettigrew 2001), and the micronaire tends to deteriorate above temperature regimes of 28-33 °C (Pettigrew 2008; Reddy et al. 1999). The sensitivity of fiber to temperature varies with its developmental stages, with the early stages of fiber elongation being more temperature-sensitive than the later stages (Gipson and Joham 1969; Xie et al. 1993). Night temperatures also play a vital role in fiber quality, with the optimal temperature being 15-21 °C (Abbas and Ahmad 2018), and temperatures above 21 °C or below 15 °C significantly decreases fiber length (Gipson and Joham 1969; Pettigrew 2008; Zhang et al. 2012). HNT stress increases respiration, leading to a restricted carbohydrate supply and thereby lowering fiber weight (Soliz et al. 2008). It was also demonstrated that heat-tolerant genotypes not only exhibit remarkable stability in yield but also produce superior quality fibers compared with the heat-sensitive genotypes under diverse environmental conditions (e.g., Azhar et al. 2009; Manan et al. 2022). With the predicted increase in both day and night temperatures, it is imperative to fill the gaps in our understanding of the different aspects of the fiber quality that determine the economic value of the crop.

Chamber versus field experiments to screen for heat stress tolerance in cotton

Over the last two decades, considerable information has been generated by the cotton research community on heat stress impacts on physiology and yield. Literature collected (a total of 110 studies) browsing through various websites/online repositories, including Google Scholar (<https://scholar.google.com/>) and Web of Science (<https://www.webofscience.com/wos/woscc/basic-search>) indicated that heat stress impact on cotton was mainly quantified under controlled environments using either growth chambers or glass houses where temperature was artificially controlled (Fig. 2; Supplementary Table 4; Birrer et al. 2021; Demirel et al. 2016; Khan et al. 2020; Loka et al. 2010, 2016a, 2016b, 2020; Manan et al. 2022; Masoomi-Aladizgeh et al. 2021; Mishra et al. 2017;

Najeeb et al. 2017; Raphael et al. 2017; Van der Westhuizen et al. 2020; Xu et al. 2020). Controlled environment studies allow for precise temperature control and experimental conditions but may not fully reflect the complexities of real-world field conditions. In field-based studies (39 out of 110), staggered sowing and/or irrigation management were used to synchronize the targeted developmental stage with high natural temperatures, i.e., summers (e.g., Abbas and Ahmad 2018; Abro et al. 2015, 2022; Aslam et al. 2022; Emine et al. 2012; Li et al. 2020; Ma et al. 2021; Mercado Álvarez et al. 2022; Rani et al. 2022; Saleem et al. 2021; Thompson et al. 2022). These studies aimed to bridge the gap in information between controlled environments and field conditions, recognizing the importance of understanding cotton responses to heat stress under more realistic field conditions. For instance, field trials conducted over two consecutive cotton growing seasons revealed that heat stress exhibits a substantial detrimental effect on several agro-morphological, physio-chemical, and fiber-related parameters in various cotton genotypes (Yousaf et al. 2023).

A systematic screening for heat tolerance in cotton using field-based heat tents or structures where temperature can be controlled and monitored accounted for the lowest proportion (11 out of 110) of studies (Fig. 2; Supplementary Table 4; Soliz et al. 2008; Cottee et al. 2010; Chen et al. 2017a, 2017b; Gao et al. 2021; Zafar et al. 2022). Soliz et al. (2008) used heat shelters (4 m wide × 5 m long × 1 m tall) and observed no significant effect of HNT on carbon balance and fiber weight per seed, which was mainly attributed to

inadequate replications, shorter period of stress (4 h per day for 1 and 2 weeks) and single cultivar ‘Suregrow 215BR’. In contrast, heat stress imposed by using polyethylene UV-stabilized film (2.8 m long × 2.8 m wide × 2.6 m tall) over the crop canopy for one week, induced significant negative impacts on cotton (Cottee et al. 2010). However, under small field tents/enclosures, the humidity builds up, creating a more stressful environment from temperature and humidity interactions, leading to confounding impacts on the overall physiology and molecular responses, in addition to increasing crop vulnerability to pest/disease incidence (Bahuguna et al. 2015).

Further, only a few studies (8 out of 110) investigated the effects of heat stress on cotton under both controlled and natural (field) conditions (Fig. 2; Azhar et al. 2009; Burke et al. 2015; Sarwar et al. 2018, 2022; Wu et al. 2014). This comparative approach is helpful for a comprehensive understanding of heat stress responses in cotton across scales, which provides insights into cotton’s adaptability and potential for improved heat stress tolerance. For instance, in a recent study, Sarwar et al. (2022) investigated the impact of varying temperature regimes on the medium heat-tolerant cotton variety, AA-802, across three reproductive stages (squaring, flowering, and boll formation) under both glasshouse and field conditions. Heat stress increased relative cell injury, total soluble proteins, reactive oxygen species, and reduced the total number of bolls per plant, the number of sympodial branches per plant, and fiber quality traits under both glasshouse and field environments (Sarwar et al. 2022).

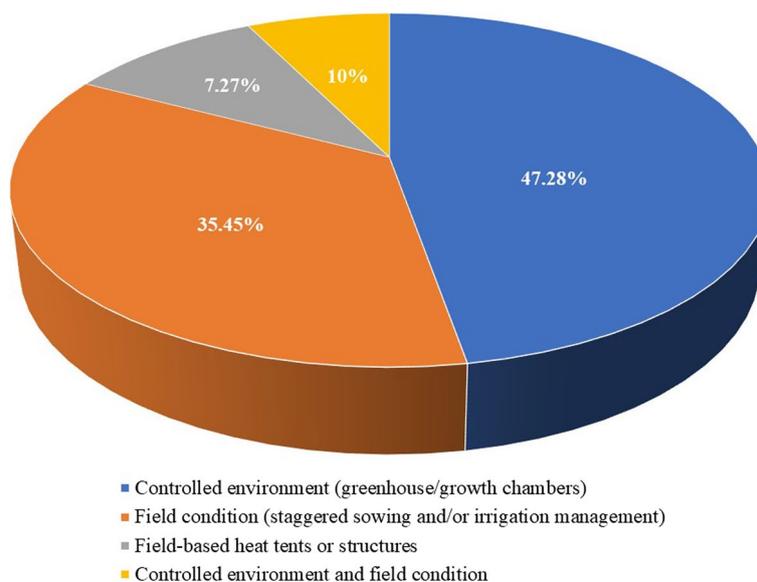


Fig. 2 Pie chart illustrating the distribution of published studies evaluating the impact of heat stress on cotton across different scales

Combined heat and water-deficit stress

Heat and water-deficit stresses often occur simultaneously under natural field conditions (Mittler 2006) and heat stress is further exacerbated under water-limited conditions. Plant responses under combined heat and drought stress have been strikingly different compared with individual stresses. The detrimental effects of combined heat and water-deficit stress on the growth and development of cotton are emphasized in several published studies (Hejnák et al. 2015; Singh et al. 2018; Li et al. 2020; Gao et al. 2021; Hu et al. 2022, 2023; Iqbal et al. 2017). However, understanding the combined stress impacts has received considerably less attention than the individual stresses. Plants tend to close their stomata soon after exposure to water deficit conditions, which helps reduce transpiration water loss but also lowers the intercellular CO₂ concentration, resulting in stomatal or diffusional limitation to photosynthesis (Chaves et al. 2003). The reduction in transpiration further lowers transpiration cooling and amplifies canopy temperatures, impeding photosynthesis (Carmo-Silva et al. 2012). In a recent study, when the changing trends of both elevated temperature and drought effects aligned, there was a more pronounced decrease in photosynthetic rate, RuBP (ribulose-1,5-bisphosphate), and starch content compared with single stress exposures (Hu et al. 2023). The changes in antioxidant mechanisms, ROS scavenging, carbohydrate content, and yield components in cotton exposed to combined heat and drought stress were similar to drought stress (Iqbal et al. 2017; Loka et al. 2020). Living organisms including plants have developed several protective mechanisms to provide thermo-tolerance and one such acquired heat resistance mechanism is the accumulation of heat shock proteins (HSPs) (Rehman et al. 2021a). Similar polypeptides were accumulated in cotton grown under dryland conditions in the field and cotton exposed to 40 °C under controlled environment growth chambers indicating that both heat and water-deficit stresses have similar endogenous protection mechanisms and produce HSPs (Burke et al. 1985). Under moderate soil relative water content, the heat-sensitive genotype (Sumian 15) experienced a yield reduction of 23 to 35%, while the heat-tolerant genotype (PHY370WR) showed a reduction of 8% to 13% (Gao et al. 2021). However, under low soil relative water content, the reductions intensified, with 44 to 54% in heat-sensitive and 37% to 43% in the heat-tolerant genotypes (Gao et al. 2021). These results indicate that water-deficit stress exacerbated heat stress. Under severe drought, an elevated temperature had a negative effect on cottonseed protein synthesis, whereas under mild drought, it had a positive effect (Xu et al. 2022). Combined elevated temperature

and drought stresses during the cotton fiber thickening stage inhibited fiber biomass accumulation and cellulose synthesis (Hu et al. 2022). Heat and or water-deficit stress during the fiber cuticle wax deposition in cotton decreased fiber wax content under individual stresses but increased it under combined stress (Birrner et al. 2021). In another study, simultaneous exposure of cotton to elevated temperature and drought stress had significant interaction effects on fiber length, strength, and micronaire, depending on cultivars and years. The negative impacts of drought on fiber length were exacerbated by elevated temperature but on the contrary, both fiber strength and micronaire were increased under elevated temperature (Gao et al. 2021). However, the authors also hypothesize that extended periods of elevated temperature would have negative effects on fiber strength and micronaire (Gao et al. 2021). A reduction in fiber length under elevated temperatures was mainly due to a shortened fiber elongation period, whereas drought stress disrupts the balance of turgor pressure in the fiber cells, leading to shorter fiber length (Ruan et al. 2007). A reduction in seed number per boll and shorter fibres under elevated temperature results in more available assimilates for fiber development, further increasing fiber strength and micronaire (Pettigrew 2008).

Osmoprotectants and antioxidants are widely recognized to play a vital role in the adaptive response to the synergistic impact of drought and heat stresses (Fig. 3). The accumulation of proline in cotton genotypes occurred to varying extents under drought and combined drought and heat stress conditions (De Ronde et al. 2000). In one study, the proline content in the drought-sensitive genotype (84-S) increased under drought, heat, and combined drought and heat stress conditions, though not to the levels observed in the tolerant genotype (M-503), highlighting the importance of this compatible solute in cotton's stress tolerance (Sekmen et al. 2014). However, the activities of some antioxidant defense enzymes, particularly SOD, CAT, and APX, were suppressed in both genotypes when exposed to combined drought and heat stresses compared with drought stress alone (Sekmen et al. 2014).

Management options to minimize heat stress-induced damages

The unpredictable alterations in climatic conditions pose a challenge to the effective implementation of management options to minimize heat stress-induced damages. Early planting to allow plants to complete their critical growth stages (e.g., peak flowering) before the onset of extremely high temperatures in the summer is considered a good heat escape strategy (Killi and Bolek 2006). Cotton sown post-recommended planting

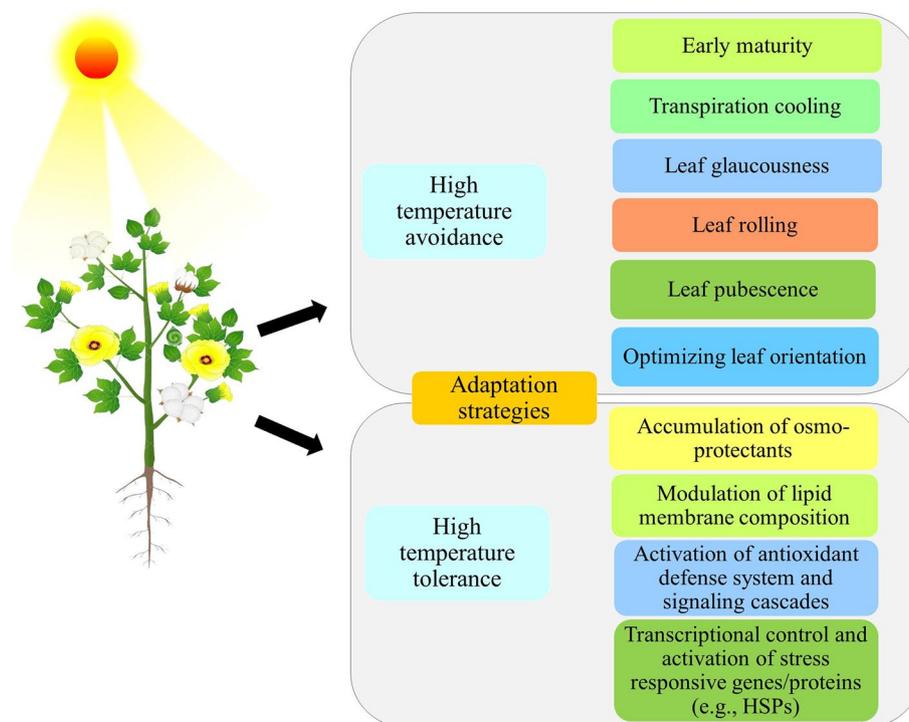


Fig. 3 Various adaptive strategies adapted by cotton plants to overcome high temperature stress induced damage

time is vulnerable to heat stress episodes, and altering the sowing time impacts growth, lint yield, and photosynthate supply to reproductive organs (Mumtaz et al. 2015; Carmo-Silva et al. 2012; Killi and Bolek 2006; Mercado Álvarez et al. 2022; Rahman et al. 2006). The other option would be to grow early maturing varieties, which would complete the critical growth stages/life cycle before the onset of high temperatures (Fig. 3; Ahsan et al. 2017). However, with both these options the effectiveness of escape cannot be guaranteed as the occurrence of heat spikes are unpredictable and could well impact the crop negatively, even though they are planted early or with a short-duration variety.

High-day temperature stress-induced acceleration in transpiration and evaporation rates result in increased water loss from the plant and soil, respectively (Sadok et al. 2021). To alleviate the negative impact of elevated temperatures, proper irrigation management must be implemented, taking into account the plant’s water requirements and canopy temperature monitoring. Insufficient water availability can lead to the modulation of stomatal conductance by the plants, causing water stress in cotton. In such circumstances, irrigation is necessary to maintain a cooler canopy. Further, in dry climates where crops rely solely on rainfall and soil moisture levels are low, adjusting the row spacing can enhance cotton lint yield (Echer and Rosolem

2015). For instance, in a previous study, it was observed that planting with an extended growing season, and lower plant density (or wider spacings) enhanced fiber yields. In contrast, late planting with limited irrigation and narrower spacings increased seed yields (Echer and Rosolem 2015).

Application of synthetic and/or natural growth regulators through foliar sprays (EL Sabagh et al. 2022), exogenous compatible solutes (Ahmad et al. 2014), signaling molecules (Sarwar et al. 2019; Larkindale and Huang 2004), and foliar nutrient spray (Sarwar et al. 2022; Saleem et al. 2018) minimizes the negative effects of environmental factors on cotton. Phytohormones, such as gibberellic acid, auxin/indole acetic acid, abscisic acid, ethylene, cytokinins, brassinosteroids, strigolactone, salicylic acid, and jasmonic acid, are critical molecular players in controlling plant growth in response to various abiotic stress stimuli, including heat stress (Jha et al. 2022). These phytohormones play a crucial role in various cellular, physiological, and developmental processes such as osmolyte accumulation, stomatal movement, photosynthesis, and pollen development, as well as reducing ROS accumulation thereby imparting heat stress tolerance (Sharma et al. 2019). Although phytohormones have seldom been utilized in cotton to manage heat stress, their beneficial effects on other important cotton traits, such as fiber

development, have been well-established under optimal conditions (Wang et al. 2020). Signaling molecules, such as hydrogen peroxide (H_2O_2), can effectively activate the defense system in plants and improve leaf CAT, SOD activity, chlorophyll contents, net photosynthetic rate, boll weight, the number of sympodial branches, and fiber quality components in cotton under heat stress (Larkindale and Huang 2004; Sarwar et al. 2019).

Elevated temperatures reduce nutrient acquisition, utilization, and partitioning. Foliar application of macro and/or micronutrients is known to stimulate the plant defense system and strengthen physiological functions under heat stress (Raghunath et al. 2021). For instance, Sarwar et al. (2019) demonstrated that the exogenous application of macro and micronutrients (K-1.5%, Zn-0.2%, and B-0.1%) minimized the adverse effects of HDT on cotton. Recently, Sarwar et al. (2022) reported that foliar application of potassium (K) and zinc (Zn), followed by boron (B), increased the relative water content, total soluble proteins, the number of sympodial branches per plant, fiber, the number of bolls per plant, fiber length, fineness, and strength. Furthermore, foliar sprays of K, Zn, and B reduced H_2O_2 under high-temperature regimes ($45/30^{\circ}C$ and $38/24^{\circ}C$) compared with the optimal temperature regime ($32/20^{\circ}C$). This reduction in H_2O_2 indirectly resulted in good fiber quality and improved yield component traits by reducing the relative cell injury and membrane leakage (Sarwar et al. 2022). Numerous macro- and micronutrients have the potential to elicit thermotolerance in cotton by enhancing biochemical and membrane stability, augmenting yield, and improving fiber quality through water-mediated interactions. These nutrients can be administered prior to exposure to high-temperature stress for optimal results. Further investigations are needed to elucidate the precise mechanisms through which these nutrients facilitate thermotolerance signaling under high-temperature stress, particularly in relation to the synthesis of heat-shock proteins mediated by K and Zn. Apart from these management options, plants also employ different adaptive strategies to overcome heat stress induced damage (Fig. 3).

Breeding for heat-resilient cotton

Conventional breeding strategies

Developing high-yielding, climate-resilient cotton cultivars that can thrive in changing climatic conditions is the primary goal of current cotton breeding programs. Conventional breeding of heat-tolerant cotton has primarily relied on selection, with the most generalized approach of selecting genotypes for heat tolerance by growing breeding materials in hot target production environments and identifying genotypes with a higher

yield (Majeed et al. 2021). Several studies on the identification of heat stress tolerant genotypes from the available gene pool have been published (Aslam et al. 2022; Asha and Lal 2013; Zafar et al. 2022; Singh et al. 2018; Demirel et al. 2016; Abro et al. 2015, 2022; Wu et al. 2014; Emine et al. 2012; Iqbal et al. 2017). Cotton breeding programs are also increasingly utilizing wild, exotic, and distant relatives (including *G. herbaceum*, *G. arboreum*, *G. barbadense*, and *G. raimondii*) because of their distinctive traits that are associated with abiotic stress tolerances (Bibi et al. 2010). However, there are multiple challenges such as genetic incompatibility, hybrid sterility, ploidy, climbing growth habit, photoperiodism, and agronomic issues that arise with gene transfer from wild to domesticated species (Mammadov et al. 2018).

Identification/selection of appropriate traits that can improve stress tolerance is a crucial initial step in any breeding program. Targeting traits including cell membrane thermostability, trichome size, stomatal conductance and size, chlorophyll content, canopy temperature, and reproductive performance that are closely linked to plant adaptation to warmer environments may allow for accelerated genetic gain in cotton yield (Ahmad et al. 2020; Abro et al. 2015, 2022). The next step after finding a suitable trait is to transfer it to an elite background or to selectively purify the selected plant. The most popular conventional breeding techniques in cotton for this purpose include pedigree breeding, single plant selection, and bulk selection (Percy 2003). These methods can be supplemented with advanced tools for rapid and precise screening and improved genetic gain (Tokatlidis et al. 2011). The utilization of cutting-edge genomics and biotechnological approaches has increased as cotton production faces diversified challenges from changing climates.

Molecular breeding

Advances in plant genomics have the potential to enhance our comprehension of the genetics underlying the key traits and provide molecular or DNA-based markers that could accelerate genetic improvement in crops. Researchers have used quantitative trait loci (QTLs) mapping and genome-wide association studies (GWAS) to identify QTLs/genes and markers associated with various important traits in cotton (Dabbert 2014; Ma et al. 2021; Pauli et al. 2016; Rani et al. 2022). To date, three studies have examined QTL mapping for heat tolerance, with Dabbert (2014) identifying 138 QTLs for eight heat-responsive traits, including cotton seed yield, lint yield, and quality traits using two recombinant inbred line (RIL) populations. In another study, Pauli et al. (2016) used a high-throughput plant phenotyping (HTPP) system to identify QTLs for leaf area index,

normalized difference vegetation index, canopy temperature, and canopy height, with individual QTL explaining phenotypic variation ranging from 4.35% to 12.42%. Similarly, Rani et al. (2022) evaluated an F_2 population derived from a cross between a heat-tolerant genotype MNH-886, and a heat-sensitive genotype MNH-814, and identified 17 QTLs associated with various morphological and yield traits with individual QTL explaining phenotypic variation ranging from 7.76% to 36.62%. Among these, the major QTLs, such as *qFSha1* and *qFSha2*, explained 35.98% and 36.62% of the phenotypic variations, respectively, for first sympodial node height. Additionally, the QTL, *qTNSa3*, was responsible for explaining 16.93% of the phenotypic variation in the total number of sympodes, while *qNOB1* and *qTNB1* explained 21.52% and 17.67% of the phenotypic variation in the length of the bract and total number of buds, respectively. These major QTLs hold the potential as targets for selective breeding approaches aimed at developing heat-tolerant cotton cultivars.

The recent advances in Next Generation Sequencing (NGS) technologies have facilitated the identification of expression QTL (eQTL) by studying the genome-wide expression of genes across populations. Integration of eQTL analysis and GWAS in cotton have enabled researchers to identify the genetic regulatory networks that control various traits such as seedling fresh weight, stem length, seed germination rate, cell wall biosynthesis, and the initiation of secondary cell wall development (Han et al. 2022; Li et al. 2020; Ma et al. 2021). By using Genome-Wide and Transcriptome-Wide Association Studies, Ma et al. (2021) identified genetic factors responsible for male sterility in cotton under high-temperature stress. Further, the application of Genomic Prediction (GP) in cotton breeding has increased selection effectiveness while reducing breeding cost and time (Billings et al. 2022; Gapare et al. 2018). Gapare et al. (2018) genotyped 215 upland cotton breeding lines with 13 330 single-nucleotide polymorphisms (SNPs) and evaluated them for fiber length and strength in different hot, central, and cool regions in Australia. They then applied different single-site and Marker-by-Environment (M x E) interaction models for various fiber quality traits. The GP accuracy for fiber length ranged from 0.27 to 0.77, while for fiber strength, it ranged from 0.19 to 0.58 based on a single-site model. The M x E model's prediction accuracy was better than that of single-site and across-site models, with an average accuracy of 0.71 and 0.59 for fiber length and strength, respectively. By identifying genotypes with consistent effects across different environments and those responsible for G x E, the M x E model may help cotton breeding programs reduce the phenotypic screening efforts required to identify adaptable genotypes.

Recently, Billings et al. (2022) conducted GWAS to identify markers associated with 20 fiber quality, seed composition, and yield traits in a panel of 80 important historical upland cotton lines evaluated in 14 individual field trials across the mid-south and southeast US cotton belt. They reported that combining GWAS results with GP can significantly improve prediction accuracies for various traits.

Transgenic approaches

Transgenic approaches have also been utilized to improve abiotic stress tolerance in cotton (Hussain and Mahmood 2020), including heat stress (e.g., Hozain et al. 2012; Burke and Chen 2015; Mishra et al. 2017; Batcho et al. 2021; Esmaeili et al. 2021). Ectopic expression of *AtSAP5*, encoding an A20/AN1 zinc finger domain-containing protein, enhances drought and heat stress tolerance by up-regulating stress-responsive genes (Hozain et al. 2012). Cotton overexpressing *AtHSP101* showed improved pollen tube growth under heat stress compared with the wild cotton (Burke and Chen 2015), highlighting the potential to boost crop yields in challenging climates by enhancing reproductive-stage heat tolerance. In another study, over-expression of the rice SUMO E3 Ligase gene, *OsSIZ1*, in cotton increased net photosynthesis and growth compared with non-transgenic cotton and significantly improved fiber yields under abiotic stresses, including drought and heat (Mishra et al. 2017). A recent study showed that *OsSIZ1/AVP1* co-overexpressed cotton outperformed and yielded 133% and 81% more fiber than non-transgenic cotton in the dryland environments of West Texas (Esmaeili et al. 2021). Similarly, over-expression of *AsHSP70* in cotton significantly reduced cell electrolyte leakage and membrane injury and improved membrane stability index under combined drought and heat stresses (Batcho et al. 2021). Recently, it was demonstrated that cotton plants overexpressing *RCA/AVP1* had a 6.5-fold increase in net photosynthetic rates under heat stress conditions, and a remarkable 96% increase in seed fiber yield as compared with wild-type cotton under combined drought and heat stresses (Smith et al. 2023). Overall, transgenesis could be an effective method for developing climate resilient cotton cultivars with higher yield potential under warmer climates, and aid in addressing the demand for global fiber even under changing climates.

Genome editing

The advent of clustered regularly interspaced short palindromic repeats and CRISPR-associated protein 9 (CRISPR/Cas9)-mediated genome editing technology has opened new avenues for precise genetic modification of cotton traits, offering potential solutions for improving

heat stress tolerance. Unlike traditional transgenic technology, CRISPR/Cas9-based genome editing allows for the targeted modification of genes at the epigenetic and transcriptional levels, as well as the possibility of knock-out or knock-in mutations (Lee et al. 2019; Fiaz et al. 2021). Although both academic and industrial communities have shown interest in this technology for improving agriculturally important traits in cotton (Ghosh and Dey 2022), no study has yet targeted a gene associated with heat stress tolerance. In general, abiotic stress-induced gene expression can be divided into three categories: (1) genes encoding proteins with known structural or enzymatic functions [viz., water channel proteins, key enzymes for osmolyte (betaine, proline, and sugars) biosynthesis, detoxification enzymes, and transport proteins], (2) uncharacterized proteins, and (3) proteins with regulatory functions (involving transcription factors and signal transduction genes) (Bhatnagar-Mathur et al. 2008). A better understanding of the specific roles played by these genes could lead to more effective ways of enhancing heat tolerance in cotton through genome editing.

Abiotic stresses can cause changes in the expression pattern of numerous plant genes, resulting in either up-regulation or down-regulation. The study of cotton gene expression patterns under long-term heat stress has shown increased expressions of *TH1*, *IAR3*, *GhHS126*, *FPGS*, and *GhHS128* genes, while the expressions of *CTL2*, *CIPK*, *ABCC3*, *Lsm8*, and *RPS14* genes were down-regulated (Demirel et al. 2014; Tahmasebi et al. 2019). The CRISPR-Cas system presents an exciting opportunity to modulate these differentially regulated genes and mitigate the negative effects of heat stress. Integrating gene editing, genome sequencing, and other omics analyses may help to identify key genes that confer heat stress tolerance in cotton. As an allotetraploid, cotton has numerous homologous gene pairs located in the A and D sub-genomes with significant single-nucleotide polymorphisms. Creating adenine base editors for efficient and accurate A-to-G single-base editing without double-strand breaks in such a complex genome could be advantageous for functional genomics and precise cotton breeding under heat stress (Wang et al. 2022).

Future line of work

- *Robust field phenotyping*—Scaling of information generated from highly precise controlled environment chambers to field conditions using robust custom-built heat tents that continuously control and monitor temperature and relative humidity inside the tents and impose heat stress throughout critical developmental stages is crucial in developing heat

tolerant cotton that can adapt to the real-world conditions.

- *Identifying heat tolerant mechanisms*—The level of tolerance/sensitivity and the mechanisms that are altered under high day, high night, and combined high day and night temperature stresses need to be characterized in cotton.
- *Management options to minimize heat stress damage*—The role of management options such as irrigation and exogenous application of plant growth regulators, compatible solutes, signaling molecules, and nutrients in minimizing heat stress damage needs further attention.
- *Integrating genomic advances with conventional breeding*—Genomic advances must be integrated with conventional breeding to accelerate genetic mapping, identification, and characterization of causal genes driving heat stress tolerance to facilitate genomics-assisted breeding.

Conclusions

In cotton, heat stress (≥ 35 °C) profoundly impacts growth, development, physiology, biochemical process, and overall productivity. Heat stress accelerates growth and promotes early maturation, reducing overall crop duration, thereby reducing internodal length, the number of nodes, and sympodial branches per plant. Flower abortion and square and boll abscission are the major causes of yield loss under heat stress, which are mainly attributed to lower carbohydrate accumulation in these sink tissues. Temperatures > 30 °C induced abnormalities in flower development, and reduced pollen viability, germination, tube growth, and pollen-pistil interaction. Considerably less information is available on the impacts of heat stress on female gametophyte development versus male reproductive organ development. Most of the published studies on heat stress in cotton either looked at the effects of HDT or combined HDT and HNT on yield and yield components, with less attention to HNT induced changes in lint yield and fiber quality. Fiber quality traits are significantly affected at day/night temperatures $> 35/25$ °C. Early stages of fiber elongation were more sensitive than later stages. One of the major limitations to screening cotton for heat tolerance is the lack of robust field-based heat tents where temperature can be controlled and monitored. Management options including irrigation management, altering planting date and plant density, and exogenous application of growth regulators and nutrients contribute to minimizing heat stress-induced damage. Recent improvements in producing high-quality genome sequences of domesticated diploid and tetraploid cotton species have offered novel insights into different traits contributing to heat stress tolerance.

A number of cutting-edge techniques, such as QTL mapping, GWAS, GS, genetic engineering, and genome editing offer great potential for developing heat-tolerant cotton.

Abbreviations

CAT	Catalase
HDT	High day temperature
HNT	High night tempera
QTL	Quantitative trait loci
ROS	Reactive oxygen species
POD	Peroxidase
SOD	Superoxide dismutase
HSP	Heat shock protein
G x E	Genotype-by-environment interaction
APX	Ascorbate peroxidase
K	Potassium
B	Boron
Zn	Zinc
RIL	Recombinant inbred line
GWAS	Genome-wide association study
SNP	Single nucleotide polymorphism
CRISPR/Cas9	Clustered regularly interspaced short palindromic repeats and CRISPR-associated protein 9
TF	Transcription factor

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42397-023-00154-x>.

Additional file 1: Supplementary Table 1. Average maximum and minimum temperatures observed during summer seasons in various years across the major cotton growing countries.

Additional file 2: Supplementary Table 2. Average maximum and minimum temperatures observed during summer seasons in various years across major cotton producing states in the USA.

Additional file 3: Supplementary Table 3. Published data on the effect of high day, high night and combined high day and night temperature stresses on yield and yield related traits in cotton (Kamal et al. 2017; Zafar et al. 2021).

Additional file 4: Supplementary Table 4. A summary of published studies evaluating the impact of heat stress on cotton across different scales.

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Authors' contributions

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Consent for publication

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Competing interests

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