Chapter 20
Heat Stress in Cotton: Responses and Adaptive Mechanisms

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Abstract Cotton is vital cash besides fiber crop and plays pivotal role in economy in many countries. It thrives well under optimal temperature. Too high and too low temperatures affect badly its growth and yield. Too low temperature affects its germination and seedling establishment stages. Particularly, high temperatures influence many physiological and biochemical processes within cotton plant that result in poor seed cotton yield. Several researches in different agroecological zones employed different agronomic practices and modern breeding techniques to mitigate the heat stress for better cotton production. A bevy of literature regarding heat stress is presented here.

Keywords Global warming · Climate change · *Gossypium hirsutum* · Abiotic stresses

Abbreviations

APX	Ascorbate peroxidase
ASC	Ascorbate
B	Boron
Ca	Calcium
CAT	Catalase
CER	CO_2 exchange rate
CICR	Central Institute for Cotton Research
GDP	Gross domestic product
GHG	Greenhouse gas

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GPX	Glutathione peroxidase
GSH	Glutathione
HSFs	Heat shock factors
HSPs	Heat shock proteins
K	Potassium
LAI	Leaf area index
LAR	Leaf area ratio
LEA	Late embryogenesis abundant
LEL	Leaf electrolyte leakage
Mg	Magnesium
Mn	Manganese
N	Nitrogen
NAR	Net assimilation rate
POD	Peroxidases
PRK	Phosphoribulokinase
PSII	Photosystem II
ROS	Reactive oxygen species
RuBP	Ribulose-1,5-biphosphate
SA	Salicylic acid
Se	Selenium
SOD	Superoxide dismutase

20.1 Introduction: Climate Change Scenario

20.1.1 Global Warming and Its Impact on Agriculture

The worlds' agricultural growth has declined from 3.2% in 1980s to 2% in 2000, which is alarming and a threat to food security (Ahmad et al. 2014, 2018; Abbas and Ahmad 2018; Ahmad and Raza 2014; Ali et al. 2011, 2013a, b, 2014a, b; Usman et al. 2009). The change in climate conditions particularly rise in temperature is the major factor affecting growth of agricultural sector leading to food security at risk (Christensen and Christensen 2007; Ahmad et al. 2017; Amin et al. 2017, 2018; Rahman et al. 2018; Tariq et al. 2017, 2018). Temperature is anticipated to rise by 2–3 °C in the next 25–45 years. The rise in temperature will also affect rainfall pattern making it more erratic. Pakistan is anticipated to be one of the most vulnerable countries in South Asia to climate change. Projected increase in CO_2 concentration is anticipated to raise the mean temperature from 1.4 to 5.8 °C resulting rise of 20–149 cm in sea level in future (IPCC 2007).

Agriculture sector itself, although a noteworthy contributor to gross domestic product (GDP) and most vulnerable to climate change, may also harm the environment through greenhouse gas (GHG) emissions adding 20% in the form of methane, nitrous oxide, and carbon dioxide. About 37% of the total worlds' emissions from agriculture production are accumulating from Asia and the Pacific (ADB 2009).

Table 20.1 Greenhouse gasses emissions through different activities associated with agriculture

Source/activity	Emission ($Mt\ CO_2$)	Year of estimate	Reference
Emissions of GHG through direct agricultural activities	5120–6116	2005	Smith et al. (2007)
Emissions of GHG through indirect agricultural activities	2198–6567	2008	van Der Werf et al. (2009)
Fertilizer manufacturing	282–575	2007	Bellarby et al. (2008)
Utilization of energy for animal feed production	60	2005	Steinfield et al. (2006)
Pesticide industries	3–140	2007	Bellarby et al. (2008)

Earth temperature is increasing exponentially; it has been raised doubled in number as compared to 50 years ago; greenhouse gases (GHGs) being the major cause. Since 2000, the emission of these gases is increasing due to burgeoning population and industrialization, thereby the number has reached up to 6 billion metric tons of "CO_2 equivalent" worldwide, which is more than 20% increase. Greenhouse gases added equivalent to CO_2 to the environment by different components of agriculture sector are given in Table 20.1.

Now a days global warming is the main issue for rapid cause of environmental adversities that needs to be addressed. Temperature is increasing and causing devastating effects to our planet and our crops. It results in poor germination, poor seedling emergence, and aberrant vegetative and reproductive growth. High temperatures have direct influence on increasing the rate of plants reproductive growth that shortens period for photosynthesis thereby restricting ideal seed production. Plants need optimum growth conditions as both higher and lower temperature interferes with the robust growth of plant, contrarily crop species differ in their behavior towards changing temperature some are highly tolerant while some exhibit sensitivity.

Geographical location has significant importance for the change in climate for crops growth; therefore, Pakistan is more prone to climate change due to its geographical location (Janjua et al. 2010). Precipitation is also decreased with the raise in temperature. Mean temperature across the country has increased by 0.5 °C in the past 30 years, and forecasts indicate a further increase of 1.4–3.7 °C by 2060: higher than the expected global average. Schlenker et al. (2006) estimated impact of climate uncertainty on crop yields in United States and established threshold levels of temperatures for different crops such as 29 °C for corn and soybeans and 33 °C for cotton. Moreover, temperature more than optimum requirement halts growth of aforementioned crops with severe yield losses.

20.1.2 Cotton Production in the Perspective of Global Warming

A brief change in temperature leading to exceed plants thermal capability, or thermal capacity of a plant is considered heat stress (Gür et al. 2010). Cotton yield is determined by the surrounding environment which has dramatic effects on growth and development. The temperature fluctuations affect growth and developmental processes and thus determine up to 70% yield variations in cotton (Farooq et al. 2015; Luo et al. 2014; Nasim et al. 2016; Rahman et al. 2017). Heat stress is often associated with other ecological stresses like drought (Rehman 2006).

Heat stress decreases the potential of the crop, and it is estimated that crop exhibit only 25% of its potential due to such environmental stress (Boyer 1982). High temperature and change in rainfall pattern are major drawbacks in achieving higher and stable cotton yields (Bange and Milroy 2004; Gwimbi and Mundoga 2010; Iqbal et al. 2016). Cotton growth and development is maximum at 33 °C, and significant decline in fruit retention is observed above 36 °C (Luo 2011; Nasim et al. 2016; Singh et al. 2007). Heat stress is a severe threat to cotton productivity globally (Hall 2001).

20.2 Effects on Cotton Plant

High-temperature stress influences cotton plant in a number of ways such as by inducing morphological, physiological changes and biochemical alterations thus limiting the crop performance and lower seed cotton production. Heat stress has effects on seed germination, seedling and root growth. High temperature effects on diverse growth phases in cotton are depicted in Fig. 20.1.

The temperature range of 28–30 °C is considered optimum for seed germination besides cotton seedling development. Cotton root growth is maximum at day/night temperatures of 30/22–35/27 °C and rise in temperatures to 40/32 °C alter root distribution pattern resulting in limited downward extension of roots (Reddy et al. 1997a, b). Temperatures higher than 30 °C, but not exceeding 40 °C, increase seed germination rate leading to early seedling development. Increase in temperature beyond 40 °C has damaging effects on cotton seedlings. In such conditions, heat-tolerant genotypes withstand better due to activation of acquired thermo-tolerance until the temperature approaches 37.7–40 °C (Burke 2001). The extent of damage is much higher in heat-sensitive genotypes, and the entire fields may be wiped out due to rapid loss of water when hot winds blow across the cotton fields. Such events often take place in major cotton-growing countries like India and Pakistan.

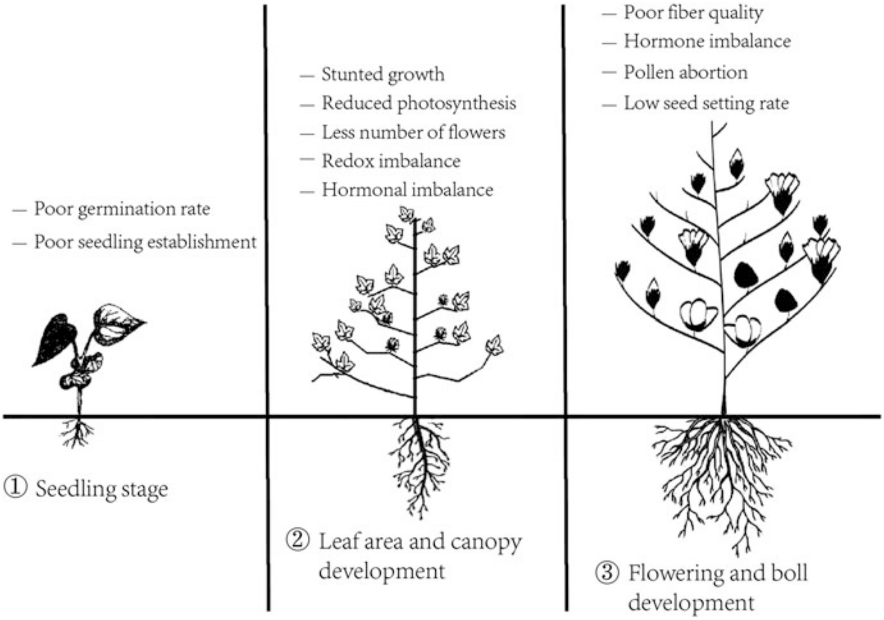

Fig. 20.1 Effect of higher temperature on agronomic besides physiological attributes of cotton at numerous stages of development (Zafar et al. 2018)

20.2.1 Effects on Plant Growth Besides Development

Although, cotton has a well-defined growth and developmental pattern, however, it is highly temperature dependent (Iqbal et al. 2016). The rise in temperature generally results in accelerated growth of plants making crop to mature early and at the same time limiting the crop to achieve its genetic potential (Reddy and Zhao 2005). The developmental processes of the plants are more rapid during increased daytime temperature (Reddy et al. 1996), while the leaf expansion rate in cotton is more under dark conditions (Krieg and Sung 1986). Continuous increase in temperature throughout the cotton-growing season shortens the crop duration up to 24 days (Reddy et al. 1996) or even 35 days earlier from germination to maturity if the average temperature at global level rises 5 °C (Reddy et al. 1992a, b, c, 1997a, b).

Leaves are more sensitive to temperature variations during early stage of development. At about 3 weeks after emergence, leaves expanded six to eight times more at 28–30 °C temperatures than those at 20–21 °C (Reddy et al. 1992a, b, c, 1997a, b). Unlike roots, shoots require higher temperature for optimum growth (Arndt 1945; Pearson et al. 1970). Cooler temperatures cause accumulation of metabolites through slowing down the plant growth and development, thus making plant to develop more vegetative branches (Reddy et al. 1992a, b, c). That is why excessive vegetative growth does not take place at higher daytime temperatures. Plant growth traits like

LAI, LAR, and NAR respond positively to an increasing temperature up to a maximum of 35 °C (Jackson 1967).

Temperatures above 30/22 °C are conducive for stem elongation, fruiting branches as well as fruiting branch nodes at early crop stage (Reddy et al. 1992a, b, c). The number of fruiting sites increases greatly with the increase in mainstem nodes (Reddy et al. 1992a, b, c). Night temperatures have relatively more effect in controlling flower initiation (Gipson and Ray 1969). For example, the night temperature of 25 °C caused delayed flowering and first fruiting branch in upland cotton (Mauney 1966), and boll maturity was delayed when the night temperatures were lower (Gipson and Joham 1969).

Temperature variations dramatically affect growth besides potential yield of cotton (Nasim et al. 2011; Luo et al. 2014; Rahman et al. 2017). Cotton plant grows efficiently at 33 °C temperature, but the effective fruit bearing declines considerably when temperature rises beyond 36 °C (Luo 2011; Singh et al. 2007). Under higher temperatures, production and assimilation of carbohydrates are inhibited which promotes boll shedding as well as smaller and malformed bolls (parrot beak), lesser lint quantity, and decreased yields (Hatfield et al. 2008, 2011; Oosterhuis 2009). However, the cotton genotypes in India and Pakistan are well adapted to the high-temperature conditions and are successfully grown at temperatures as high up to 46 °C.

Environmental stresses including high temperature at floral development stage are crucial and limit potential yields (Boyer 1982). The most sensitive growth phase for cotton to heat stress is reproductive growth stage which includes its pollen tube growth and development and fertilization (Zinn et al. 2010). Unfavorable weather variations adversely affect development of ovule, pollen fertility, and anther dehiscence or dispersal of pollens (Zinn et al. 2010; Young et al. 2004). Healthy pollen grains have key roles in fertilization process, but they are more susceptible to damage by high-temperature stress (Kakani et al. 2005). Therefore, this stress during anthesis may lead to improper fertilization resulting in lesser number of seeds and bolls (Kakani et al. 2005; Reddy et al. 1992a, b, c; Snider et al. 2009). Development of fiber takes place on seeds in the boll; therefore seed number in boll besides ovules in a locule would determine the quantity and quality of lint fiber to be produced (Stewart 1986). Variation in seed number in a boll reflects either inadequate fertilization of seed or post-fertilization growth termination of the embryo depending upon both cultivar and unfavorable ecological conditions (Karmakar et al. 2016; Stewart 1986). Heat-induced sterility has been a common issue in commercially grown varieties in Pakistan where most of the initial fruit produced is shed, due to high temperature, which often triggers extra vegetative growth (Taha et al. 1981).

Increasing temperatures accelerate crop growth and developmental processes (Rawson 1992; Ziska and Bunce 1997) but also have detrimental effects on overall crop performance if temperature exceeds than the desirable limits. While cotton is highly sensitive with raise in high temperature creating heat stress for all growth stages, fruiting phase is reported to be more sensitive among other growth phases (Snider et al. 2009, 2010, 2011). For example, 1 °C rise in temperature produced squares, flowers, and matured bolls by 1.6, 3.1, and 6.9 days earlier, respectively

(Reddy et al. 1997a, b). Disruption and shortening of fruit maturation period, as a result of high-temperature stress, limit productivity, causing subsequent yield losses in cotton (Rawson 1992; Stewart 1986; Wullschleger and Oosterhuis 1990; Ziska and Bunce 1997) owing to increased shedding of fruit forms and production of smaller bolls (Reddy et al. 1999; Yfoulis and Fasoulas 1978; Zhao et al. 2005).

Fruit retention is highly sensitive to increased temperature stress, besides duration of stress is very crucial as it determines the fruit load on a plant. The ideal temperature for healthy cotton growth is 20–32 °C (Mohamed and Abdel-Hamid 2013; Reddy et al. 1992a, b, c). It is described that maximum growth of cotton especially number of bolls which is essential for higher lint yield occurs during both day and night with a temperature of 30 °C day besides 22 °C night, respectively (Burke et al. 1988; Reddy et al. 1996). For example, Reddy et al. (1992a, b, c) found 30/32 °C temperature to be the most appropriate to gain maximum boll weight. The cotton plants retained only 50% of the squares and bolls when exposed to 33 °C average daily temperature and fruit retention declined sharply to none when daily average temperature was rose to 36 °C (Reddy et al. 1992a, b, c). Similarly, a 12 h exposure of cotton plants to 40 °C produced only 1% of their mass as bolls (Reddy et al. 1991). It has been observed that young bolls are relatively more vulnerable to temperature stress and often shed when the plant faces 32 °C or higher average daily temperatures (Reddy et al. 1996). However, the cotton crop ably tolerates to short duration stress imposed by temperatures as high up to 43/45 °C provided there is ample moisture in the soil.

Among the C_3 plants, cotton has relatively more heat-tolerance capability; however, temperatures higher than optimum stimulate shedding of squares and bolls resulting in sharp decreases in yield (Oosterhuis 1997; Schlenkera and Roberts 2009). Apart from the intensity and duration of temperature stress having a critical role in fruit retention, high night temperatures at fruiting phase of cotton are very deleterious and cause more damage to the seed cotton yield than the high day time temperatures. Investigations have revealed that high temperatures at night promote respiration rates, decrease concentrations of leaf soluble carbohydrates (Loka and Oosterhuis 2010), and increase abscission leading to significantly lower production (Gipson and Joham 1969).

20.2.2 Effects on Physiological and Biochemical Parameters

Cotton crop is usually grown in arid besides semiarid areas in different countries where temperatures are quite high during the crop growth periods. The higher temperatures have limiting effects on growth, physiological, and biochemical processes.

20.2.2.1 Effects on Water Relations

The presence of optimum leaf water content maintains cell turgidity and key cell functions like stomatal regulation, net photosynthetic rate, and translocation of assimilates to different parts of the plant. Variation in ambient temperature greatly influences plant water status. A change in the surrounding environment like increase in temperature than the desired level disturbs the plant water status. Increased transpiration rates triggered by high temperature result in water loss from the plant when soil water content is not sufficient. Although high temperatures severely disrupt the tendency to maintain cell water status under limited moisture conditions, the plants are able to maintain steady tissue water status under conditions of ample moisture content. Limited water availability under field conditions often results in high-temperature stress due to lower rate of evaporative cooling. Increased transpiration rates due to high day temperatures cause reduction in water potential that leads to perturbation of numerous physiological processes (Tsukaguchi et al. 2003).

20.2.2.2 Effects on Cell Membrane, Anther Dehiscence, and Pollen Viability

Cell membrane, that surrounds the cytoplasm, is a selectively permeable structure which separates the interior of cells from outside environment. The cell membrane should maintain its integrity for normal cell functions by allowing selective substances to move into or out of cell. Cell membrane is mainly composed of lipids (up to 80%) and proteins. Under stressful environments such as high temperature, lipid peroxidation occurs within the membrane causing increase in the fluidity of the thylakoid membranes thus negatively affecting the efficiency of the photosystem complex. Under continued heat stress, cyclic photophosphorylation is increased to disperse excess energies and preserve the more sensitive photosystem II complex (Schrader et al. 2004; Sharkey 2005). In cotton plant, the ability of membrane structure to adjust under high-temperature conditions has been identified as a physiological adaptation toward heat stress (Rahman et al. 2004). Defensive role of antioxidants cannot be understated when high-temperature stress occurs. Reactive oxidative species (ROS) increase extensively with increased levels of heat stress (Wahid et al. 2007) which also activate enzymatic pathways needed to initiate stress response (Dat et al. 1998; Foyer and Noctor 2005). Though, if stress conditions prolong, then ROS can also initiate programmed cell death (Gechev et al. 2006). During stressful periods, sufficient antioxidant pools are necessary to moderate heat-related responses for proper growth and continued development of cotton (Snider et al. 2011).

In cotton fruiting period is highly temperature sensitive, and higher temperature can disrupt the fruit setting process due to pollen abortion at temperatures of 35–39 °C (Min et al. 2014). Often growth of filaments is restricted, while stigmas elongate properly giving rise to asynchronous development (Brown 2008). Such

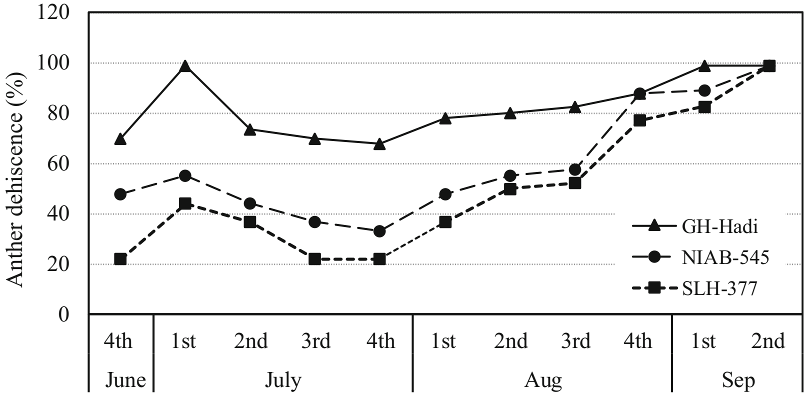

Fig. 20.2 Dehiscence of anthers in three cotton genotypes during the fruiting period (CCRI 2017)

flower abnormalities develop in cotton when high night temperatures cause rise in canopy temperatures and limit cotton reproductive performance (Zeiher et al. 1994) due to a decline of up to 84% in anther dehiscence and 78% in pollen viability when night temperature increased to 30 °C (Ahmed et al. 1992).

The dehiscence of anthers which is highly temperature sensitive is the primary step in fertilization process. Monitoring of anther dehiscence on daily basis in field evaluation trials gives handsome information about performance of cotton varieties under prevailing environmental conditions. For this purpose, up to three flowers from each varietal plot are collected between 09:30 and 10:30 h and transported to laboratory in zip-locked polythene bags. The flowers are examined under the microscope to assess the number of pollen grains that have burst out from the anthers. The anther dehiscence percentage is calculated on the basis of dehiscent anthers, i.e., 90% (fully dehiscent), 50% (partially dehiscent), and 10% (non-dehiscent).

The field studies conducted at Central Cotton Research Institute (CCRI), Multan Pakistan have revealed that dehiscence of anthers started to decline from first week of July, remained lowest during third and fourth week and then increased gradually from first week of August reaching its maximum up to 100% in September. Although heat-tolerant genotypes maintained highest anther dehiscence during the period, the trend was, however, similar in all genotypes (Fig. 20.2).

Pollen viability refers to the health of pollens, and it provides information about the ability of pollens to fertilize. Pollen viability is determined by gently tapping the inverted flower on a glass slide. The pollens collected on the slide are stained with vital dye Acetocarmine and observed under the microscope after 6 h at 200×. The viable pollens show bold red color of the dye, while nonviable pollens remain colorless (Fig. 20.3). Different physiological and other yield-contributing traits have positive correlations such as pollen viability, % boll set on first besides second positions along sympodia, and bolls per plant besides boll weight along with SCY,

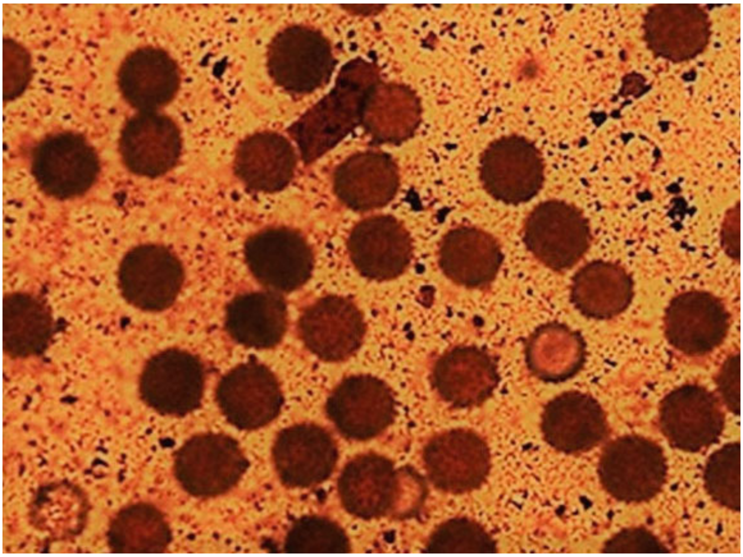

Fig. 20.3 Pollen viability in cotton: Pollens with bold red color are viable and those without color are non-viable (unpublished data of Physiology/Chemistry Section CCRI, Multan)

Table 20.2 Relationship between cotton yield and physiological traits determining heat tolerance

	AD%	PV (%)	% BSFP	% BSSP	RCIL (%)	EC	NBPP	BW (g)
PV (%)	0.97^{**}							
% BSFP	0.90^{**}	0.89^{**}						
% BSSP	0.88^{**}	0.88^{**}	0.98^{**}					
RCIL (%)	-0.97^{**}	-0.97^{**}	-0.86^{**}	-0.84^{**}				
EC (μS cm^{-1})	-0.90^{**}	-0.88^{**}	-0.90^{**}	-0.89^{**}	0.85^{**}			
NBPP	0.60^{**}	0.58^{**}	0.58^{**}	0.60^{**}	-0.59^{**}	-0.54^{**}		
BW (g)	0.12^{ns}	0.15^{ns}	0.08^{ns}	0.10^{ns}	-0.12^{ns}	-0.08^{ns}	-0.34^{**}	
SCY (kg ha^{-1})	0.99^{**}	0.97^{**}	0.91^{**}	0.90^{**}	-0.98^{**}	-0.90^{**}	0.60^{**}	0.11^{ns}

AD anther dehiscence, *PV* pollen viability, *BSFP* boll set on first position, *BSSP* boll set on second position, *RCIL* relative ell injury level, *EC* electrical conductivity, *NBPP* number of bolls per plant, *BW* boll weight, *SCY* seed cotton yield

**Significant at $p < 0.01$ ^{ns}Non-significant

while cell injury and electrical conductivity have negative correlations with seed cotton yield (Table 20.2).

20.2.2.3 Effects on Photosynthesis and Photorespiration

The process of photosynthesis is vital for different plant functions and survival. Optimum temperature, light intensity, ample availability of water, and carbon dioxide have positive influence on photosynthesis. However, extreme temperature stress is considered the most important limiting factor for photosynthesis (Salvucci and Crafts-Brandner 2004). Restricted photosynthetic efficiency as a result of temperature stress has been stated in diverse crops counting cotton (Bibi et al. 2008; Reddy et al. 1991). Maximum net photosynthesis in cotton is noticed at optimum temperature of 28 °C, and it tended to decrease when temperature reached at 35 °C (Bibi et al. 2008; Crafts-Brandner and Salvucci 2000; Reddy and Hodges 1995; Snider et al. 2009; Wise et al. 2004) owing to significant reduction in photosynthetic pigments at higher temperature (Mohamed and Abdel-Hamid 2013). High temperatures during the vegetative stage can destroy components of leaf photosynthesis, reducing CO_2 gain rates thereby limiting the export of assimilate from leaves to developmental parts (Jiao and Benhua 1996). Higher-temperature stress affects photosynthetic efficiency of cotton through decreased chlorophyll content (Snider et al. 2009, 2010), inhibited CO_2 exchange rate through limiting activity of rubisco (Crafts-Brandner and Salvucci 2000; Law and Crafts-Brandner 1999), decreased membrane integrity (Schrader et al. 2004; Bibi et al. 2008; Rahman et al. 2004), and increased photorespiration (Perry et al. 1983). Inhibition of photosynthesis due to higher temperature stress precedes the other detectable stress symptoms (Berry and Bjorkman 1980) such as the activity of rubisco, regeneration rate of ribulose-1,5-biphosphate (RuBP), and metabolism of triose phosphate (Wise et al. 2004). Higher temperature disrupts the fixation of photosynthetic CO_2 by damaging photosystem II (PSII) electron transport mechanism in thylakoid membrane (Berry and Bjorkman 1980). Since PSII function is the most unstable component in electron transport (Havaux et al. 1996; Quinn and Williams 1985), its inhibition results in enhanced chlorophyll fluorescence (Krause and Weis 1991). That is why the magnitude of heat-induced changes in photosynthesis mechanism is quantified on the basis of chlorophyll fluorescence (Govindjee 1995; Krause and Weis 1991; Strasser 1997).

Photorespiration is a process during which plants take up oxygen instead of CO_2 when the light intensity is high. High temperatures during the daytime increase photorespiration and decrease net carbon assimilation in C_3 species and thus result in the loss of carbohydrates (Guinn 1974; Krieg and Sung 1986; Ludwig et al. 1965). The conditions of continued high temperatures adversely affect plant growth through increased photorespiration (Arevalo et al. 2004, 2008). During photorespiration, carbohydrates produced by photosynthesis get utilized for respiratory energy rather than to fulfill the need of plant developmental processes such as filling of developing bolls (Loka and Oosterhuis 2010). Moreover, under conditions of high-temperature plants are unable to accumulate and provide enough quantity of carbohydrates to match with the plants' needs (Oosterhuis 1999). Perry et al. (1983) reported that photorespiration increased linearly with the rise in temperature from 22 to 40 °C:

photorespiration representing less than 15% to almost 50%, respectively, of the net photosynthesis. This highlights that the components of photorespiration and photosynthesis are highly influenced by temperature variations.

20.2.2.4 Effects on Enzyme Activation

Enzyme activity within plants is highly temperature dependent. Elevated temperatures beyond the desirable limits significantly lower the activity of different enzymes. The enzyme Rubisco activase regulates activation of ribulose-1,5-bisphosphate carboxylase/oxegenase (Rubisco) in light (Andrews et al. 1995; Portis Jr 1992; Salvucci and Ogren 1996). Vital role for Rubisco activase in sustaining active state of Rubisco during light at levels which are sufficient for photosynthesis has been reported in numerous studies (Andrews et al. 1995; Eckardt and Portis Jr 1997; Salvucci et al. 1986). Isolated Rubisco activase is mainly sensitive to inactivation by raised temperatures (Crafts-Brandner et al. 1997; Crafts-Brandner and Salvucci 2000; Salvucci et al. 2001). Therefore, the inactivation of Rubisco activase offers a potential biochemical explanation of decreased activeness of Rubisco at raised temperatures (Kobza and Seemann 1989; Krause and Weis 1991; Weis 1981).

20.2.2.5 Effects on Reactive Oxygen Species, Antioxidants, and Heat Shock Proteins

High-temperature stress induces a number of biochemical alterations in plants as a defense mechanism including production of antioxidants and heat shock proteins. ROS are chemically active and unstable compounds which consist of singlet oxygen, superoxide radical, peroxides, hydroxyl radical, and alpha oxygen. ROS, a natural byproduct in normal metabolism of oxygen, is involved in cell signaling besides homeostasis. ROS are produced in excess, in chloroplasts, and mitochondria under environmentally stressed conditions like heat stress causing damage to cell structures; the state termed as oxidative stress (Apel and Hirt 2004). The presence of excess ROS affects normal cell functions due to oxidative damage leading to cell death if the stress conditions prevail.

As a defense mechanism, plants synthesize different antioxidants to protect cells from oxidative damage caused by production of excess ROS. For normal cell functions and growth, there needs to be maintained balance between production and breakdown of ROS by antioxidants. Antioxidants prevent the oxidation of other molecules and neutralize the free radicals making them less reactive. The defense mechanism of plant comprises of different enzymatic components like superoxide dismutase (SOD), ascorbate peroxidase (APX), ascorbate (ASC), and glutathione (GSH) (Foyer and Noctor 2005).

Proteins in plant cells are temperature sensitive and are prone to denaturation by heat stress. As a phenomenon of thermotolerance, plants synthesize proteins which are termed as HSPs. The HSPs act as chaperones and prevent denaturation of cell proteins (Moriarty et al. 2002), promote refolding of denatured proteins (Frydman 2001), and are involved in other stress response mechanisms (Wang et al. 2004). Synthesis of HSPs increases with the gradual rise in temperature (Abrol and Ingram 1996). The production and accumulation of HSPs has been evidenced in cotton under controlled temperatures of 38–41 °C (Burke et al. 1985). The HSPs have been categorized into five groups on basis of molecular weights as HSP100s, HSP90s, HSP70s, HSP60s, and sHSPs (12–40 kDa) (Wang et al. 2004). In contrast to the other parts of plants, germinating pollens upon exposure to heat do not exhibit HSPs synthesis and therefore lose viability (Hopf et al. 1992).

20.2.3 Effects on Fiber Quality

Cotton crop is grown primarily to obtain lint fiber which is composed mainly of cellulose (>85%). Cellulose is a linear chain polysaccharide made up of glucose molecules mutually linked by beta-1,4 glycosidic bonds. The ideal temperature range reported for the synthesis of cellulose is from 25 to 30 °C, and cellulose synthesis decreases if temperature drops or exceeds this range (Roberts et al. 1992). Sucrose (carbohydrate), the product of photosynthesis in plants, is the basic compound in cellulose synthesis (Tian et al. 2013); therefore, any change in the concentration of sucrose would directly affect the synthesis of cellulose. Cotton photosynthetic capacity decreases if average daily temperature rises above 32 °C (Crafts-Brandner and Salvucci 2000), thus decreasing sucrose synthesis. To produce healthy fiber, plant should be able to maintain a steady rate of photosynthesis under varied conditions. Generally, 12,000–15,000 fibers are produced by a single seed under favorable temperature conditions (Oosterhuis 1997).

Adequate supply of carbohydrates is very crucial in healthy fiber development. Unfavorable conditions such as high temperatures inhibit assimilation of carbohydrates thereby decreasing seed number, seed size, number of fibers per seed, and also the weight of fiber produced on a seed thus ultimately leading to yield reduction (Arevalo et al. 2004; Oosterhuis 1999). Rising temperatures have marked effects on cotton fiber characteristics which may be either positive or negative under different circumstances. The quality of fiber is determined on the basis of different indices like fiber length, fiber strength, and fiber micronaire (fineness) which exhibit variable degree of sensitivities to the environmental factors (Bowman and Gutiérrez 2003; Bradow and Davidonis 2000; Gokani and Thaker 2002; Gou et al. 2007; John and Keller 1996; Pettigrew 2008). Increased temperatures may lead to development of altered fiber traits such as higher micronaire value, more fiber strength, and increased fiber maturity (Ton 2011). Increased fiber maturity and strength are desirable, while fiber with higher micronaire is of lower economic value.

Temperature variations have predominant effects on fiber quality parameters (Pettigrew 2008) and particularly on fiber strength during thickening of secondary cell wall (Ruan 2007). An average daily temperature of 26 °C is considered optimal for fiber development (Rahman et al. 2007). Increase in average everyday temperature beyond 30 °C or peak day temperature above 35 °C (Pettigrew 2001; Reddy et al. 1991) inhibits development of quality fiber depending upon the duration of high-temperature stress (Oosterhuis 1999; Rahman et al. 2007; Reddy et al. 1995). Similarly, night temperatures also affect fiber quality. Fiber length was found maximum between 15 and 21 °C night temperatures, and length decreased when nigh temperature rose above 21 °C (Gipson and Joham 1969; Pettigrew 2008) or decreased below 15 °C (Gipson and Joham 1969; Zhang et al. 2012). Decrease in lint index, percentage of lint and lint produced per boll at higher and lower temperature limits have been evidenced. Fiber growth duration and rate of fiber elongation may vary among the varieties and with the change in environmental factors (Gipson and Ray 1969). Fiber elongation, however, requires lower temperature than that optimally required for boll development (Pettigrew 2001). Fiber micronaire (fineness) has been reported to deteriorate above 33/28 °C temperature regimes (Pettigrew 2008; Reddy et al. 1999).

Sensitivity of fiber to temperature varies with stage of fiber development. The early stage of fiber elongation such as up to 2 weeks after anthesis has been reported to be more to night-temperature sensitive than the later stages of fiber elongation (Gipson and Joham 1969; Xie et al. 1993; Gipson and Ray 1969). Initiation of fiber elongation starts with the flowering and continues up to 25 days after flowering, while the secondary cell wall thickening continues during 20–60 days after flowering, although these processes vary with varieties and overall temperature conditions or cumulative heat units (Bradow and Davidonis 2010). Relationships between fiber quality characters besides temperatures are mentioned in Table 20.3.

20.2.4 Effects on Genetics and Molecular Responses

In nature plants suffer from various abiotic stresses throughout the course of their growth, while heat stress has a unique action mode on physiology of plant cells. While mostly heat stress becomes exacerbated with the occurrence or severity of salt

Table 20.3 Relationship of fiber quality parameters with temperature conditions

Fiber trait	Correlation	Temperature condition	References
Length of fiber	Negative	Difference amid maximum and minimum temperatures	Hanson et al. (1956)
Strength of fiber	Positive	Maximum or mean maximum temperature	Hanson et al. (1956)
Strength of fiber	Positive	Heat-unit-accumulation during boll development	Snipes and Baskin (1994)
Secondary wall deposition (fiber maturity)	Positive	Temperature/heat unit accumulation	Johnson et al. (1997), Bradow et al. (1996)
Fiber fineness (micronaire increase)	Positive	Heat unit accumulation	Johnson et al. (1997), Bradow et al. (1997)

Source: Singh et al. (2007)

and drought stress, it is imperative to investigate influence of independent stress besides biological impact of heat stress in order to alleviate combined effect of these abiotic stresses. Plant susceptibility to higher temperature depends on developmental stages, high temperature negatively affecting growth stages of plants. Effects of high temperature vary within species and among genotypes (Barnabás et al. 2008; Sakata and Higashitani 2008). The exposure of plants to heat shock by an increase in 5 °C exceeding from its optimum temperature requirement significantly alters and influences metabolic and cellular machinery essential for heat stress tolerance (Guy 1999). Plant adaptation under thermal includes changes in cellular structural organization, i.e., changes in function of organelles besides cellular membrane functions (Weis and Berry 1988), inhibiting biosynthesis of essential proteins besides enhancing transcription and translation of HSPs (Bray et al. 2000; Demirel et al. 2014), and the production of phytohormones, e.g., ABA and antioxidants enzymes (Maestri et al. 2002).

Fluctuation in temperature is sensed by plants with the aid of complex group of sensors present in different cellular compartments. Fluidity of cell membrane increases to activate the lipid-based signaling pathways likely augmented Ca^{2+} influx besides cytoskeleton reorganization. Signaling between the two pathways leads to increased production of osmolytes besides osmoprotectants in reaction to heat stress. However, *Arabidopsis* CNGC2 gene encrypts a component of membrane cyclic nucleotide-gated Ca^{2+} channels which are responsible for sensing and resultantly increase the temperature in plasma membrane in order to tackle heat shock reaction (Saidi et al. 2009). Mechanism illuminates crucial role of lipid membranes against heat stress (Horváth et al. 2012). Newly, it was illustrated that signaling pathways activate specific tissues under heat stress (Mittler et al. 2011).

Heat stress triggers changes in photosynthesis besides respiration, hence leading to reduction in life cycle resulting in reduced yield of plant (Barnabás et al. 2008). Initial effect of thermal stress encompasses structural changes in chloroplast protein with decreased enzyme activity (Ahmad et al. 2010). Furthermore, it causes injuries in cellular membrane structure with the alteration in cell elongation, expansion, and differentiation (Potters et al. 2009; Rasheed 2009; Smertenko et al. 1997). Homeostasis of plants is also disturbed with heat stress including biosynthesis of, and metabolites compartmentalization in plant tissues (Maestri et al. 2002) modification in activities of starch accumulation, sucrose synthesis, carbon metabolic enzymes, and down regulation of specific genes responsible for carbohydrate metabolism (Ruan et al. 2010).

Biosynthesis of various phytohormones increases under heat stress that causes premature senescence (Larkindale et al. 2005; Larkindale and Huang 2004; Talanova et al. 2003) such as a bscisic acid synthesis increases due to heat stress causing abscission of reproductive organs (Binder and Patterson 2009).

Transcriptomic changes in plants occurr in regulating gene expression to combat with adverse effect of temperature; approximately 5% of plants genes become upregulated via heat stress, while chaperones are minor part of general heat shock reaction (Saidi et al. 2011; Aksoy et al. 2015). Most of genes are involved in primary/secondary metabolisms, transcription besides translation in response to high temperature.

Higher accumulation of ROS species works as indicator of heat stress causing oxidative/cellular damages to plants whereas peroxidation of lipids disturb consist membrane permeability besides function. Heat stress causes denaturation and misfolding of freshly synthesized protein. Heat shock factors (HSFs) activate heat shock proteins (HSP); however, their expression pattern varies between species (Banti et al. 2010).

Plant development and physiological processes are adversely effected due to heat stress. Its damage to plant varies depending upon its developmental stage with a severity during reproduction stage which handicap plants to adapt with changing environmental conditions (Hall 2001). Higher temperature affects cotton reproductive development by decrease in pollen viability (Hejnák et al. 2015).

Flowering of plants is decreased due to heat stress which ultimately limits sexual reproduction (Hedhly et al. 2009; Thakur et al. 2010; Zafar et al. 2018). Numerous researches were conducted to unravel the effect of temperature under different conditions by artificial application of high temperature under glass or subjecting plants to high light intensity in growth chambers, and it was inferred to be deleterious for bud initiation and other growth stages of plants (Hedhly et al. 2009; Nava et al. 2009). Agronomic leguminous besides cereal crops depicted higher sensitivity at flowering, whereas horticultural crops depicted decreased fruit formation (Frank et al. 2009; Saha et al. 2010), which was speculated to be due to reduced availability of water and nutrients uptake by plant organs for their normal growth and higher yield (Young et al. 2004).

In depth it was revealed that male gametophyte is sensitive to heat stress as compared to pistil and female gametophyte which exhibited tolerant behavior (Hedhly et al. 2009). Heat stress generally stimulates rather than delays the process of anthesis to hasten flower opening and abnormal reproductive development without accumulation of necessary resources (Zinn et al. 2010). As we abovementioned about the gene expression changes with heat stress, it also varies in other plant parts such as tapetum degeneration is observed with a high rate of plant sterility among a group of species (Endo et al. 2009; Oshino et al. 2007).

Heat stress is also the cause of male sterile plants especially for sensitive species with impaired pollen development, a major factor for reduced plant yield in such scenario of environmental pressure (Wassmann et al. 2009; Sakata and Higashitani 2008). For cotton the raise in temperature from 34 to 43 °C during its growth abruptly disrupts anther formation and limiting physiological processes (Zahid et al. 2016). It also alters transport of nutrients and minerals within plants due to disrupted balance of symplastic besides apoplastic phloem loading (Taiz and Zeiger 2006). Cotton plants under pressure of heat stress exhibit lower concentration of sugars (soluble) in anther walls, pollen-grains, resultantly decreased locular fluid and pollen viability (Snider et al. 2009). Heat stress promotes development of aborted tapetal cells, which causes swift progress toward meiotic prophase triggering programmed cell death and pollen sterility (Parish et al. 2012; Sakata and

Higashitani 2008). In cotton higher temperature damages developing microspores e.g., anthers (Min et al. 2013).

20.2.5 Molecular Mechanisms of Heat Tolerance

Plants are capable to adjust themselves according to climate drift by activating genes responsible to circumvent harsh existing conditions; in this way they protect themselves from heat stress (Sánchez-Rodríguez et al. 2011; Qi et al. 2011). This ability of plants to help them to acclimate to higher temperature by maintaining homeostasis to prevent heat injury and another unprecedented mechanism such as huge production of HSPs (Vierling 1991). The heat tolerance in plants is due to various multigenic traits directly or indirectly involved during development and maintenance of thermal tolerance, the main players are antioxidant enzymes, gene regulations, lipid membrane stability, and compatible solutes accumulations (Kaya et al. 2001).

A number of studies have highlighted the importance of HSFs which are critical for heat tolerance, while some have lesser critical part such as HSP101, HSA32, HSFA1, HSFA3, and knockout of variants showed less impact for heat tolerance (Schramm et al. 2008; Yoshida et al. 2011). It indicates that complex network is involved for conferring differential protection against heat stress. Nonetheless, HSPs have significant role for tolerance which work as molecular chaperones to circumvent denaturation of targeted proteins besides likely facilitating refolding of protein (Ahuja et al. 2010; Lohar and Peat 1998; Scharf et al. 2012).

Heat stress tolerance is dependent upon induction of heat shock proteins (HSP70 and HSP90) in cotton (Gurley et al. 2000). The inhibited expression of HSP70 and HSP90 in cotton stimulated oxidative stress and reduced the tolerance for heat stress in cotton genotypes, which exhibited that HSP70 and HSP90 are involved for heat tolerance (Sable et al. 2018). Although, HSP101 and HSP70 are not normally required for growth under normal conditions but, however, have significant importance for tolerance and protein oxidative protection in cotton (Zhang et al. 2016). It is supported from several studies that HSFs can role as molecular sensors which sense ROS species and regulate the expression of oxidative stress responsive genes in cotton (Miller and Mittler 2006; Sable et al. 2018; Sekmen et al. 2014). Moreover, in cotton HSPs are associated with membrane to form heat shock lipids which stabilize the membrane during earlier temperature stress (Cottee et al. 2014).

Plants facing any abiotic stress immediately produce ROS-scavenging enzymes to alleviate oxidative stress produced by ROS species; therefore, plants suffering from heat stress also produce antioxidant enzymes (SOD, POD, CAT, APX and GPX) (Sekmen et al. 2014). It was reported that in tolerant plant species the production of these enzymes is higher as compared to susceptible for protection from oxidative damages (Abiko et al. 2005). Antioxidant enzymes are found in almost all the cellular components of plants for detoxification and cellular survival (Asada 2006; Iba 2002; Mittler et al. 2004). It was reported from dicot model plant

(Arabidopsis) that APX gene family starts expression during heat stress which is solely dependent on HSF for heat tolerance (Panchuk et al. 2002).

The LEA proteins, i.e., ubiquitin, besides dehydrins, are key players for protecting from heat and drought stress moreover drought stress further aggravates heat stress with least availability of water for plant growth. In cotton, LEA proteins aid in preventing aggregation and protection from desiccation (Magwanga et al. 2018). The role of ubiquitin was against heat stress, and it was reported that it is important for the first 30 min for short exposure of plants to heat stress (Huang and Xu 2008).

Different approaches have been exploited to discover molecular mechanisms rendering heat tolerance during reproductive organ development especially at the stage of pollen formation which is necessary to understand and pave path for developing heat-tolerant cultivars, thereby various genome-wide approaches have been deployed for heat tolerance cotton breeding program (Min et al. 2014). It was concluded that numerous mechanisms such as several hormones, antioxidants, and HSPs are important for reproductive structures tolerance in cotton (Min et al. 2014).

Higher temperature stress has devastating effect on crop yield. In cotton, tolerant cultivars exhibit higher chlorophyll content, maintain photosynthesis machinery by adjusting stomatal conductance during heat stress (Hejnák et al. 2015), although to ensure higher fruit setting and seed cotton production, are important parameters to be considered with elevated temperatures (Reddy et al. 1992a, b, c). Genetic resources need to be exploited when there are limited options available for heat tolerance in cotton; sometimes wild cultivars are used to fix trait through breeding for achieving higher tolerance (Pradhan et al. 2012).

In heat-tolerant plants, expression of multiple proteins has been observed with an increase in concentration of phosphoribulokinase (PRK), which is the main component of calvin cycle for final RuBP production. Protective proteins (HSP70, HSP90 besides Cpn60) also accumulated with an elevated gene expression to confer protective role against heat stress (Scafaro et al. 2010).

Likewise, a proteomic study was conducted for comparing protein expression in cotton among susceptible and tolerant cultivars, and it was observed that accumulation of HSPs was higher in tolerant cultivars making them more tolerant under adverse temperature (Min et al. 2014). In cotton genetic variation occurs with the ability of each cotton cultivars to withstand heat stress with increased membrane stability and chlorophyll contents and minimum electrolyte leakage from tolerant cultivars (Asha and Ahamed 2013).

Currently global warming is the main issue as we know earth temperature is increasing every year around the globe which will have severe impact on the crops growth. On the other hand, human population is also increasing rapidly and to ensure food security heat-tolerant crops development is necessary to be sure to cope with future changing climatic conditions. That is also necessary to understand behavior of crop to changing climatic conditions that what kind of physiological adaptations take place in plants. Modern genetic approaches are also paving path for tolerant crops development within a less period of time. Figure 20.4 explains different mechanisms of heat-tolerance initiated in plants under high-temperature stress.

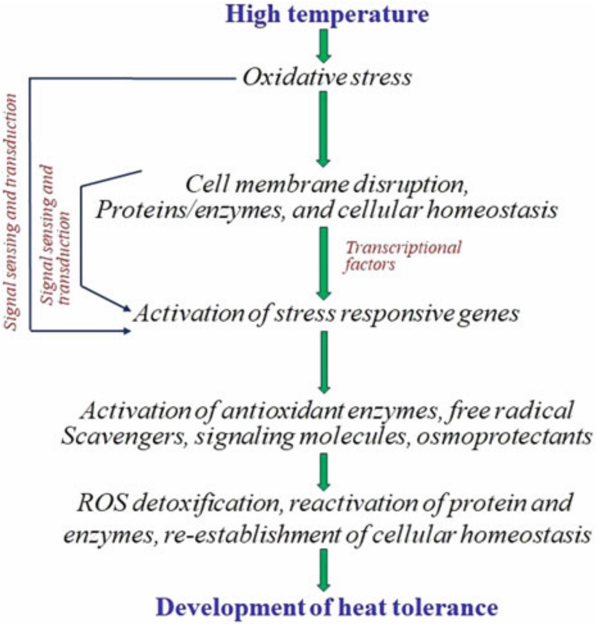

Fig. 20.4 Schematic diagram of mechanisms involved in heat tolerance of plants (Hasanuzzaman et al. 2013)

20.3 Strategies to Cope with High-Temperature Stress in Cotton

20.3.1 Variety Selection, Sowing Time Adjustment, and Irrigation Management

Cotton plant is able to respond with the severity of stress and adopt according to the harsh environmental conditions. High-temperature stress in cotton is most important due to its impact in early growth including germination, flowering besides during boll formation stages. High night temperature also increases overall mean temperature. Relative humidity has direct role to inhibit cooling phenomena during night leading to higher nighttime canopy and air temperatures. Moreover, higher humidity during daytime limits transpiration rates thus resulting in higher daytime canopy temperatures as well.

Cotton growth is influenced due to temperature stress which induces differential physiological, biochemical, and metabolic changes, by changing plant photosynthetic performance, stomatal conductance, maintaining oxidative balance, carbohydrate production, lipid peroxidation, and synthesis of protein for heat tolerance (Bibi et al. 2008; Roy and Ghosh 1996).

Heat stress is a hard to control phenomenon due to climate change. Different strategies should be applied to adapt to temperature stress. There exists genetic variability in cotton varieties and available germplasm express either susceptibility or tolerance in heat stress (Khan et al. 2008). Selection of heat-tolerant varieties is, therefore, one of the prime management options to avoid heat stress impacts on cotton crop. Varieties owing leaf characteristics with thick cuticle and waxy surfaces are better heat tolerant as they can reflect solar radiation to decrease damage of heat stress (CICR 2000). Generally, most of the commercial cotton varieties are good absorber of solar radiation and suffer increased heat stress impact. Selection of short season cultivars might be helpful as they are lesser exposed to heat stress.

The other viable choice is to reduce the exposure of fruiting phase to heat stress through planting time adjustment. The change in planting time is a good option to protect the early stages of crop from severe temperatures. Sowing of cotton after recommended planting time is more vulnerable to damages from heat stress. Sowing time changes affect the cotton growth, lint yield, and assimilate supply to reproductive organs (Khan et al. 2017). Planting time needs to be adjusted in such a way that flowering phase of crop should not face the highest day/night temperatures of the season allowing it to escape from heat stress damage.

High temperature accelerates water losses from the soil and plant through increased rates of evaporation and transpiration. Timely irrigation management would minimize the impacts of heat stress. Irrigation ought to be applied according to plant needs by observing canopy temperature for ameliorating detrimental effects of higher temperature (White and Raine 2008). Inadequate availability of water forces plant to adapt to such conditions by physiological changes through adjusting stomatal conductance, which increase the incidence of water stress in cotton. It is necessary to apply water to cope such situations which keeps the canopy cool. In arid conditions crop is totally dependent on rain, and with deficient soil moisture conditions, adjustment of row spacing helps to increase lint yield of cotton (Bange et al. 2008).

20.3.2 Screening for Heat Tolerance

In Pakistan cotton is mostly cultivated in hottest regions (Riaz et al. 2013). The genotypes commercially grown often face extremely high temperature up to 50 °C during months (May and June), which is almost 20 °C above than optimal temperature required for its normal growth, thus retarding crop's performance to a high extent. Development of heat-tolerant commercial cotton genotypes is a main challenge (Moreno and Orellana 2011; Zhang et al. 2006). Identification besides confirmation of traits that confer tolerance to high temperature remains elusive due to dynamic responses of plants subjected to heat stress (Rodríguez et al. 2005; Wahid et al. 2007). Scientists are also working to examine in what way plants could be managed in high-temperature conditions. Based on importance of high-temperature stress, physiological, biochemical, and molecular responses have been studied to screen the newly evolved cotton germplasm. Identification and development of potential genotypes which possess better tolerance to heat stress could give better yield performances in heat-prone areas.

Fig. 20.5 Reproductive tissues of cotton flowers exposed to heat-stress (left) and optimum thermal conditions (right). Heat-stressed-flowers commonly have short filaments which creates illusion of an elongated stigma. (Modified and adopted from Brown 2008)

Several methods in natural field environmental conditions are generally being in practice for selection of heat tolerance. Field research is more advantageous for understanding the behavior as compared to controlled conditions; however; it has also limitations to control the environment under field conditions.

Studies have revealed that there exists a relationship between temperature besides cotton reproductive performance (Brown 2001; Zeiher et al. 1994). Heat stress damages young squares 15 days prior to flowering. Once developed into flowers most of these do not open fully owing to their smaller size. Moreover, the flowers show asynchronous development of male besides female reproductive structures, and anthers fail either to release pollen or are unable to fertilize due to incompatible elongation (Fig. 20.5) of filaments and stigmas (Brown 2008). High temperature affects anther developmental phases causing abnormalities in the structures, pollen sterility, and premature abortions. For instance, pollen germination and pollen tube growth at 82.4–86.0 °F (28–30 °C) negatively affect cotton reproductive performance. Pollen germination which was maximum at 82.4 °F/28 °C (Burke et al. 2004) showed a moderate to sharp decline when temperature increased beyond 28 °C to up to 98.6 °F/37 °C. Likewise, length of germinating pollen tubes increased maximum at temperatures between 82.4 °F/28 °C and 87.8 °F/31 °C but decreased significantly at 93.2 °F/34 °C approaching zero at 109.4 °F/43 °C. Higher temperature results in membrane modification and its composition with higher leakage of ions. Stability of cell membrane for thermal stability is evaluated with the ability of plants against hardens reaction to higher temperature besides tolerate harmful metabolic changes for heat stress (Alexandrov 1964).

Heat tolerance test was developed to understand stability of cellular membrane by measuring electrolyte leakage from leaf discs washed in deionized water immediately after exposure to heat-stress (Sullivan 1972). The EC of exudates from tissues discs is expressed as measures of CMT to stress (Blum and Ebercon 1981). The method is, however, more applicable to plants at mature stages.

Temperature variation effects on plants are multifaceted and greatly influence pollen viability, fruit setting along sympodial branches (% boll set on first and second positions), and biochemical parameters such as chlorophyll content, crude protein and proline levels. These parameters may also be considered, while testing cotton genotypes for heat tolerance as well as yield performance. Relatively new physiological techniques like CMT, LEL, and anther dehiscence have been established as reliable and efficient screening methods (Singh et al. 2007).

Stomatal conductance is worthy criteria for higher yield of irrigated crops grown under environmental adversities (Lu et al. 1998; Rahman 2005; Ulloa et al. 2000). Canopy temperature is a sensitive technique for measuring tolerance to high temperatures under filed conditions (Oosterhuis and Snider 2009; Snider et al. 2010). Photosynthesis is also dependent upon stomatal conductance, thereby it is also sensitive under heat stress conditions, nevetheless it is not practical approach for screening of germplasm against stress tolerance (Bibi et al. 2008). Important traits for selection of heat tolerance in pants are given in Table 20.4.

20.3.3 Chemical and Biochemical Interventions to Induce Heat Tolerance

Various approaches have been employed to induce thermal stress tolerance in plants such as foliar application of chemicals, seed treatment prior to sowing with some inorganic salts, oxidants (e.g., H_2O_2), and osmoprotectants (e.g., growth hormones) (Wahid et al. 2007).

Seed treatment with high temperature (42 °C) before sowing enhances tolerance ability of plant and to combat overheating and overcome dehydration; likely it also aids in higher accumulation of water soluble proteins. Exogenous application is also a good option such as Ca^{2+} applications increases plants' heat tolerance. Calcium in the form of $CaCl_2$ application just before stress treatment increases antioxidant enzyme activity leading to protection from heat stress (Kolupaev et al. 2005; Tikhomirova 1985). Glycine betaine and polyamines, low molecular weight organic compounds, which confer fruitful to induce heat tolerance in numerous plant species. Seeds pre-treated with glycine betaine produced plants having low membrane damage, improved photosynthetic rate, and enhanced leaf water potential besides more shoot growth (Wahid and Shabbir 2005).

The protective mechanisms activated within plants in response to higher-temperature stress are described schematically in Fig. 20.6. Plants tolerate to high-temperature stress by morphological, physico-biochemical changes. In physiological

Table 20.4 Important morpho-physiological selectable traits conferring heat tolerance

No.	Trait	Characteristics	References
(A) Morphological traits amenable to direct selection			
1.	Okra leaf type	High leaf N content High CO_2 exchange rate (CER) High photoelectron transport rate Reduced non photochemical quenching	Pettigrew (2004)
		Reduced individual leaf area Higher photosynthesis	Wells et al. (1986)
2.	Lower fruiting height	Greater heat tolerance	Feaster and Turcotte (1985)
3.	Thicker leaves	High N content	Hall (2001)
		High photosynthetic capacity	Wright et al. (1993)
4.	Abundant flowering and fruiting at higher temperature	Heat tolerance	Ehlig and LeMert (1973)
5.	Earliness	Reproductive heat tolerance	Ahmed et al. (1993), Ehlers and Hall (1996)
6.	Stay-green effect	Heat tolerance	Reynolds et al. (1997)
7.	Pollen selection	Pollen selection through heat treatment Reproductive stage heat tolerance	Rodriguez-Garay and Barrow (1988)
(B) Physiological traits for both direct and/or indirect selection			
1.	Cell membrane thermostability (CMT)	Measures resistance of protoplasmic proteins to denaturation	Bibi et al. (2003), Rahman et al. (2004)
		Heat and drought tolerance	Ashraf et al. (1994)
2.	Leaf electrolyte leakage (LEL)	Heat tolerance	Thiaw (2003)
3.	Anther dehiscence and pollen viability	Reproductive heat tolerance	Singh et al. (2007), Brown and Zeiher (1998)
4.	Stomatal conductance		Ulloa et al. (2000), Rahman (2005)
5.	Canopy temperature		Oosterhuis et al. (2009)
6.	Photosynthesis		Bibi et al. (2008)

Source: Singh et al. (2007)

response, plants accumulate compatible osmolytes, which aid in increasing retention of water in plants for improved stomatal regulation and photosynthetic rate. The morpho-physiological changes include decrease in cell size, stomata closure to curtail water, increased stomatal and trichomes densities besides greater xylem vessels. In biochemical alterations, accumulation of stress-related antioxidant enzymes takes place which augment activities of antioxidants enzymes in plant cells. Antioxidants alleviate ROS and reduce photo-oxidation damage with

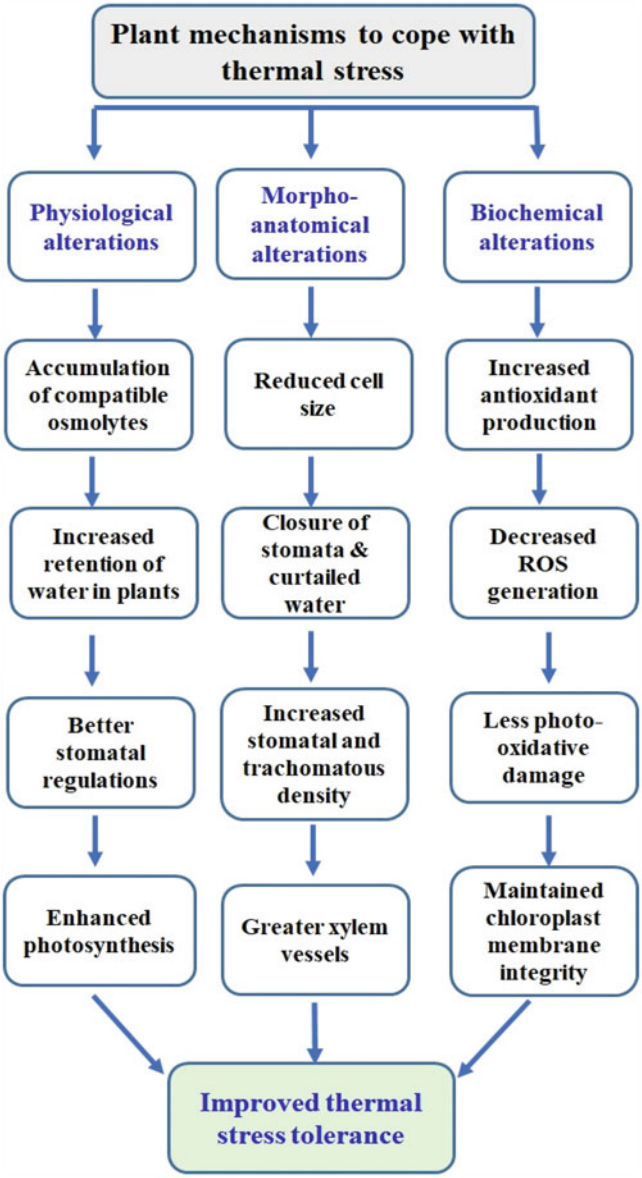

Fig. 20.6 Schematic presentation of morphological, physiological and biochemical alteration of plants to cope with high temperatures. (Modified and adopted from Waraich et al. 2012)

maintenance of chloroplast integrity. Plant growth regulator's exogenous applications are an important alternative to decrease negative impact of temperature stress by enhancing the antioxidant defense (Sarwar et al. 2017).

Foliar applications of essential macronutrients (N, K, Ca, and Mg) and micronutrients (B, Mn, Se), and Salicylic acid (SA) also help in alleviating adverse effects of temperature stress. These nutrients enhance antioxidants enzyme concentration in plant cells. Nutrients like K and Ca improve uptake of water with improved stomatal regulation that makes plant able to survive during exposure of heat stress. Moreover, K and Ca also help in osmotic balance and maintenance of higher tissue water potential under temperature stress conditions (Waraich et al. 2012).

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