

# Novel Breeding and Biotechnological Approaches to Mitigate the Effects of Heat Stress on Cotton



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## 1 Introduction

Cotton belongs to the family Malvaceae, which contains more than 200 genera and about 2300 species. More than 50 species of *Gossypium* are native to Africa, Australia, Central and South America, and Asia (Wendel and Grover 2015). *Gossypium barbadense*, known as Egyptian or American pima cotton, produces 8% of the total cotton in the world. *G. hirsutum* is called upland cotton; native to Mexico and Central America, this species produces 90% of the total cotton in the world (McCarty et al. 2004). Upland cotton is an important fibre crop that is cultivated in more than 80 countries and occupies more than 32 million hectares worldwide. It is an important source of oil and livestock feed (Singh et al. 2007). Pakistan, China, India, and Sudan contain 75% of the total cotton cultivated area in the world, and these countries have the potential to produce cotton at high temperatures. Although cotton is a warm-season crop, this plant does not yield best at a very high temperature. Researchers have reported that high temperature has negative association with boll development and plant growth in *G. hirsutum* (Pettigrew 2004). The reproductive growth of a cotton crop is more sensitive to heat stress than is its vegetative growth, and high temperature exerts a negative effect during the flowering period. High temperature also causes sterility of pollen grains, disruption of plasma membranes, dropping of flowers, poor retention of bolls, and reduction in the fibre quality (Kakani et al. 2005).

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There are several ways to overcome this problem of the cotton plant but development of heat-tolerant germplasm is one of the best solutions to combat high temperatures. Several projects on cotton breeding are being executed for the development of new and improved upland cotton germplasm resistant to various abiotic stresses (Wahid et al. 2007). Researchers have found a considerable level of tolerance in cotton, but the mean temperature of the Earth is rising continuously, which warns the cotton breeders to identify potential in existing germplasm by using efficient screening techniques based on physiological and molecular parameters. The molecular techniques are also time-saving and reliable (Saranga et al. 2004). Conventional breeding methods along with molecular tools are reliable and efficient methods to breed new lines of crop plants with improved qualities *i.e.* yield and tolerance to abiotic stresses.

## 2 Effects of High Temperature on Crop Plants

Increase in temperature produces heat stress in both arid and semi-arid regions, and this is becoming an alarming problem for agriculture around the globe (Hall 2000). The global population is ever increasing, so now it is necessary to increase the yield of crop plants. Night temperature is the most important factor reducing per acre yield according to some researchers, with the secondary role played by the day temperature (Willits and Peet 1998). Several studies have been conducted to assess the effect of increased temperatures on various stages of plant development and yield of crops. Knowledge of plant response to elevated temperatures is allowing farmers to grow crops for greater production in a harsh environment and gain justifiable crop yields (Paulsen 1994). In tropical regions, growth and development are damaged by high temperatures in various ways: damage before and after harvesting, sunburn of leaves, scorching of twigs, abscission and senescence of leaves, inhibition of root and shoot growth, discoloration and damage of fruits, and yield reduction of crop plants (Vollenweider and Günthardt-Goerg 2005).

Under heat stress, the response of the plant varies with species and with the degree and duration of temperature. At high temperature, growth of the plant is stopped, but uptake of water from soil is increased, stomata are closed, the internal temperature of the plant is increased, and wilting of leaves takes place. If water is not provided at this stage, wilting of leaves becomes permanent, and ultimately cellular damage or cell death may occur, leading to the catastrophic collapse of cellular organization (Ahuja et al. 2010). Increase in temperature affects the efficiency of enzymes, RNA synthesis, stability of membranes, and proteins that are involved in major physiological processes (Pagamas and Nawata 2008). The effects of heat stress are summarized in the following paragraphs.

## 2.1 *Morphological and Yield Traits*

### 2.1.1 **Seedling and Root Growth**

The best germination of cotton seed is reported to be at 22–24 °C and the best seedling development is at 26 °C, although in some parts of the world, especially the state of Mississippi of the United States, the optimal range of temperature for germination of seeds and for development of seedlings is 28 °C and 30 °C, respectively. Low temperature also causes many problems in cotton during germination and initial growth stages. Different cotton genotypes exhibit differently for their germination and the development of roots during cool soil temperature conditions (Nathan et al. 2005). In spite of sufficient moisture and nutrient availability, the existence of temperature stress (40/32 °C), plants produce poorly developed and wilted roots. The cotton plant shows its best development at day and night temperature ranges of 30/22 °C and 35/27 °C, respectively (Reddy et al. 1997). In many dry areas of the world, seedlings of the cotton plant have been found to be heat tolerant because this plant provides seed cotton during moist conditions (Burke 2001). The moisture of the soil is depleted quickly at the time of sowing in North Indian and Pakistan regions because of increased temperature and high wind velocity, so the seedlings of cotton varieties grown in these regions are said to be tolerant to high temperature and water deficit conditions (Lather et al. 2001).

### 2.1.2 **Vegetative Plant Growth**

When we talk about the growth stages of a plant affected by heat stress, it is the germination stage which is affected significantly. In various cultivated plant species, it is observed that germination percentage, the emergence of plants, normal seedlings, good seedling vigor, and growth of germinated seedlings are greatly reduced during high-temperature conditions (Toh et al. 2008). Reduced seed germination is also reported through induction of abscisic acid (ABA) (Essamine et al. 2010). Although reproductive stages of the cotton crop are more sensitive to heat stress as compared to vegetative stages, high temperatures also cause irreversible damage to the vegetative parts of cotton plants. It has been observed that cotton plants grown at high temperature showed poor growth, very short stature, fewer fruiting branches, and poor crop stand. The vegetative growth of many other crops is also affected adversely under heat stress *e.g.* in wheat, the germination rate is inhibited and burning of embryos takes place at high temperature (45 °C). In rice, the number of tillers, plant height, and biomass are reduced in response to heat stress. In sugarcane, it has been observed that leaf tips and leaf margins are damaged, like rolling and drying of leaves (Omae et al. 2012).

High temperatures can reduce the life period of field crops. The cotton crop completes its life cycle in a short time under heat stress, and the optimal time period required for proper growth of cotton bolls and development of its fibre is reduced, resulting in reduced boll size and poor fibre characteristics. In cereals, a small increase of temperature, 1–2 °C from optimum temperature, is responsible for shortening the time period for grain filling and negatively affects the yield (Nahar et al. 2010).

### 2.1.3 Square, Flowers, and Bolls

The yield of cotton depends on fruit settings and retention as well as boll weight. In the beginning of fruit development, squares appear, then flowers are developed which finally become the boll. Squares and flowers are aborted at their peak when day and night temperatures are 30 °C and 20 °C for 13 h, respectively (Reddy et al. 1991). Approximately 65–70% of fruiting points, namely, squares, buds, and small bolls of the cotton plant, fell from abiotic stresses, but heat stress is one of the factors in this loss. Pollen grain viability is severely decreased at a temperature above 35 °C; as a result, unfertilized flowers are produced that cannot form bolls (Baloch et al. 2000). Although cotton is a C3 plant, it is more heat tolerant than other plants of this class, but excessive temperature stress, that is, above 36 °C, results in severe losses to the plant (Fisher 1973). All existing squares and flowers were found to be aborted in many cotton cultivars at extreme day temperatures *i.e.* 40 °C, whereas pima cotton was found to be highly susceptible and unable to produce branches.

Retention of few bolls has been observed in cotton plant with increased temperature. Under high temperature conditions, plants also produce poor flowers. Furthermore, both of these traits vary extensively in different years according to environmental conditions and the cultivars. It has been established that abortion of young bolls takes place on exposure to an average daily temperature of more than 28 °C. In the Yangtze Valley of China, many periodic shocks related to temperature, with an air temperature more than 35 °C, usually in the months of July and August when cotton flowering and boll formation are at the peak, result in senescence of leaves, boll abortion, and a reduction in lint yield (Liu et al. 2006). Boll retention in cotton plant is strongly controlled by temperatures regimes. For the maintenance of bolls, 28 °C is the best temperature, and young bolls drop when the mean daily temperature becomes more than the optimum temperature. The main effect of higher temperature is lesser fruit holding, resulting in lower seed cotton yield, poor lint quality, and late crop maturation (Reddy et al. 1999).

### 2.1.4 Seed Cotton Yield

Yield is the most important trait for the farmer, and it has been observed that seed cotton yield is significantly affected by adverse environmental conditions (Brown et al. 2003). Negative effects on crop yield are observed during water deficit and high-temperature stress conditions (Lewis et al. 2000). It is noted that an increase in

temperature during day and night can produce adverse effects on crop yield. It is suggested that an optimal temperature is necessary for obtaining a good yield from the cotton plant. Optimum temperature is not well defined in the literature because every variety has differential response to temperature. A strong negative relationship between high temperature and yield of seed cotton is observed in the fields of Arkansas (USA) (Oosterhuis 2002). Pakistan and India are two of the four top cotton-producing countries of the world. The cotton belt of Pakistan experiences very high temperatures during the cotton season and similar conditions are observed in India. About 48 °C is observed during the cotton growth in these regions. Although the yield of seed cotton in these two countries is quite low as compared to other cotton-producing countries, the genotypes cultivated in these regions give optimal yield even at this very extreme temperature. It can be assumed that this very high temperature during summer is one of the reasons for low seed cotton yield in these countries.

There is no defined threshold level of heat stress in plants, but the temperature of 32 °C is found to be stressful, causing deterioration of more than 50% of cotton boll development. Furthermore, high temperature results in insufficient production of carbohydrates, reflected by high boll shedding percentage, smaller bolls, lesser lint percentage, and reduced yield production (Oosterhuis 1999). The fibre of the cotton plant is predominantly developed from plant carbohydrates, and decreased amounts of carbohydrates lead to less fibre and reduce ginning turn out. Increase in temperature above the optimum level may also reduce the size of cotton seeds and fibre length. Temperature influences both the rate of elongation of the fibre and secondary wall thickness. The boll maturation period is shortened by increased temperature, and incomplete boll maturation takes place during increased night temperatures. It has been validated that initial stages for elongation of fibre are sensitive to higher night temperature whereas the later stages are less sensitive to increased temperatures (Gipson and Joham 1969).

### 2.1.5 Quality of Fibre

Cotton fibres are the outgrowth of single epidermal cells. These fibres consist of various carbohydrates with cellulose as the key component. The cotton crop is generally grown for its fibre because the textile industry utilizes these fibres for making cloth. Cotton fibres or mature cotton bolls exposed to sunlight or at high temperature for many days will decrease in fibre quality. As a cotton crop completes its life cycle rapidly under high-temperature stress, thus the time required for fibre elongation and maturity also decreases, resulting in less growth of the epidermal cells with poor deposition of cellulose. The fibre quality parameters are fibre length, fibre strength, and fibre fineness. All these traits are poor in quality under heat stress conditions (Azhar et al. 2009).

Breeding with the purpose of high lint yield is still the primary goal for any cotton breeding program, and improvement in fibre quality has become increasingly important. The presence of heritable variation and the favorable correlation between

the different traits is important for launching any cotton breeding program designed for selection of desired genotypes. Cotton genotypes vary significantly for fibre length, fibre strength, fibre fineness, and fibre uniformity. Heat-tolerant genotypes of cotton provide high and stable seed cotton yield with better quality of fibre than heat-susceptible genotypes. Cotton is extremely responsive to changes in humidity, soil moisture content, and temperature, which affect its yields, the components of the yield, and the fibre properties (Killi et al. 2005).

## **2.2 *Physiological and Biochemical Traits***

### **2.2.1 *Viability and Development of Pollen***

During heat stress, pollen is adversely affected because it is the most sensitive organ in the plant. The number of fruit points are decreased in response to pollen sterility caused by heat. The yield of the crop depends upon temperature during the development of the pollens (Van Ploeg and Heuvelink 2005). Although cotton is a warmer-season crop, the viability of cotton pollen is greatly decreased under heat stress. The decreased viability of the pollen grains in cotton results in poor boll formation and fewer fruit sets, causing reduced yield. The adverse effects of heat stress on pollen viability are also reported in several crops such as tomato, barley, rice, chickpea, rapeseed, common bean, bell pepper, soybean, and strawberry (Djanaguiraman et al. 2013; Porch and Jahn 2001; Prasad et al. 2006).

High temperatures adversely affect the development of pollen at the early development of the stages (De Storme and Geelen 2014). In several crops, the most sensitive stages are 7–15 days before anthesis and typically at the time of meiosis. However, heat stress does not affect pollen quality components or meiosis stage when the temperature is above optimum level after the release of tetrads has occurred (Ahmed et al. 1992). The development of microspores (4 days before anthesis) and anthesis are the most sensitive stages in peanut (Prasad et al. 2001). Similarly, heat stress in bell pepper during the development of microspore mother cells leads to the reduction of pollen viability while heat stress at the time of lateral developmental stages does not affect pollen viability (Erickson and Markhart 2002).

Major loss of yield in plants has been observed to be caused at the time of flowering by a small increase in temperature because the reproductive stage is the most important and most sensitive stage of plant development (Lobell et al. 2011). Although variations in responses to heat stress have been found in plant species, increase in temperature at the reproductive stage is responsible for reduction in floral buds and increased flower abortion (Sato et al. 2006). Heat stress increases the rate of male sterility by reduced pollen germination, reduced development of the pollen tube, reduced ovule viability, irregularity in positions of stigma and style, reduction in numbers of pollen grains, and decreased fertilization processes (Yun-Ying et al. 2008).

### 2.2.2 Tapetum and Pollen Germination

The tapetum is the key organ of plants, providing metabolites to the pollen. The growth and development of the tapetum are significantly affected by increases in temperature. A temperature increase leads to the early meiotic phase I and degradation of the tapetum (Oshino et al. 2007). In wheat (Saini et al. 1984), cowpea (Ahmed et al. 1992), and purple false brome (Harsant et al. 2013), degradation of the tapetum has been reported during heat stress. Increase in temperature before anthesis affects the tapetum, causing structural abnormalities. In response, premature degradation of the tapetum occurs (Suzuki et al. 2001).

In plants, germination of the pollen and formation of the pollen tube are sensitive processes adversely affected by increase in temperature. It was found in many crop plants that decreased fruit setting taking place at elevated temperatures was primarily caused by reduction in pollen germination (Hazra and Ansary 2008). Pollen germination may be reduced when pollen development occurs under heat stress. Reduction in pollen germination is observed at 36 °C in such crops as cotton (Kakani et al. 2005), tomato (Vasil 1987), and cucurbit (Jóhannsson and Stephenson 1998). Poor pollen germination also delays fruit development and parthenocarpy (Abdelmageed and Gruda 2009). As a result of temperature increase, pollen germination is reduced and lesser yield is obtained from different plants.

### 2.2.3 Photosynthesis

In plants, photosynthesis is the most important and heat-sensitive physiological process (Crafts-Brandner and Salvucci 2002). High temperature exerts significant influence on the photosynthetic activity of C<sub>3</sub> and C<sub>4</sub> plants (Yang et al. 2006). Chloroplasts of plants, especially the photochemical reactions and carbon metabolism of thylakoid membranes and stroma, have been thought to be the primary sites of heat injury (Wang et al. 2009). Increased temperatures change the structural organization of thylakoids with swelling of the grana, so that the plant cannot synthesise its food, and reduction in yield occurs (Ashraf and Hafeez 2004). In leaves of plants, increase in temperature significantly affects stomatal conductance, water status, and intercellular CO<sub>2</sub> concentration (Greer and Weedon 2012). The closing of stomata at high temperature is another reason for decreased photosynthesis, which seriously affects intercellular CO<sub>2</sub> and photosystem II activity. The amount of photosynthetic pigments is greatly reduced by heat shock in plants (Marchand et al. 2005). In sorghum, when the temperature is increased (40/30 °C, day/night), reduction in chlorophyll pigment has been observed (Mohammed and Tarpley 2010). Heat tolerance is positively correlated with the efficiency of plants to assimilate CO<sub>2</sub> and maintain gas exchange under heat conditions (Yang et al. 2006). In plants, photochemistry of photosystems and stomatal conductance were also observed to be reduced when the temperature increased. Other reasons are also responsible for the reduction in photosynthesis and plant yield as a result of heat stress. Reduction in the binding of soluble proteins and damage to subunits of RuBisCo is also caused

by heat stress (Sumesh et al. 2008). Synthesis of starch and sucrose is also affected by increased temperature, causing decreased activity of sucrose phosphate synthase (Djanaguiraman et al. 2009). Increase in temperature is also responsible for lowering of the water potential in leaves and leaf area, so that premature leaf senescence takes place with a negative impact on total plant photosynthesis (Greer and Weedon 2012).

#### **2.2.4 Carbohydrates/Sugar Content**

Carbohydrates are a source of energy needed for the development and germination of pollen; they protect the membranes from adverse effects of stress including heat stress. Disruption in the metabolism of carbohydrates by elevated temperatures can affect the nutrient uptake of plants with resulting reduction in crop yield. The effect of heat stress on pollen carbohydrates has been studied in tomato, sorghum, chickpea, cotton, okra, and pepper. Production of fluorescence in the cotton crop is significantly affected at high temperatures and the viability of pollen is also reduced. From heat stress, the flowers show decreased levels of their soluble sugars in both anthers and pollen (Pressman et al. 2002). It is speculated that at the time of high-temperature stress soluble sugars are blocked in the locular fluid and fail to reach the pollens. In contrast to heat stress, during normal conditions of pollen development starch is accumulated in the pollen 3 days before anthesis and is then converted into soluble sugar. During heat stress, the concentration of starch does not reach at the required level, and ultimately the amount of soluble sugar is decreased in mature pollen. These facts indicate that even a minor change in temperature causes a change in sugar transport and metabolism.

#### **2.2.5 Proline**

Proline is an amino acid acting as an osmolyte in the cells. It has three vital roles in the plant during stress: maintenance of stability of the cell membrane and prevention of leakage of electrolytes helps optimize the concentration of reactive oxygen species and detoxification of effects of metals by acting as a chelator. It is suggested that a high concentration of proline in the cells during heat stress is desirable for normal growth and functioning of the plant (Rana et al. 2017). The concentration of proline in plants increases in response to different biotic and abiotic stresses such as increase or decrease in temperature, salinity, and pathogen attack. When proline contents in anthers of heat-sensitive and heat-tolerant cultivars of different crop plants were analyzed at 45 °C, it was found that mature pollen of tolerant cultivars had higher proline content than sensitive cultivars (Mutters et al. 1989). Under prolonged heat stress conditions, the expression of genes responsible for proline transfer in cotton is decreased.



### 2.2.6 Lipids and Polyamine

Lipids have a key role in membrane stability and fluidity during heat stress. The content of ROS in plants increases with a rise in temperature, which causes changes in phospholipids concentration from lipid phosphorylation. High temperature increases unsaturated fatty acids and reduces the quantity of saturated fatty acids. It was reported that the cellular membrane is damaged by an increase in the quantity of unsaturated fatty acids, which enhances membrane fluidity. The unsaturated fatty acids make the membrane more vulnerable to ROS. Pollen viability is correlated with changes in saturation of phospholipids (Djanaguiraman et al. 2013).

Polyamines are considered as a source of tolerance to abiotic stresses such as heat, cold, drought, and high metal content (Fariduddin et al. 2013). They sustain membrane integrity and work as scavengers against ROS (Alcázar et al. 2006). During the period of heat stress, alterations in polyamine content occur and pollen germination is decreased by the reduction of *S*-adenosylmethionine decarboxylase (SAMDC). The blocking of SAMDC translation with cycloheximide could phenocopy the effect of heat stress, which leads to decreasing pollen germination in controlled conditions. Some other proteins have also been reported to affect pollen germination.

### 2.2.7 Reactive Oxygen Species

Reactive oxygen species (ROS) act as signaling molecules under normal and stress conditions for the activation, upregulation, and downregulation of many genes involved in various metabolic pathways. When the concentration of ROS increases from optimal levels, then these species cause irreversible damage to plants by oxidative stress. High-temperature stress affects metabolic and enzyme pathways by causing the addition of ROS: hydroxyl radical ( $\text{OH}^-$ ), singlet oxygen ( $\text{O}_2^-$ ), and hydrogen peroxide ( $\text{HO}_2^-$ ). These molecules are also responsible for oxidative stress in plants (Asada 2006). The major sites of ROS generation are the chloroplast photosystem I (PSI) and photosystem II (PSII). ROS are produced in different organelles such as mitochondria and peroxisomes (Soliman et al. 2011). There is a direct relationship between the accumulation of ROS and the maximum efficiency of PSII. The optimal quantity of ROS is required for proper functioning of plant cells and tissues. Less absorption of a photon occurs from the thermal damage of photosystems. Under stress conditions, PSI and PSII absorb the intensity of photons; the extra quantity is necessary for the incorporation of  $\text{CO}_2$  and is known as extra electrons (Halliwell 2006). During the ROS in photooxidation reactions (flavoprotein, redox cycling),  $\text{O}_2^-$  is produced by the Mehler reaction in chloroplasts. Singlet oxygen is formed in chloroplasts during the process of photoinhibition and PS II reactions of electron transfer (Karuppanapandian et al. 2011).

### 3 Plant Response Under Heat Stress

#### 3.1 Post-transcription and Post-translation Gene Regulation

Various post-transcriptional and post-translational gene regularities have been noted when plants experience stress. The expression level of various genes also changes accordingly. These changes make target at a different level to the same transcript. The activity of stress-related genes responds in the form of the transcript as a signal stress including heat stress. Post-transcriptional and post-translational changes can subsequently affect the specific transcripts for integrating with other signals, including the specific type of the main stress, photoperiod, internal growth, or developmental signals and the hormonal pathway. It is revealed from recent studies that there is an interaction between alternative splicing and micro-RNAs (miRNAs). Different kinds of a given miRNA may be produced from the same gene as a result of alternative splicing (AS). It is also reported that modification in the binding sites of miRNA of the target transcript can be done by AS. In heat induction, pre-mRNA splicing has been reported in *Arabidopsis thaliana* by participating in miRNA processing of the intronic miR400, which illustrates the first type of interaction (Yan et al. 2012). It is also reported that miR400 can be co-transcribed with the help of its host gene At1g32583. During heat stress conditions, an event arises in the intron, carrying the miR400 results in the accumulation of miR400 primary transcripts. In *A. thaliana* overexpression of miR400 results in plants hypersensitive to heat stress. Heat induced a negative regulatory mechanism using miR400 expression, resulting in positive effects on the plant during heat tolerance. Several miRNAs, namely, miR842 and miR846, are produced as a result of AS (Jia and Rock 2013).

Some classes of small RNAs are involved in regulation of genes having different biological processes such as plant growth and biotic and abiotic stress responses. Much relevant evidence of the small RNA-based regulatory mechanism has been studied in reaction to heat stress. They make a class of endogenous small noncoding RNAs 20–24 nucleotides in length that act according to sequence pairing of mRNAs of their target genes and obstructing their translation by cleaving them (Axtell 2013). It shows the effect on different stress-related traits such as opening and closing of stomata, root development, osmo-protection, and antioxidant defense, as well as on crosstalk between pathways of auxin and ABA signaling. For example, *miR398* is associated with antioxidant defense. This miRNA controls different genes, such as Cu/Zn superoxide dismutase (CSD). CSD enzymes scavenge on oxidative stress. On exposure to heat, *miR398* is induced by heat shock transcription factor (HSF), thus masking the expression of the targeted genes *csd1*, *csd2*, and *ccs* (Guan et al. 2013). The heat response results in downregulation of several miRNAs. For example, the expression of *miR159* is decreased in bread wheat when exposed to heat stress (Wang et al. 2012). Transgenic wheat plants with overexpressing *miR159* or the *Arabidopsis* double mutant (*myb33 myb65*) are more susceptible to high temperatures.

Several genes are reported in the literature to have a potential role in heat stress response by utilizing genetic screening and genome-wide expression analysis (Yeh et al. 2012). In response to environmental and developmental signals, plants have post-transcriptional mechanisms by encoding miRNAs. Many miRNAs related to the responses of increase in temperature are recognized, and their response has been studied under heat stress conditions. Stress-upregulated miRNAs can downregulate their target genes in thermal stress. Understanding the roles of miRNAs in cellular tolerance, transcriptome homeostasis, and the phenological and developmental plasticity of plants during stress conditions will be helpful in engineering stress-tolerant crops in future (Jenks et al. 2007).

### 3.2 *Hormonal Pathways*

Different hormones are produced in plants in response to different environmental signals such as heat stress. One of those phytohormones is auxin, which affects many physiological mechanisms during heat stress conditions. Endogenous auxin is reduced in response to heat stress in developing anthers (Teale et al. 2006), whereas the expression of the *YUCCA* auxin biosynthesis gene was repressed through the increase of temperature and male sterility was caused in barley (Oshino et al. 2007). Salicylic acid (SA) has a role during heat stress for growth and development. SA prevents oxidative damage through detoxification of superoxide radicals, although the capacity of antioxidants prevents membrane damages of the plant. SA can increase heat resistance, improve fertility, and increase yield (Sakata et al. 2010). The antioxidant capacity in rice and *Arabidopsis* is found to be increased after the application of SA. The key stress hormone, abscisic acid (ABA), is responsible for stomatal closure during osmotic stress. ABA is also related to Rboh regulation, and Rboh mediates ABA-induced ROS in the guard cells of leaves. RbohD and RbohF are the major catalytics involved in this process (Miller et al. 2008). A high level of ABA increases growth during the vegetative period and reduces growth during the reproductive period, causing male sterility and a reduction in the rate of seed setting (Todaka et al. 2012).

### 3.3 *Phospholipids Pathways*

Many reports are available for the role of phospholipid-based signaling in response to increases in temperature (Zonia and Munnik 2006). Change in the composition of membrane phospholipids is the property of this response. The signals of phosphoinositide (PI) occur in the early events following the onset of heat stress. During subsequent incubation at 40 °C, the metabolism of membrane lipids is not affected significantly. The low level of PI signaling produces stress resistance, and higher

levels can increase damage of the cells. Phosphatidylinositol 4,5-bisphosphate (PIP) and phosphatidic acid are key mediators of pathways of signaling and of cytoskeletal and membrane dynamics organization (Zhu 2002; Staiger and Blanchoin 2006; Mellman et al. 2008). Transfer of phosphate to PI is catalyzed by the PIK enzyme during high temperature. By the activation of PIPK and PDL, heat stress induced the increase of PA and PIP levels. The G protein transduces signals initiated by heat required for PIP and PA accumulation and may be required for activation or localization of PIPK. The role of G protein is based on signaling, which has been identified as a component of heat stress response that is regulated negatively through AIFx (Misra et al. 2007).

### 3.4 Ubiquitination Pathways

The ability of a plant to survive under abiotic stresses depends upon proteomic plasticity. The ubiquitin-proteasome system (UPS) empowers the plants under heat stress to change the proteome for an effective response (Kurepa et al. 2008). UPS response to specific stress governed by the type of substrate protein such as ubiquitin-dependent dilapidation is a positive regulator which can suppress the various pathways under heat stress conditions. It also promotes the cellular changes that help the plants to acclimatize in stress environments. The negative regulator, ubiquitin ligase, is involved in the modification of regulatory proteins (Chen and Hellmann 2013). It also activates signaling pathways in response to stress stimuli under stress conditions. Many examples of UPS working to attenuate stress signals have been reported, such as degradation of ubiquitin-dependent positive regulation after receiving the stress signal. Maintenance of an optimum level of intensity of a signal and the end of its transduction could permit a plant to retain its normal growth and development when normal environmental conditions are recovered. The gene expression of ubiquitin is upregulated in plants when they are exposed to increased temperature conditions. In fact, overexpression of the ubiquitin gene has been proved to improve plant tolerance during abiotic stresses (Guo et al. 2008). After these findings, the role of many ubiquitin enzymes has been demonstrated in plants. Different E2 coding genes have been reported to regulate under stress conditions. For example, transcription levels of *CUBC<sub>2</sub> Glycine max (Gm CUBC<sub>2</sub>; soybean)*, *Arabidopsis UBC32 (At UBC32)*, and *Arachis hypogaea UBC<sub>2</sub> (AhUBC<sub>2</sub>; peanut)* are upregulated by abiotic stress conditions (Cui et al. 2012).

The response of plants during unfavorable environmental conditions is a complex and coordinated process that involves the starting of their signaling network and changes the expression of thousands of genes. By modifying many factors of transcription, the UPS can affect the variations in the expression of genes necessary to lessen the impact of biotic and abiotic stresses. E3 ligases do not allow the transcriptional activity of different transcriptional factors for change from normal conditions, such as the regulation of dehydrated responsive element-binding proteins DREB 2A

through RING type E3 ligase DREB 2A interacting proteins DRIP 1 and DRIP 2. DREB 2A is one of the transcription factors that control the expression of inducible genes during different abiotic stresses (Qin et al. 2008).

### 3.5 Heat Shock Proteins

Besides biochemical, physiological, and morphological mechanisms, molecular techniques are also being used to understand the basics of abiotic stress tolerance in plants. Plants can tolerate all types of stresses through modifying their gene expression and through coordination of gene expression in various pathways (Vinocur and Altman 2005). Similar to some other abiotic stresses, heat stress upregulates inducible genes and their production increases several fold during heat stress conditions. These genes are commonly referred as “heat shock genes” (HSGs) that encode “heat shock proteins” (HSP), proteins that are necessary for the survival of plants under high-temperature stress (Chang et al. 2007; Prasinis et al. 2004). HSPs are grouped into five different classes: HSP20, HSP60, HSP70, HSP90, and HSP100. HSP20 is also called small heat shock proteins (sHSPs). Because of their thermotolerance in nature, HSP expression could be enhanced through heat treatment and conserved heat shock elements (HSEs), which are present in the promoter region of any HSG. These elements are called *cis*-acting elements and consist of different palindromic nucleotide sequences that assist as recognition and binding sites for HSFs (Nover et al. 2001). In many species of plants, HSFs are expressed constitutively during normal conditions. It is reported that HSPs are present in the cytoplasm as monomer bonded, such as HSP70. When plants are exposed to heat stress, HSP70 is dissociated from cytoplasmic monomeric HSFs and enter into the nucleus where they form a trimer that can bind with HSEs (Lee et al. 1995). HSFs can recruit new transcriptional components, resulting in the expression of genes within seconds during high temperatures. Almost all HSGs have HSFs, and overexpression of HSFs switch on the HSGs, which provide protection to living organisms against high-temperature stress. This system is common in all the eukaryotes, but it is very complicated in plants. All plants have many copies of such genes, at least 17 in tomato, and at least 21 HSGs have been reported in *Arabidopsis*. These genes have been categorized into three different classes (A, B, C) that differ in their linkers, which are flexible and have specific domains (Nover et al. 2001).

HSPs are responsible for protein renaturation, stabilizing denatured proteins and repairing of broken membranes in plants during heat stress conditions (Török et al. 2001). Protein denaturation occurs in heat stress because reduced cell volume enhances interaction between damaged molecules. These proteins also target nonactive and imperfectly aggregated proteins in the cells, removing them from the cells (dos Reis et al. 2012). These proteins also function primarily for controlling the proper folding and conformation of both structural and functional proteins, that is, cell membranes and enzymes, respectively. They also ensure the normal functioning

of different cellular proteins during high temperatures. NtH SP70-1 is an example of such proteins that are overexpressed under heat stress in the cotton plant and have an important function during high-temperature conditions.

## **4 Heat Tolerance and Heat Avoidance**

### **4.1 Heat Tolerance**

Heat tolerance is defined as the ability of plants to produce optimal yield during conditions of high-temperature stress. Heat stress tolerance is a specific character in similar species, and even different organs, as well as the tissues of a plant, might show a variable degree of tolerance to high-temperature conditions. Development of heat-tolerant genotypes in a crop is one of the major challenges for a plant breeder (Moreno and Orellana 2011). Plants have developed various mechanisms for survival during high temperature. Tolerance mechanisms include osmoprotectants, late embryogenesis abundant (LEA) proteins, and factors involved in signaling pathways, antioxidant defense, and transcriptional control (Wang et al. 2004). Initial stress signals establish the stress-responsive mechanism through the ionic and osmotic process by changes in membrane fluidity: this helps the plant to reestablish and repair damaged membranes and proteins. In heat stress conditions, modifications in the physiological, biochemical, and molecular processes help to produce heat-tolerant genotypes by identification of potential lines from the germplasm.

### **4.2 Heat Avoidance**

During increased temperature conditions, plants show different mechanisms for their survival. These mechanisms include long-term evolutionary phenological and morphological adaptations and short-term avoidance mechanisms such as changing of leaf orientation, transpiration cooling, and alteration of membrane lipid composition. The closing of stomata, increases in stomata density, reduced water loss, and larger xylem vessels are common heat-induced features in plants (Srivastava et al. 2012). Plants growing in a hot climate avoid heat stress by reducing the absorption of solar radiation. This ability is supported by the presence of small hairs, called tomentose, which form a thick coat on the surface of the leaf, the cuticle. In these plants, blades of a leaf usually turn away from light and position themselves corresponding to the rays of the sun. The effects of radiation from the sun can also be decreased by rolling of leaf blades. Those plants that have small leaves avoid heat stress in a better way than plants with larger leaves. Their heat is evacuated more quickly because of the smaller resistance of the air boundary layer. In well-hydrated plants, the leaves are protected from heat stress by increased transpiration rate. The leaf temperature can be decreased from 6 to 15 °C relative to ambient temperature.

Different plant species have different mechanisms that help them to avoid the hottest period of the year, including abscission of leaves, heat-resistant buds, and in desert plants by completing their entire reproductive cycle during the cool season (Fitter and Hay 2012).

## 5 Screening for Heat Tolerance

Successful breeding programs for heat tolerance always depend upon reliable selection criteria. The first requirement for improvement of a crop involves the characterization of available germplasm for high temperature. It is necessary that dependable and inexpensive screening methods be used to identify agronomic, eco-physiological, and reproductive traits related to stress tolerance. Studies in field conditions have more importance than studies in a controlled environment. Greenhouse and growth chamber studies have also been used to assess the germplasm of cotton for heat stress tolerance. The plants sown in these experiments experience damage to their roots and shoots on exposure to hot conditions, whereas the field-sown plants subjected to increased temperature show more damage to their shoots as compared to roots because of the buffering effects in field conditions (Hall 2004). The basic objective of screening of cotton germplasm and new breeding lines for increased temperature tolerance is to stabilize yield. A reliable selection criteria is required for the valuable breeding program for heat tolerance. Following are some parameters that indicate plant tolerance to high-temperature stress. According to some reports, cell membrane thermostability (CMT) is considered as the most appropriate screening method for determining heat tolerance accessions in germplasm (Blum and Ebercon 1981). Cell membranes are necessary parts of each living cell, acting as a boundary between the environment and the cell protoplasm. These membranes function as a central location for cellular activity and continue their function during stress conditions as well (Raison et al. 1980). The hydrogen bonds of cell membranes are weakened by high temperatures as changes in composition and structure of cell membranes occur. Damage to cell membranes from high-temperature stress modifies their penetrability, which results in the leakage of electrolytes and effects on respiration and photosynthesis. Outflow of electrolytes indicates injury of the cell membrane (McDaniel 1982). It is well known that the static cell membrane has reduced electrolyte outflow, showing heat tolerance, and unstable cell membranes with greater electrolyte leakage indicate heat sensitivity.

Cell membrane thermostability was used for the first time in sorghum for determining heat-tolerant and heat-susceptible genotypes (Sullivan 1972). Later on, this technique was used successfully to determine the degree of heat tolerance in several field crops *i.e.* soybean, wheat, legumes, cowpea, tomato and cotton (Ashraf et al. 1994; Malik et al. 1999; Rahman et al. 2004). Relative cell injury percentage (RCI%) was described as a measure for cell membrane thermostability and could be used to evaluate heat tolerance in *G. hirsutum* (Azhar et al. 2009). It was further described that heat tolerant varieties had stable yield and provide a quality of fibre

superior to that of the susceptible varieties. So, RCI% at the seedling stage could be used as the best screening parameter for cotton germplasm. Loss or decrease of chlorophyll content in plants is associated with a reduction in yield. Genotypes vary significantly under heat stress for their rate of photosynthesis, loss of chlorophyll content, and change in the ratio of chlorophyll *a* to *b* (Reynolds et al. 1994). Okra type leaves are more tolerant to loss of chlorophyll content under high temperature conditions as compared to normal leaves of cotton. Plants with more and stable chlorophyll content are more productive as they produce stable yield under adverse environmental conditions. A higher rate of photosynthesis is observed in plants with more and stable chlorophyll content (Pettigrew et al. 1993). The measurement of leaf chlorophyll content is simply done with chlorophyll meters, available in botanical and agronomic laboratories. Thus, these selection criteria can determine heat-tolerant lines.

A screening technique based on pollen germination can also be used in vitro with the combination of boll retention percentage. Retention of bolls was found to be highly correlated with a maximum number of pollen germination. Some experiments showed the existence of genetic variation for the number of bolls per plant, boll retention, germination of pollen, and pollen tube length: pollen germination, growth of pollen tubes, and their responses to minimum, maximum, and optimum temperatures was noted. This method could be used for differentiating high-temperature-tolerant cultivars from those that are susceptible (Kakani et al. 2005). Length of pollen tube and pollen germination in cotton were found to be decreased during high temperature conditions, with resulting fertilization failure and reduced fruit setting. Along with the aforementioned techniques, other useful screening techniques for high-temperature stress tolerance include pollen viability, proline content, chlorophyll fluorescence, carbon isotopes discrimination, stomatal conductance, canopy temperature, and heat tolerance index (Singh et al. 2007).

## 6 Breeding Strategies for Heat Tolerance

### 6.1 Genetic Variation

Genetic variation is the prerequisite for developing heat-tolerant genotypes through breeding. Much information on the diversity of heat tolerance in different crops such as tomato (Abdul-Baki and Stommel 1995), wheat (Ibrahim and Quick 2001), mung bean (Collins et al. 1995), cowpea (El-kholy et al. 1997), rice (Yoshida et al. 1981), and cotton (ur Rahman et al. 2004) is available in the literature. The existence of genetic variation is essential for improving any trait of a crop. Differential behavior of varieties of cotton has been observed in response to temperature. Information for genetic variability for plant height, plant shape, plant color, number of bolls per plant, number of seeds per boll, and seed weight has been recorded. Unfortunately, the present commercial cultivars of cotton have limited genetic variation for most of these traits (Bradow and Davidonis 2000). The presence of genetic



variation in the germplasm of cotton suggests that genetic improvement can be achieved in this species through breeding and selection, provided that the variation is effected through significant genetic components (Khalid et al. 2010). Presence of significant variability in the gene pool is essential for breeding crop plant tolerance against heat stress. It is more important that variation for heat tolerance is available in plant species such as cotton, soybean, legumes, sorghum, cowpeas, tomato, and wheat (Galiba 1997; Ibrahim and Quick 2001).

Genetic variation for heat stress tolerance is available in cultivars of pima cotton, related to the plant ability for setting bolls at lower nodal positions (Feaster and Turcotte 1985). During higher temperature conditions selection has been found effective for developing lines showing good production in a broad range of environmental conditions (Feaster et al. 1980). Similar results have been observed in upland cotton. Genetic variability for photosynthesis, photo-respiration, chlorophyll fluorescence, chlorophyll content, CMT, and other morphological characters exists in the germplasm. Furthermore, other investigations also proved that high genetic variability in pollen germination, pollen viability, development of pollen tube length, and number of bolls is available in upland cotton, which provides the opportunity for the genetic enhancement for heat tolerance. Besides the normal cotton leaf shape, other leaf shapes range from super-okra (highly cleft leaf) to sub-okra (cleft leaf) (Meredith 1984). This variation in the shape of leaves can bring significant changes in plant traits and aid light interception (Wells et al. 1986). It is found that heat and drought tolerance has similar mechanisms (Reynolds et al. 2001). Nevertheless, all the characters concerning heat tolerance have also been found to be related to drought tolerance; the best example is cell membrane thermostability (Blum 2018).

## 6.2 Gene Action

Gene action for certain traits has been extensively studied in cotton. Some of the results obtained after the study of gene action controlling various traits are discussed here. Plant height, average boll weight, number of bolls per plant, yield of seed cotton, gin turnout, fibre length, fibre strength, and fibre traits are controlled by the additive type of gene action with partial dominance, except for boll weight and gin turnout (Iqbal et al. 2013). Genetic analysis for yield and yield-contributing traits in a diallel analysis of upland cotton genotypes showed that additive dominance was fully adequate for the trait of plant height whereas it was only partially suitable for number of bolls per plant, boll weight, gin turnout, and seed cotton yield (Batoool et al. 2013). Genetic analysis of different morphological and physiological traits in six generations ( $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BC_1$  and  $BC_2$ ) of cotton revealed that plant height, number of bolls per plant, boll weight, gin turnout, fibre length, fibre strength, and fibre fineness are influenced by three types of gene actions, namely, additive, dominance, and interaction. It was also suggested that selection in later segregating generations would help in improving the studied traits (Ahmad et al. 2009).

Inheritance of a number of bolls per plant, seed cotton yield, and height of the main stem was studied in a diallel scheme, indicating that both additive and dominance effects were present in the studied material. Additive and non-additive genetic components could be used through adopting parental matings in an earlier generation for improving the yield-related traits during the crosses of cotton genotypes (Murtaza et al. 2006). In genetic analysis of Egyptian cotton genotypes, it was found that the additive–dominance model was acceptable for demonstrating genetic variability and that it was important for inheriting most of the studied characters. For most studied cases, additive into additive and dominance into dominance were found to be highly significant. Inheritance of all characters was found to be controlled by additive and non-additive types of gene action, but dominant genetic effects had a major role for controlling most studied characters (Abd-El-Haleem et al. 2010). In a complete diallel cross, gene action was studied for number of seeds per boll in  $F_1$  and  $F_2$  populations. The trait was found to be controlled by the additive–dominance model in  $F_1$  whereas  $F_2$  showing partial adequacy (Khan et al. 2007). Six generations ( $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BC_1$  and  $BC_2$ ) of cotton were studied to assess the inheritance pattern of various morphological and yield-contributing traits using generation mean analysis. It was also found that number of bolls per plant and boll weight were controlled by overdominance whereas seed cotton yield was controlled by a partial dominance type of gene action (Hussain et al. 2009).

Eight varieties of cotton were hybridized in diallel mating fasion and produced 64 combinations. The inheritance pattern for the traits (number of bolls per plant and boll weight) was found to be influenced by a non-additive over-dominance type of gene action (Murtaza 2006). Plant height, number of bolls per plant, boll weight, and seed cotton yield were studied to determine the inheritance of four parents of cotton. The inheritance of plant height, number of bolls per plant, and boll weight was influenced by the additive type of gene action with partial dominance whereas seed cotton yield was governed by an over-dominance type of gene action; it was suggested that seed cotton yield could be improved by hybrid breeding. It was also found that epistasis has no effect on the aforementioned traits (Latif et al. 2014). The six generations *i.e.*  $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BC_1$ , and  $BC_2$  were developed to study the gene action involved in controlling yield, yield components, and quality characters of different crosses of cotton by using generation mean analysis. Significantly high mean values were assessed for number of bolls per plant, boll weight, fibre length, fibre strength, fibre fineness, seed cotton yield, and gin turnout. Additive and dominance genetic effects were significantly high for number of bolls per plant and boll weight for all four crosses, where dominant effects were high than additive effects. Similarly, additive and dominance genetic effects were found significantly high for fibre length in the second cross and fibre fineness in a first and fourth cross, having larger dominance effects than additive effects. In the first cross, number of bolls per plant, fibre length, and fibre fineness, in first and second cross, seed cotton yield and gin turnout, in the fourth cross boll weight, and in the second cross fibre strength, showed that these traits were controlled by dominance and nonallelic interactions (El-Refaey and El-Razek 2013).

### 6.3 Heritability of Heat Tolerance

Efforts have been made to modify various plant characteristics, such as insect resistance and yield enhancement, by selecting promising plants for the next generation. The primary purpose of this selection is to identify genotypes that can fulfill the food and fibre requirements. Nowadays, increase of yield in stressful conditions is the main breeding objective for plant breeders. The existence of available genetic differences for heat tolerance allows identifying thermo-sensitive and thermo-tolerant genotypes. Heat-sensitive genotypes can be transformed into tolerant genotypes through different breeding methods. There are two types of heritability: broad-sense heritability and narrow-sense heritability. Broad-sense heritability is the ratio of genotypic variance to phenotypic variance and narrow-sense heritability is the ratio of additive variance to phenotypic variance. Cotton breeders rely on traits having narrow-sense heritability. Breeding methods depend upon heritability of certain traits, whereas heritability depends upon environmental and genetic variances (Nyquist and Baker 1991). If a genetic variance has significant contribution for the expression of traits compared to environmental variance then heritability of particular traits will be high (Acquaah 2009). Percentage of heritability indicates that the specific trait will remain stable in later generations, which is important for the breeding aspect. Studies conducted to understand the heritability of thermotolerance in cotton, thermo-tolerant as well as thermo-sensitive cotton genotypes, were analyzed in populations of F<sub>2</sub> generations. Low heritability was found for fruit set, which indicated that the environment has relatively more influence in the inheritance of thermotolerance as compared with the genetic architecture (Hanson et al. 2002). Low heritability might be due to sub-optimal and less robust methods of phenotyping.

### 6.4 Genetic Engineering

To mitigate the adverse effect of heat stress, various genetic engineering and transgenic approaches are being used by plant scientists (Rodríguez et al. 2005). Constitutive expression of specific proteins has been reported to result from enhanced heat stress (Katiyar-Agarwal et al. 2003). Several studies of the expression of chaperones and manipulation of HSFs resulting in altered gene expression have been described. The genetically modified plants with different degrees of heat tolerance have been developed, but less molecular research work is done on heat tolerance as compared to drought, salt, and cold stress tolerance. Efforts have been made by scientists to utilize HSPs by inducing alterations in transcription factors (*AtHSF1*) in *Arabidopsis*: transgenic *Arabidopsis* was produced for heat stress tolerance. The mitochondrial small HSP (*MT-sHSP*) gene is also utilized for the development of transgenic tobacco (Sanmiya et al. 2004). The *Arabidopsis HSP101* gene was successfully overexpressed in transgenic rice for enhancing thermotolerance.

Similarly, overexpression of the small heat shock protein *sHSP*<sub>17.7</sub> confers heat tolerance in rice (Murakami et al. 2004). Thermotolerance was obtained by transformation of RuBisCo activase. This gene is involved in reversible decarboxylation of RuBisCo, and also protects the photosynthetic apparatus affected by heat stress, which indicates that several technologies could be used for the development of transgenic plants for heat tolerance (Grover et al. 2013).

## 6.5 Omics Approaches

Several technologies are being used to identify transcription, translation, and post-translation procedures and pathways of signaling that control plant response against biotic and abiotic stresses (Hasanuzzaman et al. 2013). In plants, various “omics” techniques such as metabolomics, proteomics, transcriptomics, and genomics are needed for genetic analysis. These techniques allow the minning of genes involved in various pathways involved in response to high temperature. Regulation of genes is determined by attachment of transcriptional factors, chromatin morphology, and *cis*-regulatory sequences shown by transcript profiling.

A number of genes have been reported with their potential role in heat stress response by utilizing genetic screening and genome-wide expression analysis (Yeh et al. 2012). In response to environmental and developmental signals, plants have post-transcriptional mechanisms by encoding miRNAs. These miRNAs have a specific function, so micromics helps to understand the mechanisms involved in developing tolerance to various stresses. Microarray technique has recently become a reliable tool for the systematic examination of the expression profile of a number of genes related to high temperatures (Liu et al. 2011). Transcripts of 170 cDNAs of tobacco were examined under abiotic stress conditions with or without the stimulus of heat stress (Rizhsky et al. 2002). A large number of unique genes that were not upregulated through increased temperatures or drought conditions have been upregulated later on by using both stresses. Complete genome arrays have also been used in *Arabidopsis* to study transcript alterations in response to higher temperatures (38 °C for 6 h), drought (70% relative water content), and the combined effect of these stresses. It was found that many genes were active under both stresses although some specific genes are active under a particular stress (Rizhsky et al. 2004).

## 7 Conclusion

Climate change is caused by the increase in greenhouse gases which is the most serious issue for scientists now a days. This change in climate is the primary factor for increases in global mean temperature, drought, irregular rainfall, and floods. Increase in global mean temperature is a great challenge to crop scientists, especially crop physiologists and plant breeders. Because plant growth and production

of yield are greatly influenced by temperature, the current need is to find new sources to cope with these limiting factors and to ensure the food security of the increasing population. Among several field crops, cotton is one of the top crops grown in the tropical and subtropical regions of the world. Although the cotton plant is called “sun-loving,” high temperature during its growth period exerts adverse impacts on the yield of seed cotton. This issue must be solved by cotton breeders by developing heat-tolerant lines with enhanced quality parameters to meet the requirements of the textile industry. Plant breeders have developed several heat-tolerant cultivars in the past, but these cultivars are now becoming susceptible to heat stress because the temperature of the earth is steadily rising. Previously, scientists used simple morphological assays to select heat-tolerant lines, but now the need of the time is shifting the research paradigm in cotton breeding. Screening based on only morphological and conventional breeding approaches is not sufficient to develop new cultivars. Currently, scientists have begun using various physiological and biochemical assays along with morphological parameters in breeding programs. Use of molecular markers in plant breeding is also becoming common among cotton breeders. Several genetic engineering and omics approaches are also seeking the attention of molecular plant breeders. It is concluded that the use of these modern approaches along with conventional breeding methods will allow plant breeders to develop heat-tolerant lines more efficiently for the sustainable production of cotton crops under changing environmental conditions.

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