INFLUENCE OF HIGH TEMPERATURE AND BREEDING FOR HEAT TOLERANCE IN COTTON: A REVIEW

Rishi P. Singh,[1] P. V. Vara Prasad,[2] K. Sunita,[1]
S. N. Giri[3] and K. Raja Reddy[4]

[1]Division of Genetics, Indian Agricultural Research Institute,
New Delhi 110012, India
[2]Department of Agronomy, Kansas State University,
Manhattan, Kansas 66506
[3]Birsa Agriculture University, Hazaribagh,
Jharkhand 835006, India
[4]Department of Plant and Soil Sciences,
Mississippi State University, Mississippi 39762

Advances in Agronomy, Volume 93

0065-2113/07 $35.00
DOI: 10.1016/S0065-2113(06)93006-5

Cotton (*Gossypium* spp.) is an important crop in several parts of the world, which is highly sensitive to environmental stresses. In the last century, carbon dioxide concentration [CO_2] has risen rapidly from about 350 μmol mol^{-1} in 1980 to about 378 μmol mol^{-1} at present. At the current rate of gas emissions and population increase, it is predicted that CO_2 will double by end of this century. These changes in CO_2 and other greenhouse gases are predicted to increase surface mean temperature in the range of 1.4–5.8 °C. In addition, studies also show that future climates will have more frequent short episodes of high temperature (heat). Most crops are highly sensitive to heat stress and often result in progressively decreasing yields at temperatures above the optimum. In most of the cotton-producing regions, current temperatures are already close to or above the optimum temperature for its growth and yield, particularly during flowering and boll growth period. Therefore, any increase in mean temperature or episodes of heat stress will further decrease yields. One of the most important and economic ways to overcome negative effects of heat stress is to identify and/or develop heat-tolerant cultivars. At present, the major constraint for identifying heat-tolerant cultivars is the lack of reliable screening tool. Better understanding of the possible impact of high-temperature stress on physiological, morphological, and yield processes would not only help in mitigating the adverse effects of high-temperature stress but also in developing reliable field-screening tools. This chapter reviews effects of high temperature on the cotton plant as a whole, including important physiological, growth and yield processes, and fiber properties. In addition, various new screening techniques based on physiological, ecophysiological, and morphological traits to identify tolerant germplasm are discussed in detail. Finally, the genetic, biotechnological, and breeding approaches are discussed herewith to improve understanding of heat tolerance in cotton.

I. INTRODUCTION

Cotton (*Gossypium* spp.) is produced in about 76 countries, covering more than 32 million ha across a wide range of environmental conditions. World cotton commerce is about US$20 billion annually (Saranga *et al.*, 2001). As the world's leading textile fiber plant, cotton forms a vital part of global agriculture and is a mainstay of the economy of many developed and developing countries. Cotton is the main source of employment for millions engaged in production, processing, ginning, textile, and trade-related activities, and contributes to a significant portion of the gross national product of many countries, including India, China, Pakistan, Uzbekistan, Australia, and Greece (FAO, 2005).

About 65% of world cotton production is between 30° N and 37° N latitudes, which includes United States, parts of the former Soviet Union, and China. Approximately 25% of the total production comes from the northern tropics up to 30° N. Small cotton-production areas in Greece, Bulgaria, Romania, China (45° N), and parts of the former Soviet Union are farther north (Lee, 1984). Similarly, small quantities of cotton are grown 40° N in Bulgaria, Russia, and Korea, but the summers are short and only suitable for varieties which mature very quickly (Munro, 1987). The farthest north the crop seems to be Hungary at 46° N and Ukraine at 47° N (Wendel *et al.*, 1992). Today, upland cotton is being grown globally across both tropical and temperate latitudes. The Egyptian crop is grown near sea level or a little higher, while those in East Africa are mostly grown at altitudes over 900 m in Rhodesia, and those of the higher plains of Texas (United States) are probably the highest lying commercial cotton crops in the world. The Sea Island cotton crop of West Indies is grown under fairly high humidity levels. Perennial cottons in parts of Sierra Leone receive annual rainfall of 3300 mm, and perennial cottons under the Himalayas may receive several meters of rainfall in the year (Prentice, 1972).

Cotton is generally regarded as a crop of the hot, semi-arid regions of the world, but is also an important crop in arid-irrigated regions and extends to semi-humid tropics. The area under rainfed cotton varies among countries, but at the global level, cotton area under water-limited conditions is estimated to be around 47% (Hearn, 1994). Outside the tropical belt, temperature rather than rainfall determines the cropping cycle and the crops 30° N can only be grown in the summer months maturing in September–November. The wild cottons generally occur in the tropics and subtropics, that is, in frost-free areas. Wild species of *Gossypium* occur in habitats where maximum temperatures are often very high, especially in the arid regions where insolation rates are very high (Fryxell, 1986). Daytime maximum temperatures in excess of 43°C and high-minimum-nighttime temperatures (27°C or more) are characteristics at low elevations (<450 m) in Arizona (Feaster and Turcotte, 1985). In the United States, Pima cotton (*Gossypium barbadense* L.) is grown primarily in the arid southwest, an area where air temperatures >40°C are common throughout the growing season (Radin, 1992). Similar extremes may occur in areas of the Arabian Peninsula and the deserts of southwestern Africa, where other species of cotton are grown. In the US Cotton Belt, temperature variation is quite large with seasonal variation exceeding 20°C and with greater diurnal variation (Reddy *et al.*, 1995a,b). High temperature had a strong negative correlation with lint yields, with yields decreasing about 110 kg ha^{-1} for each 1°C increase in maximum day temperature. Lobell and Asner (2003) estimated that there was as much as 17% decrease in yields of corn and soybean for each degree centigrade increase in average growing season temperature above the optimum in the United States.

High temperature rarely occurs alone and is often accompanied by high solar irradiance, drought, and wind, all of which exacerbate plant injury from high temperature (Paulsen, 1994). Saranga *et al.* (2001) stressed the coexistence of water and heat stress under arid region field conditions. They emphasized the need for a balance between tolerance of heat and drought, and the need for changing crop water use to improve crop productivity under arid conditions. This need is further strengthened by the fact that changes in cotton germplasm over the past 30 years may have resulted in reduced tolerance of modern cultivars to environmental stresses (Brown *et al.*, 2003; Lewis *et al.*, 2000). Polley (2002) stressed that understanding the interactive effects of rising [CO_2] and temperature for crop yields and water economy is among the major challenges confronting research.

The detrimental effects of high diurnal temperature on various physiological processes impacting crop yields are complex. These complicated effects support the need to merge physiological and genetic approaches to address the problem in a systematic manner and to improve the tolerance to heat stress. It is imperative that more heat-tolerant germplasm be identified (Brown and Zeiher, 1998). In this chapter, the effects of high temperature on cotton plant as a whole, including important physiological, growth and yield processes, and fiber properties, are reviewed. The various ecomorphophysiological screening techniques to identify the tolerant germplasm are discussed in detail. Finally, the genetic, biotechnological, and breeding approaches to improve understanding of heat tolerance in cotton are also discussed.

II. EFFECTS OF HIGH TEMPERATURE

High-temperature stress is among the least understood of the adversities that affect plants (Paulsen, 1994). However, significant progress has been made in the last decade on better understanding of high-temperature stress in several crops, including cotton. Furthermore, in recent years, due to the importance of, and concern about climate change there is a renewed interest in better understanding high-temperature stress and its association with other climate-change factors such as elevated CO_2, UV-B radiation, ozone, and drought. Numerous experiments have been conducted in the last two decades to determine the effect of high temperature at different plant growth stages individually and collectively on yield. A better understanding of plant responses to high temperatures is essential for developing cultivars for production in many hostile environments. Knowledge of high-temperature effects will also help to predict the agronomic consequences of global warming associated with greenhouse gases and to ensure the sustainability of agriculture (Paulsen, 1994; Reddy and Hodges, 2000). The effects of high temperatures at seedling, vegetative, and reproductive stages, including yield and fiber quality of cotton, are summarized in this section.

A. Morphological and Yield Traits

1. Seedling and Root Growth

Optimum temperatures for seed germination and seedling development of cotton range from 28 to 30°C. The base temperature for seed germination is near 12°C, while that for growth is about 15.5°C. Cool temperatures during germination and initial growth are a problem in several locations in the United States particularly across the Mississippi Delta region. Genotypic differences for germination and root development under cool soil temperatures have been observed (Mills *et al.*, 2005). The optimum range of temperature (day/night) for cotton root growth is 30/22–35/27°C, and high temperatures (40/32°C) altered the distribution of roots, causing shallower roots, even under optimum water and nutrient conditions (Reddy *et al.*, 1997b,c).

Burke (2001) reported that seedling heat tolerance is essential in most dryland cotton production areas because producers plant cotton when moisture becomes available. Similarly in North India, the soil temperature and wind velocity at sowing time are very high, resulting in rapid loss of soil moisture (Lather *et al.*, 2001). Under these conditions, emerging cotton seedlings have poorly developed root system, with a primary tap root and the beginnings of lateral root development. Burke (2001) observed that when seedling temperature increases above optimal levels, acquired thermotolerance system is induced. Maximum protection levels are induced when plant temperature reaches 37.7–40°C, but at higher temperatures protection levels decline rapidly.

Root temperature stress alters hydraulic conductivity and nutrient uptake, and regulates hormone synthesis and transport (Burke and Upchurch, 1995; Clarke and Reinhard, 1991). The impact of soil temperatures on the rate of downward extension of the cotton root system has been documented in controlled environments (Bland, 1993). From this study, increase in rooting depth appears predictive for much of the crop lifecycle, because of the temperature-dependent growth responses of seedling roots. Taylor and Klepper (1978) found that cotton roots extend deeper in the soil profile with gradual soil drying. In locations where drip irrigation or shallow wetting of the soil surface occurs, root growth may be restricted to the upper soil layers, with plants becoming prone to drying conditions in a shorter period.

McMichael and Burke (1994) found that the differences in the temperature optima appear to be associated with dynamic changes in seedling development, which may be related to changes in stored seed reserves. Cotton has a strong tap root that can penetrate to more than 3 m, but low pH, compact soil layers, and low [O_2], which can result from water logging, may limit root growth to only 0.45 m (Hearn, 1980). Cotton roots can penetrate at rates up to

90 mm day^{-1} in a rhizotron (Taylor and Ratliff, 1969). In the field on coarse soil, the maximum rate recorded was 50 mm day^{-1}, but was decreased to 8 mm day^{-1} in cool soil temperatures (Bassett *et al.*, 1970). Taylor and Klepper (1974) found that roots continued to grow in drying soil until the water content was 6–7% (−0.1 MPa). However, moisture stress can increase root growth (Brouwer and de Wit, 1969). Numerous functions of roots, including uptake of nutrients and water, assimilation and synthesis of metabolites, and translocation, are very sensitive to temperature. Root temperature may be more critical than shoot temperatures for plant growth because roots have a lower temperature optimum and are less adaptable to extreme fluctuations (Nielsen, 1974). Synthesis of cytokinins which originate predominantly in roots is among the most sensitive processes (Paulsen, 1994).

2. Vegetative Growth

Leaf area development is highly sensitive to temperature. Optimum temperature for leaf area development is 26°C (Reddy *et al.*, 1992a,b). Leaf expansion in cotton occurs at a greater rate in the dark than in the light (Krieg, 1981). At 20 days after emergence (DAE) the leaf area of plants grown at 28°C was found to be six times more than that of plants grown at 21°C (Reddy *et al.*, 1997b,c). Reddy *et al.* (1992a) reported that in upland cotton main stem elongation, leaf area expansion, and biomass accumulation rates were very sensitive to temperature at about 21 DAE. The temperature optimum for stem elongation, leaf area expansion, and biomass accumulation was 30/22°C. Development rates, as depicted by number of main stem nodes produced, number of fruiting branches and fruiting branch nodes were not as sensitive to temperatures above 30/22°C as were growth rates. The length of fruiting branches increased as temperature increased to 30/22°C and then decreased about 25% among plants grown at the two higher temperatures (35/27 and 40/32°C), due to shortening of branch internodes. Growth of fruiting branch length responded to temperature in a similar fashion to main stem elongation and to fruiting branches produced when temperature treatments were imposed at first flower (Reddy *et al.*, 1990). The total length of vegetative branches increased rapidly as temperature increased from 20/12 to 25/17°C. But with further increase in temperature, vegetative branch length declined linearly to near zero at 40/32°C. The leaf area per plant increased rapidly between 28 and 56 DAE at all temperatures. Nearly eight times more leaf area was produced at 30/22°C than at 20/12°C. About 50% more leaf area was produced at 40/32°C than at 30/22°C. Leaf growth rates were 20% and 50% smaller at cooler (20/12°C) and higher (40/30°C) temperatures, respectively, when compared to growth rates at 30/22°C.

Heitholt (1994) speculated that extremely high air temperatures from 31 to 44 days after planting, which reached 34°C or greater each day, reduced canopy growth. In other studies, Reddy *et al.* (1991b, 1992a,b) observed that both upland and Pima cotton main stem elongation rates and node development rates responded significantly to temperature. While in Pima cotton (Reddy *et al.*, 1992b), the main stem elongation rates were very sensitive to temperature after about 21 DAE. Before that time, the differences were small. Main stem node addition rate increased as temperature increased from 20/12 to 40/32°C (Reddy *et al.*, 1992a). The temperature optimum for fruiting branch growth, square and boll production, and retention was 30/22°C. Above 30/22°C, average fruiting branch length was less and square initiation was completely inhibited at 40/32°C, while vegetative branch length kept increasing up to 40/22°C (Reddy *et al.*, 1992a,c). In India, Sikka and Dastur (1960) gave the optimum range for vegetative growth of Asiatic cotton as 21–27°C and cool nights are needed for the best results, but given good moisture conditions the plant can stand temperatures even as high as 43–46°C.

3. Flower Production and Fruit Set

Flowering intervals on vertical and horizontal branches are influenced by temperature (Munro and Farbrother, 1969; Reddy *et al.*, 1997c). Mauney (1966) found similar relationships between temperature and flowering interval. Farbrother (1961) found that the horizontal flowering interval was approximately 11 days in Uganda, where temperatures in the field are fairly uniform throughout the year.

Ehlig and LeMert (1973) observed that the number of flowers per meter of row declined approximately 3 weeks after periods when the maximum temperature exceeded 42°C. Heat stress during flowering resulted in square and flower drop when day temperatures exceeded 30°C (Reddy *et al.*, 1992c). At day temperatures above 40°C, all the squares and flowers were aborted and dropped in several upland cotton cultivars (Reddy *et al.*, 1991a). Pima cotton was more sensitive to high temperature than upland cotton and some of the Pima cotton varieties failed to produce fruiting branches and reproductive sites when the average daily temperature was 36°C (Reddy *et al.*, 1995a, 1997c, 2004, 2005). Although upland type cotton did produce fruiting branches and formed squares at high temperature, it did not successfully produce bolls (Reddy *et al.*, 1991b, 1992a).

High-temperature stress prior to and during flowering significantly influences several reproductive processes leading to decreased fruit set in cotton. Oosterhuis (1999) observed that high temperature could lead to decreased pollen viability and fertilization and this effect usually occurred approximately 17 days before flowering. Similar observations were previously reported (McDonald and Stith, 1972; Meyer, 1969; Powell, 1969; Sarvella, 1966). High temperature of 32 °C at 15–17 days before anthesis caused pollen sterility in temperature-sensitive male sterile lines. Even fertile lines begin to show sterile anthers when temperatures were above 38 °C (Meyer, 1969). The exact stage of development at which the sensitivity occurs is not known; however, based on the timescale of Sarvella (1964) or Quintanilha *et al.* (1962) it occurs after, rather than during, meiosis.

If the plant is able to sustain the flower, high temperatures during anthesis influences pollination and processes leading to fertilization (pollen shed, pollen germination, pollen tube growth, and fertilization). Cotton flowers typically open in the morning between 0700 and 1100 h depending upon the environmental conditions (Pundir, 1972). Once pollen is shed it germinates within 30 min, but actual fertilization occurs between 12 and 24 h after the release of pollen (Pundir, 1972). In west Punjab of Pakistan, the occurrence of nondehiscent anthers and abnormal pollen was observed during the hot months of June, July, and August (Taha *et al.*, 1981). Pollen germination is highly sensitive to temperature, and Burke *et al.* (2004) reported optimal temperature of 28 °C for pollen germination. Suy (1979) found that the rate of pollen tube elongation was near zero below 19 °C and above 45 °C, and the rate of pollen tube growth was linearly related to temperature up to 37 °C, but pollen tube growth declined rapidly above that temperature. Kakani *et al.* (2005) estimated cardinal temperatures for 12 cultivars and reported as 15.0, 31.8, and 43.3 °C (T minimum, T optimum, and T maximum, respectively) for pollen germination and 11.9, 28.6, and 42.9 °C for pollen tube length. Weaver and Timm (1988) suggested that pollen is more sensitive to high temperature than other reproductive organs, which could account for a lack of fertilization under high-temperature stress.

The position of the flower on plant canopy can also affect pollen viability. Burke (2001) demonstrated that pollen harvested in the afternoon from flowers within the canopy had normal pollen viability, while pollen harvested from flowers at the top of the canopy showed a drastic reduction in pollen viability. This differential response may be related to lower temperature in the microenvironment due to lower radiation levels. Under controlled experiment, Zeiher *et al.* (1995) demonstrated that the poor boll set was associated with elevated night temperature. In contrast, night temperature appears to specifically affect square development either by suppressing the development of the reproductive meristem or by increased abortion of young squares. Hesketh and Low (1968) observed that the late-maturing varieties were more susceptible to fruit shedding when grown in temperatures above 30 °C day and 25 °C night. Powell (1969) reported that plants grown at a constant temperature of 29.4 °C did not produce viable pollen. Furthermore, plants grown at 32.2°C did not set fruit even when pollinated with viable pollen, and it was concluded that night temperature had a more pronounced effect on fruit set and boll development.

4. Fruit Growth

Rawson (1992) and Ziska *et al.* (1997) demonstrated that higher temperatures could accelerate crop development and reduce the time during which carbon (dry matter) is gained. Hodges *et al.* (1993) observed that most of the shortening of development time occurs during the boll growth period, resulting in smaller bolls, lower yields, and poor quality lint. At high temperature, crop developmental rate will proceed at much faster rate. Accordingly, the time required to produce squares, flowers, and mature fruits was reduced by an average of 1.6, 3.1, and 6.9 day $°C^{-1}$ of increased temperature, respectively (Reddy *et al.*, 1997c). Furthermore, assuming that temperature increase will be equally distributed throughout the growing season, a 5°C increase in average global temperature should speed development from emergence to maturity by 35 days (Reddy *et al.*, 1997a,b).

High temperatures can have a detrimental effect on boll development. Stockton and Walhood (1960) found that boll size and fiber length decreased with increasing temperatures. Plants exposed to 40°C for 12 h during the fruiting period had less than 1% of the plant mass as bolls (Reddy *et al.*, 1991a). Reddy *et al.* (1992c) observed that boll weight was greatest at 30/32°C and was less at both higher and lower temperatures; moreover, boll growth was more temperature sensitive than vegetative growth. Reddy *et al.* (1992a,b,c) reported that above-optimum temperatures caused considerable problems with boll retention. Furthermore, it was observed that only about 50% of the squares and fruit produced were retained when the average daily temperature was 33°C, and none were retained when the average daily temperature was 36°C. Morris (1964) demonstrated that high temperature shortened the boll maturation period. High temperatures induced square and boll shedding and decreased boll size leading to lower cotton yield (Brown *et al.*, 1995; Reddy *et al.*, 1991a; Zeiher *et al.*, 1995). In the conventional commercial varieties grown in Pakistan, heat-induced sterility was observed when cotton was sown during May or early June. These crops shed almost all their early bolls and they developed excessive vegetative growth due to loss of fruit (Taha *et al.*, 1981).

Gipson and Joham (1968a) observed that low night temperature was negatively correlated with the boll maturation period. High night temperature (25°C) delayed flowering in upland cotton regardless of day temperature (Mauney, 1966). Furthermore, it was observed that both maximum and minimum temperatures influenced the first fruiting branch; higher night temperature progressively delayed the appearance of the first fruiting branch. Night temperature generally exerts more impact than day temperature in controlling flowering (Gipson and Ray, 1969).

5. Yield and Fiber Components

Brown *et al.* (2003) proposed that environmental stresses, particularly water deficit, and temperature stress were mainly responsible for year-to-year variability in cotton yield (Lewis, 2000). Oosterhuis (2002) observed that high temperature during day, followed by high night temperatures, might exacerbate this detrimental effect and provide an important cause of yield variability. Temperature effects on yield are complex; crop responses to changes in temperature depend on the temperature optima for photosynthesis, growth, and yield processes and these optimal values are all different (Conroy *et al.*, 1994; Polley, 2002). When temperature is below the optimum for net photosynthesis, a small increase in temperature can stimulate crop growth. The converse is true when temperature is near the maximum for yield. A small increase in temperature can dramatically reduce yield. Johnson and Wadleigh (1939) reported increases in yields with increases in July average maximum temperature up to 35°C and decreases in yields as the July average maximum temperature exceeded 35°C. All these findings support the concept that there is an optimum temperature for cotton growth and development and growth decreased at temperatures above and below this optimum. However, the optimum temperature was not well defined and may be a characteristic of cultivar differences.

There was a strong negative correlation between high temperature and cotton yield in Arkansas (Oosterhuis, 2002). Under field conditions, cotton foliage in monsoon (rainy season) nights can be warmer by 4–5°C than foliage during nights of drier times (summer season), which significantly decreases vegetative dry matter production, fruit retention, and lint yield (Brown *et al.*, 1995). Bibi *et al.* (2003) observed that average maximum temperatures during boll development in the Mississippi Delta are always well above the optimum range (20–30°C). Oosterhuis (1999) reported that there was no sharp threshold, but rather a gradual decline to more than a 50% decrease in boll development at about 32°C. Furthermore, he reported that the overall result of high temperature was insufficient carbohydrate production to satisfy the plant's needs. This insufficiency can be reflected in increased boll shedding, malformed bolls (e.g., parrot beak), smaller boll size decreased lint percent, and lower yield. Cotton fiber is made predominantly of carbohydrate, therefore, decreased availability of carbohydrate can also be manifested in less fiber and lower ginning turnout. Excessively

Table I
Correlation of Fiber Quality Parameters with Temperature

Fiber trait	Correlation	Temperature condition	References
Fiber length	Negative	Difference between maximum and minimum temperature	Hanson *et al.* (1956)
Fiber strength	Positive	Maximum or mean maximum temperature	Hanson *et al.* (1956)
Fiber strength	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)

high temperature can also decrease seed size, fibers per seed, and fiber length. Oosterhuis (1999) concluded that the end result of high temperature and decreased carbohydrate is fewer seeds, lower fibers per seed, and smaller bolls. The same situation was evident in Arkansas (United States) in 1995 and 1998. The correlations between fiber quality traits and temperatures are given in Table I.

Haigler *et al.* (2005) reported that in central and south Texas, high temperature coupled with water stress during boll filling resulted in relatively short fibers with high micronaire (increase roughness). Bradow *et al.* (2001) demonstrated that temperature (as cumulative heat units or degree) altered the rates of fiber wall deposition and fiber cross-sectioned growth and micronaire. The heat units accumulated in the first 50 days after planting had the most significant effect on micronaire at harvest. The rates of fiber elongation and secondary wall thickening were both influenced by temperature. In experiments with constant growth conditions, Grant *et al.* (1966) found that the shortest period between flowering and boll opening (41 days) was at 29.5°C. Since secondary wall development in fibers and other epidermal cells of the same cotton seed are synchronous (Berlin, 1977), the temperature-dependent rate of cellulose synthesis is probably only a part of more general temperature dependence at the level of the cotton boll. Higher temperatures shorten the boll maturation period while incomplete boll maturation is due to low minimum night temperatures (Yfoulis and Fasoulas, 1978).

Gipson and Joham (1969) and Gipson and Ray (1969) demonstrated that initial stages of fiber elongation were highly sensitive to high night temperatures, whereas the later stages appeared to be less sensitive to temperature. Smutzer and Berlin (1975) confirmed that in upland cotton, var. Dunn, fiber elongation was optimal at 15°C. Night temperatures below 22°C increased the time required for fibers to reach the genetic potential for length of fiber (Gipson and Joham, 1969; Gipson and Ray, 1969). The maximum length of fiber was obtained when night temperatures were between 15 and 21°C, and reduction in length occurred above and below this temperature range (Gipson and Joham, 1968b). Lint index, lint percentage, and lint per boll were decreased by either high (37°C) or low (13°C) night temperatures (Gipson and Ray, 1976). Hesketh and Low (1968) found that among fiber characters the greatest effect was an increase in fiber strength with increased temperature, along with reduced ginning percentage; however, changes in fiber length and micronaire were less consistent. Seed N content was linearly related with night temperature (Gipson and Ray, 1970; Gipson *et al.*, 1969) and the percent oil tended to respond hyperbolically, with the optimum being near 20°C.

6. Growth Traits

It is evident from literature that growth of cotton is highly influenced by temperature. Studies by Jackson (1967) in Sudan (Northeast Africa) revealed that relative growth rate (RGR) and net assimilation rate (NAR) increased with increasing temperature during August through mid-October, but subsequent decrease in temperature decreased NAR. Rajan *et al.* (1973) studied the impact of temperature on growth components at the seedling stage within the range of 10–35°C and showed that NAR, leaf area index (LAI), and leaf area ratio (LAR) increased with increasing temperature. Studies by Singh *et al.* (1987) showed that increasing temperature decreased crop growth rate (CGR) and mean LAI, but improved NAR, specific leaf weight (SLW), and leaf weight ratio (LWR). LAR was, however, not influenced by change in temperature. It appears that if temperature regimes(s) experienced by the crop were supraoptimal it decreased leaf area and biomass production.

B. PHYSIOLOGICAL AND BIOCHEMICAL TRAITS

Temperatures that routinely occur in many cotton-producing regions strongly limit various physiological, biochemical, and growth processes (Reddy *et al.*, 1997a,b,c, 2004, 2005). The most commonly influenced processes include membrane disruption, gas exchange (photosynthesis, photorespiration, stomatal conductance, and transpiration), and translocation.

Table II
Effect on Important Physiological Processes and/or Their Association with High Temperature in Cotton

No.	Physiological processes	Impact/Association	References
1	Crop growth rate (CGR) and maximum and minimum temperature	Negative	Bhardwaj and Singh (1991)
2	Photosynthetically active radiation (PAR) and maximum and minimum temperature	Negative	Bhardwaj and Singh (1991)
3	CGR and mean temperature	Positive	Pettigrew and Meredith (1994)
4	Canopy temperature depression (CTD) and leaf conductance	Positive	Amani *et al.* (1996)
5	Mean leaf area index and maximum and minimum temperatures	Negative	Bhardwaj and Singh (1991)
6	Fraction of PAR absorbed (Fp) and maximum and minimum temperatures	Negative	Bhardwaj and Singh (1991)
7	Photosynthesis (PSII) and high temperature	Negative	Schrader *et al.* (2004)
8	Photorespiration and high temperature	Positive	Krieg (1986) Perry *et al.* (1983)
9	Dark respiration and high temperature	Positive	Guinn (1974); Ludwig *et al.* (1965)
10	Stomatal conductance and transpiration	Positive	Kolb and Robberecht (1996)

The physiological processes affecting the overall performance of cotton and their associations with high temperature are presented in Table II. Although most examples discussed are taken from cotton, at places where such information in cotton is not available, the processes are discussed generally and should be put in perspective of cotton.

1. Membrane Disruption

The plasmalemma and membrane of cell organelles play vital roles in the functioning of cells. Temperature stress on the membranes leads to disruption (Chaisompongopan *et al.*, 1990; Hall, 1993). Horvath *et al.* (1998) and Orvar *et al.* (2000) demonstrated that temperature-induced change in membrane fluidity is one of the immediate consequences during temperature stresses in plants and might represent a potential site of injury. Furthermore, they concluded that membrane fluidity plays a central role in sensing both high- and low-temperature conditions. Research on ultra structural effects of high temperature has focused on chloroplasts because of the extreme sensitivity of many photosynthetic reactions (Paulsen, 1994). Increased thylakoid membrane ionic conductance and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) deactivation have been suggested as the primary cause that inhibits photosynthesis. Schrader *et al.* (2004) demonstrated that in dark-adapted cotton leaves, heating caused an increase in thylakoid permeability at 36°C. The increased permeability did not cause a decline in adenosine 5-triphosphate (ATP) levels during steady state or transient heating. Rapid heating caused a transient decline in ribulose-1, 5-bisphosphate without a decrease in Rubisco activation. However, sustained heating caused a decline in Rubisco activation and also oxidized the stroma as judged by NADP-MDH activation and this is hypothesized to result from increased cyclic photophosphorylation, explaining the maintenance of ATP content in the face of increased thylakoid membrane ion leakiness.

2. Gas Exchange

Reddy *et al.* (1995b) observed that net photosynthesis in cotton was less at both higher and lower temperatures than at optimum (28°C). Net photosynthesis decreases with increasing temperature, while dark respiration increases exponentially with increasing temperatures (Bednarz and van Iersal, 2001). Heat stress inhibited CO_2-exchange rate (CER) primarily by decreasing the activation state of Rubisco via inhibition of Rubisco activase (Law and Crafts-Brander, 1999). Although Rubisco activation was more closely correlated with CER than the maximum quantum yield of photochemistry of photosystem II (PSII), both processes could be acclimated to heat stress by gradually increasing the leaf temperature.

High temperature also increases rates of photorespiration (Krieg, 1986), thus reduces net carbon gain in C_3 species. Perry *et al.* (1983) observed that in cotton a linear increase in photorespiration was recorded as air temperature increases from 22 to 40°C at saturating photon flux density. At 22°C photorespiration was less than 15% of net photosynthesis and was comparable to the dark respiration rate. At 40°C, photorespiration represented about 50% of the net photosynthesis. This indicates that temperature is the major factor influencing the ratio of photorespiration to photosynthesis. Arevalo *et al.* (2004) demonstrated that rates of respiration in the dark were significantly increased in cotton plants grown in elevated night temperatures, and the photosynthetic activity was decreased when measured the next day.

Pima cotton was bred for irrigated production in high-temperature environments. Stomatal conductance in cotton varies genetically over a wide temperature range and has increased with each release of new higher yielding cultivars (Radin *et al.*, 1994). In the high-yielding lines such as Pima S-6, net photosynthesis was constant between 24 and 36°C. Stomatal conductance, on the other hand, increased linearly with temperature in that temperature range from about 0.55 to about 0.8 mmol m^{-2} s^{-1}. Since the increase in stomatal conductance at higher temperatures did not result in higher photosynthetic rates, there was no apparent advantage for higher conductance in the advanced lines in terms of carbon gain (Lu and Zeiger, 1994). However, increased stomatal conductance or transpirational cooling is an important trait by which some plants keep their canopy cool and thus potentially avoid heat stress. Therefore, it is important to consider measuring and using tissue temperatures wherever possible. With the emphasis shifted to plant temperature rather than air temperature, all factors that limit evaporative cooling must also be considered important (Radin *et al.*, 1994), particularly water supply and humidity.

Diurnal trends of canopy conductance and transpiration were measured at four temperatures (20/12, 25/17, 30/22, and 35/27°C) (Reddy *et al.*, 1995c, 1997a, 2005). Conductance and transpiration rate closely followed the diurnal trend in photosynthetic photon flux density on a cloud-free day at all temperatures. Canopy conductance and transpiration increased with increasing temperatures from 20/12 to 35/27°C. Canopy water-use efficiency declined with increased temperature due to increased water loss. Similar observations were observed on leaf-level stomatal conductance and transpiration rates (Reddy *et al.*, 1998). Leaf stomatal conductance increased as temperature increased from 26/18 to 31/23°C and thereafter further increase to 36/28°C did not influence leaf level stomatal conductance. However, leaf transpiration rates increased linearly with increasing temperatures from 26/18 to 36/28°C.

Wright *et al.* (1993) reported that the genotypes with high transpiration efficiency (TE) had higher assimilation (A). Moreover, the genotypes with thicker leaves (low SLA) had significantly higher nitrogen content, indicative of higher photosynthetic capacity. Similarly, Subbarao *et al.* (1995) while discussing the basis of variation in TE through SLA (i.e., leaf thickness) pointed out that it might result from a difference in photosynthetic capacity on a unit leaf area basis.

3. Heat-Shock Proteins

Synthesis and accumulation of proteins during a rapid heat stress is one of the established phenomena. These proteins are designated as heat-shock proteins (HSPs). It has been reported that increased production of these proteins also occurs when plants experience a gradual increase in temperature more typical of that experienced in a natural environment (Abrol and Ingram, 1996). In arid and semi-arid drylands, crop may synthesize and accumulate substantial levels of HSP in response to elevated leaf temperatures. The induction temperature for synthesis and accumulation of HSPs in laboratory-grown cotton ranged from 38 to 41 °C (Burke *et al.*, 1985). In genetic studies it was observed that HSP expression was cosegregating with heat tolerance (Abrol and Ingram, 1996). Genetic variability in the synthesis of HSP in cereal plants was reported by Ougham and Stoddart (1986), Zivy (1987), and Nguyen *et al.* (1989). These reports indicate the possibility of using physiological and genetic approaches in studying the role of HSP genes in plants.

Plant cells respond to heat stress by rapidly accumulating HSPs. However, there is only correlative evidence for HSPs protecting cells from high-temperature stress. There are three main classes of proteins as distinguished by molecular weight of HSP, namely HSP90, HSP70, and low molecular weight (LMW) proteins of 15–30 kDa. The proportions of the three classes differ among species. Under maximum heat stress conditions, HSP70 and HSP90 mRNAs can increase 10-fold and LMW proteins increase as much as 200-fold. Certain proteins, mainly of 15–30, 70, and 90 kDa, are induced in plants at all stages of development by sudden exposure to high temperature. These HSPs are implicated in acquired thermotolerance, maintenance of cell integrity, prevention of protein denaturation, and protection of PSII, but neither these roles nor any involvement in inheritance of high-temperature hardiness have been documented (Vierling, 1991). Attempts have been made with some success to modify plant thermotolerance by over expressing HSP–protein fusions. Lee *et al.* (1995) and Hinderhofer *et al.* (1998) have demonstrated that the basal thermotolerance of *Arabidopsis* can be increased when HSP-reporter fusion genes are introduced into plants.

The appearance of plant HSP is strongly correlated with the development of stress conditions and acquired thermo-tolerance (Burke, 2001). The acquired thermo-tolerance is a complex physiological phenomenon that has been shown to involve some HSPs (Vierling, 1991). Nover *et al.* (2001) reported that the multiplicity and diversity of heat-shock factors in plants is greater than in other organisms. Law and Craft-Brandner (2001) suggested that in response to high temperature, *de novo* protein synthesis rapidly shifted from mainly expression of Rubisco large and small subunits to the major HSPs. The rigidification of thylakoid membrane, but not the plasma membrane, appears to invoke altered expression profiles of heat-shock genes suggesting that the temperature-sensing mechanism could reside in the thylakoid membrane (Horvath *et al.*, 1998). Although varying in magnitude among plant cultivars, most vegetative tissues exhibit an inducible heat-shock response. Germinating pollen, however, has not been found to exhibit the HSP induction pattern upon exposure to elevated sublethal temperatures, and concomitantly exhibits rapid losses in viability upon heat exposure (Hopf *et al.*, 1992). According to Burke *et al.* (2004), this may explain Boyer's observation that those crops with economically valuable reproductive structures show the greatest discrepancy between average and record yields (Boyer, 1982).

III. HEAT STRESS AND HEAT TOLERANCE

A. Definition and Levels of Heat Stress

Brown (2001) reported that heat stress conditions typically develop during monsoon (rainy) season when high air temperatures combined with rising humidity, thus forcing the canopy temperatures to rise above the optimal range for proper fruit development. Brown (2002) defined two levels of heat stress. Level 1 heat stress develops when crop temperature averages between 28 and 30 °C for the 24-h day. Periods of level 1 stress commonly generate light to moderate fruit shed and smaller bolls. Fruit shed usually subsides rather quickly when the stress is relieved. The impact of level 1 stress on cotton reproductive development is often variable. Possible reasons for this variable response include: relative heat tolerance of varieties, field microclimates (e.g., topography and canopy development), crop condition (e.g., fruit retention and crop vigor), and errors associated with estimating crop temperature. Level 2 heat stress develops when average crop temperature is in excess of 30 °C for the 24-h day. Level 2 stress is the more severe stress and typically produces heavier fruit shed as well as malformed and/or smaller bolls. Fruit shed generally subsides once the stress is alleviated, but level 2 stress also impacts the viability of young (14 days prebloom) squares and thus can produce a second, delayed fruit shed nearly two weeks after the stress episode.

B. Heat Tolerance

Hall (2004) defined heat tolerance as where a genotype is more productive than another genotype in environments where heat stress occurs. Heat tolerance can also be defined as the relative performance of a plant or plant process under heat compared with performance under optimal temperature. Resistance to heat is more relevant to the needs of farmers than heat tolerance, whereas heat tolerance often is of interest to scientists studying mechanisms of adaptation. However, there may only be a little or no possibility of complete resistance to high temperatures. Heat tolerance is generally associated with cellular mechanisms that facilitate the maintenance of essential plant structures and functions when the tissues are heated to supraoptimal temperatures (Blum, 1988).

Fischer and Maurer (1978) partitioned stress effects on yield (Y) into parameters measuring susceptibility to stress (S), the extent of the stress (D), and yield potential (YP).

$$Y = \mathrm{YP}(1 - S \times D)$$

where $D = (1 - X/\mathrm{XP})$, and X and XP are the mean yields of all cultivars under stressed and optimal conditions, respectively. With D being a constant for a particular trial, it can be shown that:

$$S = \left(1 - \frac{Y}{\mathrm{YP}}\right) = \frac{(\mathrm{YP} - Y)}{\mathrm{YP}}$$

where S is the yield decrease due to stress relative to the potential yield with a low value of S being desirable. Thus S is the inverse of heat tolerance.

Greater heat tolerance is defined as a specific plant process being damaged less by high tissue temperature and can involve constitutive effects or require acclimation (Hall, 2004). According to Paulsen (1994), numerous characteristics that are associated with resistance of plants to high temperature indicate that thermo-tolerance is highly complex. Stress tolerance to temperature extremes involves complex traits dependent on many attributes. The ability to survive a temperature stress that otherwise would be lethal can be conferred by exposure to a mild nonlethal temperature stress. This induced ability to survive a normally lethal stress is known as acquired thermo-tolerance (Sung *et al.*, 2003).

A heat-resistant cultivar is defined as one that has higher productivity than other cultivars when grown in environments where heat stress occurs. High tissue temperature may be either an advantage or a disadvantage depending on whether the canopy temperature is above or below optimum temperature (Reddy *et al.*, 1991a,b, 1992a,b).

IV. SCREENING FOR HEAT-TOLERANCE TRAITS

Increases in season-long average temperature and periodic episodes of heat stress exacerbate the effect on many aspects of crop growth and development, thereby reducing grain/seed numbers, yield, and fiber content and quality (Reddy *et al.*, 1996). As discussed earlier, different physiological mechanisms may contribute to heat tolerance. In any crop-improvement program, the first and foremost requirement is to identify the suitable stock(s) to be used in breeding. Therefore, it is imperative to use cost-efficient and reliable techniques to screen the available germplasm for various ecophysiological, morphological, and reproductive traits to assist their utilization in crop-breeding programs. Breeding programs may measure such traits to assist in the selection of heat-tolerant parents, segregating generations or advanced lines (Reynolds *et al.*, 2001). A brief description of some new emerging ecological, morphological, and physiological techniques, which are being used in many crop improvement programs particularly at various international crop improvement centers (mainly CIMMYT and IRRI) and other national research centers, are discussed in this section.

Several methods in both field and controlled-environment facilities are commonly being used for screening heat tolerance. Field studies are more advantageous than controlled environment as they represent the true nature of the farmer's and breeder's field conditions. However, the major limitation is the lack of control of the environment, which makes the screening process difficult. Multilocation tests to obtain variable temperature environment should be used for field evaluation of the genotypes for tolerance. Keeping in view the limitations of field studies, several studies are conducted in controlled environment, mainly greenhouses and growth chambers for evaluation of heat tolerance. In such conditions, it is recommended to use a natural soil profile rather than doing pot studies. According to Hall (2004), when plants growing in pots are subjected to high air temperatures, both the shoot and the roots are subjected to hot conditions. In contrast, when plants growing in the field are subjected to high air temperatures, the shoot is subjected to more extreme temperatures than the root system. In field conditions, temperature of the soil below 10 cm is buffered and does not warm as much or cool as much as the air. Consequently, using plants in pots, when studying effects of heat stress can subject roots to unnaturally high temperatures and generate artifacts. However, these controlled environments can be used for preliminary screening but it will be important to also test the performance of the genotypes identified under controlled condition in field conditions before they are used extensively in the breeding programs.

A. Physiological and/or Biochemical Traits

1. Cellular Membrane Thermostability

High temperature modifies membrane composition and structure and can cause leakage of ions. Membrane disruption also causes the inhibition of processes such as photosynthesis and respiration. Alexandrov (1964) concluded that thermostability is determined by the ability of plants to harden in response to high temperature and resist injurious metabolic changes at moderately high temperature, resistance of protoplasmic proteins to denaturation at extremely high temperature, and reparatory capacity of cells after injury. Stability of proteins and other macromolecules may be conveyed by very minor changes in amino acid residues, hydrogen bonds, hydrophobic interactions, addition of glycolic unit, and net free energy of stabilization (Brock, 1985). Sullivan (1972) developed a heat-tolerant test that determines cellular membrane thermostability (CMT) through measuring the amount of electrolyte leakage from leaf disks bathed in deionized water after exposure to heat treatment. Later modification to this method has also been proposed for specific crops. Blum and Ebercon (1981) used this technique to measure both heat and drought tolerance in wheat.

Electrical conductivity of exudates from tissues disks, which is usually expressed as the ratio of values at experimental and lethal temperatures, measures the CMT to stress (Blum and Ebercon, 1981). Some studies showed that these results were similar and associated with field performance (Saadalla *et al.*, 1990a). The method might be less applicable to plants at younger stages than at mature stages; however, cell membranes are less sensitive than thylakoid activities to high temperature in young plants, whereas their liability increases during maturation (Paulsen, 1994). Bibi *et al.* (2003) demonstrated that membrane leakage was the most sensitive technique for quantifying temperature tolerance in cotton under field conditions.

Cell membrane thermal stability has been used as a measure of heat tolerance in several other crops, including rice (Tripathy *et al.*, 2000), soybean (Martineau *et al.*, 1979), potato and tomato (Chen *et al.*, 1982), and cotton (Kakani *et al.* (2005). CMT in rice was used as a major selection index of drought tolerance in cereals (Tripathy *et al.*, 2000). The use of CMT to measure heat tolerance has been successful in cowpea (Hall, 2004). Genetic experiments conducted by Thiaw and Hall (2004) confirmed that leaf-electrolyte-leakage (LEL) under heat stress was negatively correlated with heat tolerance for pod set in cowpea. The LEL protocol (Thiaw, 2003) consisted of subjecting leaf disks to 46°C for 6 h in aerated water, then measuring electrical conductivity of the solution followed by boiling the leaf disks, and then measuring the electrical conductivity of the solution again. The percent leakage during heat stress was calculated from the two measurements. Blum (1988) and others have proposed that plants should be heat-hardened prior to sampling the tissue, and four measurements of electrolyte leakage should be used in calculating CMT. An advantage of the LEL method used by Thiaw (2003) over the CMT method used by Blum *et al.* (2001) is that samples for the LEL method can be taken from plants growing in any field nursery or glasshouse without the need for acclimated plants. Also, only two measurements of electrolyte leakage are needed with the LEL method, so more plants can be evaluated than with the CMT method which requires four measurements.

The LEL protocol (Thiaw and Hall, 2004) has an advantage over direct selection that it can be conducted in the off season with plants grown in moderate temperatures. Thiaw and Hall (2004) proposed an improved method for breeding heat-resistant cowpeas. This method consists of direct selection for abundant flowering and pod set in very hot summer field nurseries or glasshouses, followed by indirect selection using slow LEL in the fall and winter with plants grown under moderate temperatures in greenhouses. However, some studies did not show strong correlation between CMT with reproductive traits such as pollen viability and seed set in several cultivars of peanut (Kakani *et al.*, 2002), cotton (Kakani *et al.*, 2005), and rice (Prasad *et al.*, 2006).

Recent studies on cotton showed that CMT was positively and significantly correlated with biomass and yield under stress conditions but not with biomass or yield under nonstress conditions (Rahman *et al.*, 2004). Blum *et al.* (2001) observed that the associations between CMT and yield under heat stress were reasonably strong and significant but not perfect. Furthermore, they reported that other factors besides CMT may support yield under heat stress, and that CMT alone cannot be used as the criterion in the "final breeding stage" or as a rough selection tool to reduce a large population into the most likely heat-tolerant core at the early stages of the breeding program.

2. Chlorophyll Content

Reynolds *et al.* (1994) exhibited physiological evidence indicating that loss of chlorophyll during grain filling was associated with reduced yield in the field of wheat. Wardlaw *et al.* (1980) and Blum (1986) demonstrated the presence of genetic variability under controlled environmental conditions among wheat cultivars when exposed to high temperature. Similarly, Al-Khatib and Paulsen (1984) and Harding *et al.* (1990) detected similar differences in photosynthesis under heat stress that were associated with a loss of chlorophyll and changes in the ratio of chlorophyll a to b.

Pettigrew *et al.* (1993) showed that the higher assimilation in cotton cultivars with "okra" shaped leaves to had a high SLW (g m^{-2} leaf area) and higher leaf chlorophyll concentration compared with "normal" leaf cultivars. They postulated that the genotypic differences in assimilation were due to a higher concentration of the photosynthetic apparatus per leaf caused by increased leaf thickness. In drought experiments, it was reported that the cotton lines having the highest carbon isotope discrimination values also had the lowest chlorophyll a and b contents (Cohen, 2001; Saranga *et al.*, 2004). High seed cotton-producing lines were characterized by low canopy temperature and high chlorophyll a. There were strong correlations between chlorophyll a and dry matter production under both water-limited and well-watered treatments of cotton (Saranga *et al.*, 2004). Reynolds *et al.* (2000) observed high leaf chlorophyll content in the Mexican wheat landrace collection where the best genotypes showed substantially greater leaf chlorophyll concentration than the standard check. They also established that while high chlorophyll content does not guarantee heat tolerance. However, stay-green trait has been associated with heat tolerance in wheat and similarly high chlorophyll content was associated with heat tolerance of sister lines in some wheat crosses (Reynolds *et al.*, 1997).

3. Chlorophyll Fluorescence

Chlorophyll fluorescence emission kinetics from plants provides an indicator of plant photosynthetic performance (Kaustsky *et al.*, 1960). Siebke *et al.* (1997) demonstrated that fluorescence parameters were related directly to the photosynthetic CO_2 assimilation rate of leaves. The sensitivity of chlorophyll fluorescence to perturbations, in metabolism coupled with the ease and speed of measuring chlorophyll fluorescence, makes fluorescence a potentially useful for noninvasive screening to identify metabolic disturbances in leaves. The ratio of variable to maximum fluorescence (Fv:Fm) of PSII measures the efficiency of excitation energy captured by PSII. Decrease in Fv:Fm indicates an increase in the nonphotochemical quenching of PSII excitation energy, and Fv:Fm can be used to monitor responses to environmental stress (Warner and Burke, 1993). The main drawback in part to use chlorophyll fluorescence has been the small sampling area of commercially available fluorimeters that use fiber optics for collecting fluorescence emissions. Recently, the development of chlorophyll fluorescence imaging systems that can image fluorescence parameters from areas in excess of 100 cm^2 has allowed the application of the technique for the screening of many plants simultaneously. Fv:Fm estimates the maximum quantum efficiency of PSII photochemistry (Butler, 1978). As Fv:Fm is a widely used parameter that estimates the maximum quantum efficiency of PSII photochemistry and can be determined in less than a second, Barbagallo *et al.* (2003) suggested that this should be the preferred parameter for screening where possible. They also demonstrated that a strong correlation exists between Fv:Fm and the leaf area exhibiting chlorophyll fluorescence.

Hall (2004) suggested that for crops where the limiting effect of heat stress involves damage to photosynthesis, there is some merit in trying measurements of chlorophyll fluorescence as an indicator of damage to PSII. Equipment is available that permits rapid field measurement of the Fv:Fm parameter which provides an estimate of the damage to PSII. For this approach, also, key tests have not yet been reported for any species that demonstrate whether selection based on chlorophyll fluorescence is effective in enhancing heat tolerance.

It should be noted that when determining whether a selection method is effective it is also necessary to determine the efficiency of the method: the costs of the selection procedure in relation to the gains that are compared with other selection procedures. Bibi *et al.* (2003) showed significant differences between the obsolete and modern cultivars only at 30.5°C for chlorophyll fluorescence. This technique showed some sensitivity for quantifying temperature tolerance in that it is a much easier technique for field use. Moffat *et al.* (1990) suggested that chlorophyll fluorescence may be more promising as a screening trait, given that association between plant tolerance and lower fluorescence signals have been reported in a number of crops, including wheat. Images of fluorescence parameter (Fv:Fm) have been widely used to detect stress in plants (Maxwell and Johnson, 2000). Jiang and Huang (2000) demonstrated that under the combined drought and heat stresses, the reduction in Fv:Fm was correlated with that of net photosynthesis. The interaction of drought and heat caused more rapid and severe damage to the photochemical efficiency of PSII than either stress alone, similar to the effects on net photosynthesis.

4. Carbon Isotope Discrimination

There are two naturally occurring stable isotopes of carbon, ^{12}C and ^{13}C (Farquhar *et al.*, 1989). Most of the carbon is ^{12}C (98.9%), with 1.1% being ^{13}C. The overall abundance of ^{13}C relative to ^{12}C in plant tissue is commonly less than in the carbon of atmospheric CO_2, indicating that carbon isotope discrimination occurs during the incorporation of CO_2 into plant biomass. This fractionation between ^{13}C and ^{12}C is caused by differences in the diffusivities in air between the heavier and lighter isotope and by the initial carboxylating enzyme (Rubisco) which discriminates against heavier isotope. Carbon isotope analysis integrates the ratio of stable isotopes of carbon (^{13}C:^{12}C) across the life of plant tissue being analyzed. There are strong negative correlations between carbon isotope discrimination (Δ) and water-use efficiency in several plant species (Craufurd *et al.*, 1999; Farquhar and Richards, 1984; Farquhar *et al.*, 1989; Wright *et al.*, 1993). The underlying principle of negative relationship is related to stomatal conductance (Farquhar *et al.*, 1989). As water becomes limiting, stomatal closure occurs, therefore, discrimination against ^{13}C decreases as water stress increases because the ratio of ^{13}C:^{12}C increases in stressed leaves of C_3 plants, and Rubisco has less opportunity to discriminate (Farquhar *et al.*, 1989). The carbon isotope discrimination has not been used to study the effects of high temperature alone or in combination with water stress, despite the fact that heat stress is an important component of drought stress (Williams and Boote, 1995).

Stable carbon isotope discrimination differences among cultivated Pima cotton lines were positively associated with degree of selection for lint yield and heat resistance (Lu *et al.*, 1996). Similarly, Saranga *et al.* (2001) demonstrated that the relatively large quantitative trait loci (QTL) associated with carbon isotope discrimination may help to identify the important physiological traits that contribute to stomatal conductance/photosynthetic capacity relationships under heat and other abiotic stresses.

B. ECOPHYSIOLOGICAL TRAITS

1. Aerodynamic Resistance

Aerodynamic resistance of a crop plays a major role in determining the relative importance of stomatal conductance to TE. If the canopy resistance to heat and water vapor diffusion is large, an increase in stomatal conductance would tend to cool and humidify the air in the boundary layer, thus lowering the leaf-air vapor pressure deficit (VPD); TE would then increase (Farquhar *et al.*, 1989; Reddy *et al.*, 1991b). Thus, cultivars with greater stomatal conductance could assimilate more at the same level of TE (Cowan and Farquhar, 1977; Farquhar *et al.*, 1988). Under field conditions, the boundary layer that forms over crop canopies could cause gas exchange to be less dependent on stomatal conductance, and is thus one of the important factors affecting TE (Jarvis and McNaughton, 1982). A plant with high TE may be able to decrease the aerodynamic conductance of its canopy boundary layer through greater rigidity of the canopy, while maintaining a high stomatal conductance (Walker and Lance, 1991).

Boundary layer resistance at the canopy level depends on canopy architecture, which is determined by leaf size, leaf arrangement, growth habit (i.e., prostrate vs erect), and height of the canopy. With a low canopy conductance, leaf water equilibrates with adjacent airspace of higher humidity than the bulk atmosphere (Walker and Lance, 1991). O'Toole and Real (1986) have shown that aerodynamic resistance and canopy resistance to water vapor transfer can be determined from the linear relationship of difference between canopy and air temperature ($T_c - T_a$) and VPD. Change in either aerodynamic resistance or stomatal resistance among cultivars would influence canopy temperature through an effect on either sensible or latent heat exchanges. Cultivars with warmer canopy temperature, given that all other conditions are equal, will have decreased evapotranspiration (Hatfield *et al.*, 1987). They reported that consistent canopy temperature differences occurred among cotton varieties grown in the irrigated plots even though the environmental conditions varied. In the dryland plots, canopy temperature showed significant cultivar-by-day interaction suggesting that some varieties use available soil water faster than other varieties. Those varieties, which had warmer canopies in the irrigated plots, had the larger biomass in the dryland plots.

Hatfield *et al.* (1987) reported that leaf conductance was positively correlated with leaf water potential (ψ), which indicates that leaf conductance differences among the varieties were influenced by the leaf water status and by factors causing increased canopy temperature and decreased leaf conductance that may have a positive effect on growth. Canopies that were warmer had lower leaf conductance, which would result in decreased transpiration, for example, 10% reduction in evapotranspiration induces a canopy with a temperature 1.5 °C warmer than another (Hatfield *et al.*, 1987). They observed maximum potential differences in evapotranspiration rates of 13%. The decreased transpiration rate in the warmer environment should decrease the rate of water uptake from the profile and increase the period of water availability to the plant.

2. Quantification of Stress Index Using Canopy Temperature

Leaf, foliage, and canopy temperatures have excited plant physiologists and atmospheric physicists alike for more than 100 years (Jackson, 1982). Tanner (1963) stated that plant temperature might be a valuable qualitative index to differences in plant water regimes. In the last 25 years, there has been rapid development in the use of foliage temperature to quantify plant stress. Several indices have been developed based on the comparison of midday foliage and air temperature and their differential.

a. Canopy Temperature Depression. The difference between air and foliage temperature is referred to canopy temperature depression (CTD). The ability of the plant to decrease temperature through transpirational cooling will keep the plant cool and benefits plants at above optimal stress conditions. As much as 10 °C difference between air and leaf temperatures have been reported in cotton (Burke and Upchurch, 1989). Hatfield *et al.* (1987) demonstrated that canopy temperature of field-grown cotton tracked air temperature at night and became cooler than air temperature each morning when the leaf temperature approached 27.5 °C. This temperature was approximately midpoint of an identified thermal kinetic window (TKW) (Burke and Upchurch, 1989). Mahan *et al.* (1995) reported that various factors including leaf area, root to leaf ratio, leaf orientation, size and shape, surface characteristics (e.g., pubescence), leaf thickness and size, and distribution of stomata are known to affect transpiration. Nobel (1999) reported that the sun tracking of leaves could reduce their temperature by up to 6°C. Accordingly, small leaf has thinner boundary layer that is more conducive to sensible and latent heat transfers and as a consequence is often cooler than bigger leaves in similar environments.

CTD has been used to quantify stress within a given species (Idso *et al.*, 1981; Jackson *et al.*, 1981). In cotton, the relationships among canopy temperature, VPD, and stress have allowed the development of crop stress indices. Amani *et al.* (1996) reported that for a given genotype, CTD is a function of a number of environmental factors, principally soil water status, air temperature, relative humidity, and incident radiation. Moreover, they have also demonstrated that the trait is best expressed at high VPD conditions associated with low relative humidity and warm air temperature. The relative importance of the characteristic of individual leaves decreases as the plant canopy becomes denser. Under these conditions the aerodynamic characteristics of the canopy play a major role in the energy transfer between the plant and environment. Ham *et al.* (1991) and Mateos *et al.* (1991) studied the effect of canopy closure on the energy balance of plants and concluded that rapid closure of the canopy will reduce the occurrence of high leaf temperature.

b. Crop Water Stress Index. Initially stress degree day (SDD) was defined as the difference in foliage and air temperature (Idso *et al.*, 1977; Jackson *et al.*, 1977) to account water stress of crops. Later, Idso *et al.* (1981) incorporated VPD to account for differences among environments and the concept of crop water stress index (CWSI) was refined to include this parameter. Ehrler (1973) concluded that using leaf-air temperature differences for scheduling irrigations in cotton was useful. Ehrler *et al.* (1978) demonstrated that the difference in leaf and air temperature of well-irrigated cotton and wheat was linearly related to VPD of the atmosphere 1 m above the crop canopy. Idso *et al.* (1981) and Idso (1982) confirmed this observation at four different locations in the United States and further illustrated that a unique linear relationship between canopy-air temperature ($T_c - T_a$) and VPD could be found for 26 agricultural crop species.

The relationship between canopy temperature, air temperature, and transpiration is not simple and involves atmospheric conditions (VPD, air temperature, and wind velocity), soil (soil moisture), and plant morphophysiological characteristics (canopy size, canopy architecture, and leaf adjustment to water deficit). These variables are considered when canopy temperature is used to develop the CWSI. The CWSI is a measure of the relative transpiration rate occurring from a plant at the time of measurement using a measure of plant temperature and VPD (refers to dryness of the air). Jackson *et al.* (1981) presented the theory behind the energy balance that separates net radiation from the sun into sensible heat that heats the air, and latent heat that is used for transpiration. The CWSI incorporates midday values of net radiation, canopy and air temperature, VPD, aerodynamic resistance, and canopy resistance into an energy balance for a crop surface. The CWSI has been related to yield in cotton (Burke *et al.*, 1990). When a plant is transpiring fully the leaf temperature is 1–4 °C below the air temperature and CWSI is zero. As the transpiration decreases, the leaf temperature rises and can reach to 4–6 °C above the air temperature. When the plant is no longer transpiring the CWSI is 1. However, O'Toole and Hatfield (1983) found that wind speed influenced the canopy to air temperature difference. Some researchers (Hatfield, 1985; Wanjura *et al.*, 1984) demonstrated that the unstressed baseline of cotton for the CWSI varies slightly from those initially defined by Idso *et al.* (1981).

Keener and Kircher (1983) studied the effectiveness of SDD, water stress index, and CWSI which were developed for arid or semi-arid regions. It was demonstrated by these authors that CWSI would be of limited utility under humid conditions. Jackson *et al.* (1981) also acknowledge the potential problems in humid environments and pointed out that the occurrence of leaf temperature warmer than air temperature presents a limitation of any of the current canopy temperature-based stress indices.

c. Thermal Stress Index. The CWSI method often exhibits values below 0 and above 1 in areas with VPD below 1.0 kPa. This effect is due to the limitations in resolving differences in T_c and T_a in regions of high humidity as reported by Burke *et al.* (1990). These authors stressed that the impact of changing air temperature on plant growth and performance can be understood only when the temperature providing optimum enzyme function is known. Burke *et al.* (1988) reported that the temperature range for which the value of the apparent K_m remained within 200% of the minimum observed value was defined as the TKW for optimum enzyme function. For crop plants, the TKW is generally established as a result of thermally induced lipid phase, changes in Rubisco activity, and the starch synthesis pathway in leaves and reproductive organs. The temperature response curves for recovery of PSII fluorescence following illumination compare favorably with the TKW in several crop species (Burke, 1990). Overall, the TKW is useful in defining the bounds of thermal stress in plants and exploring the genetic improvement of heat tolerance using a molecular approach (Nguyen, 1994).

Burke and Upchurch (1989) found the TKW for cotton is 23.5–32 °C through the relationship between leaf and air temperatures and plant water use. Burke *et al.* (1988) demonstrated that canopies of both wheat and cotton were only within their TKW for approximately 30% of the growing season in west Texas. The length of time the plant temperature was within the TKW was related to biomass production. Furthermore, Burke *et al.* (1990) suggested the potential use of the crop-specific biochemical temperature optimum (the midpoint temperature 27.5 °C of the TKW for cotton) as baseline temperature for a TSI. The formula for TSI suggested by the author is

$$\mathrm{TSI} = \frac{(T_\mathrm{f} > T_\mathrm{b})}{T_\mathrm{b}}$$

where T_f is foliage temperature and T_b is the biochemically determined base line temperature of 27.5°C. The values of TSI range from zero to some positive limit and are restricted to a thermal stress resulting from an inability of the plant to cool either because of soil water deficit or because of physical limitation to cooling resulting from high humidity levels. The biochemical-based TSI and the physically based CWSI were highly correlated ($r^2 = 0.92$) for cotton across a range of environmental conditions.

C. ASSOCIATION AMONG ECOPHYSIOLOGICAL, MORPHOLOGICAL, AND YIELD TRAITS

In any breeding program the knowledge of association among different traits is of paramount importance. The information generated from character association studies can be utilized to determine the correlated response (if any) and to decide the breeding methodology/strategy for the successful incorporation of useful traits in optimum combination. The association among various ecophysiological, morphological, and yield components reported elsewhere is summarized in this section and presented in Table III.

Feaster and Turcotte (1985) reported a highly significant negative correlation ($r^2 = 0.79$) between fruiting height and yield. Empirically the first fruiting nodes number has been associated with earliness of a particular genotype. Again earliness has been found to be negatively correlated with yield in Pima cotton. Temperature is an important factor modulating the interrelationship(s) of the above parameters. Bhardwaj and Singh (1991) demonstrated that CGR is positively correlated with photosynthetically active radiation (PAR) (absorbed), fraction of photosynthetically active radiation absorbed (Fp), and mean LAI but negatively with maximum and minimum temperatures. On the other hand, PAR absorbed is correlated positively with Fp and LAI but negatively with maximum and minimum temperatures. Furthermore, LAI and Fp also had negative correlation with temperature (maximum and minimum), and Fp was correlated negatively with SLW.

Pettigrew and Meredith (1994) reported that CER was positively correlated with N fertilization ($r = 0.768$) and SLW ($r = 0.568$). CGR was correlated positively with light utilization efficiency (LUE) along with LAI, mean temperature, and SLW. CGR possesses a positive correlation with

Table III
The Association Among Eco-Morpho-Physiological Parameters and Yield

No.	Parameters	Association with yield	References
1	Cell membrane thermostability (CMT)	Positive	Bibi *et al.* (2003), Rahman *et al.* (2004), Reynolds *et al.* (2001), Saadalla *et al.* (1990b)
2	Canopy temperature depression (CTD)	Positive	Idso and Reginato (1982), Reynolds *et al.* (1998)
3	Leaf and stomatal conductance	Positive	Amani *et al.* (1996), Lu *et al.* (1994)
4	Crop water stress index (CWSI)	Positive	Burke *et al.* (1990)
5	Thermal stress index	Positive	Burke *et al.* (1990)
6	Carbon isotopes discrimination differences	Positive	Lu *et al.* (1996)
7	Leaf chlorophyll content	Positive	Reynolds *et al.* (2001), Saranga *et al.* (2004)
8	Stay-green effect	Positive	Reynolds *et al.* (2001)
9	Chlorophyll fluorescence	Positive	Bibi *et al.* (2003)
10	Dark respiration	Negative	Oosterhuis *et al.* (2002), Hodges *et al.* (1991)
11	Photosynthesis	Positive	Lu *et al.* (1994), Reynolds *et al.* (2001)

LUE and mean LAI (Bhardwaj and Singh, 1991). They speculated that the crop follows the same strategy to combat higher temperatures. When temperatures approach 41/30°C (maximum and minimum, respectively) leaf area growth ceases and is followed by no crop growth (i.e., zero CGR) at 42/31°C. Photosynthesis is evenly balanced by respiratory activity (i.e., compensation point). PAR was not absorbed by the crop at 43/32°C whereas light interception ceases at 46/34°C. At this stage the crop would register negative growth owing to stoppage of photosynthesis but continuation of photo and dark respirations.

Abrol and Ingram (1996) reported that correlation between synthesis and accumulation of HSPs and heat tolerance suggests, but does not prove that the two are causally related. Cell membrane thermostability was found to be highly correlated to heat stress at the seedling and anthesis stages in cotton (Saadalla *et al.*, 1990b). However, it was observed that there is no correlation between CMT and tolerance during anthesis particularly related to pollen germination and tube growth of cultivars which had higher temperature optima and greater pollen germination (Kakani *et al.*, 2005). It was shown that in cotton, heat tolerance does not correlate with degree of lipid saturation (Rikin *et al.*, 1993). Similar observations in genotypes of other crops species in relation to heat tolerance and membrane lipid were reported (Kee and Nobel, 1985).

Idso *et al.* (1984) established a strong correlation of CTD with yield. Similarly, Reynolds *et al.* (1998) observed that CTD had high genetic correlation with yield and high values of proportion of direct response to selection indicating that the traits are heritable and therefore, amenable to early generation selection. Since CTD is directly or indirectly affected by a number of physiological processes, it is a good indicator of genotype fitness in a given environment. CTD and leaf conductance show an association with each other and with yield (Amani *et al.*, 1996). The possibility of coupling selection for both traits is attractive. Reynolds *et al.* (2001) suggested that CTD could be used to select among early generation bulks that are heterogeneous and may still be segregating. CTD also seems to be affected by the ability of a genotype to partition assimilation to yield and is indicated by the fact that CTD frequently shows a better association with yield (Reynolds *et al.*, 2001).

Radin *et al.* (1994) reported a positive relationship between photosynthetic rate and stomatal conductance in the low range of conductance values up to about 0.4 mmol m^{-2} s^{-1}, but apparent relation at higher conductance values, and therefore, failed to support the hypothesis that the observed variation in stomatal conductance was mediated by variation in photosynthetic rates. There is a strong correlation between assimilation and stomatal conductance over a wide range of cultivar of plant species and under a diversity of environmental conditions (Wong *et al.*, 1979).

Reynolds *et al.* (1994) demonstrated that loss of chlorophyll during grain filling is associated with reduced yield of wheat. The difference in photosynthesis under heat stress has been shown to be associated with a loss of chlorophyll and a change in the chlorophyll a:b ratio due to premature leaf senescence (Al-Khatib and Paulsen, 1984; Harding *et al.*, 1990). The CTD which is a function of stomatal conductance (Amani *et al.*, 1996) is a mechanism of heat escape in cotton (Cornish *et al.*, 1991).

Under high-temperature conditions the respiration costs are higher, leading eventually to carbon starvation because assimilation cannot keep pace with respiratory losses (Levitt, 1980). This process would seem unavoidable, as evidenced by the positive association recorded between dark respiration at high temperature and heat tolerance in sorghum lines (Gerik and Eastin, 1985). On the other hand, high rates of respiration may be severely detrimental to yield in wheat (Wardlaw *et al.*, 1989) and cotton (Hodges *et al.*, 1991; Oosterhuis *et al.*, 2002). Reynolds *et al.* (1998) demonstrated that there is positive association between heat tolerance and both leaf respiration and CMT; thereby indicating that nonphotosynthetic cellular metabolism is associated with sensitivity to warmer environments in wheat. Significant positive genetic correlations between wheat yield and CTD, CMT and leaf chlorophyll during grain filling, leaf conductance and photosynthesis have been reported under heat stress conditions (Reynolds *et al.*, 2001).

A strong positive correlation has been observed between carbon isotope discrimination and specific leaf area among groundnut genotypes (Rao and Wright, 1994). This is consistent with the hypothesis that high TE genotypes have higher assimilation. Indeed, the genotypes with thicker leaves (low SLA) had significantly higher leaf nitrogen contents, again indicative of higher photosynthetic capacity. The significant application of these observations is that breeders could use the inexpensively measured specific leaf area in lieu of carbon isotope discrimination, to screen for high TE among genotypes within a specific environment (Craufurd *et al.*, 1999; Wright *et al.*, 1993). Correlated traits such as specific leaf area, which has been shown to be related with carbon isotope discrimination, could thus be used as a surrogate to ^{13}C discrimination analysis (Craufurd *et al.*, 1999; Subbarao *et al.*, 1995). El-Sharkawy *et al.* (1965) found a negative correlation between leaf thickness and CER among several cotton species.

Reddy *et al.* (1992c) observed that flower retention was negatively associated with the number of hours per day the plants were exposed to 40°C. Ehlers and Hall (1996) reported the association present between reproductive-stage heat tolerance and extreme earliness. Ahmed *et al.* (1993) speculated that this association may be due to heat susceptibility being caused by certain phytochromes that also cause late flowering. This association between extreme earliness and heat tolerance has been observed in other species.

McDonald and Stith (1972) had seen simple correlations between maximum temperature at 17 days preanthesis and sterility. Fisher (1973) did not find significant correlations between boll set and maximum temperature, though he observed highly significant negative correlations between boll set and minimum night temperature. Yfoulis and Fasoulas (1973) observed a negative correlation between the 24-h cycle mean temperature and boll period and genetic responses to temperature changes. Oosterhuis (1997) observed a strong negative correlation between yield and temperature in August when boll development occurs.

Cotton canopy architecture, particularly with respect to plant height and branch formation, is modified temperature (Hanson *et al.*, 1956; Reddy *et al.*, 1990, 1997c). Higher temperature can have significant negative impact on photosynthesis, reduced photosynthetic rates, and the modulation of other metabolic factors, in association with lower light intensities, may result in lower micronaire, fiber strength, and yield (Pettigrew, 1996). The micronaire reading of fiber produced in the warmest environment was highest (Quisenberry and Kohel, 1975).

V. BREEDING FOR HIGH-TEMPERATURE TOLERANCE

A. Trait Selection

Nasyrov (2004) emphasized that the selection of plants on a physiological and genetic basis will make it possible to get varieties and hybrids with high photosynthetic efficiency and a balanced ratio between source and sink that will provide the maximum expression of yield potential. This task cannot be solved by geneticists alone because it is necessary to overcome the accursed negative correlation between yield and plant resistance.

Tolerance to high soil temperatures during seed germination would appear to require constitutive genetic effects; although the mother-plant environment during seed development and maturation can influence the heat tolerance of seed during germination. Tolerance to high tissue temperatures during plant emergence and early seedling growth involves both constitutive and acclimation effects. Seedlings subjected to moderately high temperatures synthesize a novel set of proteins that have been called HSPs, and the plants become more tolerant, in terms of plant survival, to more extreme temperatures (Vierling, 1991). These proteins are thought to enable cells to survive the harmful effects of heat by two general mechanisms: as molecular chaperones and by targeting proteins for degradation. As an example of chaperone activity, it has been shown that a specific small HSP cooperates with other HSPs to reactivate a heat-denatured protein (Lee and Vierling, 2000). HSPs do not appear to be the only mechanism whereby plants differ in heat tolerance (Hall, 2004). In cotton, Rahman *et al.* (2004) reported that CMT could be a useful technique for differentiating heat-tolerant and heat-susceptible cottons; however, they cautioned regarding its indirect selection on the basis of seed cotton yield under non-heat-stressed environments.

While working on the development of heat-tolerant Pima cotton cultivars in the late 1950s in Arizona, several indices were developed to select the heat-tolerant Pima cotton genotypes (visual index in 1962, and phenotypic index and fruit-height response index in 1964). Feaster and Turcotte (1985) concluded that fruiting-height response at low elevation in Arizona was an effective indicator of heat tolerance. The lower fruiting genotypes have greater heat tolerance since they are capable of fruiting well during July and August when minimum night temperatures are high.

Faver *et al.* (1996) suggested that a genetic base may exist for improving the photosynthetic capacity, and genetic differences have been reported in the rate of carbon assimilation in cotton. Light distribution can be affected by the species of cotton (Sassenrath-Cole, 1995). Upland cotton exhibited regular leaf shapes throughout the growing season and was diaheliotropic. Pima cotton leaves were large and fairly flat early in the season, but progressively became more cupped at increasing main stem positions and showed no heliotropic response. As a result of the solar-tracking response and leaf shape, the canopy light environment differed for two species. Genotypic differences in CER could be due to a greater concentration of photosynthetic apparatus per unit leaf area caused by leaf thickness differences. Genetic differences in photosynthetic capacity may be detected indirectly by selecting for leaves that have more dry weight per unit leaf area, because they usually have higher levels of photosynthetic enzymes and photosystem components per unit leaf area (Hall, 2001). The functional relationship between smaller leaf areas and higher yield potential and heat resistance is also of interest. Boundary layer resistance and heat transfer are markedly dependent on leaf dimensions (Nobel, 1991). Use of the energy balance model to stimulate the effect of leaf width on leaf temperature at high irradiance and high stomatal conductance showed that leaf temperature decreases with width (Lu *et al.*, 1992) thus, the smaller leaf area of the advanced Pima lines might contribute to their enhanced heat resistance (avoidance). It is of interest that leaves from the more productive upland cotton are smaller than leaves from Pima S-7, the commercial Pima line currently in use. In contrast, the stomatal conductance, which was uniformly high in all elite lines. This observation suggests that selection pressures for higher stomatal conductance have been stronger than those for leaf area. Lu *et al.* (1997) suggested that higher stomatal conductance and photosynthetic rate and smaller leaf areas are functionally important for the attainment of higher heat tolerance and yields.

Pettigrew *et al.* (1993) suggested that photosynthetic rate could be a selection criterion for plant breeders especially if lines with superior photosynthesis could be identified and coupled with those lines with suitable partitioning of photosynthates between reproductive and vegetative growth. Establishing why certain lines may differ in photosynthetic rate could provide more tools for selection. Plant breeders can use photosynthetic rate as a selection criterion for improved lines. These improved lines in turn could be crossed with other lines that possess suitable partitioning of photosynthates between reproductive and vegetative growth (Pettigrew and Meredith, 1994). Significant negative correlation has been shown between photosynthetic capacity and specific leaf area (Dornhoff and Shibles, 1976). According to Subbarao *et al.* (1995), this evidence suggests indirectly that basis of variation in TE through specific leaf area (i.e., leaf thickness) may result from difference in photosynthetic capacity on a unit leaf area basis. El-Sharkawy *et al.* (1965) reported the presence of significant genetic differences in photosynthetic rate in cotton and suggested the possibility of differences in ratio of photosynthesis to photorespiration.

The extent to which respiration can be increased through selecting for leaf traits that influence photosynthesis is controversial (Evans, 1983). However, some studies reported that increasing productivity of wheat, cotton, and soybean was positively associated with stomatal conductance and photosynthetic rate (Condon and Hall, 1997; Fischer *et al.*, 1998; Lu *et al.*, 1998; Morrison *et al.*, 1999). Lu *et al.* (1996, 1998) concluded decisively that independent selection pressure exists independent of photosynthetic rates for higher stomatal conductance and for a relationship between stomatal conductance and yield. Radin *et al.* (1994) emphasized that one cycle of selection solely for conductance from a segregating population led to decreased leaf temperature and enhanced yield. Furthermore, they reported that the stomatal component of heat resistance was apparently dependent upon evaporative cooling. This represents a "heat avoidance strategy" in that leaf temperature decrease without necessarily increasing tissue tolerance to thermal stress. The genetic variability for an avoidance of heat resistance has been reported. Lu *et al.* (1994) and Radin *et al.* (1994) in follow-up studies under field and laboratory conditions have demonstrated that independent selection processes for higher net photosynthesis and stomatal conductance. The stomatal response to temperature is as a key stomatal property altered by selection for higher yields and heat tolerance (Lu and Zeiger, 1994). Ulloa *et al.* (2000) worked on the hypothesis that selection for high yields had imposed indirect selection pressure for elevated stomatal conductance at supraoptimal temperature under irrigated environments. This increased conductance may reduce leaf temperature and confer tolerance (or avoidance) to high temperatures especially during critical fruiting periods. Lu and Zeiger (1994) reported that the selection pressure for higher stomatal conductance cannot be explained by an adaptive advantage of enhanced carbon gain.

Saranga *et al.* (2004) suggested that there are important opportunities for developing polyploid crop genotypes that retain commercial levels of quality and productivity. Different cotton species have evolved different alleles related to physiological responses for improved adaptation to abiotic stress. Furthermore, the discovery in several cases of complementary favorable alleles on homologous chromosome showed that by assembling interspecific hybrid genotypes both *Gossypium hirsutum* and *G. barbadense* could be improved relative to their native state. This exemplifies the unique opportunities to evolve favorable new traits that accrue as a result of polyploid formation; the evolution of the genus *Gossypium* has included a very successful experiment in polyploid formation. The merger of two genomes A and D with different evolutionary histories in a common nucleus appears to offer unique avenues for phenotypic response to selection (Jiang *et al.*, 1998). Burke (2001) suggested on the basis of research in wheat that it is possible that chromosomal deletions in the A or D genome of cotton would provide an enhanced, acquired thermo-tolerance system.

B. Correlated Response of Selected Trait

In the past, the breeding of agricultural crops for higher yields has been very successful. Breeders usually select for high-yielding genotypes by using empirical methods, paying less attention to specific plant traits that might be conducive to higher yields. However, comparing old, low-yielding lines of any crop with advanced, high-yielding lines shows clearly that many morphological, physiological, and biochemical traits have been altered by the intense selection pressure for higher yield. These changes indicate that selection for high-yielding genotypes has generated indirect selection pressure on the altered traits. If one excludes effects of genes that regulate the expression of two or more unrelated traits (pleiotrophic genes), the study of high-yielding lines might reveal specific traits and genes associated with higher yield. With this information, breeders could explicitly select for yield-enhancing traits to further improve yields. Lu *et al.* (1997) speculated that intensive selection for higher yield and heat resistance in Pima cotton has generated indirect selection pressure on photosynthetic rate, stomatal conductance, and leaf areas that parallel the interspecific trait difference between upland and Pima cotton and their agronomic performance. This is an example of correlated response to selection. Lu and Zeiger (1994) found that selection for agronomic traits such as yield potential can lead to genetically stable changes in stomatal properties. These changes could be functionally related to other agronomic traits under selection and thus the selection for higher yields has imposed selection pressures for higher photosynthetic rates (Cornish *et al.*, 1991). The higher stomatal conductance would have resulted from a coupling between photosynthesis and conductance (Wong *et al.*, 1979) rather than from selection pressures on higher stomatal conductance per se. Lu and Zeiger (1994) studied conductance in an F2 population derived from an interspecific cross showed a segregation pattern typical of other genetically determined traits. Selection for heat resistance might have favored genotypes having an enhanced evaporative cooling and lower leaf temperature mediated by higher stomatal conductance.

Reynolds *et al.* (2001) used CTD as an indirect selection criterion for genetic gains in wheat yield. They reported that CTD is affected by many physiological factors, which makes it a powerful integrative trait. Since CTD is directly or indirectly affected by a number of physiological processes, it is a good indicator of a genotype's fitness in a given environment. Furthermore, CTD also seems to be affected by the ability of a genotype to partition assimilates to yield, indicated by the fact that CTD frequently had a closer association with yield and grain number than it does with total above ground biomass. Indirect selection procedures based on the measurement of canopy temperatures using remote sensing could be more effective than direct selection based on the measurement of the stomatal conductance of individual leaves. Promising progress has been made in applying this

Table IV
Important Morphophysiological Selectable Traits Against Heat Tolerance/Heat Stress

No.	Trait	Characteristics	References
(A) Morphological traits amenable to direct selection			
1	Okra leaf type	Higher leaf (N) content	Pettigrew (2004)
		Higher CO_2-exchange rate (CER)	
		Higher photoelectron transport rate	
		Reduced nonphotochemical quenching	
		Reduced individual leaf area	Wells *et al.* (1986)
		Higher photosynthesis	
2	Lower fruiting height	Greater heat tolerance	Feaster and Turcotte (1985)
3	Thicker leaves	Higher N content	Hall (2001)
		Higher photosynthetic capacity	Wright *et al.* (1993)
4	Abundant flowering and fruiting at high 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	Rodriguez-Garay and Barrow (1988)
		Reproductive stage heat tolerance	Hall (1992)
(B) Physiological traits for both direct and/or indirect selection			
1	Cell membrane thermostability (CMT)	Measures the resistance of protoplasmic proteins to denaturations	Saadalla *et al.* (1990a), Blum and Ebercon (1981), Bibi *et al.* (2003), Rahman *et al.* (2004)
		Heat and drought tolerance	Ashraf *et al.* (1994), Saadalla *et al.* (1990b)
		Heat tolerance	
		Independent of developmental stage	

2	Chlorophyll contents and chlorophyll a:b ratio	Dry matter and yield	Al-Khatib and Paulsen (1984), Saranga *et al.* (2004)
3	Carbon isotopes discrimination differences	Heat tolerance	Lu *et al.* (1996)
(C) Screening of traits through infrared/remote sensing for direct selection			
1	Leaf conductance	Heat tolerance	Lu *et al.* (1994)
2	Crop water stress index (CWSI)	Transpiration rate	Jackson *et al.* (1981)
		Vapor pressure deficit (VPD)	
		Plant temperature	
		Net radiation	
		Air temperature	
		Canopy temperature	Burke *et al.* (1990)
		Aerodynamics resistance	Burke *et al.* (1990), Jackson *et al.* (1981)
3	Chlorophyll fluorescence	Efficiency of PSII	Butler (1978)
		Indication of damage to PSII	Hall (2004)
4	Canopy temperature depression (CTD)	Leaf conductance	Reynolds *et al.* (1998)
		Air temperature	Amani *et al.* (1996)
		Soil water status and RH	Amani *et al.* (1996)
		Incident radiations	Amani *et al.* (1996)
		Heat escape	Cornish *et al.* (1991)
5	Thermal stress index (TSI)	Quantify thermal stress	Burke *et al.* (1990)
		Measures enzymatic functions at high temperature	
		The CWSI and TSI are highly correlated	
		Can work at any level of VPD	

technique to spring wheat (Fischer *et al.*, 1998; Reynolds *et al.*, 1998). Important morphophysiological selectable traits against heat tolerance/ heat stress are given in Table IV.

Heat tolerance has been a primary selection criterion for higher lint yield in Pima cotton-breeding programs (Feaster and Turcotte, 1985; Percy and Turcotte, 1991). It has been estimated that nearly 50% of the lint yield increase in Pima cotton at lower elevations of southwestern United States has been the result of increased heat tolerance in improved cultivars (Kittock *et al.*, 1988). It has been demonstrated by Srivastava *et al.* (1995) that selection pressure for higher lint yield and heat tolerance in Pima cotton has altered intrinsic guard cell properties. Furthermore, Lu *et al.* (2000) stressed that the characterization of the properties of Pima cotton guard cells may be of importance for design of future programs that incorporate physiological traits into breeding strategies. Remarkable similarity in relationship between stomatal conductance and yield (Lu *et al.*, 1998) in the historical series of Pima cotton and wheat supports the hypothesis that selection pressures for higher yields in irrigated crops grown at supraoptimal temperatures generate strong indirect pressures for higher stomatal conductance.

Pollen selection through heat treatment allows screening for a large number of genetic combinations and may be a valuable method of breeding for heat tolerance. Breeding for heat tolerance during reproductive development has been effective in cowpea (Hall, 1992) and cotton (Rodriguez-Garay and Barrow, 1988). Burke (2001) speculated that improvements in vegetative heat tolerance might also provide improved heat tolerance during pollen development. Genes for heat tolerance during reproductive development enhance sink strength and harvest index (Ismail and Hall, 1998), and there are indications that they may enhance responsiveness to elevated CO_2.

Traits affecting radiation use efficiency like early ground cover; stay green and photosynthetic rate could be expected to be important under heat stress. The stay-green trait has been used widely in breeding for heat tolerance (Reynolds *et al.*, 2001). In addition, Bibi *et al.* (2003) studied several physiological parameters of obsolete and modern cultivars and found significant differences in chlorophyll fluorescence. Modern cultivars exhibited higher fluorescence than the obsolete cultivars indicating greater stress tolerance of modern cultivars at higher temperatures. There is a need for developing systematic-screening tools in evaluating stress tolerance in cotton genotypes for high-temperature stress (Burke, 2004; Kakani *et al.*, 2005).

C. Isogenic Lines to Study Individual Trait Performance

Prior to widespread use of specific phenological, physiological, or morphological traits in breeding programs, their value must be clearly established. A rigorous test involves the development of pairs of lines with and without the trait but with otherwise similar genetic background (i.e., almost isogenic lines). Ideally, several pairs of isogenic lines should be developed with different genetic backgrounds, because the agronomic value of a gene(s) can depend on the other genes present in the genome (Hall, 2001). Understanding the relationship between traits and yield is being mediated by the identification and marking more of the controlling genes and their alleles. Isogenic comparisons have their limitations, but as more are carried out, the importance of certain genes for yield and other traits are being confirmed.

One of the important traits for which isogenic lines were widely used is the okra-type cultivars with various morphological and physiological traits. The okra leaf trait in upland cotton determines a leaf shape that is duly cleft with narrow lobes, in contrast with normal broad leaf. In addition to a radically different leaf shape, the okra leaf trait exhibits a large change in growth characters (Wells *et al.*, 1986). Pettigrew (2004) demonstrated that okra leaf trait reduced individual leaf area by 37% relative to the comparable normal leaf type, but okra leaf type had 16% greater chlorophyll content compared with normal leaf type isogenic pair. Similarly, Heitholt and Meredith (1998) found that okra leaf types were usually 1–4 days earlier in maturity than their normal-leaf counterparts, possibly contributing to their overall yield advantage. Meredith *et al.* (1996) evaluating the effect of three traits such as subokra leaf, semi smooth leaf, and nectarless in different isolines demonstrated that subokra leaf types produced significantly higher (35 kg ha^{-1} or 4% more seeds) first harvest than normal leaf types, and seeds of semismooth isolines were heavier than those of hirsutum cottons. Leaf canopy photosynthesis of subokra type was 7% greater than that of normal leaf near isolines and was one of the causes for increased yields associated with subokra leaf trait (Wells *et al.*, 1986). Similarly, Peng and Krieg (1991) reported that okra leaf plants had greater canopy photosynthesis per unit leaf area than normal leaf plants, but Elmore *et al.* (1967) observed no difference in the leaf CER between superokra and normal isolines. The intensity of competition for solar radiation differs among the leaf types with less mutual shading in communities of superokra leaf plants than in communities of other leaf types. Furthermore, solar radiation interception and dry matter production of cotton are affected by leaf type and total leaf area development (Kerby and Buxton, 1978). Karami *et al.* (1980) observed that an okra leaf cotton genotype had significantly higher assimilation under water stress than its isolines with "normal" leaf morphology. Pettigrew *et al.* (1993) examined cotton leaf-type isolines and showed superior leaf CER in supraokra and okra leaf cotton compared with normal leaf genotype, Deltapine 50. Dark adapted Fv:Fm was not different for the okra leaf type genotypes compared with normal leaf type genotypes; however, the okra leaf type lines had a 14% greater light adapted PSII efficiency and 14% greater photosynthetic electron transport rate compared with normal leaf type genotypes (Pettigrew, 2004). Nonphotochemical quenching was also 11% lower in the okra leaf type relative to normal leaf type genotypes. The two okra leaf type cultivars exhibited 30% higher CER, on average, than any of the normal leaf type varieties. Okra leaf type genotypes had lower stomatal conductance, it has also been reported that the okra leaf trait has higher photosynthesis per unit leaf area and higher water-use efficiency (Baker and Myhre, 1968; Pettigrew *et al.*, 1993).

On the basis of modeling studies, Landivar *et al.* (1983) concluded that okra leaf cottons are very competitive in yield with normal leaf under favorable growing conditions, but are likely to be less competitive than normal leaf under adverse conditions. In contrast, Stiller *et al.* (2004) observed that okra leaf cotton cultivars gave higher yield in most of the water stress environments. Meredith and Wells (1986) conclusively demonstrated that certain population has the genetic potential of producing okra leaf cotton with higher yielding ability than that of normal leaf cotton.

D. Genetic Variability

The value of any trait as a selection character depends on whether it satisfies four basic criteria (Mahon, 1983). These criteria are as follows: (1) presence of sufficient genetic variability in its expression, (2) the characters should be characterized genetically, (3) the character must be related to agronomic benefit (e.g., yield, aspects of quality, and production cost), and (4) it must be measurable in large scale trials. Therefore, in this section the results of various reports with regard to genetic variability of different eco-morpho-physiological traits related to high-temperature tolerance are presented and discussed.

McMichael and Burke (1994) found differences in temperature characteristics of root growth responses in young cotton seedlings. The root growth in response to temperature was maximal within the optimal temperature predicted by TKW. Farbrother (1960) and Hearn (1976) reported varietal differences in root density and their ability to extract water. Burke (2004) also reported genetic diversity in heat tolerance among the six greenhouse-grown cotton cultivars.

Bradow and Davidonis (2000) reviewed that the cotton canopy architecture, particularly with respect to plant height and branch lengths that can be modified by environmental conditions such as temperature, light intensity, and herbivory by insects and management strategies such as growth regulator application. The energy exchanges within a plant canopy can be affected by size, shape, and orientation of the leaves. In upland cotton germplasm great variability with respect to leaf size and shape has been reported elsewhere (Heitholt *et al.*, 1992). In addition to the normal leaf shape, cotton leaf shapes range from highly cleft (superokra) to only slightly cleft leaves (subokra)

(Meredith, 1984). It has been established that the variation in leaf shapes can greatly alter canopy light interception characteristics (Wells *et al.*, 1986). The increase in SLW grown under dryland conditions has been reported by Pettigrew (2004) and Wilson *et al.* (1987). Pettigrew (2004) observed that smaller leaves with occasionally greater SLW for the dryland plants lead to speculation of a higher concentration of photosynthetic apparatus per unit leaf area for the water-stressed plants. This was further confirmed by the fact that there was 19% higher chlorophyll content in dryland leaves in upland cotton. McNamara *et al.* (1940) demonstrated that varieties differing in leaf size and degree of lobing had differences in monopodial plastochrons. Bednarz and van Iersel (2001) found that morphological characters, such as deep lobed leaf and pubescence, did not provide enhanced heat tolerance. Kerby and Buxton (1978) speculated that when leaf area per plant is reduced genetically, plastochrons are reduced. It may be related to greater solar radiation penetration into canopies resulting in increased photosynthetic activity of lower leaves and much of the earliness associated with the okra leaf types results from small plastochrons.

Sassenrath-Cole (1995) observed that different leaf type and row spacing altered canopy structure. Furthermore, the boll temperature tracked air temperature due to the absence of evaporative cooling by the bolls. Temperature of the lower canopies was warmer during the day and cooler at night for more open canopies such as okra leaf. The differences in temperature profiles within canopies have significant impact on boll maturation over the course of the growing season and may account for the observed increases in rate of earliness of bolls of okra leaf types (Heitholt, 1993). Alterations in leaf size and shape can affect the temperature of canopies (Mahan *et al.*, 1995).

According to Reynolds *et al.* (2001), heat stress is almost certainly a component of drought stress, since one of the principal effects of drought is to reduce evaporative cooling from plant surface. Nonetheless not all traits conferring heat tolerance are also associated with genetic variability for drought tolerance, a good example being CMT (Blum, 1988). Genetic variation in CMT has been observed in various field-grown crops including cotton (Bibi *et al.*, 2003; Rahman *et al.*, 2004). Saadalla *et al.* (1990a,b) found a high correlation in wheat for CMT between seedling and flag leaves at anthesis for genotypes grown under controlled environmental conditions. Similar results were reported in cotton for this trait. Ashraf *et al.* (1994) reported the stable performance of cotton genotypes identified during seedling stage for their CMT. The physiological basis for the association of CMT with heat tolerance has not been understood. Plasma membranes are known to be more heat tolerant than the photosynthetic thylakoid membranes. Wise *et al.* (2004) demonstrated that photosynthesis in field-grown Pima cotton leaves is functionally limited by photosynthetic electron transport and RuBP regeneration capacity, not by Rubisco activity presumably because of limitation in thylakoid reactions needed to support RuBP regeneration.

Despite the strong environmental dependence of stomatal conductance, existing genetic variation can be successfully manipulated to produce stable populations with contrasting conductance levels. Crop plants show genetic variation for stomatal characteristics such as stomatal density, aperture size, opening pattern, and sensitivity to changes in internal plant water status and soil water status (Ludlow, 1980; Markhart, 1985). Percy *et al.* (1996) observed stomatal conductance differences in the low- and high-yielding Pima cotton lines and reported that stomatal conductance is genetically controlled. Variation in stomatal conductance to water is also linearly correlated with assimilation with the result that Ci/Ca remains relatively constant across [CO_2] (Morison, 1993). Genotypic variation in photosynthetic capacity on a unit leaf area basis has been reported in many crops (Bhagsari and Brown, 1986; Wallace *et al.*, 1972). Perry *et al.* (1983) confirmed these genetic differences in the ratio of photorespiration to net photosynthesis in cotton and found that rates were directly attributed to source:sink ratio differences. Lu *et al.* (1997) observed that an upland cotton cultivar Deltapine 90 (DP-90) showed 25–35% higher stomatal conductance, 35–50% higher photosynthetic rate, and 45% smaller leaf area than Pima S-6 (PS-6). Furthermore, the higher photosynthetic rate and stomatal conductance of DP-90 leaves were partly related to their sun-tracking ability. The cultivars DP-90 and PS-6 had comparable photosynthetic rate, but the stomatal conductance was higher in DP-90. Moreover, in the 25–35 °C temperature range, photosynthetic rate as a function of temperature remained nearly constant in both cultivars and was higher in upland cotton at all temperatures. In contrast, stomatal conductance showed strong temperature dependence. The slope of the stomatal response to temperature was higher in DP-90. They also suggested that upland cotton could be used as a source of genetic variability for higher stomatal conductance in Pima cotton-breeding programs. The Pima cultivars have lower heat tolerance than advanced upland cultivars (Kittock *et al.*, 1988; Reddy *et al.*, 1992b) and lower lint yield in hot environment (Radin, 1992; Silvertooth *et al.*, 1992). Cantrell *et al.* (1998) reported 12% of the variation in stomatal conductance based upon QTL analysis and confirmed that stomatal conductance is a heritable trait and seems to be significantly associated with lint yield in heat stress environments.

Taha *et al.* (1981) found differences in boll set in cultivars ST 3 and B 557 and suggested that in selecting for heat tolerance it is important to choose varieties that develop a large number of bolls of good size before the plants reach cutout phase. Brown and Zeiher (1998) found cultivar response to heat stress during reproductive development, to identify stages during reproductive development and plant processes that distinguish heat-tolerant from heat-sensitive cultivars. Recent studies showed that there were differences among cotton cultivars in temperature response of pollen grains under artificial conditions (Kakani *et al.*, 2005). Cultivars ST 4793R, DP 458B/RR, and DP 5415RR not only had higher pollen germination and longer pollen tubes when germinated at high temperature but also had higher temperature optima, and thus were classified as heat-tolerant cultivars (Kakani *et al.*, 2005). Rodriguez-Garay and Barrow (1988) demonstrated that genes for heat tolerance could be selected in the pollen and effectively transferred by the backcross method. They observed that cultivars developed in warmer areas were more fertile than those developed in areas where cotton is widely grown. This indicates that genes that allow the sporophyte to function at high temperatures also allow the pollen to retain fertility after heat stress.

The literature suggests the presence of genetic variation in cotton for various characteristics such as seed germination, seedling establishment, vegetative stage of development, photosynthesis, photorespiration, chlorophyll contents, chlorophyll fluorescence, CMT, CTD, stomatal conductance, and various morphological traits like, leaf area, leaf thickness, leaf shape, height, and first fruiting node number. Similarly, genetic variation in reproductive development traits (pollen shedding, pollen germination, pollen tube lengths, and boll set) has also been reported in cotton thereby indicating the scope for genetic improvement for heat tolerance.

E. INHERITANCE STUDIES

After identification of genotypes suitable for potential utilization in a breeding program for improvement of the trait(s) under consideration, the inheritance studies of the desired trait are necessary to decide the breeding methodologies. On the basis of the existing survey of literature, the inheritance pattern/heritability of the various eco-morpho-physiological traits are mentioned.

Various reports using transgenic approaches, as reviewed by Sung *et al.* (2003), have largely validated that tolerance is a multigenes trait. It has been demonstrated that modifying membrane fluidity can influence gene expression (Horvath *et al.*, 1998; Orvar *et al.*, 2000). The importance of proper membrane fluidity in temperature tolerance has been delineated by mutation analysis, transgenic, and physiological studies. Alfonso *et al.* (2001) reported that a soybean mutant deficient in fatty acid unsaturation showed strong tolerance to high temperature. Similarly, Hugly *et al.* (1989) showed that the thylakoid membranes of two Arabidopsis mutants deficient in fatty acid unsaturation (fad 5 and 6) showed increased stability to high temperature.

Tripathy *et al.* (2000) reported that CMT indicating the polygenic nature of its inheritance with broad-sense heritability of 34%. Blum *et al.* (2001) reported the broad-sense heritability for CMT for high-temperature tolerance to be 71% in the winter and 67% for the summer wheat. Fokar *et al.* (1998) reported high heritability for CMT in wheat.

Cotton is related to the plants with maternal type inheritance of chloroplasts, so during the selection of parents, a pair with high photosynthetic activity of the apparatus (Nasyrov, 2004) to improve photosynthetic productivity. For example, the cultivar Taskent-1, which was bred from wild germplasm (*Gossypium mexicanum*), had higher rates of photosynthesis. In crossing Taskent-1 and C-6030 varieties, Nasyrov (2004) observed pronounced effects of heterosis and there was an increase of Rubisco activity with a coefficient of 18% and a slight increase of chloroplast number. All these factors lead to considerable increase in yield. Under the reciprocal combination when the cultivar C-6030 with low photosynthetic activity served as maternal form it got very weak effect of heterosis.

The inheritance of stomatal conductance in Pima cotton varied in complexity from a simple additive-dominance model to a model displaying digenic epistatic interaction (Percy *et al.*, 1996). The alleles from the dominant markers from the upland cotton parent contributed the highest mean values of stomatal conductance and further suggested that genes from upland cotton may contribute to the increases in conductance in advanced Pima-breeding lines (Ulloa *et al.*, 2000). Percy *et al.* (1996) reported broad-sense heritability estimates of stomatal conductance were 0.16–0.44 mmol m^{-2} s^{-1} in cotton. In interspecific populations, additive as well as dominance effects for stomatal conductance were observed for QTLs.

Using genetic mapping to dissect the inheritance of different complex, traits in the same segregating population can be a powerful means to distinguish common heredity from casual association between such traits (Paterson *et al.*, 1988). QTLs have been identified in cotton that confer physiological variations thought to be associated with stress tolerance such as osmotic adjustment (Morgan and Tan, 1996), carbon isotope ratio (^{13}C:^{12}C), stomatal conductance (Ulloa *et al.*, 2000), chlorophyll content, and canopy temperature (Saranga *et al.*, 2001). They showed that the genetic control of difference in canopy temperature was markedly influenced by water regime. Among four QTLs found to confer genetic differences in canopy temperature, one was specific to arid conditions and a second was specific to relative canopy temperature (GH allele conferring higher stability across environments). The GH allele at the chromosome 6 canopy temperature QTL was associated with higher seed cotton yield and lower osmotic potential. Furthermore, the relatively large number of QTLs associated with ^{13}C may help identify the important physiological traits that contribute to stomata conductance/photosynthetic capacity relationship.

Saranga *et al.* (2004) documented an association between carbon isotope discrimination (Δ) and chlorophyll content in two genomic regions. These researchers reported that the likelihood that 2 out of 11 Δ QTLs would be associated with 2 of the 4 chlorophyll a/b QTLs in a genome size of cotton is about 0.02%. Furthermore, QTL alleles associated with higher Δ under arid conditions coincided with lower chlorophyll contents. This unexpected finding was further supported by the results of a subsequent study of F4 and F5 progenies of the plants from a current study in which the line having the highest Δ values also had the lowest chlorophyll a and chlorophyll b contents (Cohen, 2001). Saranga *et al.* (2004) on the basis of QTLs' analysis concluded that QTLs conferring low canopy temperature and high chlorophyll a (one QTL each); with two QTLs conferring high chlorophyll b and there was a positive correlation between chlorophyll a and dry matter production in both water stress and well-watered conditions.

F. IMPACT OF HEAT-TOLERANT GENES

Impact of heat-tolerant genes is well documented in cowpea (Ismail and Hall, 1998, 1999). In cowpea, heat-tolerant genes progressively enhanced grain yield from first flush of flowers by increasing pod set on the main stem nodes, and enhancing the overall partitioning of carbohydrates into grain with increases in nighttime temperatures above 20 °C (Ismail and Hall, 1998). Heat-tolerant genes (or closely linked genes) also had a progressive dwarfing effect, mainly resulting from shorter main stem internodes and involving reduced shoot biomass production at night temperatures above 15 °C. They concluded that heat-tolerant (or associated) genes and the dwarfing and reduced biomass production associated with the heat-tolerant genes could have negative effects in some environments. Ehlers and Hall (1996) suggested that in the tropical zone, the dwarfing effect of the heat-tolerant genes is more pronounced than in subtropical zones, and in the tropics it will be necessary to combine the heat-tolerant genes with genes that enhance vegetative growth.

Cowpea lines that are heat tolerant at both early flowering and pod set produced the highest grain yield, whereas lines that are susceptible to both stages produced the lowest grain yield. The lines that are heat tolerant during early flowering but heat susceptible during pod set had intermediate yield (Ismail and Hall, 1999). Furthermore, the harvest index increased by four- to ninefold and pod per peduncle increased by three- to sevenfold for lines with heat tolerance during early flowering and pod set, respectively. These results suggest that the heat-tolerant genes, that are effective at early flowering and pod set, contribute equally to the final grain yield through their effects on pod set and harvest index.

Heritability of high-temperature resistance has not been clearly ascertained. Transgressive segregation toward higher relative injury values in progeny than in parents of wheat suggests that the parents contributed different genes for high-temperature tolerance and the trait is not simply inherited (Saadalla *et al.*, 1990b). Cytoplasmic and nuclear interactions in response to high temperature are indicated by significant reciprocal effects. General and specific combining abilities for heat tolerance in a similar diallel of rice genotypes also are highly significant (Yoshida *et al.*, 1981). Broad-sense and narrow-sense heritability are both high, indicating that most genetic variation is additive and breeding for the trait should be successful.

G. BREEDING FOR HIGH-TEMPERATURE TOLERANCE

Hall and Allen (1993) hypothesized that cultivars with heat tolerance during reproductive development, high harvest index, high photosynthetic capacity per unit leaf area, small leaves, and low leaf area per unit ground area, under the present level of CO_2 will be most responsive under both hot and intermediate temperatures. Ismail and Hall (1998) reported that the heat-tolerant genes confer some of the hypothesized traits, heat tolerance during reproductive development, particularly higher harvest index and less leaf area per unit ground area in cowpea. Similarly, the Pima cotton-breeding program has achieved large changes in plant architecture and substantial decreases in leaf size (Lu *et al.*, 1994) and both trends have facilitated increased plant density. Furthermore, denser canopies tighten the coupling between leaf and canopy temperature (Lu *et al.*, 1994) and should enhance adaptive advantages of higher stomatal conductance associated with lower leaf temperature (Lu *et al.*, 1998).

The strategy of modern breeding is to improve the intensity of the productive process under optimal partition of assimilates. The increase in productivity must be realized not by means of the vegetation period but by activation of productive process by increased rate of photosynthesis combined with higher number of bolls, increased boll weight, and harvest index up to 50% (Nasyrov, 2004).

The productivity of a crop can be limited by any of the physical properties of its environment. However, the concept of environmental limitation is meaningful only in reference to a specific plant type, since the productivity of crop species or cultivars can vary within a single environment. The physiological processes, which restrict productivity in an environment, are referred to as physiological limits. These limits can be overcome by modifying either the environment or the physiological characteristics of the crop and the development of cultural practices and crop cultivars to exploit specific agricultural environments (Mahon, 1983).

Crop physiology and ecology provide information on plant function and environment that, in principle, could be used to determine the suites of traits and their level that should be adaptive in specific environments (Hall, 2001). Key physiological traits affecting crop productivity are likely to already have been modified by the extensive genetic manipulation typical of breeding programs. These physiological traits can be identified by comparing obsolete and modern lines grown in the same environment. In cotton, this type of study was conducted by Bridge and Meredith (1983). Lu *et al.* (1998) observed that stomatal conductance associated with lower canopy temperatures of obsolete and advanced lines exhibits maximal differences in the early afternoon, a time at which daily temperature are also maximal. Bibi *et al.* (2003) observed significant differences in chlorophyll fluorescence between the obsolete and modern cultivars at 30.5°C. The obsolete cultivars experienced lower fluorescence than the modern cultivars. This indicates that the obsolete cultivars suffer from more stress than the newer cultivars. Characterization of physiological traits altered in the process of selection for higher yields could make it possible to identify the nature of the selection pressure causing the changes, and the relationship between the altered trait and yield increase. Desirable physiological traits could then be specifically targeted for selection (Lu and Zeiger, 1994).

Plant breeders have attempted to increase the capacity for root growth in breeding programs to improve drought resistance of agricultural crops. Most crops show considerable genetic variability in growth rate of roots, indicating that breeding for increased root growth can be effective. In cotton, it has been demonstrated that root growth is under genetic control (McMichael and Burke, 1994). They suggested that the evaluation of cotton root growth responses to shoot and root temperatures within or below cotton's TKW enhanced root growth.

Breeding for specific canopy architecture has the potential to reduce the occurrence of plant temperature above the optimal thermal range. Such a trait would improve the plant's ability to resist high temperature through changes in canopy architecture that serve to reduce thermal stresses with minimal effects on water consumption (Mahan *et al.*, 1995). The development of plant varieties with desirable canopy architecture coupled with management practices designed to avoid temperatures beyond the optimal thermal range may result in improved agronomic performance. Pettigrew *et al.* (1993) advocated that consideration should be given to utilize the high photosynthetic potential of okra or superokra leaf type in breeding programs. Moreover, another example of okra leaf productivity can be found in Australia where substantial increase in area and yield were reported with okra leaf genotypes (Thomson, 1995).

A physiological character can be defined as the measurable expression of the rate or duration of a physiological process. Physiological characters are hierarchical in the same sense as yield components. The physiological characters are closely linked to morphology because morphological changes are the end results of physiological processes. Morphological expression can be considered as a physiological or "morpho-physiological" character if it is assumed to control the rate of a process (Mahon, 1983). On theoretical grounds, it has been suggested that independent selection and controlled recombination of individual physiological traits could be a valuable addition to the normal methods of plant breeding. Perry *et al.* (1983) suggested that in the long term, genetic modification to reduce photorespiration and increased photosynthetic efficiency would be most desirable. Many studies have shown that attained yield advances in most agricultural crops have resulted from a higher harvest index, rather than from higher photosynthetic rates (Evans, 1983). In the absence of selection pressure for higher photosynthetic rates (as in Pima cotton), higher stomatal conductance could be disadvantageous because of wasteful water use (Lu *et al.*, 1998).

Abrol and Ingram (1996) emphasized that increased temperature would affect the crop calendar in tropical regions. In the tropics, however, global warming, though predicated to be of only small magnitude, is likely to reduce the length of effective growing season, particularly where more than one crop per year is grown. In semi-arid regions and other agroecological zones where there is wide diurnal temperature variation, relatively small changes in mean annual temperatures could markedly increase the frequency of higher temperature injury. In cotton, canopy temperature can be 10–15 °C higher in dryland cotton than in irrigated cotton (Burke *et al.*, 1988). The global warming would reduce dry matter accumulation in dryland cotton because of increased respiration and reduced photosynthesis (Abrol and Ingram, 1996).

Increased cotton yields could be achieved by breeding for simultaneous increases in both the reproductive sink and the photosynthetic source (Evans, 1983). In any breeding program projected changes in climate must be considered. Increases in atmospheric CO_2 concentrations will tend to make photosynthetic sources more effective per unit leaf area. Consequently, maintaining a balance between photosynthetic sources and reproductive sink may require selecting plants with much greater reproductive sinks. Breeding to maintain an appropriate balance will be of particular importance for cases where high temperatures result in greater damage to reproductive development than to the photosynthetic source.

From the present literature, it can be seen that different physiological mechanisms may contribute to heat tolerance in the field such as heat-tolerant metabolism as indicated by higher photosynthetic rates, increased stomatal conductance, chlorophyll content, fluorescence, stay green and CMT, or heat avoidance as indicated by CTD in addition to leaf types and thickness and crop duration. Breeding programs may measure such traits to assist in the selection of heat-tolerant parents, segregating generation, or advanced lines. According to Evans and Fischer (1999), the identification of yield-related physiological selection traits (as distinct from morphological or visual ones) has been of great interest to many physiologists and some breeders. Reasons for generally frustrating results have been thoughtfully discussed by Jackson *et al.* (1996). Accordingly, as field instruments continue to improve, new opportunities arise, as with air borne infrared images to register canopy temperature and other remote-sensing techniques (Araus, 1996). Such techniques could complement molecular-aided selection.

Carbon dioxide concentration has increased rapidly during the last few decades, and it is expected that CO_2 concentration will double by the end of this century. Making full use of elevated CO_2 may also require selection to enhance those components of the photosynthetic system, other than Rubisco, that become limiting if the CO_2 assimilation per unit leaf area of C_3 species is to reach much higher rates. Selection for more open stomata may be useful, except for environments with extreme drought, since elevated CO_2 will tend to cause partial stomatal closure. Overall, elevated atmospheric CO_2 and global climate change will provide both opportunities that may be exploited by plant breeding to increase productivity and some additional problems for plant breeders and other scientists to solve in the twenty-first century (Hall and Ziska, 2000). It has been observed by a number of researchers (Drake *et al.*, 1997; Idso and Idso, 1994; Reddy *et al.*, 1997d, 2000, 2005) that CO_2 enrichment alone may increase yields under water-limited conditions. Prior *et al.* (1994) observed that increasing CO_2 increased root length and dry weight densities of cotton. Cotton is the most important candidate for such a response. The impacts of elevated CO_2 on various physiological and morphological traits of cotton are summarized in Table V. In addition Idso *et al.* (1987), Long (1991), and Polley (2002) suggested that the effects of higher temperature and CO_2 on plants are not additive, moreover, direction of crop responses to CO_2 enrichment and temperature change are species and even cultivar specific (Ziska *et al.*, 1997). The heat-tolerant genes may enhance adaptation to the climatic conditions of the twenty-first century with elevated CO_2 expected to be warmer (Hall and Allen, 1993). In addition to enhancing grain yield under hot conditions, the heat-tolerant genes have been shown to enhance responses to elevated CO_2 with respect to pod production under both optimum and high night temperature (Ahmed *et al.*, 1993). High-temperature injury on reproductive development will not likely be ameliorated by high CO_2. Controlled environment studies have shown that grain and fruit production will be limited in high-temperature environments (Baker *et al.*, 1990; Prasad *et al.*, 2002, 2003; Reddy *et al.*, 1996, 1997b,d). Therefore, it becomes imperative that the positive effects of predicted future CO_2 enrichment in C_3 crops like cotton can only be exploited by developing cultivars

Table V
Effect of Elevated CO_2 on Different Morphological, Physiological Traits, and Yield Components in Cotton

Trait	Effect of CO_2	Comment	References
Square and boll	44% increase	Average of five temperature conditions at 720 μmol mol^{-1} as compared to ambient CO_2 360 μmol mol^{-1}	Reddy *et al.* (1997b)
Node addition		No effect	Reddy *et al.* (1995a,c)
Root:shoot ratio		No effect of elevated CO_2	Reddy *et al.* (2000)
Harvest index		No effect of elevated CO_2	Reddy *et al.* (2000)
Lint percentage		No effect of elevated CO_2	Reddy *et al.* (1999)
Biomass above ground	63% increase	At 650 μmol mol^{-1} in comparison to ambient CO_2 (under FACE) 350 μmol mol^{-1}	Kimball and Mauney (1993)
Biomass above ground	35% increase	At 550 μmol mol^{-1}	Mauney *et al.* (1994)
Yield	60% increase	Current ambient CO_2 + 300 μmol mol^{-1}	Reddy *et al.* (2000)
Yield	40% increase	At 550 μmol mol^{-1}	Mauney *et al.* (1994)
Lint yield	60% increase	At 550 μmol mol^{-1}	Pinter *et al.* (1996)
Photosynthetic efficiency	25% increase	At doubling the ambient CO_2	Reddy *et al.* (2000)
Root biomass	High	At all temperature in high CO_2	Reddy *et al.* (1995b)
Root biomass	Greater	At optimum temperature and twice ambient CO_2	Reddy *et al.* (1995b)

tolerant to high temperature in general and especially at the reproductive development stage.

Baker *et al.* (1990) hypothesized that future crop yields will be influenced by complex interactions between the effects of increased atmospheric CO_2 concentration and trace gases such as ozone as well as the effects of temperature increase brought about by climate change (IPCC, 1995). This could be good or bad news as agricultural productivity is expected to be sensitive to global climate change and increased CO_2 concentration should cause increased productivity at least in C_3 plants and decrease soil–water use relative to the dry matter produced. Higher temperature and periodic episodes of heat stress and drought, however, could exacerbate the effect on crop growth and development, reduce crop yields and quality (Reddy *et al.*, 1996, 1999). Acquired tolerance to high and/or low-temperature stress conditions are complex traits as demonstrated from a vast research of plant breeding and crop improvement efforts (Sung *et al.*, 2003).

Wang *et al.* (2003) suggested that a comprehensive breeding strategy for abiotic stress tolerance should include the following steps and approaches: (1) conventional breeding and germplasm selection, especially of wild relatives of a species; (2) elucidation of the specific molecular control mechanisms in tolerant and sensitive genotypes; (3) biotechnology-oriented improvement of selection and breeding procedures through functional genomic analysis, use of molecular probes and markers for selection among natural and bred populations, and transformation with specific genes; and (4) improvement and adaptation of current agricultural practices.

Hall (2001) suggested that genetic engineering is useful in ideotype breeding in that, in principle, single genes can be transferred into a cultivar without changing the genetic background, thereby creating an isogenic pair of lines in one step and a relatively short time. In practice, however, many transformed plants must be created and evaluated because factors such as the placement and manner of gene insertion can influence its expression. The traditional back-crossing procedure for creating almost isogenic lines requires many plant generations and several years, but it can be accelerated by using DNA markers to select for the genetic background of the recurrent parent. DNA markers also can be used to develop indirect selection methods. In this case, DNA markers are needed that are closely linked to the trait of interest. Indirect selection using DNA markers is powerful where it can be used for nondestructive screening of single plants in the first segregating generation. Once a set of stable lines has been bred with selection based on indirect screening procedures, one should either conduct studies to confirm that the desired trait is present, using a more reliable direct screening procedure, or proceed directly to performance trials under field conditions in the target production environment. Cheikh *et al.* (2000) stressed that molecular biology tools will never replace the input and role of crop breeders in improving agronomic traits, but these tools will enable them to be more responsive in both time and breadth of environmentally sensitive traits to meet agricultural market needs and opportunities. Biotechnology tools combined with conventional breeding should position us to be able to take greater care of the production environment and allow us to achieve adequate food production and security for the growing world population.

H. PRACTICAL ACHIEVEMENTS

At Phoenix, Arizona, systematic efforts were started in the late 1950s to develop heat-tolerant Pima cotton cultivars, and a number of cultivars have been developed and released for commercial production since 1960, Pima S-2 being the first cultivar. The realized genetic gain from Pima S-1 to Pima S-5 was 57% at low elevation (<450 m) and 30% at high elevation (>750 m). Furthermore, each release (Pima S-1 in 1951, Pima S-2 in 1960, Pima S-3 and Pima S-4 in 1966, Pima S-5 in 1975, Pima S-6 in 1983, and Pima S-7 in 1991) progressively increased lint yield (Lu *et al.*, 1998). Stomatal conductance showed a strong, positive correlation with lint yield, and increased about 30 mmol m^{-2} s^{-1} per 100 kg ha^{-1} increases in cotton lint yield (Lu *et al.*, 1998). Some studies showed that photosynthetic rates and stomatal conductance in Pima lines have increased in parallel with yields (Cornish *et al.*, 1991; Lu and Zeiger, 1994). This provides evidence that selection pressures for higher yields could have resulted in an indirect selection for higher photosynthetic rates, stomatal conductance, and heat tolerance (Lu *et al.*, 1998; Radin *et al.*, 1994). However, detailed correlation studies suggested no correlation between photosynthetic rates and lint yield or between photosynthetic rates and the order in which the cultivars were commercially released (Lu *et al.*, 1998). They conclude that overall the observed increases in stomatal conductance in the Pima series have exceeded the increase in photosynthetic rates, which provides further evidence for independent selection pressures on higher stomatal conductance and for relationship between stomatal conductance and yield to be independent of photosynthetic rate (Lu *et al.*, 1996, 1998). Radin *et al.* (1994) suggest that as breeders have increased the yield of cotton, genetic variability for conductance has allowed inadvertent selection for heat avoidance (evaporative cooling) in a hot environment.

Breeding has also increased tolerance to high temperatures in each commercial release of Pima cultivars (Feaster and Turcotte, 1962, 1984; Feaster *et al.*, 1967; Niles and Feaster, 1984). No attempts to modify physiological or morphological traits have been made in this program; instead, improvements have been achieved by genetic manipulation of available germplasm variability, extensive selection within segregating populations, and testing advanced generation lines for yield at sites with different temperature regimes. Feaster and Turcotte (1985) conclusively demonstrated that in environments where the adaptation of a cultivar depends largely on its tolerance to high night temperature, the height on the plant at which an appreciable number of bolls begin setting is an effective indicator of heat tolerance.

The stomatal conductance apparently is dependent upon evaporative cooling. This represents a heat avoidance strategy, in that leaf temperature decreases without necessarily increasing tissue tolerance for thermal stress. Genetic variability for an avoidance type of heat tolerance was reported by Radin *et al.* (1994) for the first time. Evans and Fischer (1999) discussed avoidance of heat stress and its adverse effects on boll set. Early development may be the explanation of the yield advantage, and cotton is an excellent example of the power of empirical selection for yield. Selection for higher yields and heat resistance has altered the stomatal response to temperature in Pima cotton (Lu *et al.*, 1998). They demonstrated that air temperature in the Pima cotton-growing areas of Arizona often exceeds 40°C. Leaf–air temperature difference in a heat-sensitive land race, Sea Island, a low-yielding commercial line, Pima-32 and a high-yielding line Pima S-6 were about −1, −3, and −4.5°C, respectively (Lu *et al.*, 1994; Radin *et al.*, 1994). This trend toward higher stomatal conductance and lower leaf temperature has persisted in a subsequent commercial release of Pima S-7 (Lu *et al.*, 1998).

At Cotton Research Institute, Sakrand, Sindh, Pakistan, one cultivar CRIS-134, has been developed. This cultivar is capable of producing 32 bolls after 75 days of planting (the hottest days having an average temperature of 41 °C) as compared to NIAB-78 and CRIS-9, which formed 17 and 11 bolls, respectively. This cultivar (CRIS-134) was specifically developed to tolerate the hot period of June–August (Soomro, 1998). Similarly, at Indian Agricultural Research Institute, New Delhi, India, heat-tolerant cotton genotypes have been developed using shuttle-breeding approach. Shuttle-breeding approach refers to change of environment during the selection processes. This method is used to select broadly adopted cultivars from the segregating populations. The selection was applied (Singh *et al.*, 2003) for higher numbers of fruiting structures (square/flower/bolls) per plant in addition to early maturity initially in the cultivars and later on in the segregating generations from intra- and interspecific crosses. Rosielle and Hemblin (1981) discussed selection approaches under stress and nonstress conditions and suggested that if it is imperative that yields in stress environments be increased, then selection for tolerance may be worthwhile. The genotypes were selected by using this approach for high-temperature tolerance with the objective to test the suitability to grow during spring–summer season (February–June) in Australia. This season is similar to that in north India which is characterized by low temperature during germination (mean minimum temperature of 7.5–18.3°C in second fortnight of February) and high temperatures during reproductive stages (25.4–33.7°C mean minimum temperature and 33.6–43.4°C mean maximum temperature from May 15 to June 30). On the basis of the temperature recorded from 2001 to 2004 (mid-February to June end averaged over 15 days) it became clear that during summer season both minimum and maximum temperatures are very high, while under the main crop season the maximum temperature is more or less similar to the mean minimum temperature experienced during the critical reproductive phase (mid-September onward). The success of these selected genotypes depends upon their tolerance to low temperature during germination and plant stand establishment and high-temperature/heat-stress tolerance during reproductive stage as suggested by Reddy *et al.* (1996). Breeding both high and low-temperature-tolerant cultivars is beneficial. Low-temperature tolerance in cotton would allow the producer to plant the crop earlier and permit a crop canopy to develop earlier in the growing season. This would allow flowering to occur before the mid-summer high temperature that limits fruit set. Similar conditions of cool temperatures during germination and high temperature during flowering occur in cotton-producing regions of the United States (Oosterhuis, 1999; Reddy *et al.*, 1995b). The damaging effect of high temperature on cotton production in Arizona has been recognized (Kittock *et al.*, 1988; Lu *et al.*, 1994). They found that cotton yields in Arizona were limited by high temperature especially if not planted early.

The promising heat-tolerant genotypes can be characterized phenotypically as reported by Singh *et al.* (2003, 2004). Compact plant type, as Ismail and Hall (1998) also found that the dwarfing and reduced biomass production was associated with the heat-tolerant genes in cowpea. Ismail and Hall (1998) reported that heat-tolerant genes slightly enhanced the extent of premature plant senescence occurring just after the first flush of pods was produced. Lower first fruiting node number, as also reported by Feaster and Turcotte (1985), was one of their selection criteria.

The leaves of genotype Pusa 17-52-10 are also very desirable to withstand very hot summer, and they become droopy exposing less area to direct sunlight. This genotype was shown to have higher boll weight 3 g versus 1.5–2.0 g of the heat-susceptible genotype and high boll number per plant (14–15) and reduced ginning turnout (by about 30–32% in comparison to 34%) during main season crop. The heat-tolerant cotton genotype Pusa 17-52-10 has been registered with NBPGR (INGR No 03073). This particular genotype demonstrated tolerance to high temperatures consistently with regard to its performance under multilocation centers for 3 years. Moreover, the strains having heat tolerance also exhibited wide adaptability in terms of their maturity (125–135 days), growth habit, and boll number/plant when grown in different latitudes from northwestern India to coastal eastern regions of Sunderban delta (characterized by very hot and humid conditions) to the southern part tested under rice fallow system.

Oosterhuis (1999) reported that since cotton fiber is made predominantly of carbohydrate, a decreased availability of carbohydrate can also be manifested in less fiber and lower ginning turnout. Overall the heat-tolerant genotypes confer some of the hypothesized traits reported by Hall and Allen (1993) and observed phenotypes of heat-tolerant Pima cotton genotypes reported by Feaster and Turcotte (1984).

VI. SUMMARY AND CONCLUSIONS

Projected changes in climate due to increasing "greenhouse" gases is a challenging issue to many scientists. Atmospheric CO_2 has increased by 37% during the past two centuries to its present level of 380 μmol mol^{-1}, and it is predicted that CO_2 could be in the range of 510–760 μmol mol^{-1} by the middle or later part of this century. The increasing CO_2 and other greenhouse trace gases will contribute to global climate change, which in turn is expected to warm the earth by 2–5 °C by the end of this century. As the world becomes warmer, the hydrological cycle will also become more intense resulting in more uneven and intense precipitation. This will result in increased summer drying and associated risk of both droughts and floods. The current and projected changes in climate pose a greatest challenge to crop physiologists, crop breeders, and producers to continue to produce ecosystem goods and services in a sustainable manner to the needs of growing population. Since plant growth and crop production are controlled by weather and in particular temperature, it becomes imperative to understand the implications of temperature change on crop production.

Cotton, *Gossypium* species, is of the marvels of the plant kingdom in providing the needs of humankind. It produces the basic raw materials, such as cellulose, protein, and oil, in quantity and quality surpassed by few plant species. The cellulose is pure and in the form of a natural fiber. This crop is an important commodity worldwide, valued at US$20 billion per annum is likely to suffer most by global climate change, since two-third of the global cotton production come from higher (>30° N) latitude. Nevertheless, it has been predicted that the impact of global warming will be greater in the northern than in the southern hemisphere due to more high latitude area is cultivated in the northern hemisphere.

Better understanding of the possible impact of rising temperature on crop photosynthesis and productivity would help in mitigating the adverse effects of high-temperature (heat) stress. From the literature surveyed, it has been observed that rising temperature exerts negative influence on CGR, photosynthesis, crop phenology, and yield. As the temperature increases further, interception and absorption of PAR will be drastically affected. Dark and photorespiration overtake net photosynthesis and result in loss of biomass. Breeding cultivars to any abiotic stress is very costly and time-consuming process. It requires the concerted efforts of crop physiologists, biochemists, molecular biologists, and geneticists in addition to the efforts rendered by the traditional plant breeders. The very basic and first approach is to identify the suitable donor stock(s) for their effective utilization in tailoring of new cultivars. The conventional screening of large germplasm has been very resource intensive and time consuming because the success of any breeding program depends on the effective evaluation and utilization of available and suitable germplasm.

The use of relatively new physiological techniques such as CMT, LEL, carbon isotope discrimination; ecophysiologically based remote-sensing/infrared techniques such as CTD, VPD, chlorophyll fluorescence; and biochemical parameters such as chlorophyll a and b contents and a:b ratio are gaining popularity to screen efficiently and quickly with reliability. The quantification of various environmental parameters in terms of CWSI and TSI has helped to evaluate the genotypes against water and/or heat stress, both CWSI and TSI are correlated with yield under heat stress conditions.

The association between CTD and leaf conductance with each other and with yield extends the possibility of coupled selection for both traits. The CTD which is a function of stomatal conductance itself is a mechanism of heat escape in cotton. CTD is directly affected by a number of physiological processes; it is a good indicator of the fitness of a genotype in a specific environment. Moreover, CTD also seems to be affected by the ability of a genotype to partition assimilates to yield. The significant positive genetic correlation between yield and CTD, cell membrane thermostability, leaf chlorophyll content, leaf conductance, and photosystem components have been reported under heat stress conditions.

It has also been reported in literature that the stomatal component of heat resistance is apparently dependent on evaporative cooling which represents a "heat avoidance strategy," and the genetic variability for an avoidance of heat resistance has been reported in cotton. Nevertheless, it has also been speculated that intensive selection for higher yield and heat resistance in Pima cotton has generated indirect selection pressure on photosynthetic rate, stomatal conductance, and reduced leaf areas (correlated response). Genetic differences in photosynthetic capacity may be detected indirectly by selecting for thicker leaves as they have more dry weight per unit leaf area and usually have higher levels of photosynthetic enzymes and photosystem components per unit leaf area. Direct selection can be applied for morphological traits such as lower fruiting node number, smaller and thicker leaves, okra leaf types, and abundant flowering, and fruiting under high-temperature conditions.

Heat tolerance at reproductive stage can be enhanced by using pollen selection through heat treatment.

Indirect selection procedures based on the measurement of canopy temperature by remote sensing could be more effective than direct selection based on the measurement of the stomatal conductance of individual leaves. The stay-green trait has the potential to be widely used in breeding for heat tolerance. The heritability of useful eco-morpho-physiological trait(s) for enhancing heat-tolerance needs further investigation to make it amenable to selection. From the various reports it is clear that sufficient genetic variability is present in the elite cotton germplasm which could be used effectively after critical evaluation to develop cotton cultivars for heat tolerance by adopting suitable-breeding methodologies.

ACKNOWLEDGMENTS

Part of the research was funded by the Departments of Energy, Bioenergy, and Biological and Environmental Research programs, US Department of Energy, through Mississippi State University, and the South Central Regional Center of NIGEC, respectively and USDA UV-B Monitoring and Network, Colorado State University, Fort Collins, CO. We thank Drs. Harry F. Hodges, Jack C. McCarty, and Frank B. Matta for reviewing the chapter and for their helpful comments. Contribution from the Department of Plant and Soil Sciences, Mississippi State University, Mississippi Agricultural and Forestry Experiment Station no. J-10971 and from the Department of Agronomy, Kansas State University, Manhattan, Kansas (Kansas Agricultural Experiment Station no. 07-53-B).

REFERENCES

Abrol, Y. P., and Ingram, K. T. (1996). Effects of higher day and night temperatures on growth and yields of some crop plants. *In* “Global Climate Change and Agricultural Production. Direct and Indirect Effects of Changing Hydrological, Pedological and Plant Physiological Processes” (F. A. Bazzaz and W. G. Sombroek, Eds.), pp. 1–19. John Wiley & Sons Ltd., Chichester, West Sussex, England.

Ahmed, F. E., Mutters, R. G., and Hall, A. E. (1993). Interactive effects of high temperature and light quality on floral bud development in cowpea. *Aust. J. Plant Physiol.* **20**, 661–667.

Alexandrov, V. Y. (1964). Cytophysiological and cytoecological investigations of resistance of plant cell toward the action of high and low temperature. *Quat. Rev. Bio.* **39**, 35–77.

Alfonso, M., Yruela, I., Almárcegui, S., Torrado, E., Pérez, M. A., and Picorel, R. (2001). Unusual tolerance to high temperatures in a new herbicide-resistant D1 mutant from *Glycine max* (L.) Merr. cell cultures deficient in fatty acid desaturation. *Biomed. Life Sci.* **212**, 573–582.

Al-Khatib, K., and Paulsen, G. M. (1984). Mode of high temperature injury to wheat during grain development. *Physiol. Plant.* **61**, 363–368.

Amani, I., Fischer, R. A., and Reynolds, M. P. (1996). Evaluation of canopy temperature as screening tool for heat tolerance in spring wheat. *J. Agron. Crop Sci.* **176**, 119–129.

Araus, J. L. (1996). Integrative physiological criteria associated with yield potential. *In* "Increasing Yield Potential in Wheat" (M. P. Reynolds, Ed.), pp. 150–166. CIMMYT, Mexico, DF.

Arevalo, L. M., Oosterhuis, D. M., Coker, D. L., and Brown, R. S. (2004). Effect of night temperature on plant growth, boll development and yield. *In* "Proceeding of the Beltwide Cotton Conferences" (D. A. Richter, Ed.), p. 1972. National Cotton Council America, Memphis, TN.

Ashraf, M., Saeed, M. M., and Qureshi, M. J. (1994). Tolerance to high temperature in cotton at initial growth stages. *Environ. Exp. Bot.* **343**, 275–283.

Baker, D. N., and Myhre, D. L. (1968). Leaf shape and photosynthetic potential in cotton. *In* "Proceeding of the Beltwide Cotton Conferences" (P. W. Brown, Ed.), pp. 102–109. National Cotton Council of America, Memphis, TN.

Baker, J. T., Allen, L. H., Jr., and Boote, K. J. (1990). Growth and yield response of rice to carbon dioxide concentration. *J. Agric. Sci.* **115**, 313–320.

Barbagallo, R. P., Oxborough, K., Pallett, K. E., and Baker, N. R. (2003). Rapid, noninvasive screening for perturbations of metabolism and plant growth using chlorophyll fluorescence imaging. *Plant Physiol.* **132**, 485–493.

Bassett, D. M., Anderson, W. D., and Werkhoven, C. H. E. (1970). Dry matter production and nutrient uptake in irrigated cotton (*Gossypium hirsutum* L.). *Agron. J.* **62**, 299–303.

Bednarz, C. W., and van Iersal, M. W. (2001). Temperature response of whole-plant CO_2 exchange rate of four Upland cotton cultivars differing in leaf shape and leaf pubescence. *Commun. Soil Sci. Plant Anal.* **32**, 2485–2501.

Berlin, J. D. (1977). The fine structure of the non-fiber epidermal cell during cotton seed development. *In* "Proceeding of the Beltwide Cotton Conferences" (P. W. Brown, Ed.), p. 69. National Cotton Council of America, Memphis, TN.

Bhagsari, A. S., and Brown, R. H. (1986). Leaf photosynthesis and its correlation with leaf area. *Crop Sci.* **26**, 127–132.

Bhardwaj, S. N., and Singh, M. (1991). Thermal relation of light utilization and biomass production in upland cotton (*Gossypium hirsutum* L.). *In* "Proceedings of Indo US Workshop on Impact of Global Climatic Changes on Photosynthesis and Plant Productivity, January 8–12, 1991" (I. P. Abrol, Ed.), pp. 651–662. Oxford and IBH Publishing Company Ltd., New Delhi, India.

Bibi, A. C., Oosterhuis, D. M., Brown, R. S., Gonias, E. D., and Bourland, F. M. (2003). "The Physiological Response of Cotton to High Temperatures for Germplasm Screening," pp. 87–93. Summaries of Arkansas Cotton Research 2003. AAES Research Series 521.

Bland, W. L. (1993). Cotton and soybean root systems growth in three soil temperature regimes. *Agron. J.* **85**, 906–911.

Blum, A. (1986). The effect of heat stresses on wheat leaf and ear photosynthesis. *J. Exp. Bot.* **37**, 111–118.

Blum, A. (1988). "Plant Breeding for Stress Environment." CRC Press Inc., Boca Ratan, FL.

Blum, A., and Ebercon, A. (1981). Cell membrane stability as a measure of drought and heat tolerance in wheat. *Crop Sci.* **21**, 43–47.

Blum, A., Klueva, N., and Nguyen, H. T. (2001). Wheat cellular thermotolerance is related to yield under heat stress. *Euphytica* **117**, 117–123.

Boyer, J. S. (1982). Plant productivity and environment. *Science* **218**, 443–448.

Bradow, J. M., and Davidonis, G. H. (2000). Quantitation of fiber quality and the cotton production-processing interface: A physiologist's perspective. *J. Cotton Sci.* **4**, 34–64.

Bradow, J. M., Sassenrath-Cole, G. F., Hinojasa, O., and Wartelle, L. H. (1996). Cotton fiber physical and physiological maturity variation in response to genotype and environment. *In* "Proceeding of the Beltwide Cotton Conferences," pp. 1251–1254. National Cotton Council of America, Memphis, TN.

Bradow, J. M., Wartelle, L. H., Bauer, P. J., and Sassenrath-Cole, G. F. (1997). Small-sample cotton fiber quality quantitation. *J. Cotton Sci.* **1**, 48–58.

Bradow, J. M., Johnson, R. M., Bauer, P. J., and Sassenrath-Cole, G. F. (2001). Variability in micronaire: Sources and significance. *In* "Proceeding of the Beltwide Cotton Conferences" (C. P. Dugger and D. A. Richter, Eds.), pp. 477–478. National Cotton Council of America, Memphis, TN.

Bridge, R. R., and Meredith, W. R., Jr. (1983). Comparative performance of obsolete and current cotton cultivars. *Crop Sci.* **23**, 949–952.

Brock, T. D. (1985). Life at high temperatures. *Science* **230**, 132–138.

Brouwer, R., and de Wit, C. T. (1969). A simulation model of plant growth with special attention to root growth and its consequences. *In* "Root Growth" (W. J. Whittington, Ed.), pp. 224–244. Butterworth Publishers, London.

Brown, P. W. (2001). Heat tress and cotton yields in Arizona. Arizona Cotton Report. The University of Arizona of Agriculture and Life Sciences, indexed at http://ag.arizona.edu/pubs/crops/az1224/

Brown, P. W. (2002). Cotton heat stress update: Coolidge and Maricopa. Arizona Cotton Report. The University of Arizona of Agriculture and Life Sciences. Indexed at http://ag.arizona.edu/azmet/data/cm.pdf

Brown, P. W., and Zeiher, C. A. (1998). A model to estimate cotton canopy temperature in the desert southwest. *In* "Proceeding of the Beltwide Cotton Conferences" (C. P. Dugger and D. A. Richter, Eds.), p. 1734. National Cotton Council of America, Memphis, TN.

Brown, P. W., Zeiher, C. A., and Silvertooth, J. (1995). Response of Upland cotton to elevated night temperatures. I. Results of field studies. *In* "Proceeding of the Beltwide Cotton Conferences" (C. P. Dugger and D. A. Richter, Eds.), p. 1129. National Cotton Council of America, Memphis, TN.

Brown, R. S., Oosterhuis, D. M., Coker, D. L., and Fowler, L. (2003). The dynamics of dry-matter partitioning in the cotton boll of modern and obsolete cultivars. *In* "Proceeding of the Beltwide Cotton Conferences" (D. A. Richter, Ed.), pp. 1886–1889. National Cotton Council of America, Memphis, TN.

Burke, J. J. (1990). Variation among species in the temperature dependence of the reappearance of variable fluorescence following illumination. *Plant Physiol.* **93**, 652–656.

Burke, J. J. (2001). Opportunities for improving cotton's tolerance to high temperature. *In* "Proceeding of the Beltwide Cotton Conferences" (C. P. Dugger and D. A. Richter, Eds.), p. 1453. National Cotton Council of America, Memphis, TN.

Burke, J. J. (2004). Metabolic and reproductive fitness of heat-stressed cotton. *In* "Proceeding of the Beltwide Cotton Conferences" (C. P. Dugger and D. A. Richter, Eds.), p. 2136. National Cotton Council of America, Memphis, TN.

Burke, J. J., and Upchurch, D. R. (1989). Leaf temperature and transpirational control in cotton. *Environ. Exp. Bot.* **29**, 487–492.

Burke, J. J., and Upchurch, D. R. (1995). Cotton rooting patterns in relation to soil temperatures and the thermal kinetic window. *Agron. J.* **87**, 1210–1216.

Burke, J. J., Hatfield, J. L., Klein, R. R., and Mullet, J. E. (1985). Accumulation of heat shock proteins in field-grown cotton. *Plant Physiol.* **78**, 394–398.

Burke, J. J., Mohan, J. R., and Hatfield, J. L. (1988). Crop specific thermal kinetic windows in relation to wheat and cotton biomass production. *Agron. J.* **80**, 553–556.

Burke, J. J., Hatfield, J. L., and Wanjura, D. F. (1990). A thermal stress index for cotton. *Agron. J.* **82**, 526–530.

Burke, J. J., Velten, J., and Oliver, M. J. (2004). *In vitro* analysis of cotton pollen germination. *Agron. J.* **96**, 359–368.

Butler, W. L. (1978). Energy distribution in the photochemical apparatus of photosynthesis. *Annu. Rev. Plant Physiol.* **29**, 345–378.

Cantrell, R. G., Ulloa, M., Percy, R., Zeiher, E., and Lu, Z. (1998). Genetic variation for stomatal conductance in an interspecific cotton population. *In* "Proceeding of the Beltwide Cotton Conferences" (C. P. Dugger and D. A. Richter, Eds.), p. 485. National Cotton Council of America, Memphis, TN.

Chaisompongopan, N., Li, P. H., Davis, D. W., and Mackhart, A. H. (1990). Photosynthetic responses to heat stress in common bean genotypes differing in heat acclimation potential. *Crop Sci.* **30**, 100–104.

Cheikh, N., Miller, P. W., and Kishore, G. (2000). Role of biotechnology in crop productivity in a changing environment. *In* "Climate Change and Global Crop Productivity" (K. R. Reddy and H. F. Hodges, Eds.), pp. 425–435. CAB International, UK.

Chen, T. H. H., Shen, Z. Y., and Lee, P. H. (1982). Adaptability of crop plants to high temperature stress. *Crop Sci.* **22**, 719–725.

Clarke, B., and Reinhard, N. (1991). Effects of soil temperature on root and shoot growth traits and iron deficiency chlorosis in sorghum genotypes grown in a low calcareous soil. *Plant Sci.* **130**, 97–103.

Cohen, A. (2001). Water-use efficiency of interspecific F4 and F5 cotton lines. M.Sc. Thesis, The Hebrew University of Jerusalem, Rehoboth, Israel.

Condon, A. G., and Hall, A. E. (1997). Adaptation to diverse environments: Variation in water-use efficiency within crop species. *In* "Ecology in Agriculture" (L. E. Jackson, Ed.), pp. 79–116. Academic Press, San Diego, CA.

Conroy, J. P., Seneweera, S., Basra, A. S., Rogers, G., and Nissen-Wooler, B. (1994). Influence of rising atmospheric CO_2 concentrations and temperature on growth, yield and grain quality of cereal crops. *Aust. J. Plant Physiol.* **21**, 741–758.

Cornish, K., Radin, J. W., Turcotte, E. L., Lu, Z. M., and Zeiger, E. (1991). Enhanced photosynthesis and stomatal conductance of pima cotton (*Gossypium barbadense* L.) bred for increased yield. *Plant Physiol.* **97**, 484–489.

Cowan, I. R., and Farquhar, G. D. (1977). Stomatal function in relation to leaf metabolism and environment. *Sym. Soc. Exp. Biol.* **31**, 471–505.

Craufurd, P. Q., Wheeler, T. R., Ellis, R. H., Summerfield, R. J., and Williams, J. H. (1999). Effect of temperature and water-use efficiency, carbon isotope discrimination, and specific leaf area in peanut. *Crop Sci.* **39**, 136–142.

Dornhoff, G. M., and Shibles, R. M. (1976). Leaf morphology and anatomy in relation to CO_2-exchange rate of soybean leaves. *Crop Sci.* **16**, 377–381.

Drake, B. G., Gonzalez-Meler, M. A., and Long, S. P. (1997). More efficient plants: A consequence of rising atmospheric CO_2? *Annu. Rev. Plant Biol.* **48**, 609–639.

Ehrler, W. L. (1973). Cotton leaf temperature as related to soil water depletion and meteorological factors. *Agron. J.* **65**, 404–409.

Ehrler, W. L., Idso, S. B., Jackson, R. D., and Reginoto, R. J. (1978). Diurnal changes in plant water potential and canopy temperature of wheat as affected by drought. *Agron. J.* **70**, 999–1004.

Ehlers, J. D., and Hall, A. E. (1996). Genotypic classification of cowpea based on responses to heat and photoperiod. *Crop Sci.* **36**, 673–679.

Ehlig, C. F., and LeMert, R. D. (1973). Effects of fruit load, temperature and relative humidity on boll retention of cotton. *Crop Sci.* **13**, 168–171.

Elmore, C. D., Hesketh, J. D., and Muramoto, H. (1967). A survey of rates of leaf growth, leaf aging and leaf photosynthetic rates among and within species. *J. Ariz. Acad. Sci.* **4**, 215–219.

El-Sharkawy, M. A., Hesketh, J. D., and Muramato, H. (1965). Leaf photosynthesis rates and other growth characteristics among 26 species of *Gossypium*. *Crop Sci.* **5**, 173–175.

Evans, L. T. (1983). "Crop Evolution Adaptation and Yield." Cambridge University Press, Cambridge, UK.

Evans, L. T., and Fischer, R. A. (1999). Yield potential: Its definition, measurement and significance. *Crop Sci.* **39**, 154–1551.

FAO. (2005). http://faostat.fao.org/faostat/collections?subset=agriculture

Farbrother, H. G. (1960). Progress Report Experiment Station, Uganda, 1959–1960. Empire Cotton Growing Corporation, London. p. 20.

Farbrother, H. G. (1961). Progress Report Experiment Station, 1960–1961. Uganda Empire. Cotton Growing Corporation, London. p. 56.

Farquhar, G. D., and Richards, R. A. (1984). Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Aust. J. Plant Physiol.* **11**, 539–552.

Farquhar, G. D., Hubick, K. T., Condon, A. G., and Richards, R. A. (1988). Carbon isotope fractionation and plant water-use efficiency. *In* "Stable Isotopes in Ecological Research" (Eco. Studies68) (J. R. Ehleringer and K. A. Nagy, Eds.), pp. 21–40. Springer, Berlin, Germany.

Farquhar, G. D., Wong, S. C., Evans, J. R., and Hubick, K. T. (1989). Photosynthesis and gas exchange. *In* "Plants Under Stress" (H. J. Jones, T. J. Flower, and M. B. Jones, Eds.), pp. 47–69. Cambridge University Press, Cambridge.

Faver, K. L., Gerik, T. J., Thaxton, P. M., and El-Zik, K. M. (1996). Late season water stress in cotton: II. Leaf gas exchange and assimilation capacity. *Crop Sci.* **36**, 922–928.

Feaster, C. V., and Turcotte, E. L. (1962). Genetic basis for varietal improvement of Pima cotton. USDA-ARS Bulletin 34.

Feaster, C. V., and Turcotte, E. L. (1984). Genetic contribution to commercial yields of Pima cotton. *In* "Proceeding of the Beltwide Cotton Conferences" (C. P. Dugger and D. A. Richter, Eds.), pp. 93–95. National Cotton Council of America, Memphis, TN.

Feaster, C. V., and Turcotte, E. L. (1985). Use of heat tolerance in cotton breeding. *In* "Proceeding of the Beltwide Cotton Conferences" (C. P. Dugger and D. A. Richter, Eds.), pp. 364–366. National Cotton Council of America, Memphis, TN.

Feaster, C. V., Turcotte, E. L., and Young, E. F. (1967). Pima cotton varieties for low and high elevations. USDA-ARS. pp. 34–90.

Fisher, W. D. (1973). Association of temperature and boll set. *In* "Proceeding of the Beltwide Cotton Conferences" (P. W. Brown, Ed.), pp. 72–73. National Cotton Council of America, Memphis, TN.

Fischer, R. A., and Maurer, R. (1978). Drought resistance in spring wheat cultivars. I. Grain yield responses. *Aust. J. Agric. Res.* **29**, 897–912.

Fischer, R. A., Rees, D., Sayre, K. D., Lu, Z., Condon, A. G., Larque-Saavedra, A., and Zeiger, E. (1998). Wheat yield progress associated with higher stomatal conductance and photosynthetic rate and cooler canopies. *Crop Sci.* **38**, 1467–1475.

Fokar, M., Nguyen, H. T., and Blum, A. (1998). Heat tolerance in spring wheat. I. Estimating cellular thermotolerance and its heritability. *Euphytica* **104**, 1–8.

Fryxell, P. A. (1986). Ecological adaptations of *Gossypium* species. *In* "Cotton Physiology" (J. R. Mauney and J. M. Stewart, Eds.), pp. 1–7. Memphis, TN.

Gerik, T. J., and Eastin, J. D. (1985). Temperature effects on dark respiration among diverse sorghum genotypes. *Crop Sci.* **25**, 957–961.

Gipson, J. R., and Joham, H. E. (1968a). Influence of night temperature on growth and development of cotton (*Gossypium hirsutum* L.). I. Fruiting and boll development. *Agron. J.* **60**, 292–295.

Gipson, J. R., and Joham, H. E. (1968b). Influence of night temperature on growth and development of cotton (*Gossypium hirsutum* L.). II. Fiber properties. *Agron. J.* **60**, 296–298.

Gipson, J. R., and Joham, H. E. (1969). Influence of night temperature on growth and development of cotton (*Gossypium hirsutum* L.). III. Fiber elongation. *Crop Sci.* **9**, 127–129.

Gipson, J. R., and Ray, L. L. (1969). Fiber elongation rates in five varieties of cotton (*Gossypium hirsutum* L.) as influenced by night temperature. *Crop Sci.* **9**, 339–341.

Gipson, J. R., and Ray, L. L. (1970). Temperature variety interrelationships in cotton. I. Boll and fiber development. 2. Seed development and composition. *Cotton Growers Rev.* **47**, 257–271.

Gipson, J. R., and Ray, L. L. (1976). The effect of temperature on certain seed and lint parameters of selected cotton cultivars. *In* "Proceeding of the Beltwide Cotton Conferences" (P. W. Brown, Ed.), pp. 45–46. National Cotton Council of America, Memphis, TN.

Gipson, J. R., Ray, L. L., and Flower, C. L. (1969). Influence of night temperatures on seed development of five varieties of cotton. *In* "Proceeding of the Beltwide Cotton Conferences" (P. W. Brown, Ed.), pp. 117–118. National Cotton Council of America, Memphis, TN.

Grant, J. N., Orr, R. S., and Powell, R. D. (1966). Cotton fibers structure and physical properties altered by environment. *Text Res. J.* **36**, 432–440.

Guinn, G. (1974). Abscission of cotton floral buds and bolls as influenced by factors affecting photosynthesis and respiration. *Crop Sci.* **14**, 291–293.

Haigler, C. H., Zhang, D., and Wilkerson, C. G. (2005). Biotechnological improvement of cotton fiber maturity. *Physiol. Plant.* **124**, 285–294.

Hall, A. E. (1992). Breeding for heat tolerance. *Plant Breed. Rev.* **10**, 129–168.

Hall, A. E. (1993). Physiology and breeding for heat tolerance in cowpea, and comparison with other crops. *In* "Adaptation of Food Crops to Temperature and Water Stress" (C. G. Kuo, Ed.), pp. 271–284. Publ. No. 93–410. Asian Vegetable Research and Development Center, Shanhua, Taiwan.

Hall, A. E. (2001). Consideration of crop responses to environment in plant breeding. *In* "Crop Response to Environment," pp. 197–208. CRC Press LLC, Boca Raton, Florida.

Hall, A. E. (2004). Mitigation of stress by crop management. http://www.plantstress.com/Articles/heat_m/heat_m.htm

Hall, A. E., and Allen, L. H., Jr. (1993). Designing cultivars for the climatic conditions of the next century. *In* "International Crop Science I. CSSA" (D. R. Buxton, R. Shibles, R. A. Forsberg, B. L. Blad, K. H. Asay, G. M. Paulsen, and R. F. Wilson, Eds.), pp. 291–297. Madison, WI.

Hall, A. E., and Ziska, L. H. (2000). Crop breeding strategies for the 21st century. *In* "Climate Change and Global Crop Productivity" (K. R. Reddy and H. F. Hodges, Eds.), pp. 407–423. CABI Publishing, New York, USA.

Hanson, R. G., Ewing, E. C., and Ewing, E. C., Jr. (1956). Effect of environmental factors on fiber properties and yield of deltapine cottons. *Agron. J.* **48**, 546–581.

Harding, S. A., Gurkema, J. A., and Paulsen, G. M. (1990). Photosynthesis decline from high temperature stress during maturation of wheat. I. Interaction with senescence process. *Plant Physiol.* **92**, 648–653.

Hatfield, J. L. (1985). Wheat canopy resistance determined by energy balance techniques. *Agron. J.* **77**, 279–283.

Hatfield, J. L., Quisenberry, J. E., and Dilbeck, R. E. (1987). Use of canopy temperature to identify water conservation in cotton germplasm. *Crop Sci.* **27**, 269–273.

Hearn, A. B. (1976). Response of cotton to nitrogen and water in a tropical environment: III. Fiber quality. *J. Agric. Sci.* **86**, 257–269.

Hearn, A. B. (1980). Water relationship in cotton. *Outlook Agric.* **10**, 159–166.

Hearn, A. B. (1994). The principles of cotton water relations and their applications in management. *In* "Challenging the Future. Proceeding World Cotton Conference I" (G. A. Constable and N. W. Forrester, Eds.), pp. 66–92. CSIRO, Australia.

Heitholt, J. J. (1993). Cotton boll retention and its relationship to lint yield. *Crop Sci.* **33**, 486–490.

Heitholt, J. J. (1994). Canopy characteristics associated with deficient and excessive cotton plant population densities. *Crop Sci.* **34**, 1291–1297.

Heitholt, J. J., and Meredith, W. R., Jr. (1998). Yield, flowering and leaf area index of okra-leaf and normal-leaf cotton isolines. *Crop Sci.* **38**, 643–648.

Heitholt, J. J., Pettigrew, W. T., and Meredith, W. R., Jr. (1992). Light interception and lint yield of narrow-row cotton. *Crop Sci.* **32**, 728–733.

Hesketh, J. D., and Low, A. (1968). Effect of temperature and fiber quality of cotton varieties of diverse origin. *Emp. Cott. Grow. Rev.* **45**, 243–257.

Hinderhofer, K., Eggers-Schumacher, G., and Schoffl, F. (1998). HSF3, a new heat shock factor from *Arabidopsis thaliana*, depresses the heat shock response and confers thermotolerance when over expressed in transgenic plants. *Mol. Gen. Genet.* **258**, 269–278.

Hodges, H. F., Reddy, V. R., and Reddy, K. R. (1991). Mepiquat chloride and temperature effects on photosynthesis and respiration of fruiting cotton. *Crop Sci.* **31**, 1302–1308.

Hodges, H. F., Reddy, K. R., McKinion, J. M., and Reddy, V. R. (1993). Temperature effects on cotton. *Mississippi Agric. For. Exp. Sta. Bull.* **990**, Mississippi State, MS.

Hopf, N., Plesofsky-Vig, N., and Bramb, R. (1992). The heat shock response of pollen and other tissues of maize. *Plant Mol. Biol.* **19**, 623–630.

Horvath, I., Glatz, A., Varvasovszki, V., Török, Z., Páli, T., Balogh, G., Kovács, E., Nádasdi, L., Benkö, S., Joó, F., and Vígh, L. (1998). Membrane physical state controls the signaling mechanism of heat shock response in *Synechocystis* PCC 6803: Identification of *hsp 17* as a 'fluidity gene'. *Proc. Natl. Acad. Sci. USA* **95**, 3513–3518.

Ham, J. M., Heilman, J. L., and Lascano, R. J. (1991). Soil and canopy balances of a row at partial cover. *Agron. J.* **83**, 744–753.

Hugly, S., Kunst, L., Browse, J., and Somerville, C. (1989). Enhanced thermal tolerance of photosynthesis and altered chloroplast ultrastructure in a mutant of *Arabidopsis* deficient in lipid desaturation. *Plant Physiol.* **90**, 1134–1142.

Idso, S. B. (1982). Non-water-stressed baselines: A key to measuring and interpreting land water stress. *Agric. For. Meteorol.* **27**, 59–70.

Idso, K. E., and Idso, S. B. (1994). Plant responses to atmospheric CO_2 enrichment in the face of environmental constraints: A review of the past 10 years' research. *Agric. For. Meteorol.* **69**, 153–203.

Idso, S. B., and Reginato, R. J. (1982). Leaf diffusion resistance and photosynthesis in cotton as related to a foliage temperature based plant water stress index. *Agric. For. Meteorol.* **27**, 27–34.

Idso, S. B., Jackson, R. D., and Reginato, R. J. (1977). Remote sensing of crop yields. *Science* **196**, 19–25.

Idso, S. B., Jackson, R. D., Pinter, P. J., Jr., Reginato, R. J., and Hatfield, J. L. (1981). Normalizing the stress-degree-day parameter for environmental variability. *Agric. For. Meteorol.* **24**, 45–55.

Idso, S. B., Reginato, R. J., Clarrson, K. L., and Anderson, M. G. (1984). On the stability of stress baselines. *Agric. For. Meteorol.* **32**, 177–182.

Idso, S. B., Kimball, B. A., Anderson, M. G., and Mauney, J. R. (1987). Effects of atmospheric CO_2 enrichment on plant growth: The interactive role of air temperature. *Agric. Ecosyst. Environ.* **20**, 1–10.

Intergovernmental Panel on Climate Change (IPCC). (1995). "Climate Change 1995: The Science of Climate Change" (J. T. Houghton, L. G. Meira-Filho, B. A. Callander, N. Harris, A. Katenberg, and K. Maskell, Eds.), Cambridge University PressCambridge, UK.

Ismail, A. M., and Hall, A. E. (1998). Positive and potential negative effects of heat-tolerance genes in cowpea. *Crop Sci.* **38**, 381–390.

Ismail, A. M., and Hall, A. E. (1999). Reproductive-stage heat tolerance, leaf membrane thermostability and plant morphology in cowpea. *Crop Sci.* **39**, 1762–1768.

Jackson, J. E. (1967). Studies on the sowing dates of cotton in sudan gezira. I. The influence of date of sowing on plant growth development. *J. Agric. Sci. Camb.* **69**, 305–315.

Jackson, P., Robertson, M., Cooper, M., and Hammer, G. (1996). The role of physiological understanding in plant breeding: From a breeding perspective. *Field Crops Res.* **49**, 11–37.

Jackson, R. D., Renitago, R. J., and Idso, S. B. (1977). Wheat canopy temperature: A practical tool for evaluating water requirements. *Water Resour. Res.* **13**, 651–656.

Jackson, R. D. (1982). Canopy temperature and crop water stress. *In* "Advances in Irrigation" (D. Hillel, Ed.), Vol. 1, pp. 43–85. Academic Press, New York.

Jackson, R. D., Idso, S. B., Reginto, R. J., and Pinter, P. J., Jr. (1981). Canopy temperature as a crop water stress indicator. *Water Resour. Res.* **17**, 1133–1138.

Jarvis, P. G., and McNaughton, K. G. (1982). Stomatal control of transpiration: Scaling up from leaf to region. *Adv. Ecol. Res.* **15**, 1–49.

Jiang, C.-X., Robert, J. W., El-Zik, K. M., and Paterson, A. H. (1998). Polyploid formation created unique avenues for response to selection in *Gossypium* (cotton). *Evolution* **93**, 4419–4424.

Jiang, Y., and Huang, B. (2000). Effects of drought or heat stress alone and in combination on kentucky bluegrass. *Crop Sci.* **40**, 1358–1362.

Johnson, B., and Wadleigh, C. H. (1939). Certain ecological factors and the cotton plant. *Arkanas Agr. Exp. Sta. Bull.* **376**.

Johnson, R. M., Sassenrath-Cole, G. F., and Bradow, J. M. (1997). Prediction of cotton fiber maturity from environmental parameters. *In* "Proceeding of the Beltwide Cotton Conferences" (C. P. Dugger and D. A. Richter, Eds.), pp. 1454–1455. National Cotton Council of America, Memphis, TN.

Kakani, V. G., Prasad, P. V. V., Craufurd, P. Q., and Wheeler, T. R. (2002). Response of *in vitro* pollen germination and pollen tube growth of groundnut (*Arachis hypogaea* L.) genotypes to temperature. *Plant Cell Environ.* **25**, 1651–1661.

Kakani, V. G., Reddy, K. R., Koti, S., Wallace, T. P., Prasad, P. V. V., Reddy, V. R., and Zhao, D. (2005). Differences in *in-vitro* pollen germination and pollen tube growth of cotton cultivars in response to high temperature. *Ann. Bot.* **96**, 59–67.

Karami, E., Krieg, D. R., and Quisenberry, J. E. (1980). Water relations and carbon-14 assimilation of cotton with different leaf morphology. *Crop Sci.* **20**, 421–426.

Kaustsky, H., Apel, W., and Amann, H. (1960). Chlorophyll fluorescence and kohlensaure assimilation. *Biochem. Z.* **322**, 277–292.

Kee, S. C., and Nobel, P. S. (1985). Fatty acid composition of chlorenchyma membrane fractions from three dessert succulents grown at moderate and high temperature. *Biochem. Biophys. Acta* **820**, 100–106.

Keener, M. E., and Kircher, P. L. (1983). The use of canopy temperature as an indicator of drought stress in humid regions. *Agric. Forest Meteorol.* **28**, 339–349.

Kerby, T. A., and Buxton, D. R. (1978). Effects of leaf shape and plant population on rate of fruiting position appearance in cotton. *Agron. J.* **70**, 535–538.

Kimball, B. A., and Mauney, J. R. (1993). Response of cotton to varying CO_2, irrigation and nitrogen yield and growth. *Agron. J.* **85**, 706–712.

Kittock, D. L., Turcotte, E. L., and Hofman, W. C. (1988). Estimation of heat tolerance improvement in recent American pima cotton cultivars. *J. Agron. Crop Sci.* **161**, 305–309.

Kolb, P. F., and Robberecht, R. (1996). High temperature and drought stress effects on survival of *Pinus ponderosa* seedlings. *Tree Physiol.* **16**, 665–672.

Krieg, D. R. (1981). Leaf development and function as related to water stress. *In* "Proceeding Beltiwide Cotton Production Research Conference" (J. M. Brown, Ed.), pp. 41–42. National Cotton Council of America, Memphis, TN.

Krieg, D. R. (1986). Feedback control and stress effects on photosynthesis. *In* "Proceeding of the Beltwide Cotton Conferences," pp. 227–243. National Cotton Council of America, Memphis, TN.

Landivar, J. A., Baker, D. N., and Jenkins, J. N. (1983). Application of GOSSYM to genetic feasibility studies. I. Analysis of four abscission and yield in okra leaf cottons. *Crop Sci.* **23**, 497–504.

Lather, B. P. S., Saini, M. L., and Punia, M. S. (2001). Hybrid cotton retrospect and prospects in Indian context. *Nat. J. Plant Improv.* **3**, 61–68.

Law, R. D., and Crafts-Brandner, S. J. (1999). Inhibition and acclimation of photosynthesis to heat stress is closely correlated with activation of ribulose-1,5-bisphosphate carboxylase/oxygenase. *Plant Physiol.* **120**, 173–181.

Law, R. D., and Craft-Brandner, S. J. (2001). Heat stress induces the synthesis of a new form of ribulose-1,5-biphosphate carboxylase/oxygenase activase in cotton leaves. *Planta* **214**, 117–125.

Lee, G. J., and Vierling, E. (2000). A small heat shock protein cooperates with heat shock protein 70 systems to reactivate a heat-denatured protein. *Plant Physiol.* **122**, 189–197.

Lee, J. A. (1984). Cotton as a world crop. *In* "Cotton: Agronomy Monograph 24 ASA CSSA and SSSA" (R. J. Kohel and C. F. Lewis, Eds.), pp. 1–25. ASA CSSA and SSSA Madison, WI.

Lee, J. H., Hubel, A., and Schoffl, F. (1995). Depression of the activity of genetically engineered heat shock factors causes constitutive synthesis of heat shock proteins and increased thermotolerance in transgenic *Arabidopsis*. *The Plant J.* **8**, 603–612.

Levitt, J. (1980). "Response of Plants to Environmental Stresses—Chilling, Freezing and High Temperature Stresses," p. 497. Academic Press, New York, NY.

Lewis, H. (2000). Environmental regulation of yield and quality components in Upland cotton. *In* "Proceedings Genetic Control Cotton Fiber and Seed Quality Workshop" (C. R. Benedict and G. Jividin, Eds.), pp. 8–36. Cotton Inc., North Carolina.

Lewis, H., May, L., and Bourland, F. M. (2000). Cotton yield components and yield stability. *In* "Proceeding of the Beltwide Cotton Conferences" (C. P. Dugger and D. A. Richter, Eds.), pp. 532–536. National Cotton Council of America, Memphis, TN.

Lobell, D. B., and Asner, G. P. (2003). Climate and management contributions to recent trends in US agricultural yields. *Science* **299**, 1032.

Long, S. P. (1991). Modification of the response of photosynthetic productivity to rising temperature by atmospheric [CO_2]: Has its importance been underestimated? *Plant Cell Environ.* **14**, 729–739.

Lu, Z., and Zeiger, E. (1994). Selection of higher yield and heat resistance in pima cotton has caused genetically determined changes in stomatal conductance. *Physiol. Plant.* **92**, 273–278.

Lu, Z., Chen, J., Radin, J. W., Percy, R. G., Turcotte, E. L., and Zeiger, E. (1992). Roles of stomatal conductance and leaf size in regulation of leaf temperature in pima cotton (*Gossypium barbadense* L.). *Plant Physiol.* **99**, 11.

Lu, Z., Radin, J. W., Turcotte, E. L., Percy, R., and Zeiger, E. (1994). High yields in advanced lines of pima cotton are associated with higher stomatal conductance, reduced leaf area and lower leaf temperature. *Physiol. Plant.* **92**, 266–272.

Lu, Z., Chen. J., Percy, R. G., Sharifi, M. R., Rundel, P. W., and Zeiger, E. (1996). Genetic variation in carbon isotope discrimination and its relation to stomatal conductance in pima cotton (*Gossypium barbadense*). *Aust. J. Plant Physiol.* **23**, 127–132.

Lu, Z. M., Chen, J., Percy, R. G., and Zeiger, E. (1997). Photosynthesis rate, stomatal conductance and leaf area in two cotton species (*G. barbadense* and *G. hirsutum*) and their relation to heat resistance and yield. *Aust. J. Plant Physiol.* **240**, 693–700.

Lu, Z., Percy, R. G., Qualset, C. O., and Zeiger, E. (1998). Stomatal conductance predicts yield in irrigated pima cotton and bread wheat grown at high temperatures. *J. Exp. Bot. Spec.* **49**, 453–460.

Lu, Z., Chen, J., Percy, R. G., and Zeiger, E. (2000). Photosynthetic rate, stomatal conductance and leaf area in two cotton species (*Gossypium barbadense* and *Gossypium hirsutum*) and their relation with heat resistance and yield. *Aust. J. Plant Physiol.* **24**, 693–700.

Ludlow, M. M. (1980). Adaptive significance of stomatal responses to water stress. *In* "Adaptations of Plants to Water and High Temperature Stress" (N. C. Turner and P. J. Kramer, Eds.), pp. 123–138. Wiley, New York.

Ludwig, L. J., Saeki, T., and Evans, L. T. (1965). Photosynthesis in artificial communities of cotton plants in relation to leaf area. I. Experiments with progressive defoliation of mature plants. *Aust. J. Biol. Sci.* **18**, 1103–1118.

Mahan, J. R., McMichael, B. L., and Wanjura, D. F. (1995). Methods for reducing the adverse effects of temperature stress on plants: A review. *Environ. Exp. Bot.* **35**, 251–258.

Mahon, J. D. (1983). Limitations to the use of physiological variability in plant breeding. *Can. J. Plant Sci.* **63**, 1–21.

Markhart, A. H. (1985). Comparative water relations of *Phaseolus vulgaris* L., and *Phaseolus acutifolius* gray. *Plant Physiol.* **77**, 113–117.

Martineau, J. R., Specht, J. E., Williams, J. H., and Sullivan, C. Y. (1979). Temperature tolerance in soybean. I. Evaluation of temperature for assessing cellular membrane thermostability. *Crop Sci.* **19**, 75–78.

Mateos, L., Smith, R. C. G., and Sides, R. (1991). The effect of soil surface on the crop water stress index. *Irrig. Sci.* **12**, 73–83.

Mauney, J. R. (1966). Floral initiation of upland cotton *Gossypium hirsutum* L. in response to temperatures. *J. Exp. Bot.* **17**, 452–459.

Mauney, J. R., Kimball, B. A., Pinter, P. J., Jr., LaMorte, R. L., Lewin, K. F., Nagy, J., and Hendrey, G. R. (1994). Growth and yield of cotton in response to a free-air carbon dioxide enrichment (FACE) environment. *Agric. Forest Meteorol.* **70**, 49–68.

Maxwell, K., and Johnson, G. N. (2000). Chlorophyll fluorescence: A practical guide. *J. Exp. Bot.* **51**, 659–668.

McDonald, R. G., and Stith, L. S. (1972). Effect of temperature and humidity on pollen dehiscence in cytoplasmic male-sterile stocks of *Gossypium*. *In* "Proceeding of the Beltwide Cotton Conferences" (P. W. Brown, Ed.), p. 60. National Cotton Council of America, Memphis, TN.

McMichael, B. L., and Burke, J. J. (1994). Metabolic activity of cotton roots in response to temperature. *Environ. Exp. Bot.* **34**, 201–206.

McNamara, H. C., Hooton, D. R., and Porter, D. D. (1940). Differential growth rate in cotton varieties and their response to seasonal conditions at Greenville, TX. USDA. Tech. Bull. 710. Greenville, TX.

Meredith, W. R., Jr. (1984). Influence of leaf morphology on lint yield of cotton enhancement by the sub-okra trait. *Crop Sci.* **24**, 855–857.

Meredith, W. R., Jr., and Wells, S. (1986). Normal vs okra leaf yield interactions in cotton. I. Performance of near isogenic lines from bulk populations. *Crop Sci.* **26**, 219–222.

Meredith, W. R., Jr., Pettigrew, W. T., and Heitholt, J. J. (1996). Sub-okra, semi-smoothness and nectariless effect on cotton lint yield. *Crop Sci.* **36**, 22–25.

Meyer, V. G. (1969). Some effects of genes, cytoplasm and environment on male sterility of cotton (*Gossypium*). *Crop Sci.* **9**, 237–242.

Mills, N. B., Oosterhuis, D. M., and McMichael, B. (2005). Genotypic root response of cotton at sub-optimal temperature environments. Abstract No. 240. American Society of Agronomy International Annual Meeting (November 6–10, 2005). American Society of Agronomy, Madison, WI.

Moffat, J. M., Sears, G., Cox, T. S., and Paulsen, G. H. (1990). Wheat high temperature tolerance during reproductive growth I. Evaluation by chlorophyll fluorescence. *Crop Sci.* **30**, 881–885.

Morgan, J. M., and Tan, M. K. (1996). Chromosomal location of a wheat osmoregulation gene using RELP analysis. *Aust. J. Plant Physiol.* **23**, 803–806.

Morison, J. I. L. (1993). Response of plants to CO_2 under water limited conditions. *Vegetatio* **104/105**, 193–209.

Morris, D. A. (1964). Variation in the boll maturation period of cotton. *Emp. Cott. Gr. Rev.* **44**, 2–22.

Morrison, M. J., Voldeng, H. D., and Cober, E. R. (1999). Physiological changes from 58 years of genetic improvement of short-season soybean cultivars in Canada. *Agron. J.* **91**, 685–689.

Munro, J. M., (Ed.) (1987). "Cotton," 2nd ed., p. 436. Longman Scientific and Technical, John Wiley & Sons, New York, NY.

Munro, J. M., and Farbrother, H. G. (1969). Composite plant diagrams in cotton. *Cotton. Gr. Rev.* **48**, 261–282.

Nasyrov, Y. S. (2004). Photosynthesis, global climate changes and genetic improvement of plant productivity. *In* "Strategies for Sustainable Cotton Production. A Global Vision," 2. Crop Production (B. M. Khadi, H. M. Vamadevaiah, I. S. Katageri, H. L. Halemani, and B. C. Patil, Eds.), pp. 23–25. University of Agricultural Sciences, Dharwad, Karnataka, India.

Nguyen, H. T. (1994). Genetics and molecular aspects of high temperature stress responses. *In* "Physiology and Determination of Crop Yield" (K. J. Boote, J. M. Bennett, T. R. Sinclair, and G. M. Paulsen, Eds.), pp. 391–394. American Society of Agronomy, Madison, WI.

Nguyen, H. T., Krishan, M., Burke, J. J., Porter, D. R., and Vierling, R. A. (1989). Genetic diversity of heat shock protein synthesis in cereal plants. *In* "Environmental Stress in Plants: Biochemical and Physiological Mechanisms" (J. H. Cherry, Ed.), pp. 319–330. Springer-Verlag, Berlin.

Nielsen, K. F. (1974). Roots and root temperatures. *In* "The Plant Root and Its Environment" (E. W. Carson, Ed.), pp. 293–333. University Press Virginia, Charlottesville, VA.

Niles, G. A., and Feaster, C. V. (1984). Breeding. *In* "Cotton" (R. J. Kohel and C. F. Lewis, Eds.), pp. 201–231. American Society of Agronomy, Madison, WI.

Nobel, P. S. (1991). "Physiochemical and Environmental Physiology." Academic Press Inc., New York, NY.

Nobel, P. S. (1999). "Physiochemical and Environmental Physiology," 2nd ed. Academic Press Inc., New York, NY.

Nover, L., Bharti, K., Döring, D., Mishra, S. K., Ganguli, A., and Klaus-Dieter, S. (2001). *Arabidopsis* and the heat stress transcription factor world: How many heat stress transcription factors do we need? *Cell Stress Chaperones* **6**, 177–189.

O'Toole, J. C., and Hatfield, J. L. (1983). Effect of wind on the water stress index derived by infrared thermometry. *Agron. J.* **75**, 811–817.

O'Toole, J. C., and Real, J. G. (1986). Estimation of aerodynamics and crop resistances from canopy temperature. *Agron. J.* **78**, 305–310.

Oosterhuis, D. M. (1997). Effects of temperature extremes on cotton yields in Arkansas. *In* "Proceeding of Cotton Research Meeting and Research Summaries" (D. M. Oosterhuis, Ed.), *University of Arkansas Agricultural experiment Station Special Report* **183**, 94–98.

Oosterhuis, D. M. (1999). Yield response to environmental extremes in cotton. *In* "Proceeding of the 1999 Cotton Research Meeting" (C. P. Dugger and D. A. Richter, Eds.), pp. 30–38. National Cotton Council of America, Memphis, TN.

Oosterhuis, D. M. (2002). Day or night high temperatures: A major cause of yield variability. *Cotton Grower.* **46**, 8–9.

Orvar, B. L., Sangwan, V., Omann, F., and Dhindsa, R. S. (2000). Early steps in cold sensing by plant cells: The role of actin cytoskeleton and membrane fluidity. *Plant J.* **23**, 785–794.

Ougham, H. J., and Stoddard, J. L. (1986). Synthesis of heat shock proteins and acquisition of thermotolerance in high temperature susceptible lines of sorghum. *Plant Sci.* **44**, 163–167.

Paterson, A. H., Lander, E. S., Hewitt, J. D., Peterson, S., Lincoln, S., and Tanksley, S. D. (1988). Resolution of quantitative traits into Mendelian factors by using a complete linkage map of restriction fragment length polymorphisms. *Nature* **335**, 721–726.

Paulsen, G. M. (1994). High temperature responses of crop plants. *In* "Physiology and Determination of Crop Yield" (K. J. Boote, J. M. Bennett, T. R. Sinclair, and G. M. Paulsen, Eds.), pp. 365–389. American Society of Agronomy, Madison, WI.

Peng, S., and Krieg, D. R. (1991). Single leaf and canopy photosynthesis response to plant age in cotton. *Agron. J.* **83**, 704–708.

Percy, R. G., and Turcotte, E. L. (1991). Early-maturing, short-statured American Pima cotton parents improve agronomic traits of interspecific hybrids. *Crop Sci.* **31**, 709–712.

Percy, R. G., Lu, Z. M., Radin, J. W., Turcotte, E. L., and Zeiger, E. (1996). Inheritance of stomatal conductance in pima cotton (*Gossypium barbadense* L.). *Physiol. Plant.* **96**, 389–394.

Perry, S. W., Krieg, D. A., and Hutmacher, R. B. (1983). Photosynthetic rate control in cotton. *Plant Physiol.* **73**, 662–665.

Pettigrew, W. T. (1996). Low light conditions compromise the quality of fiber produced. *In* "Proceeding of the Beltwide Cotton Conferences" (P. Dugger and D. A. Richter, Eds.), pp. 1238–1239. National Cotton Council of America, Memphis, TN.

Pettigrew, W. T. (2004). Physiological consequences of moisture deficit stress in cotton. *Crop Sci.* **44**, 1265–1272.

Pettigrew, W. T., and Meredith, W. R., Jr. (1994). Leaf gas exchange parameters vary among cotton genotypes. *Crop Sci.* **34**, 700–705.

Pettigrew, W. T., Heitholt, J. J., and Vaughn, K. C. (1993). Gas exchange and comparative anatomy among cotton leaf-type isolines. *Crop Sci.* **33**, 1295–1299.

Pinter, P. J., Jr., Kimball, B. A., Garcia, R. L., Wall, G. W., Hunsaker, D. J., and LaMorte, R. L. (1996). Free-air CO_2 enrichment: Responses of cotton and wheat crops. *In* "Carbon Dioxide and Terrestrial Ecosystems" (G. W. Koch and H. A. Mooney, Eds.), pp. 215–249. Academic Press, San Diego, CA.

Polley, H. W. (2002). Implications of atmospheric and climatic change for crop yield and water use efficiency. *Crop Sci.* **42**, 131–140.

Powell, R. D. (1969). Effect of temperature on boll set and development of *Gossypium hirsutum*. *Cotton Grow. Rev.* **46**, 29–36.

Prasad, P. V. V., Boote, K. J., Allen, L. H., and Thomas, J. M. G. (2002). Effect of elevated temperature and carbon dioxide on seed-set and yield of kidney bean (*Phaseolus vulgaris* L.). *Global Change Biol.* **8**, 710–721.

Prasad, P. V. V., Boote, K. J., Allen, L. H., and Thomas, J. M. G. (2003). Super-optimal temperatures are detrimental to peanut (*Arachis hypogaea* L.) reproductive processes and yield at both ambient and elevated carbon dioxide. *Global Change Biol.* **9**, 1775–1787.

Prasad, P. V. V., Boote, K. J., Allen, L. H., Jr., Sheehy, J. E., and Thomas, J. M. G. (2006). Species, ecotype and cultivar differences in spikelet fertility and harvest index of rice in response to high temperature stress. *Field Crops Res.* **95**, 398–411.

Prentice, A. N. (1972). "Cotton with Special Reference to Africa," p. 282. Longman, London, UK.

Prior, S. A., Rogers, H. H., Runion, G. B., and Mauney, J. R. (1994). Effects of free-air CO_2 enrichment on cotton root growth. *Agric. Forest Meteorol.* **70**, 69–86.

Pundir, N. S. (1972). Experimental embryology of *Gossypium arboreum* L. *and G. hirsutum* L., and their reciprocal crosses. *Bot. Gaz.* **133**, 7–26.

Quintanilha, A., Salazar, D. L., and Cabral, A. (1962). Desenvolvimeto do butao flora do algodoeiro em funaco do tempo. *Bol. Soc. Broteriana* **36**, 189–215.

Quisenberry, J. E., and Kohel, R. J. (1975). Growth and development of fiber and seed in Upland cotton. *Crop Sci.* **15**, 463–467.

Radin, J. W. (1992). Reconciling water-use efficiency of cotton in field and laboratory. *Crop Sci.* **32**, 13–18.

Radin, J. W., Lu, Z. M., Percy, R. G., and Zeiger, E. (1994). Genetic variation for stomatal conductance in Pima cotton and its relation to improvements of heat adaptation. *Proc. Natl. Acad. Sci. USA* **91**, 7217–7221.

Rahman, H., Malik, S. A., and Saleem, M. (2004). Heat tolerance of upland cotton during the fruiting stage evaluated using cellular membrane thermo stability. *Field Crops Res.* **85**, 149–158.

Rajan, A. K., Betteridge, B., and Blackman, G. E. (1973). Differences in the interacting effects of light and temperature on the growth of 4 species in the vegetative phase. *Ann. Bot.* **37**, 287–313.

Rao, R. C. N., and Wright, G. C. (1994). Stability of the relationship between specific leaf area and carbon isotope discrimination across environment in peanut. *Crop Sci.* **34**, 98–102.

Rawson, H. M. (1992). Plant responses to temperature under conditions of elevated CO_2. *Aust. J. Plant Physiol.* **22**, 23–32.

Reddy, K. R., and Hodges, H. F. (2000). "Climate Change and Global Crop Productivity." CAB International, Oxnard, UK.

Reddy, V. R., Baker, D. N., and Hodges, H. F. (1990). Temperature and mepiquat chloride effects on cotton canopy architecture. *Agron. J.* **80**, 190–195.

Reddy, V. R., Reddy, K. R., and Baker, D. N. (1991a). Temperature effects on growth and development of cotton during the fruiting period. *Agron. J.* **83**, 211–217.

Reddy, V. R., Baker, D. N., and Hodges, H. F. (1991b). Temperature effects on cotton canopy growth, photosynthesis and respiration. *Agron. J.* **83**, 699–704.

Reddy, K. R., Reddy, V. R., and Hodges, H. F. (1992a). Effects of temperature on early season cotton growth and development. *Agron. J.* **84**, 229–337.

Reddy, K. R., Hodges, H. F., McKinion, J. M., and Wall, G. W. (1992b). Temperature effects on Pima cotton growth and development. *Agron. J.* **84**, 237–243.

Reddy, K. R., Hodges, H. F., and Reddy, V. R. (1992c). Temperature effects on cotton fruit retention. *Agron. J.* **84**, 26–30.

Reddy, K. R., Hodges, H. F., and McKinion, J. M. (1995a). Carbon dioxide and temperature effects on Pima cotton development. *Agron. J.* **87**, 820–826.

Reddy, K. R., Hodges, H. F., and McKinion, J. M. (1995b). Cotton crop responses to a changing environment. *In* "Climate Change and Agriculture: Analysis of Potential International Impacts" (C. Rosenzweig, J. T. Ritchie, J. W. Jones, G. Y. Tsuji, and P. Hilderbrand, Eds.), pp. 3–30. ASA Spec. Publ. No. 59, Madison, WI.

Reddy, V. R., Reddy, K. R., and Hodges, H. F. (1995c). Carbon dioxide enrichment and temperature effects on canopy cotton photosynthesis, transpiration, and water use efficiency. *Field Crops Res.* **41**, 13–23.

Reddy, K. R., Hodges, H. F., and Mckinion, J. M. (1996). Food and agriculture in the 21st century: A cotton example. *World Resour. Rev.* **8**, 80–97.

Reddy, A. R., Reddy, K. R., and Hodges, H. F. (1997a). Dynamics of canopy photosynthesis in pima cotton as influenced by growth temperatures. *Indian J. Exp. Biol.* **35**, 1002–1006.

Reddy, K. R., Hodges, H. F., and McKinion, J. M. (1997b). A comparison of scenarios for the effect of global climate change on cotton growth and yield. *Aust. J. Plant Physiol.* **24**, 707–713.

Reddy, K. R., Hodges, H. F., and McKinion, J. M. (1997c). Crop modeling and applications: A cotton example. *Adv. Agron.* **59**, 225–290.

Reddy, K. R., Reddy, A. R., Hodges, H. F., and McKinion, J. M. (1997d). Water and nutrient deficits, crop yields and climate change. *World Resour. Rev.* **10**, 23–43.

Reddy, A. R., Reddy, K. R., and Hodges, H. F. (1998). Interactive effects of elevated CO_2 and growth temperature photosynthesis in cotton leaves. *Plant Growth Regul.* **26**, 33–40.

Reddy, K. R., Davidonis, G., Johnson, J., and Vinyard, B. (1999). Temperature regime and carbon dioxide enrichment alters cotton boll development and fiber properties. *Agron. J.* **91**, 851–858.

Reddy, K. R., Hodges, H. F., and Kimball, B. A. (2000). Crop ecosystem response to climatic change: Cotton. *In* "Climate Change and Global Crop Productivity" (K. R. Reddy and H. F. Hodges, Eds.), pp. 161–187. CAB International, Oxnard, UK.

Reddy, K. R., Kakani, V. G., Zhao, D., Koti, S., and Gao, W. (2004). Interactive effects of ultraviolet-B radiation and temperature on cotton growth, development, physiology and hyperspectral reflectance. *Photochem. Photobiol.* **79**, 416–427.

Reddy, K. R., Prasad, P. V., and Kakani, V. G. (2005). Crop responses to elevated carbon dioxide and interactions with temperature. *In* "Ecological Responses and Adaptations of Crops to Rising Atmospheric Carbon Dioxide" (Z. Tuba, Ed.), pp. 157–191. Food Products Press, Binghamton, NY.

Reynolds, M. P., Balota, M., Delgado, M. I. B., Amani, I., and Fischer, R. A. (1994). Physiological and morphological traits associated with spring wheat yield under hot, irrigated conditions. *Aust. J. Plant Physiol.* **21**, 717–730.

Reynolds, M. P., Nagarajan, S., Razzaue, M. A., and Ageeb, O. A. A., (Eds.) (1997). "Using Canopy Temperature Depression to Select for Yield Potential of Wheat in Heat-Stressed Environmental." Wheat Special Report No. 42, CIMMYT, Mexico.

Reynolds, M. P., Singh, R. P., Ibrahim, A., Ageeb, O. A. A., Larqué-Saavedra, A., and Quick, J. S. (1998). Evaluating physiological traits to complement empirical selection for wheat in warm environment. *Euphytica* **100**, 84–95.

Reynolds, M. P., Delgado, M. I., Gutierrez-Rodriguez, M., and Larqué-Saavedra, A. (2000). Photosynthesis of wheat in a warm, irrigated environment. I. Genetic diversity and crop productivity. *Field Crops Res.* **66**, 37–50.

Reynolds, M. P., Nagarajan, S., Razzaque, M. A., and Ageeb, O. A. A. (2001). Heat tolerance. *In* "Application of Physiology in Wheat Breeding" (M. P. Reynolds, J. I. Ortiz-Monasterio, and A. McNab, Eds.), pp. 124–135. CIMMIT, Mexico, DF.

Rikin, A., Dillworth, J. W., and Bergman, D. K. (1993). Correlation between circadian rhythm of resistance to extremes temperature and changes in fatty acid composition in cotton seedlings. *Plant Physiol.* **101**, 31–36.

Rodriguez-Garay, B., and Barrow, J. R. (1988). Pollen selection for heat tolerance in cotton. *Crop Sci.* **28**, 857–859.

Rosielle, A. A., and Hamblin, J. (1981). Theoretical aspects of selection for yield in stress and non-stress environments. *Crop Sci.* **21**, 943–946.

Saadalla, M. M., Quick, J. S., and Shanahan, J. F. (1990a). Heat tolerance in winter wheat. II. Membrane thermostability and field performance. *Crop Sci.* **30**, 1248–1252.

Saadalla, M. M., Shanahan, J. F., and Quick, J. S. (1990b). Heat tolerance in winter wheat. I. Hardening and genetic effects on membrane thermostability. *Crop Sci.* **30**, 1243–1247.

Saranga, Y., Jiang, C. X., Wright, R. J., Yakir, D., and Paterson, A. H. (2004). Genetic dissection of cotton physiological responses to arid conditions and their inter-relationships with productivity. *Plant Cell Environ.* **27**, 263–277.

Saranga, Y., Menz, M., Jiang, C.-X., Robert, J. W., Yakir, D., and Andrew, H. P. (2001). Genomic dissection of genotype X environment interactions conferring adaptation of cotton to arid conditions. *Genome Res.* **11**, 1988–1995.

Sarvella, P. (1964). Vital-stain testing of pollen viability in cotton. *J. Hered* **55**, 154–158.

Sarvella, P. (1966). Environmental influences on sterility in cytoplasmic male-sterile cottons. *Crop Sci.* **6**, 361–364.

Sassenrath-Cole, G. F. (1995). Dependence of canopy light distribution on leaf and canopy structure for two cotton (*Gossypium*) species. *Agric. Forest Meteorol.* **77**, 55–72.

Schrader, S. M., Wise, R. R., Wacholtz, W. F., Ort, D. R., and Sharkey, T. D. (2004). Thylakoid membrane responses to moderately high leaf temperature in Pima cotton. *Plant Cell Environ.* **27**, 725.

Siebke, K., Von Caemmerer, S., Badger, M., and Furbank, R. T. (1997). Expressing an RbcS antisense gene in transgenic *Flaveria bidentis* leads to an increased quantum requirement for CO_2 fixed in photosystems I and II. *Plant Physiol.* **105**, 1163–1174.

Sikka, M. A., and Dastur, R. H. (1960). Climate and soils. *In* "Cotton in India: A Monograph" (R. H. Dastur, R. D. Asana, K. Sawhney, S. M. Sikka, R. S. Vasudev, Q. Khan, V. P. Rao, and B. L. Setti, Eds.), Indian Central Cotton Committee. Vol. I. Chapter 2.

Silvertooth, J. C., Watson, T. F., Malcuit, J. E., and Brown, P. W. (1992). Evaluation of date of planting and irrigation termination on the yield of Upland and Pima. *In* "Cotton a College of Agriculture Report," pp. 252–273. University of Arizona, Series P-91.

Singh, K. P., Bhardwaj, S. N., and Singh, M. (1987). Parameters controlling crop growth rate and their relationship with photosynthetically active radiation and temperature in Upland cotton. *Indian J. Agric. Sci.* **57**, 828–832.

Singh, R. P., Singh, J., Lal, C. B., Sunita, K., and Elayaraja, K. (2003). Development of suitable cotton *G. hirsutum* L. plant type tolerant to high diurnal temperature with suitability to grow during spring/summer season. *ICAR News* **9**, 14–16.

Singh, R. P., Singh, J., Lal, C. B., Sunita, K., and Elayaraja, K. (2004). Evaluation of punjab American cotton (*G. hirsutum* L.) genotypes tolerant to high temperature and their performance during spring summer season. *Ann. Agric. Res.* **25**, 268–273.

Smutzer, G., and Berlin, J. D. (1975). Ultrastructural aspects of cotton fiber differentiation as influenced by night temperature. *Tex. Rep. Biol. Med.* **33**, 362–363.

Snipes, C. E., and Baskin, C. C. (1994). Influence of early defoliation on cotton yield, seed quality and fiber properties. *Field Crops Res.* **37**, 137–143.

Soomro, A. R. (1998). Central Cotton Research Institute, Pakistan, The Institute Profile. *SAIC (SAARC Agricultural Information Center) Newsletter* **8**, 4.

Srivastava, A., Lu, Z. M., and Zeiger, E. (1995). Modification of guard cell properties in advanced lines of pima cotton bred for higher yields and heat resistance. *Plant Sci.* **108**, 125–131.

Stockton, J. R., and Walhood, V. T. (1960). Effect of irrigation and temperature on fiber properties. *In* "Proceedings of 14th Annual Beltwide Cotton Defoliation Conference" (C. W. Smith and J. T. Cothren, Eds.), pp. 11–14. John Wiley and Sons Inc., New York.

Stiller, W. N., Reid, P. E., and Constable, G. A. (2004). Maturity and leaf shape as traits influencing cotton cultivars adaptation to dry land conditions. *Agron. J.* **96**, 656–664.

Subbarao, G. V., Johansen, C., Rao, R. C. N., and Wright, G. C. (1995). Transpiration efficiency: Avenues for genetic improvement. *In* "Handbook of Plant and Crop Physiology" (M. Pessarakli, Ed.), pp. 785–806. Marcel Dekker Inc., NY.

Sullivan, C. Y. (1972). Mechanism of heat and drought resistance in grain sorghum and methods of measurement. *In* "Sorghum in the Seventies" (N. G. P. Rao and L. R. House, Eds.), Oxford and IBH Publishing Co., New Delhi, India.

Sung, D.-Y., Kaplan, F., Lee, K., and Charles, L. (2003). Acquired tolerance to temperature extremes. *Trends Plant Sci.* **8**, 179–187.

Suy, T. B. (1979). Contribution of l'etude de la croissance des tubes polliniques chez *Gossypium hirsutum* L. en function des conditions du milieu. *Cotton Fib. Trop.* **34**, 295–300.

Taha, M. A., Malik, M. N. A., Chaudhry, F. L., and Makhdum, I. (1981). Heat induced sterility in cotton sown during early April in West Punjab. *Exp. Agric.* **17**, 189–194.

Tanner, C. B. (1963). Plant temperatures. *Agron. J.* **55**, 210–211.

Taylor, H. M., and Klepper, B. (1974). Water relations to cotton. I. Root growth and water use as related to top growth and soil water content. *Agron. J.* **66**, 584–588.

Taylor, H. M., and Klepper, B. (1978). The role of rooting characteristics in the supply of water to plants. *Adv. Agron.* **30**, 99–128.

Taylor, H. M., and Ratliff, L. F. (1969). Root elongation rates of cotton and peanuts as a function of soil strength and soil water content. *Soil Sci.* **108**, 113–119.

Thiaw, S. (2003). Association between slow leaf-electrolyte-leakage under heat stress and heat tolerance during reproductive development in cowpea. Ph.D. Dissertation, University of California, Riverside, CA.

Thiaw, S., and Hall, A. E. (2004). Comparison of selection for either leaf-electrolyte-leakage or pod set in enhancing heat tolerance and grain yield of cowpea. *Field Crops Res.* **86**, 239–253.

Thomson, N. J. (1995). Commercial utilization of okra leaf mutant: The Australian experience. *In* "Challenging the Future. Proceedings of the World Cotton Research Conferences" (G. A. Constable and N. W. Forrester, Eds.), pp. 393–401. CSIRO, Canberra, Australia.

Tripathy, J. N., Zhang, J., Robin, S., Nguyen, T. T., and Nguyen, H. T. (2000). QTLs for cell membrane stability mapped in rice under drought stress. *Theor. Appl. Genet.* **100**, 1197–1202.

Ulloa, M., Cantrell, R. G., Percy, R. G., Zeiger, E., and Lu, Z. M. (2000). QTL analysis of stomatal conductance and relationship to lint yield in an interspecific cotton. *J. Cotton. Sci.* **4**, 10–18.

Vierling, E. (1991). The roles of heat shock proteins in plants. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **42**, 579–620.

Walker, C. D., and Lance, R. C. N. (1991). The fractionation of ^{2}H and ^{18}O in leaf water of barley. *Aust. J. Plant Physiol.* **18**, 411.

Wallace, D. H., Ozbun, J. L., and Munger, H. M. (1972). Physiological genetics of crop yield. *Adv. Agron.* **24**, 97–146.

Wang, W., Vinocur, B., and Altman, A. (2003). Plant responses to drought, salinity and extreme temperatures: Towards genetic engineering for stress tolerance. *Planta* **218**, 1–14.

Wanjura, D. F., Kelly, C. A., Wendt, C. W., and Hatfield, J. L. (1984). Canopy temperature and water stress of cotton crops with complete and partial ground cover. *Irrig. Sci.* **5**, 37–46.

Wardlaw, I. F., Sofield, I., and Cartwright, P. M. (1980). Factors limiting the rate of dry matter accumulation in the grain of wheat grown at high temperature. *Aust. J. Plant Physiol.* **7**, 387–400.

Wardlaw, I. F., Dawson, I. A., Munchi, P., and Fewster, R. (1989). The tolerance of wheat to high temperatures during reproductive growth. I. Survey procedures and general response patterns. *Aust. J. Agric. Res.* **40**, 1–13.

Warner, D. A., and Burke, J. J. (1993). Cool night temperatures alter leaf starch and photosystem II chlorophyll fluorescence in cotton. *Agron. J.* **85**, 836–840.

Weaver, M. L., and Timm, H. (1988). Influence of temperature and water status on pollen viability in bean. *J. Am. Soc. Hort. Sci.* **113**, 13–15.

Wells, R., Meredith, W. R., Jr., and Williford, J. R. (1986). Canopy photosynthesis and its relationship to plant productivity in near-isogenic cotton lines differing in leaf morphology. *Plant Physiol.* **82**, 635–640.

Wendel, J. F., Brubaker, C. L., and Percival, A. E. (1992). Genetic diversity in *Gossypium hirsutum* and the origin of upland cotton. *Am. J. Bot.* **79**(1), 1291–1310.

Wilson, R. F., Burke, J. J., and Quisenberry, J. E. (1987). Plant morphological and biochemical responses to field water deficits II. Responses of leaf glycerolipid composition in cotton. *Plant Physiol.* **84**, 251–254.

Williams, J. H., and Boote, K. J. (1995). Physiology and modeling—predicting the unpredictable legume. *In* "Advances in Peanut Science" (H. E. Pattee and H. T. Stalker, Eds.), pp. 301–353. APRES, Stillwater, OK.

Wise, R. R., Olson, A. J., Schrader, S. M., and Sharkey, T. D. (2004). Electron transport is the functional limitation of photosynthesis in field-grown pima cotton plants at high temperature. *Plant Cell Environ.* **27**, 717–724.

Wong, S. C., Cowan, I. R., and Farquhar, G. D. (1979). Stomatal conductance correlates with photosynthetic capacity. *Nature* **282**, 424–426.

Wright, G. C., Hubick, K. T., Farquhar, G. D., and Rao, R. N. C. (1993). Genetics and environmental variation in transpiration efficiency and its correlation with carbon isotope discrimination and specific leaf area in peanut. *In* "Stable Isotopes and Plant Carbon-Water Relations" (J. E. Ehleninger, A. E. Hall, G. D. Farquhar, and B. Saugier, Eds.), pp. 247–267. Academic Press, New York.

Yfoulis, A., and Fasoulas, A. (1973). Interactions of genotype and temperature on cotton boll period and their implication in breeding. *Exp. Agric.* **9**, 193–201.

Yfoulis, A., and Fasoulas, A. (1978). Role of minimum and maximum environmental temperature on maturation period of the cotton boll. *Agron. J.* **70**, 421–425.

Yoshida, S., Satake, T., and Mackill, D. J. (1981). "High Temperature Stress in Rice". Paper Series No. 67. International Rice Research Institute Research (IRRI), Manila, Philippines.

Zeiher, C., Matumba, N., Brown, P., and Silvertooth, J. (1995). Response of upland cotton to elevated night temperatures. II. Results of controlled environmental studies. *In* "Proceeding of the Beltwide Cotton Conferences" (C. P. Dugger and D. A. Richter, Eds.), p. 1129. National Cotton Council of America, Memphis, TN.

Ziska, L. H., Namuco, O., Mayo, T., and Quilang, J. (1997). Growth and yield response of field grown tropical rice to increasing carbon dioxide and air temperature. *Agron. J.* **89**, 45–53.

Zivy, M. (1987). Genetic variability for heat shock proteins in common wheat. *Theor. Appl. Genet.* **74**, 209–213.