Chapter 4
Heat Tolerance

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Abstract Predicted global warming would make it more difficult for farmers to achieve the increases in crop productivity needed to meet expected increases in demand for food during this century—because an increase in temperature of 1 °C has been shown to decrease grain production of some annual crop species by about 10 %. In considering strategies for breeding heat-resistant cultivars that have greater yield than current cultivars under hot conditions, high-temperature effects on germination, vegetative growth, reproductive development, and yield are reviewed. For several annual crop species, pollen development and seed or fruit set have been shown to be particularly sensitive to high temperatures occurring in the late-night to early-morning period. The few studies that have been conducted indicated that elevated atmospheric carbon dioxide concentration will not enable plants to overcome this problem. For a few crop species, heat-resistant cultivars have been bred by conventional hybridization and selection for heat tolerance during reproductive development and/or yield. The progress that has been made in breeding for heat resistance in cowpea, common bean, cotton, tomato, rice, and wheat are reviewed. The successes achieved in breeding with these crops using conventional hybridization and selection provide guidelines whereby further progress can be made in increasing the heat resistance of these and other crop species. For the future, DNA markers for what appear to be major genes conferring heat tolerance during reproductive development would be valuable because their use in selection could substantially enhance the efficiency whereby heat-resistant cultivars

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are bred. More upstream research on the development of crops with facultative apomictic breeding systems is warranted. Cultivars with an appropriate type of apomixis could have tolerance to the many stresses that damage reproductive development including chilling and drought, in addition to heat, because these cultivars do not require pollen development to achieve seed production. Apomictic cultivars have additional values including the ability of hybrids to produce true-breeding seed permitting the development of hybrid cultivars for crop species where it currently is not economically feasible.

4.1 Introduction

Predicted global warming would make it more difficult for farmers to achieve the increases in crop productivity (yield per unit area) needed to meet expected increases in demand for food and animal feed during this century. Due to projected increases in human population and the need for people who currently are poorly fed to receive more, higher-quality food, farmers will need to produce twice as much food and feed crops on about the same area of cultivated land by the end of this century (World Bank 2010). It may be difficult to achieve this goal because the productivity of some crops has not increased in recent years.

Doubling productivity of food and feed crops in about 69 years would require yield increases of 1 % per year. During these 69 years it has been predicted that temperatures could increase several degrees celcius, and high temperatures already are reducing yields of some crops in some climatic zones. For example, rice (*Oryza sativa* L.) yields for crops grown under optimal management on the experimental farm of the International Rice Research Institute in the Philippines over a 12-year period from 1992 through 2003 were negatively correlated with temperatures during the growing seasons (Peng et al. 2004). Day temperatures had increased 0.35 °C while night temperatures had increased 1.13 °C from 1979 to 2003. Grain yields exhibited a 10 % decrease per °C increase in night temperature with no correlation with day temperature. This indicates that increases in temperature of 0.05 °C per year, equivalent to 3.5 °C over 69 years, could cause yield decreases of 0.5 % per year. Apparently, the development of heat-resistant cultivars that produce greater yields than current cultivars under hot conditions could contribute to maintaining or hopefully increasing productivity during a period of global warming.

As will be discussed later, heat-resistant cultivars of a few crop species have been developed by selecting for greater heat tolerance during reproductive development. But, in general, there has been little emphasis on selecting for heat tolerance in public plant breeding programs. We do not know the extent of selection for heat tolerance in commercial plant breeding programs, but it likely has not been done to a major extent, since virtually none of these programs advertise their cultivars as having heat resistance.

In this review we will examine plant responses to high temperature during germination, vegetative growth, and reproductive development to provide a physiological basis for choosing selection criteria in breeding for heat tolerance in annual crops. We will emphasize those crops that produce grain and/or fruit because most of the earlier research on heat tolerance has been conducted with these types of crops, and the cereals and grain legumes are major sources of food and feed. Studies of these types of crops provide an opportunity to determine whether heat stress is reducing reproductive yield through detrimental effects on the photosynthetic source of carbohydrate or through damage to reproductive development. Whether heat stress is mainly damaging the source or the sink or both processes will determine which heat tolerance selection strategies are most likely to enhance heat resistance.

We will review methods for breeding for heat tolerance building on general reviews of this topic by Singh et al. (2011) and Hall (1992), a web site on breeding for heat tolerance (http://www.plantstress.com), and reviews of specific crops: cotton (*Gossypium hirsutum* L.) by Singh et al. (2007), cowpea (*Vigna unguiculata* L. Walp.) by Hall (2011), rice by Lafarge et al. (2011), and wheat (*Triticum* spp.) by Trethowan and Mahmood (2011). Finally, we will describe those programs we are aware of where breeding for heat tolerance has made significant progress in developing heat-resistant cultivars.

4.2 Plant Responses to High Temperatures

Relatively hot temperatures can impair plant function or development through either direct effects of high tissue temperature or indirect effects of the high evaporative demand and water stress that accompany hot weather. Evaporative demand exhibits a near exponential increase with increase in temperature and can result in large increases in transpiration and substantial decreases in leaf water potential (Hall 2001). Through transpirational cooling and traits influencing radiation loading, plants can avoid high tissue temperatures. This review, however, will mainly consider the direct effects of high tissue temperature on plants.

Hot temperatures can have either reversible effects on plant function or irreversible damaging effects on plant development and/or function. This review will consider only the irreversible damaging effects of heat stress on plants. The magnitude of heat stress depends on intensity (temperature), duration of exposure, and rate of increase, because plants have some ability to acclimate and more rapid increases in temperature can be more damaging. Threshold temperatures where heat stress begins in natural environments are particularly relevant to understanding effects on crops under field conditions.

4.2.1 Germination and Seedling Survival Under Heat Stress

In the semiarid tropics, inadequate seedling establishment due to heat stress can reduce productivity and stability of production of sorghum (*Sorghum bicolor* L. Moench) (Peacock 1982) and pearl millet (*Pennisetum glaucum* L. R. Br.) (Peacock et al. 1993). Inadequate seedling establishment has occurred when soil seed-zone temperatures exceed 45 °C and soil surface temperatures exceed 55 °C. This could be due to failed germination, inhibited epicotyl emergence from the soil, or death of seedlings caused by heat girdling (Peacock et al. 1990).

Maximum threshold temperatures for germination and emergence are higher for warm-season annuals than for cool-season annuals (as defined in Hall 2001). For example, the maximum threshold seed-zone temperature for cowpea is about 37 °C (El-Kholy et al. 1997), compared with about 33 °C for lettuce (*Lactuca sativa* L.) (Argyris et al. 2005). Inadequate seed germination due to heat stress can be a problem for cool-season crops such as lettuce when they are sown in late summer to accommodate a fall harvest (Borthwick and Robbins 1928).

Maximum threshold temperatures at which high temperatures kill seedlings can depend on plant preconditioning. Seedlings subjected to high but sublethal temperatures for a few hours subsequently can survive higher temperatures than seedlings that have been maintained at moderate temperatures (Yarwood 1961). This acclimation to heat can be induced by the gradual diurnal increases in temperature that occur in hot natural environments (Vierling 1991). The "heat-shock" response involves repression of the synthesis of most normal proteins and mRNAs, and the initiation of transcription and translation of a small set of heat-shock proteins (Vierling 1991). Studies of loss-of-function mutants of *Arabidopsis thaliana* demonstrated that the enhanced thermotolerance can be associated with at least three independent effects: the synthesis of a novel set of proteins (specifically Hsp101), protection of membrane integrity, and recovery of protein activity/synthesis (Queitsch et al. 2000; Hong et al. 2003). The heat-shock protein Hsp101 likely functions as a molecular chaperone in the renaturation of cellular proteins that have a tendency to unfold and aggregate at very high temperatures. With increases in temperature, membranes become more fluid and electrolytes leak more readily from plant tissues. Heat acclimation reduces the tendency for membranes to leak under hot conditions.

Variation occurs among species in the maximum threshold temperatures that result in the death of seedlings. Among the cool-season annuals, pea (*Pisum sativum* L.) is very sensitive, dying when daytime temperatures exceed about 35 °C for sufficient duration, whereas barley (*Hordeum vulgare* L.) can withstand hotter temperatures. Warm-season annuals usually can withstand higher temperatures than cool-season annuals. For example, cowpea and cotton can survive about the highest temperatures experienced in crop production zones (maximum daytime air temperatures in a weather station shelter of 50 °C) and produce substantial amounts of vegetative biomass providing the crops have an adequate supply of water.

Germination, emergence, and seedling survival are relatively simple systems, and methods have been developed that can screen large numbers of plants to detect genotypic differences in heat tolerance (Wilson et al. 1982; Soman and Peacock 1985; Peacock et al. 1993). This type of selection, however, only will confer a useful level of heat resistance for those field conditions where heat stress has major detrimental effects on plant stands because many crops have some capacity to exhibit compensatory growth when the population of seedlings is low.

4.2.2 Effects of High Temperatures on Vegetative Growth and Development

The rate of vegetative growth decreases when canopy photosynthesis is reduced by heat stress. If a maximum threshold temperature is imposed on a plant for sufficient duration, the photosynthetic system is damaged such that the rate of CO_2 uptake is substantially reduced and the damage may be irreversible. Sensitivity of photosynthesis to heat may be primarily due to damage to components of photosystem II (PSII) located in the thylakoid membranes of the chloroplast (Al-Khatib and Paulsen 1999). The extreme sensitivity of PSII may be due to effects of temperature on the membranes in which it is embedded. Murakami et al. (2000) developed transgenic tobacco (*Nicotiana tabacum* L.) plants with altered chloroplast membranes by silencing the gene encoding chloroplast omega-3 fatty acid desaturase. The transgenic plants had less trienoic fatty acids and more dienoic fatty acids in their chloroplasts than the wild-type plants. The transgenic plants also had greater photosynthesis and growth rates than the wild-type plants in hot environments. In addition, there are indications that a small heat-shock protein in the chloroplast may protect PSII electron transport during heat stress (Heckathorn et al. 1989).

In comparisons of contrasting species, PSII of the cool-season species wheat was more sensitive to heat than PSII of either rice or pearl millet, which are warm-season species adapted to much hotter climates (Al-Khatib and Paulsen 1999). Portable instruments are available to rapidly measure chlorophyll fluorescence parameters of intact leaves that could be used to screen many plants to quantify the extent that PSII has been damaged and hopefully detect genotypic differences in heat tolerance. Selection of this type with grain crops only will enhance heat resistance where grain yield is being limited by heat-stress effects on the supply of carbohydrate through effects on PSII.

For spring wheat growing in hot, irrigated environments, cultivar differences in grain yield were positively correlated with photosynthetic rate per unit leaf area (Reynolds et al. 1994). Even stronger positive associations were observed between grain yield and stomatal conductance. This indicates that the more open stomata of the heat-resistant cultivars may be enhancing photosynthesis both by facilitating the diffusion of CO_2 into leaves and by enhancing transpirational cooling bringing leaf temperatures below damage thresholds. In addition, cultivar differences in grain yield of spring wheat growing in a hot, irrigated environment were positively correlated with the number of kernels per spike (Shpiler and Blum 1991). This could be explained by either cultivar differences in heat tolerance during reproductive development or the possibility that processes determining kernel number may be linked to photosynthesis. Cultivar variation in kernel number was correlated with spike dry weight at anthesis and the ratio of solar irradiance to air temperature for the 30-day period prior to anthesis (Fischer 1985). Consequently, there are circumstances where damaging effects of heat on photosynthesis can reduce both the photosynthetic source and the reproductive sink, making it difficult to determine which of them is most limiting to grain yield. Also, pollen development in wheat is very sensitive to heat stress (see for review, Dolferus et al. 2011; Farooq et al. 2011).

The source versus sink issue concerning the limiting effects of heat stress on yield is further complicated by the possibility that photosynthetic capacity and stomatal behavior may be influenced by the extent of the reproductive sink through complex, long-term feedback effects. Pima cotton (*Gossypium barbadense* L.) cultivars were bred that have greater boll yields in hot environments by selecting plants with the ability to set more bolls on low nodes under very hot irrigated conditions (Feaster and Turcotte 1985). Subsequent studies showed that these heat-resistant cultivars also had greater rates of photosynthesis and higher stomatal conductances in hot conditions (Cornish et al. 1991). Plants that have higher photosynthetic capacity often have higher maximal stomatal conductance, and the mechanism of this long-term regulation is not known (Hall 2001). The mechanisms whereby the cotton cultivars are heat-resistant are not known. The simplest explanation is that they have greater ability to set bolls under hot conditions, because this is what they were selected for. But then why do they also have higher photosynthetic rates? Is this a consequence of or a cause for the greater boll set?

When grains are developing, leaves begin to senesce and this can be accelerated by late-season heat stress. Delayed-leaf-senescence traits have been sought as a means to enhance grain filling and lengthen the reproductive period under late heat stress or drought. This trait can be easily screened for visually in field nurseries providing one only selects plants that have both delayed leaf senescence and abundant fruit and/or grain because plants that have low fruit and/or grain set typically also exhibit a type of delayed leaf senescence that has limited agronomic value. Cultivars and genetic lines with delayed-leaf-senescence traits have been bred for sorghum (Reddy et al. 2011), cowpea (Gwathmey and Hall 1992), and wheat (Farooq et al. 2011). The extent to which they enhance heat resistance has not been adequately quantified.

4.2.3 *Reproductive Development Under Heat Stress*

In very hot environments many crop plants produce significant amounts of biomass but few flowers, fruits, or seeds. In these cases, reproductive development clearly is more sensitive to heat than photosynthesis and biomass production.

4.2.3.1 Flowering Under Heat Stress

Some emphasis is given to cowpea because much work has been done on heat-stress effects on flowering with this crop and several other warm-season crops appear to have similar responses (Hall 2004). Under long-day very hot field conditions, some cowpea genotypes produced floral buds, but they did not produce any flowers (Ehlers and Hall 1996). Prior to discussing growth chamber studies of this heat-stress effect, it is important to note that it depends on light quality. Floral bud development of a heat-sensitive cowpea genotype was arrested by high night temperatures and long days only in growth chambers that had red (655–665 nm)/far-red (725–735) ratios of 1.3–1.6 but not with an R/FR ratio of 1.9 (Ahmed et al. 1993b). Note that sunlight has an R/FR ratio of 1.2 above the canopy and a lower ratio within dense canopies, and suppression of floral buds does occur with heat-sensitive genotypes in very hot long-day field conditions. Also note that growth chambers that mainly use either fluorescent or metal-halide lamps and have a high F/R ratio often have been used in plant growth studies and could have produced results that are not relevant to natural environments.

The suppression of floral buds under high night temperatures and long days appears to be a phytochrome-mediated effect, except that a night-break of red light during a long night did not result in floral bud suppression (Mutters et al. 1989b). Suppression of floral buds was greater under a combination of hot nights and very hot days than under only hot nights (Dow El-Madina and Hall 1986). Experiments involving the transfer of plants between growth chambers with optimal or hot night temperatures for different periods demonstrated that plants did not have a particular stage of development where they were sensitive to high temperature but that the duration of the heat experience may be critical for the suppression of floral bud development (Ahmed and Hall 1993). A period of 2 weeks or more of consecutive or interrupted hot nights during the first 4 weeks after germination caused complete suppression of the first five floral buds on the main stem. The minimum day length required to elicit heat-induced suppression of floral bud development may be as short as 13 h, including civil twilight. Days that are longer than this minimum occur in all subtropical and some tropical zones during the season when cowpeas are grown. We are using the definitions of subtropical and tropical zones of Hall (2001) that are based on temperature.

It should be noted that genotypes of cowpea with “classical” sensitivity to photoperiod do not produce floral buds under long days. Under inductive short days and high night temperature, a cultivar with “classical” sensitivity to photoperiod produced floral buds and the buds were not sensitive to heat and developed normally, producing flowers (Mutters et al. 1989b).

In genetic studies, segregation of cowpea plants for heat tolerance during floral bud development was consistent with the hypothesis that it is conferred by a single recessive nuclear gene (Hall 1993). The presence or absence of flowers is easy to screen for in field nurseries, and subsequent breeding demonstrated that this trait can be reliably selected in the F_2 generation (Hall 2011) supporting the argument that the inheritance is controlled by a single recessive gene. Multiple forms of phytochrome are present in plants that have different physiological roles (Smith and Whitelam 1990). The dominant nuclear gene involved in conferring sensitivity to heat during floral bud development in cowpea might be involved in the synthesis of one of these phytochromes (Hall 1992).

Some cultivars of common bean (*Phaseolus vulgaris* L.) have been shown to exhibit floral bud suppression under hot long days (Konsens et al. 1991; Shonnard and Gepts 1994). The sensitivity to heat during early floral bud development of common bean may only occur in long days and may be consistent with the action of a single dominant gene (White et al. 1996) as it is with cowpea. Pima cotton also has been shown to not produce flowers under very hot conditions (Reddy et al. 1992).

4.2.3.2 Fruit and/or Seed Set Under Heat Stress

Growth chamber studies of heat-stress effects on cowpea produced unexpected results. Pod set was reduced much more by subjecting shoots to high temperature at night than when a higher temperature was imposed on shoots during the day (Warrag and Hall 1984a, b). The sensitivity of pod set in cowpea to high night temperature was confirmed under field conditions (Nielsen and Hall 1985b). In this study a system was used in which plots of cowpea were enclosed in plastic sheets only during the nighttime hours and a fan, air distribution system, heater, and differential thermostat were used to increase air temperature in the enclosure a fixed number of degrees above ambient air temperature (Nielsen and Hall 1985a). Growth chamber studies demonstrated that the pod set of cowpea was sensitive to heat during the last 6 h but not the first 6 h of the night (Mutters and Hall 1992).

Fruit and/or seed set has been shown to be particularly sensitive to high night temperature in several other warm-season crops including cotton (Gipson and Joham 1968), sorghum (Eastin et al. 1983), rice (Peng et al. 2004; Mohammed and Tarpley 2010), and common bean (Konsens et al. 1991). For peanut (*Arachis hypogaea* L.), high temperatures during the morning reduced fruit set, whereas higher temperatures during the afternoon had no effect on fruit set (Prasad et al. 2000). Apparently, fruit and/or seed set can be damaged by high temperatures occurring during the late night or early morning while they are not sensitive to much higher temperatures occurring later in the day. This late-night or early-morning sensitivity to heat stress has implications for the mechanism of the effect, choice of screening environments, and predictions concerning how global warming might influence productivity under field conditions.

The lack of pod set in cowpea under high night temperature was due to impaired pollination and a lack of seed set (Warrag and Hall 1984b). Artificial pollination studies demonstrated that the female part of the flower, the pistil, was not damaged by high night temperature (Warrag and Hall 1983). Reciprocal transfers of plants between growth chambers with high or optimal night temperatures demonstrated that the stage of floral development most sensitive to heat stress occurred 9–7 days before anthesis (Ahmed et al. 1992). The sensitive stage is after meiosis, which occurs 11 days before anthesis in cowpea. Damage occurred at the time when the tetrads were being released from the microspore mother cell sac (Warrag and Hall 1984b; Ahmed et al. 1992; Mutters and Hall 1992). In common bean, microsporogenesis was also found to be the period during reproductive development most sensitive to high-temperature stress using scanning and transmission electron microscopy, pollen viability, and yield (Porch and Jahn 2001). Premature degeneration of the tapetal tissue and lack of endothecium formation were observed in cowpea (Ahmed et al. 1992) and common bean (Porch and Jahn 2001), which could have been responsible for the low pollen viability, low anther dehiscence, and low pod set under high night temperature (Ahmed et al. 1992). Tapetal tissue plays an important role in providing nutrients to developing pollen grains, and its premature degeneration could thereby stunt pollen development. Mutters et al. (1989a) hypothesized that heat injury during floral development of sensitive cowpea genotypes may be due to reduced translocation of proline from anther walls and tapetal tissue to developing pollen, based on studies of cowpea genotypes with contrasting heat tolerance in field environments with either very hot or more optimal thermal regimes. Large amounts of proline are required for pollen development, pollen germination, and pollen tube growth. Tapetal malfunction has been considered the causal mechanism of some of the genetic male sterility occurring in plant species (Dundas et al. 1981; Nakashima et al. 1984).

High night temperatures damaged pollination in other warm-season crops including rice (Mohammed and Tarpley 2009), common bean (Gross and Kigel 1994; Porch and Jahn 2001), pepper (*Capsicum annuum* L.) (Wien 1997), sorghum (Eastin et al. 1983; Prasad et al. 2008), and cotton (Singh et al. 2007). High night and/or day temperatures damaged pollination in peanut (Prasad et al. 1999a, b), maize (*Zea mays* L.) (Herrero and Johnson 1980), and tomato (*Lycopersicon esculentum* Mill.) (Peet et al. 1998). Pollination in the cool-season crop wheat is particularly sensitive to high temperatures (Saini et al. 1984) and also may involve tapetal malfunction (Dolferus et al. 2011). It is likely that pollen development of many crop species is sensitive to high temperatures.

High night temperatures can be more damaging to pod set of cowpeas under the long days typical of subtropical zones than under the short days that can occur in the tropics (Ehlers and Hall 1998). Responses to red light during long nights, far-red light at the end of long days, and far-red followed by red light at the end of long days indicate that the greater sensitivity of cowpea to high night temperature under long days is a phytochrome-mediated effect (Mutters et al. 1989b). For rice also the detrimental effects of high temperatures on pollination are enhanced under long days, and this effect provides the basis for the photoperiod-sensitive genic male sterile system that has been used in the production of hybrid seed (Ziguo and Hanlai 1992; Yuan et al. 1993).

Why is the seed set of many warm-season crops sensitive to high temperatures during the late night or early morning, while they are not sensitive to higher temperatures occurring during midday and afternoon? Mutters and Hall (1992) hypothesized that there is a heat-sensitive physiological or developmental process in pollen development that is under circadian control. Note that reproductive events, such as anthesis, meiosis, and flower opening, and phytochrome-mediated events, have a degree of circadian control occurring at a particular time in the 24-h cycle. They hypothesized that natural selection would have favored plants in which the heat-sensitive process in pollen development takes place in the coolest part of the 24-h cycle, which is the late night and early morning.

Genetic control of the timing of reproductive events that has relevance to heat tolerance has been demonstrated. The time of day for flowering of different genotypes within the genus *Oryza* ranges widely from early morning to evening with many cultivars of rice exhibiting anthesis between 10 A.M. and noon. An early-morning flowering trait was introgressed from a wild rice that begins flowering at 6 A.M. into a rice cultivar with later flowering. An early-morning flowering line was bred and found to flower earlier and exhibit less spikelet sterility than the parental cultivar, which flowered when temperatures were hotter (Ishimaru et al. 2010).

In hot screening environments, fruit set of grain legumes, tomatoes, and cotton can be scored visually. For example, the number of pods per peduncle is a useful criterion for pod set in cowpea. For cereals, seed set can be scored visually. Additional criteria may be used, such as the proportion of anthers that dehisce or the extent of pollen viability.

4.2.4 Influence of Elevated Atmospheric Carbon Dioxide Concentration on Plant Responses to High Temperature

Analyses of air trapped in polar ice indicate that, prior to the year 1800, the atmospheric CO_2 fluctuated between 180 and 290 ppm for at least 220,000 years (Hall and Allen 1993). Since 1800, ice core data indicate increases in CO_2 from 280 to 315 ppm by 1958. Direct measurements of CO_2 indicate accelerating increases since 1958 from 315 to 380 ppm by the early 2000s. It has been predicted that atmospheric CO_2 could exceed 600 ppm by the end of this century.

Plants with the C_4 photosynthetic system evolved during an early period after atmospheric CO_2 became low, and this system represents a specific adaptation to the low CO_2 of the last 200,000 years. The extent and nature of the evolution of plants with the C_3 photosynthetic system, with respect to the low CO_2, are not known. It is likely that low CO_2 over 220,000 years resulted in evolutionary modifications to whole plant processes, such as increases in the ratio of the photosynthetic source to carbohydrate sink tissues. Consequently, some C_3 plants may not be well adapted to future or even present day levels of CO_2 due to inadequate investment in sink tissues (Hall and Ziska 2000). Photosynthetic rates of these C_3 plants may increase as CO_2 increases, but the rates may not increase as much as they would if the plants were adapted to function optimally at elevated CO_2. Progress during the twentieth century in increasing the productivity of several C_3 crops through plant breeding was estimated as mainly (77 %) resulting from increases in harvest index (the ratio of grain yield to total shoot biomass) with only 23 % due to increases in total shoot biomass (Gifford 1986). This indicates that these crops had an inadequate reproductive sink, for agricultural purposes, and with further increases in atmospheric CO_2, the reproductive sink may become even more incapable of supporting the full photosynthetic potential.

In early studies using controlled-environment enclosures, doubling CO_2 increased grain yield of various cereal crops by 32 % and of various grain legumes by 54 % at intermediate temperatures (Kimball 1983). More recent studies with free-air CO_2 enrichment (FACE) experiments under field conditions, however, resulted in grain yield responses to elevated CO_2 that were about 50 % lower than those obtained using enclosures (Leakey et al. 2009). FACE experiments provide crop responses that are more relevant to farming because the crops are grown under natural open-air field conditions. Yield increases in the FACE studies were less than the increases in photosynthesis that occurred with short-term doubling of CO_2 at the same temperature (Poorter 1993; Allen 1994). Limitations in sink demand were apparent in the FACE experiments where only a small proportion of the increase in photosynthate supply was partitioned to grain (Leakey et al. 2009). The results of the FACE experiments support the hypothesis that crop plants are not well adapted to the higher CO_2 likely to occur by the end of this century.

The influence of elevated atmospheric CO_2 is examined for those crops whose reproductive development is sensitive to high temperature under the current CO_2 concentration. For soybean (*Glycine max* L. Merr.) growing under controlled-environment field conditions, harvest index progressively decreased with an increase in temperature under either 330 or 660 ppm CO_2. Harvest index was lower with elevated CO_2 indicating a more severe imbalance between the reproductive sink and the photosynthetic supply (Baker et al. 1989). Reproductive development of Pima cotton can be so sensitive to high temperatures that the plants do not produce either flowers or bolls (Reddy et al. 1992). Studies in naturally sunlit, controlled-environment chambers demonstrated that at elevated CO_2 of 700 ppm, Pima cotton still did not produce any flowers or bolls when subjected to high temperatures (Reddy et al. 1995, 1997). Controlled-environment field studies with rice demonstrated that grain yield decreased 10 % per °C increase in average temperature above 26 °C at CO_2 of either 330 or 660 ppm (Baker and Allen 1993). The decrease in grain yield was mainly due to fewer grains per panicle. High day and night temperatures can cause decreases in viability of pollen grains at anthesis and decreases in seed set in rice (Ziska and Manalo 1996). Elevated CO_2 aggravated these heat-stress effects, causing a 1 °C decrease in the maximum threshold canopy surface temperature after which the percentage of spikelets having ten or more germinated pollen grains exhibited a precipitous decline (Matsui et al. 1997). Heat-induced increases in floret sterility may have been responsible for the downregulation of photosynthesis observed in rice under high temperatures and elevated CO_2 through indirect effects associated with reductions in reproductive sink strength (Lin et al. 1997).

A unique insight into the interactive effects of high night temperature and elevated CO_2 was obtained from studies with cowpea genotypes that are either heat tolerant or heat sensitive during reproductive development. With high night temperatures, many cowpea genotypes are heat sensitive and do not produce any flowers, while others are partially heat tolerant and produce flowers but no pods and a few with complete heat tolerance produce both flowers and pods (Ehlers and Hall 1996). In growth chamber studies with three contrasting genotypes under high night temperature, a heat-sensitive genotype did not produce any flowers and a partially heat-tolerant genotype produced flowers but did not set any pods under either 350 or 700 ppm CO_2 (Ahmed et al. 1993a). Interestingly, a completely heat-tolerant genotype had greater pod production under elevated CO_2 at both high and more optimal night temperatures than a genetically similar cultivar that does not have the heat-tolerance genes (Ahmed et al. 1993a).

These studies indicate that elevated atmospheric CO_2 will not overcome heat-stress effects on reproductive development. This supports the argument that these effects are direct and are not mediated by heat-stress effects on the photosynthetic source. For those many crops that are sensitive to heat during reproductive development, incorporating heat tolerance may also enhance their yield responses to elevated atmospheric CO_2 over a range of temperatures (Hall and Allen 1993; Hall and Ziska 2000). This important hypothesis should be more completely tested using field conditions with additional cultivars of cowpea and other heat-tolerant crop species. 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 will be most responsive to elevated CO_2 under both hot and intermediate temperatures.

4.2.5 Effects of High Temperature on Grain Yield

Populations of plants under field conditions must be used when seeking estimates of the effects of heat stress on grain yield that are relevant to agriculture. In studies that use year-to-year variation in temperature or different locations with contrasting thermal regimes, other aspects of the environment also vary. In the study of variation in rice yield over 12 years on the experimental farm of the International Rice Research Institute (Peng et al. 2004), night temperature, day temperature, and solar radiation level varied. The authors used partial correlation analysis to establish that grain yield decreased 10 % per °C increase in night temperature independent of the changes in solar radiation. Ismail and Hall (1998) evaluated grain yields of six pairs of cowpea lines, with differences in heat tolerance during reproductive development but with simliar genetic background, growing under optimal irrigated management in four field environments with contrasting thermal regimes over 2 years. The solar radiation levels in these eight field environments were high and similar. Heat-susceptible lines exhibited a 13.6 % decrease in grain yield per °C increase in average minimum night temperature between emergence and first flowering above a threshold of 16 °C. The reduction in grain yield was mainly due to decreases in pod set and harvest index. In the three environments with the highest night temperatures, the heat-resistant lines had 54 % higher grain yield than the heat-susceptible lines mainly due to greater pod set and harvest index.

A reliable method to determine the effects of increases in temperature on productivity is to subject different plots of plants growing in the field to increases in temperature without otherwise disturbing the environment. This can be more readily achieved for increasing night temperature than for increasing day temperature. In one of the first studies of this type, the night temperature of sorghum plots was increased 5 °C for 1 week during floret differentiation and there was a 28 % decrease in grain yield associated with a 30 % decrease in the number of grains (Eastin et al. 1983). Plots of cowpea plants were subjected to elevated night temperatures during early-flowering stages using enclosures that were only imposed at night as was described previously (Nielsen and Hall 1985a). The cowpea plants exhibited a 4.4 % decrease in grain yield per °C increase in nighttime temperature above a threshold daily minimum temperature of 15 °C (Nielsen and Hall 1985b). The reductions in grain yields were due to reductions in the proportions of flowers producing pods. When rice plots were subjected to a 4 °C increase in temperature, during both night and day using open-top chambers, there was a decrease in grain yield of 18 % (Moya et al. 1998) due to reductions in spikelet and pollen fertility (Matsui et al. 1997).

It is clear that heat stress especially at night can decrease grain and/or fruit yield. Reduced seed and/or fruit set due to a lack of pollination are often responsible for this effect. Experience with breeding for heat tolerance during reproductive development has shown that it can overcome this problem.

4.3 Breeding and Selection Methods

Development of heat-resistant cultivars has relied principally on classical breeding methods using available genetic variation. Although heat-tolerant genotypes have been identified in landrace and cultivar collections, the proportions of heat-tolerant accessions have been low, such as in tomato (Opeňa et al. 1989), cowpea (Patel and Hall 1990), the Sudan core of the sorghum collection (Dahlberg et al. 2004), a Mexican wheat collection (Hede et al. 1999), wheat cultivars (Reynolds et al. 1994), cucumber (Staub and Krasowska 1990), chickpea (Krishnamurthy et al. 2011), and the common bean core collection (Porch TG, unpublished). Wild species of crop plants provide a mainly untapped source of additional genetic diversity. For example, collection of wild *Triticum* and *Aegilops* species led to the identification of heat-tolerant accessions originating from specific high-temperature agroecological zones, including eastern Israel, western Jordan, and southwestern Syria (Edhaie and Waines 1992). Ecogeographical approaches, based on the identification of landraces or wild species in carefully identified high-temperature agroecological zones, might lead to the discovery of germplasm with high levels of heat tolerance.

4.3.1 Genetics and Heritability of Heat Resistance and Heat Tolerance

For effective yield gain in breeding, adequate additive genetic variance and heritability are needed. However, heritability of yield generally decreases under greater and more complex stress conditions. In addition, G × E interaction in the high ambient temperature stress response can be significant, e.g., effects of photoperiod (see for review, Hall 1992 and Wallace 1980), while additional abiotic or biotic stressors in the environment also need to be considered. For example, insect-pest attacks can make it difficult to assess genotypic differences in pod set in cowpea under hot field conditions, especially in West Africa. Although variance increases under stress, resulting in high CVs, the advantages to selection for yield in complex field environments include improving adaptation to the target production environment (Ceccarelli et al. 1987).

Inheritance of heat resistance, i.e., high yield in hot environments compared with other cultivars, has been shown to be complex whereas heat tolerance of individual components that contribute to yield such as flower production and seed set has been shown to be simply inherited in some cases. Research in cowpea on the interaction of heat stress under variable photoperiods showed that germplasm can be divided into two groups, day-neutral accessions and short-day accessions, and several subgroups (Ehlers and Hall 1996). Genetic analysis of heat tolerance focused on the day-neutral group. Inheritance of heat tolerance for flower production was controlled by a single recessive gene (Hall 1993). In contrast, for pod set, two genes appeared to control heat tolerance with one of them characterized as having dominant gene action (Marfo and Hall 1992). Heat tolerance for flower production was highly heritable and could be effectively selected in the F_2 generation (Hall 2011), while narrow-sense heritability of heat tolerance for pod set in cowpea was only 26 % (Marfo and Hall 1992). In snap bean, genetic control of heat tolerance, measured as pod production (Bouwkamp and Summers 1982) or as abscission tolerance (Rainey and Griffiths 2005a, b), was found to be under simple genetic control. The narrow-sense heritability for pod production, however, was less than 10 %. In dry bean, heat resistance was found to be a heritable trait with breeding potential (Román-Avilés and Beaver 2001, 2003). Indeterminate growth habit and heat resistance were correlated (Shonnard 1991; Porch 2001), indicating possible simple genetic control for this trait or escape related to indeterminacy in common bean. In tomato, a few dominant genes were found to control fruit set under heat stress but narrow-sense heritability was low (Shelby et al. 1978), while a few recessive major genes were found by Opeňa et al. (1989). In rice, high broad-sense and narrow-sense heritabiltiy, with mostly additive genetic control, was found for heat resistance (Yoshida et al. 1981). Pollen grain number under heat stress was found to be correlated with yield under heat stress and controlled by several recessive genes (Mackill and Coffman 1983).

While the majority of studies have seemed to indicate simple inheritance for reproductive traits under heat stress, there is also evidence for complex inheritance of heat tolerance. For floral development under hot conditions in common bean, Shonnard (1991) found complex inheritance with additive gene action, dominance effects, and interaction with the environment. For floral bud abscission, realized heritability was 36 %, while for seed set it was 22 %. In tomato, diallel experiments indicated both specific and general combining abilities for fruit set (El Ahmadi and Stevens 1979; Opeňa et al. 1987).

4.3.2 Selection Techniques

A major constraint to progress in breeding for heat tolerance is the identification of and access to appropriate, consistent selection environments. The selection environment plays a key role in the efficiency of the selection process. The predominant approach to breeding for heat tolerance has involved selection for reproductive traits or yield under high ambient temperature conditions in the field. This cost-effective approach for increasing productivity and multiple-stress tolerance in high ambient temperature target production environments has been shown to be effective for a number of crops such as cotton, cowpea, dry bean, snap bean, and tomato.

Characterization of field production environments is an important aspect of the response to high-temperature stress. Each crop differs in its tolerance to high ambient temperatures, thus crop-specific threshold temperatures are important for assessing those daytime and nighttime temperatures that result in significant yield reductions. These temperatures vary based on the crop and developmental stage but can also depend on other environmental conditions.

Use of significantly hotter field environments than the typical production environment has resulted in the improvement of heat tolerance during reproductive development in cowpea (Ehlers et al. 2000; Hall 2011) and dry bean (Shonnard 1991; Rosas et al. 1999; Porch et al. 2012) but may result in the exclusion of moderately tolerant germplasm with other advantageous characteristics (Abdul-Baki 1991). Different field temperatures can be attained through selection of field sites at different altitudes and/or latitudes within a production region (e.g., Wallace 1980).

Confounding factors often exist in the field, which lead to more challenging identification of specific genetic factors related to heat tolerance. Root rot, low soil fertility, foliar diseases, insect pests, and drought often occur in high ambient temperature stress locations. However, screening plants in complex field environments can produce germplasm that is tolerant to multiple stresses (e.g., Porch et al. 2012), which is a decided advantage.

In addition to temperature, relative humidity is a major environmental factor that differs between semiarid, subhumid, and humid production zones. Research in wheat has shown that the greatest source of interaction between genotypes and sites across years was due to relative humidity (Reynolds et al. 1998; Vargas et al. 1998), resulting in the recommendation that breeding for high and low relative humidity environments should be conducted separately (Reynolds et al. 2001). These findings suggested that disease pressure may be a more important constraint under high relative humidity environments, while drought stress could be a greater constraint in low relative humidity environments. Thus relative humidity, as well as soil moisture conditions, should be considered in addition to temperature stress characteristics when choosing a selection environment.

Photoperiod can be a critical parameter in selecting a screening environment for some crops. Sensitivity of reproductive development to heat has been shown to be influenced by day length in cowpea and rice (as reviewed above).

The timing of screening is important. Studies on a number of crops (e.g., cotton, cowpea, rice, tomato, and common bean), reviewed above, have shown that the greatest sensitivity to high-temperature stress occurs during reproductive development (note: some crops have shown sensitivity to high soil temperatures at planting or during vegetative growth). Since the sensitive periods during the reproductive development period tend to be relatively short, weeks to a month long, planting can be timed so that reproductive development coincides with this high-temperature period during the warm season. Some species are more sensitive to high night temperature and locations should be chosen that provide sufficiently high night temperature during reproductive development to cause stress. Differences in plant phenology between genotypes should be considered in order to avoid escapes. Field selection environments typically do not facilitate temperature control; however, nighttime temperatures can be modified using small canopies that can be placed over the crop at night.

Controlled environment, high-temperature screening, and selection methods have been used for crop improvement. Modern, tightly controlled greenhouse environments effectively control temperature, in addition to some other aspects of the environment. Greenhouse selection for heat tolerance has been widely employed in snap bean (e.g., Dickson and Petzolt 1989; Wasonga et al. 2010, 2012) and tomato (Berry and Rafique-Uddin 1988) and is effective in cowpea (Thiaw and Hall 2004). Temperatures generally differ between the field and greenhouse screening environments (often higher in the greenhouse, especially at night), in order to ensure a similar selection index. A significant advantage of the greenhouse environment is that it affords the opportunity for the application of consistent high night temperatures that are often only available in lowland tropical and subtropical but not temperate field environments. In addition, greenhouse environments generally offer better control of other sources of stress, thus eliminating the effects of interaction with drought and biotic constraints. A major advantage of hot greenhouse environments is that they can provide more consistent evaluations of plant heat tolerance than hot field environments, but they are more expensive to operate per plant tested. However, greenhouse environments are often not representative of field environments.

Correlations between genotype responses in field and greenhouse trials or between different field environments have been shown in some circumstances. For example, cowpea selection for yield in high-temperature tropical field environments (Patel and Hall 1986; Ehlers and Hall 1998) has resulted in germplasm tolerant to high temperature in subtropical field and greenhouse environments. Snap bean selected for heat tolerance in greenhouses has exhibited high yields in high-temperature field sites in Kenya and Puerto Rico (Wasonga et al. 2010, 2012). In wheat, canopy temperature depression was found to be correlated between screen-house trials and field trials (Hede et al. 1999). These results indicate that in some cases, selection in one environment has resulted in broad adaptation of heat-tolerant germplasm which could simplify breeding approaches and make germplasm useful over broad geographical areas.

Indirect selection approaches can be useful where specific traits are correlated with heat tolerance. Maintenance of membrane function has been considered a general mechanism for heat tolerance. Based on earlier research it had been proposed that selection for slow leaf-electrolyte leakage under heat stress could provide a method to breed for increased heat tolerance (Blum 1988). Genetic selection studies with cowpea demonstrated that low leaf-electrolyte leakage under hot conditions is associated with heat tolerance during pod set in cowpea and can be used as a selection criteria. Lines of cowpea that were heat tolerant during pod set were shown to have less leaf-electrolyte leakage under heat stress than a set of heat-sensitive lines (Ismail and Hall 1999). Thiaw and Hall (2004) selected two of these lines, a heat-sensitive cultivar and a heat-tolerant genetic line with similar genetic background, and used them as parents in a breeding program. They crossed the parents and then divergently selected one population for high and low pod set under heat stress and another population for low and high leaf-electrolyte leakage under heat stress. Genetically stable, selected lines were developed and evaluated in an extremely hot long-day field environment and a long-day glasshouse environment with high night temperature. In both environments, 66 lines selected in one generation for high pod set and 16 lines selected in two generations for low leaf-electrolyte leakage had greater pod set and grain yield than either the 40 lines selected for low pod set or the 16 lines selected for high leaf-electrolyte leakage. In both environments, highly significant negative correlations were obtained between leaf-electrolyte leakage and number of pods per peduncle and grain yield using data from both populations. These results indicate there is a strong association between ability to set pods under heat and maintenance of membrane function that may be pleiotropic. The indirect realized heritability for heat tolerance during pod set resulting from selection for slow leaf-electrolyte leakage was only 10–12 %. This indirect screen has value, however, in that it can be conducted at times of the year and in locations where field screening for heat tolerance is not possible. Field screening for pod set, however, still would be necessary.

Blum et al. (2001) made progress in breeding heat-resistant spring wheat cultivars that produced more grain than other cultivars in hot environments by selecting for slow leaf-electrolyte leakage under hot conditions. They proposed that selecting for slow leaf-electrolyte leakage under hot conditions could not replace selecting for yield in the field but that it can be useful for reducing a large population into the most likely heat-tolerant core in the early stages of a breeding program.

Selection of heat-shock proteins (HSP) may be another avenue to pursue for the indirect selection of heat-tolerant germplasm; however, to date, correlations have not been shown between HSPs and heat resistance as expressed in seed yield. Genetic lines of cowpea with substantial differences in heat tolerance during reproductive development and with a similar genetic background have produced the same set of heat-shock proteins in their leaves when subjected to high temperatures. Heat-shock protein profiles were examined in six common bean lines that differ in heat acclimation potential with respect to differences in heat-killing time based on leaf-electrolyte leakage (Li and Udomprasert 1993). No relationship was observed between patterns of HPSs and heat acclimation potential.

While there is no published evidence to indicate that genetic engineering has been used for the development of improved heat tolerance in a cultivar, basic research has been completed indicating that transcription factors (Yoshida et al. 2012), micro RNAs (Yu et al. 2012), and heat-shock proteins (Queitsch et al. 2000) increase tolerance of specific physiological processes in the laboratory, but this does not necessarily translate to the field environment. Some recent research demonstrated that the expression of AtSAP5 in cotton increased expression of stress-response genes and may have increased drought and heat tolerance (Hozain et al. 2012).

4.3.3 Breeding Methods

Breeding methods for heat tolerance vary based on the genetic nature of the tolerance to high ambient temperature stress and on the crop. The pedigree method has perhaps been used most extensively for breeding for heat tolerance across crops. This breeding approach has been employed for the improvement of snap bean at Cornell; dry bean at the University of Puerto Rico and USDA-ARS in Mayagüez, Puerto Rico; cowpea at the University of California, Riverside (Hall 2011); and tomato and Chinese cabbage at AVRDC (Opeña et al. 1987). Selection is often conducted in early generations. In cowpea, for example, selection of single F_2 plants with high numbers of flowers, pods per peduncle, seeds per pod, and seed quality has been conducted under very high-temperature field conditions. Recessive genes in the F_2 were thus fixed, which include photoperiod insensitivity and resistance to floral bud abortion, but this selection only provided partial heat tolerance during pod set. Early generation selection can substantially increase the speed of the breeding process when the trait of interest is under relatively simple control and has adequate inheritance. Selection of more complex or dominant traits, such as pod set in cowpea, mainly is conducted in later generations while agronomic traits can be selected in concurrent trials under commercial conditions. Evaluations of advanced lines are then conducted in multilocation trials throughout the target production zone.

Due to the simple genetic nature of heat tolerance during reproductive development in a number of crops, the backcross breeding approach has also been employed as method for introgression of tolerance into elite material. In rice, a large backcross population was advanced using single-seed descent and then selected for heat tolerance during the milky stage of seed development using differential planting dates (Liao et al. 2011). In cotton, backcross breeding was used to transfer pollen thermotolerance through treating pollen before pollination for 15 h with 35 °C temperatures, resulting in higher levels of fertile pollen in subsequent generations (Rodriquez-Garay and Barrow 1988). The backcross method is ideal for relatively simply inherited traits with adequate inheritance and can be combined with single-seed descent or the pedigree approach to result in an efficient method for germplasm improvement.

In order to combine multiple sources of heat tolerance, recurrent selection has been employed in diploid potato resulting in a 27 % increase in yield in a single cycle of recurrent selection (Gautney and Haynes 1983) and is being employed to combine heat and drought tolerance in common bean (Porch TG, unpublished).

Although quantitative trait locus (QTL) approaches have not been extensively used in breeding for heat tolerance, some QTLs that may be relevant have been identified in crop species. QTLs controlling pollen germination and pollen tube growth were identified in maize (Frova and Sari-Gorla 1994), and grain-filling duration QTLs were identified in wheat (Yang et al. 2002). While some studies have shown that heat tolerance is under relatively simple control (Porch et al. 2004; Rainey and Griffiths 2005a, b; Hall 2011), few QTL analyses have been completed and molecular markers have yet to be developed for marker-assisted selection (MAS). Additional QTL studies are needed that may show similar genetic control and similar mechanisms for heat tolerance across some species.

4.3.4 *Facultative Apomixis as an Approach for Achieving General Tolerance to Several Stresses During Reproduction*

Production of pollen and pollination are sensitive to several other stresses in addition to high temperature, including chilling, drought, and frost. A potential general solution to reproductive sensitivity is to develop cultivars that do not require sexual processes when growing in farmers' fields, i.e., apomixis.

Crop plants with an appropriate type of apomixis would be able to produce viable seed from maternal tissue without requiring either meiosis of the embryo mother cell or pollen production and pollination of the embryo or endosperm. Advantages of cultivars with this type of apomixis were described by Jefferson (1993) and are discussed below.

Because they do not require sexual processes, apomictic cultivars would have tolerance to the many stresses that have the potential to damage pollination and other aspects of sexual reproduction. Since meiosis is eliminated, apomixis would fix hybridity because all cultivars including F_1 hybrids would have true-breeding seeds. This would make possible the use of hybrid vigor in the many crop species where it is currently either not economic (e.g., cowpea, common bean, and wheat) or difficult (e.g., rice) to generate hybrid seed by crossing. Note that cowpea exhibits substantial hybrid vigor. Farmers would be able to reuse seed produced by apomictic hybrid cultivars in that the seed would retain its hybrid vigor. This would be a significant advantage to poor farmers. Seed industries would still be needed because farmers would still need to purchase high quality seed after several years of using their own seed. The quality of seed declines from year to year due to the presence of seed-borne pathogens and contamination by off-types either in the farmers' fields or due to mechanical mixing during harvesting or seed processing. Crops currently propagated vegetatively, such as most Irish potatoes (*Solanum tuberosum* L.), would benefit from apomictic cultivars because they could be propagated by seed instead. Breeding progress would be accelerated by using apomictic lines because they would confer the ability to immediately fix heterozygous genotypes.

Normal reproduction would still be needed in breeding programs to permit the continual breeding of improved cultivars. The integration of breeding with apomictic cultivar release could be achieved by using facultative apomixis systems, where the default state is apomictic and the sexual state can be "switched on" by the breeder. Switching might be achieved either by sprays with specific chemicals or by growing the plants in a specific environment. For example, there is a male sterility in rice that can be switched off by growing the plants in shorter-day cooler environments (Yuan et al. 1993). In this system a warm thermal regime combined with long days induces male sterility. This represents an extreme sensitivity of the similar system that has been observed in some other species such as cowpea (Hall 2004).

Several plant species have the genes needed to develop facultative apomictic breeding systems in crop plants. Through genetic engineering it may be possible to create and transfer the "cassette" of genes needed for facultative apomixis into crop cultivars (Jefferson 1993). This would not be an easy task but crop cultivars with facultative apomixis would result in a revolution in plant biology, plant breeding, crop production, and agriculture.

4.4 Heat-Resistant Cultivars and Breeding Lines

Relatively little progress has been made in breeding cultivars with heat resistance, i.e., cultivars with greater yields than other cultivars in hot commercial production environments. In addition to heat resistance, cultivars should have similar or greater grain yields than current cultivars in more moderate temperature environments within the target production zone and other desirable agronomic traits. Documented cases of the development of heat-resistant cultivars or breeding lines of annual crops that produce grain and/or fruit are described.

4.4.1 Grain Cowpea and Snap Cowpea

"California Blackeye 27" (CB27) was bred using a pedigree breeding procedure involving crosses among two accessions that are heat tolerant during reproductive development and two California cultivars (Ehlers et al. 2000). Segregating lines were subjected to selection for flower production and pod set over several years in a summer field nursery in Imperial Valley, California, that has extremely high night and day temperatures during early flowering (average daily maximum and minimum air temperatures of 41 and 24 °C) and long days. In addition, resistances to root-knot nematode and Fusarium wilt were incorporated. This was followed by selection for yield and other agronomic traits in experiment-station sites and farmer-managed trials in commercial production locations in California where the temperatures ranged from being cool to very hot (average daily maximum and minimum air temperatures ranging from about 26/13 to 35/17 °C during the first 60 days after sowing). As a result of this work, CB27 was bred, which is heat resistant in that it produced higher yields than cultivar CB5 in hot environments (Ismail and Hall 1998) and it had similar yields as the cultivar CB46 in more optimal environments. CB27 is a semidwarf cultivar with a higher harvest index and a more compact growth habit than CB5 and has exhibited greater yield advantages when grown on narrow row spacing (Ismail and Hall 2000).

"Marfo-Tuya" was bred by crossing a landrace from Ghana "Sumbrisogla" and breeding line 518-2 from the University of California, Riverside (Padi et al. 2004b). Line 518-2 was bred by crossing CB5 with a Nigerian landrace that has heat tolerance during reproductive development and selecting for flower production and pod set in an extremely hot, long-day summer field nursery in Imperial Valley, California. Segregating progeny from the cross between "Sumbrisogla" and 518-2 were selected for flower production and pod set in an extremely hot, long-day summer field nursery in Imperial Valley, California, and then for grain yield and other agronomic attributes in northern Ghana. In experiment-station trials over 7 years at four locations in northern Ghana, "Marfo-Tuya" had grain yields that were 52 % greater than a check cultivar. In farmer-managed agronomic trials over 3 years at 52 farm sites across northern Ghana, "Marfo-Tuya" produced significantly more grain than local checks in 72 % of the test locations.

"Apagbaala" was bred by a three-way cross involving a breeding line from the International Institute of Tropical Agriculture (IITA), a heat-tolerant cultivar from Nigeria, and a heat-tolerant breeding line from the University of California, Riverside (Padi et al. 2004a). Segregating progeny were selected for flower production and pod set in an extremely hot, long-day summer field nursery in Imperial Valley, California, over 2 years and two generations. Lines were then selected for grain yield and other agronomic attributes over 3 years in northern Ghana. In experiment-station yield trials over 7 years at four locations in northern Ghana, “Apagbaala” had grain yields that were 41 % greater than the local check cultivar. In farmer-managed agronomic trials over 4 years at 66 farm sites across northern Ghana, “Apagbaala” produced significantly higher grain yields than the local check in 74 % of the test locations.

“Mouride” was bred by crossing a landrace from Senegal that is used as a cultivar, 58-57, with a breeding line from IITA (Cisse et al. 1995). Early generation selections were conducted for resistance to cowpea weevil, cowpea aphid-borne mosaic virus, and bacterial blight. Selection for yield and other agronomic traits was conducted in Senegal at four experiment-station locations and at 35 on-farm sites over 3 years. In these trials, “Mouride” produced 18 % more grain but 17 % less forage than 58-57, and in subsequent years it has produced very high grain yields in many trials in the hot Sahelian zone. At no time was “Mouride” selected for heat tolerance, but it was selected for yield in very hot environments in Senegal. Subsequent glasshouse studies in California under short days with high night temperatures (Ehlers and Hall 1998) showed that “Mouride” had some heat tolerance during pod set, whereas another cultivar bred in Senegal using similar methods but different parents, “Melakh” (Cisse et al. 1997), was heat sensitive during pod set. Selection for grain yield in hot regions of tropical Africa does not necessarily incorporate heat tolerance, but it has produced some cultivars that may be useful donors of heat-tolerance traits.

Five vegetable (edible pod snap-type) cowpea breeding lines were developed at the Indian Agricultural Research Institute, New Delhi, India, by incorporating resistance to bacterial blight and selecting for high pod yield under very hot, long-day field conditions in northern India (Patel and Singh 1984). These lines were shown to have heat tolerance during flowering and pod set in an extremely hot, long-day summer field nursery in Imperial Valley, California (Patel and Hall 1986). Under hot long-day field conditions in Riverside, California, these breeding lines produced green pod yields between 25–28 ton/ha, whereas the US cultivar “Snapea” yielded only 13 ton/ha and a snap bean (*Phaseolus vulgaris* L.) cultivar, “Contender,” produced only 6.7 ton/ha.

4.4.2 Common Bean, Snap Bean, and Tepary Bean

Current estimates predict that the area suitable for common bean production could increase by over 50 % if beans were able to tolerate a 2 °C increase in temperature (Beebe et al. 2012). Thus, there is significant justification for investing in breeding common bean for heat tolerance (Porch et al. 2007). Plant breeding efforts have increased tolerance to heat stress in germplasm, mainly in the Mesoamerican gene pool. Early efforts to improve bean golden mosaic virus (BGMV) resistance in the lowlands of Central America resulted in the generation of heat-tolerant germplasm at CIAT, including DOR 364 and DOR 557. Specific breeding for heat tolerance at

Escuela Agricola Panamericana (Zamorano) resulted in the generation of the first heat-tolerant common bean variety, Tio Canela, with a small red seed type (Rosas et al. 1999). Significant gains in heat tolerance were achieved with the release of two additional small red genotypes, Amadeus 77 (Rosas et al. 2004) and CENTA Pipil, which resulted in significant yield improvement in lowland production environments and also in Amadeus 77 becoming the most widespread common bean variety in Central America. In the Caribbean, selection for heat tolerance led to the release of "Verano" (Beaver et al. 2008), a small white variety from the University of Puerto Rico, with heat tolerance, common bacterial blight resistance, and virus resistance. Andean beans, TARS-HT1 and HT2 kidney bean germplasm (Porch et al. 2010), were developed for heat tolerance at USDA-ARS in Mayagüez, Puerto Rico, while Mesoamerican beans TARS-SR05 (Smith et al. 2007) and TARS-MST1 (Porch et al. 2012) have multiple-stress tolerance, including heat tolerance.

At Cornell University, the snap bean breeding program has improved reproductive heat tolerance in snap bean germplasm for the USA, resulting in the development of Cornell 502 and 503. Ongoing efforts are combining heat tolerance and rust resistance for snap bean production in East Africa (Wasonga et al. 2010, 2012).

The genetic limits of heat tolerance in existing crop plants may require exploration into the development and use of new species, or historically used native species, as future food security crops. One possible example is tepary bean (*Phaseolus acutifolius* A. Gray), a native species from the Sonoran desert of Mexico and southern USA (Freytag and Debouck 2002), which has drought adaptation and heat tolerance that is superior to that of common bean. Although not currently a commercial crop, at the peak of tepary production in the 1930s, the Tohono O'odham tribe in southern Arizona grew more than 750 tons of tepary beans annually, and the crop has traditionally been produced by Native American tribes in the region (Nabhan and Felger 1978). Current production levels are far lower and dispersed through Arizona, New Mexico, Mexico, and Central America. However, there is increasing interest in tepary in the USA and production has begun in Africa by small-holder farmers in arid regions (Shisanya 2002). Tepary exhibits multiple drought and heat tolerance related traits including: stomatal control (Markhart 1985), dehydration avoidance (Mohammed et al. 2002), root characteristics (Butare et al. 2011), and yield stability (Miklas et al. 1994; Porch 2006).

Tepary landraces have been used for mass selection, resulting in the release of a dark yellow tepary (cited by Pratt and Nabhan 1988). "Redfield" tepary was released in a published registration (Garver 1934) and was the result of a selection from T.S. 3306, a Texas landrace. Recent breeding efforts at ARS-TARS, Puerto Rico, have resulted in the development of improved tepary lines, TARS-Tep 22 and TARS-Tep 32, with heat, drought, common bacterial blight, and bruchid resistance (Porch et al. 2013, accepted). They also exhibit a larger seed size and improved agronomic characteristics, which have been constraints to tepary production and consumer acceptability in the past. Virus resistance and culinary traits may also need to be improved, but further research is needed to explore these characteristics and the potential for improvement.

4.4.3 Pima Cotton and Upland Cotton

Breeding heat-tolerant Pima cotton began in the late 1950s at Phoenix, Arizona. Feaster and Turcotte (1985) established that in environments where adaptation depends on tolerance to high night temperature, the extent of boll set at low nodal positions under very hot conditions is an effective indicator of heat tolerance. Several cultivars (Feaster and Turcotte 1976, 1984; Turcotte et al. 1992) and germplasm lines (Turcotte et al. 1991; Percy and Turcotte 1997) were bred by selecting for greater boll set on low nodal positions under very hot field conditions. The realized genetic gain in lint yield from "Pima S-1" to "Pima S-5" was 57 % in very hot conditions at low elevation and 30 % at higher elevation. "Pima S-6," which was released in 1983, was estimated to have 69 % greater yield over Pima S-1 (the dominant cultivar in southwestern USA from 1955 to 1961) in hot environments and a 27–43 % yield advantage in cooler environments (Feaster and Turcotte 1985).

Average yields of Pima and upland cotton (*Gossypium hirsutum* L.) were compared for six counties in Arizona over a 30-year period (Kittock et al. 1988). Pima cotton lint yields increased substantially more than upland cotton lint yields, particularly in hot environments, as improved Pima cultivars were released over the 30-year period. The authors concluded that about 50 % of the 30-year lint yield increase of Pima cotton in hot environments resulted from the increased heat tolerance (i.e., boll set) of the improved cultivars. A historical set of eight heat Pima cultivars, which had been selected for boll set in a very hot field environment, were compared in a very hot commercial production environment (Lu et al. 1998). Genotypic differences in lint yield were positively correlated with stomatal conductance measured in the middle of the afternoon during peak flowering and fruiting. Lu et al. (1998) hypothesized that the adaptive advantage of the higher stomatal conductance is independent of photosynthesis and is associated with leaf cooling providing a heat avoidance type of heat resistance. However, this hypothesis would not explain heat-stress effects on boll set that occur in the late night or early morning when stomata would have little influence on plant temperature.

In earlier years upland cotton had greater heat tolerance than Pima cotton. Since this time, the success of commercial upland cotton breeding programs for the extremely hot environments of southwestern USA probably was also partially due to incorporation of heat tolerance during boll set.

Upland cotton cultivar CRIS-134 was bred to tolerate the hot period of June–August at the Cotton Research Institute, Sakarand, Sindh, Pakistan (Soomro 1998). This cultivar is capable of producing 32 bolls after 75 days from sowing compared with 11–17 bolls in check cultivars.

Heat-tolerant upland cotton genotypes have been developed at the Indian Agricultural Research Institute (IARI), New Delhi, India, using a shuttle-breeding approach involving changing environments during generations of selection (Singh et al. 2004). Selection was applied for high numbers of fruiting structures and early maturity (Singh et al. 2003). According to Singh et al. (2007), heat-tolerant genotype Pusa 17-52-10 has been registered with NBPGR (INGR No 03073) and the heat-tolerant upland cotton genotypes bred in India typically have compact plant type, as also was observed in heat-tolerant cowpea genotypes (Ismail and Hall 1998), and low first fruiting node number, as was observed in heat-tolerant Pima cotton genotypes (Feaster and Turcotte 1985). IARI has bred an upland cotton cultivar, "Aurobindo PSS-2," that has tolerance to high temperatures during reproductive stages and tolerance to low temperatures during germination (Singh et al. 2011). Cowpea lines also have been bred that combine tolerance to high night temperature during reproductive stages with chilling tolerance during germination and emergence (Hall 2011). It is surprising that chilling tolerance and heat tolerance, at different stages of development, can be combined because they may depend on different membrane fluidity properties (Lyons 1973).

4.4.4 Tomato

The heat-tolerant tomato cultivar "Saladette" was bred by Paul W. Leeper by selecting for fruit set under the hot summer conditions of the Lower Rio Grande Valley in Texas. Since this time, Saladette and other heat-tolerant genotypes (Stevens 1979) have been used as parents in breeding programs in the USA. Several commercial breeding programs in California have developed heat-resistant tomato cultivars for processing and fresh market use by incorporating heat tolerance during reproductive development.

Fresh market tomato breeding began at the University of Florida in 1922. A hybrid cultivar was released in 1989, "Solar Set," that was described as having a commercially acceptable level of heat tolerance (Scott 1999). Heat tolerance involved the ability to set fruit in hot field conditions. Solar Set was compared with three other heat-tolerant cultivars, nine heat-tolerant lines, and four heat-sensitive cultivars in an extremely hot glasshouse (38–40 °C/29–31 °C day/night air temperatures) and a hot (28–29 °C/18–19 °C day/night average air temperatures) field environment (Abdul-Baki 1991). "Solar Set" had higher yields than the other heat-tolerant cultivars and lines in the field environment but produced fewer flowers and normal fruits and had lower yields than the other heat-tolerant cultivars and lines in the extremely hot glasshouse. An open-pollinated heat-tolerant cultivar, "Neptune," was released that had similar field yields as "Solar Set" (Scott et al. 1995a). A heat-tolerant hybrid, "Equinox," was released that was reported to have the same high-temperature fruit-setting ability and similar field yields as "Solar Set" (Scott et al. 1995b). A heat-tolerant hybrid, "Solar Fire," was developed that was reported to have superior fruit-setting ability under high temperatures (>32 °C day/>21 °C night) than most current cultivars and to have produced greater yields than "Solar Set" in field trials in Florida (Scott et al. 2006). Note that the various tomato cultivars that were released also had differences in resistances to diseases and other traits such as those involving fruit quality.

The Asian Vegetable Research and Development Center (AVRDC) in Taiwan began its tomato breeding program in 1972 focusing on producing cultivars for use in the tropics (where night temperatures are high). Many biotic stresses constrain tomato production in the tropics, but during the first stage of the AVRDC tomato breeding program (1973–1980), heat tolerance during reproductive development was incorporated by selecting for fruit set in field nurseries grown at the hottest time of the year (Villareal and Lai 1979). As of 1992 this breeding program had contributed to the development and release of 52 tropical tomato lines in 32 countries (Opeňa et al. 1993). The relationships between reproductive-stage heat tolerance of some AVRDC lines and fruit yield under hot tropical conditions are discussed by de la Peňa et al. (2011). They recommend that screening for pollen amount and pollen viability can be useful surrogate traits to selecting for fruit set under very hot field conditions.

4.4.5 Rice

Genotypic differences in heat tolerance have been detected in rice in which there was a highly significant correlation between the percentage of florets setting seed and the number of pollen grains per stigma (Yoshida et al. 1981; Mackill et al. 1982). Many heat-tolerant lines were also early flowering (Yoshida et al. 1981). A similar association between heat tolerance at flowering and earliness also has been observed in cowpea (Ehlers and Hall 1996). In genetic studies with rice, the number of pollen grains per stigma and percentage seed set had broad-sense heritabilities of 83.7 % and 69.2 %, respectively (Mackill and Coffman 1983). Phenotypic and genetic correlations between the two traits were 0.58 and 0.65, respectively. A narrow-sense heritability of 48 % indicated that it should be possible to select for seed set under high temperature.

A breeding project was initiated at the International Rice Research Institute in 2007 to incorporate heat tolerance during seed set into rice and to change the time of flowering from between 10 A.M. and noon to earlier in the morning when it is cooler (Redoňa et al. 2007). Advanced breeding lines have been developed, some of which were selected using a shuttle-breeding approach involving naturally hot locations in different countries. These heat-tolerant rice lines are now being evaluated for yield and other agronomic traits (E. D. Redoňa, personal communication).

4.4.6 Wheat

Progress has been made in breeding heat-resistant wheat cultivars as was shown by evaluations of spring wheat cultivars (Shpiler and Blum 1991; Leithold et al. 1997) and winter wheat cultivars (Assad and Paulsen 2002; Tewolde et al. 2006). Heat-resistant cultivars usually produced more grain per spike and had greater individual grain weight. A major factor in gaining heat resistance may have been selection for grain yield in field environments where heat stress occurred. Through the use of appropriate experimental designs and field procedures and computerized combine harvesters, more extensive yield testing can be done with wheat than with most other crop species. For example, the spring wheat breeding program of E. A. Hurd in Saskatchewan, Canada, yield-tested about 1,000 lines per cross in early generations (Hurd 1971).

Spring wheat breeding programs of the International Maize and Wheat Improvement Center (CIMMYT) use selection in field nurseries with managed stress to incorporate stress tolerance (Trethowan and Mahmood 2011). For example, a late-planted field nursery in northwestern Mexico provides heat stress during grain development but is well watered to avoid confounding effects due to drought. Seed are bulk harvested, in some cases, and separated for seed size and density on a gravity table. Large well-filled grain are selected and then resown again in a late-planted field nursery where plants are subjected to heat stress during grain development.

Progress has been made at CYMMT in combining selection for physiological criteria with empirical selection for grain yield and individual seed weight. Grain yield of spring wheat cultivars in hot irrigated environments had been shown to be positively correlated with stomatal conductance, and it was shown that canopy temperature depression (CTD) as measured with an infrared thermometer is an effective method for screening for this trait (Amani et al. 1996). Based on studies with breeding lines, Reynolds et al. (1998) proposed that selection for CTD could complement empirical selection for heat resistance. Selection for CTD has now been used in the F_4 generation to favorably skew gene frequency, resulting in a higher proportion of drought-adapted materials with cooler canopies (Trethowan and Turner 2009). Blum et al. (2001) proposed that selection for slow leaf-electrolyte leakage under heat stress also might be useful for reducing a large population into the most likely heat-tolerant core in the early stages of a breeding program.

4.5 Future Directions and Conclusions

Due to global warming, more effort should be devoted to breeding for heat resistance in annual crops. Work by a few breeders with a few annual crop species has shown that this can be done by conventional hybridization with selection for heat tolerance during reproductive development. Pollen development of many species is particularly sensitive to high temperatures occurring in the late night or early morning. DNA markers should be developed for heat tolerance during pollen development since this could make breeding for heat resistance more effective and markers could be determined in plants grown in cooler as well as warmer environments. Collaboration in marker development is warranted since similar markers may be effective in several species and since comparative genomics can be employed for testing candidate genes. More consideration should be given to the development of facultative apomictic breeding systems since they could provide a general solution to the damage that many stresses cause to reproductive development in crop plants.

Future breeding methods should involve a greater integration of molecular breeding, whole genome selection, high throughput phenotyping, and reverse genetic approaches as compared to current improvement programs. Additional markers should be developed for different heat-tolerance traits. The complexity of target production environments, however, requires that phenotypic field selection likely will remain the foundation of crop improvement programs.

Where necessary, alternate crops can be considered where the reclamation of marginal high temperature agroecological zones is being pursued. For example, among the warm-season legumes, dry grain cowpea, snap cowpea, and tepary have much greater heat tolerance than common bean or snap bean.

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