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Heat stress in plants

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Contents

1-What Does Stress Mean to an Agriculturalist?

Stress in biological terms means deviation in the normal physiology, development and function of plants which can be injurious and can inflict irreversible damage to the plant system. The type of stress that crop plants suffer from can be broadly grouped as ‘temperature variation at crucial stages’. There are several sticky abiotic parameters revolving around temperature e.g., frost damage and evaporation stress.

Many living organisms parasitize plants, such as the plant pathogenic viruses, bacteria, fungi, nematodes, insects and phenerogamic plants.Abiotic stresses are inflicted by non-living things/ matter on which the plant system is dependent.

Ambient temperature, relative humidity, sunshine, microclimate, soil nutrition, soil biota and other physico-chemical properties of the soil create stress on plant.

2-Types of Abiotic Stress in Plants

Various types of abiotic stresses that plants encounter between seedling to harvest stages are:

- Unseasonal rain
- Abundant and copious soil moisture or its quick retreat
- Soil salinity
- Micronutrient (soil nutrition) shortage in the root zone
- Global change in weather patterns
- Economic and political uncertainty

In addition, many biotic stresses affect crop yield:

- Disease damage
- Insect or nematode damage
- Invasive threats

Breeding crops for specific abiotic tolerance is one of the core activities of varietal improvement program. Developing abiotic tolerant varieties and adopting good crop practices are the means by which agriculturists minimize the impact of abiotic stresses without causing a substantial yield loss. Abiotic tolerant plants have the inbuilt capacity to overcome the damage caused by stresses at various growth stages. If the abiotic stress is only for a brief period and if congenial conditions return thereafter, then the plant activates the various compensation mechanisms and succeeds in executing damage control. As a consequence, the total biomass and the yield of crops remain largely unaffected.

Often, many of the abiotic stresses occur together and in that process inflict severe yield losses. For example, crop plants are largely dependent on the availability of moisture in the top 10 cm of the soil profile. Drought stress occurs when soil moisture status is low, relative humidity is low and temperature is high. When relative humidity is low and temperature is high i.e., two stresses occur together, ‘atmospheric drought’ sets in. This is agriculturally overcome by extending irrigation; and where timely access to surface irrigation is not feasible, the ‘agricultural drought’ sets-in. And if the agricultural drought persists, crops virtually dry up, fires become common and productivity of orchard crops gets badly affected.

3-High Temperature Stress

There are three cardinal points for the types of temperatures that are vital for plant activity:

- Minimum temperature below which no plant growth and development occurs.
- Optimum temperature at which maximum plant growth and development occurs
- Maximum temperature above which plant growth and development stops

Temperature requirement of different plants vary for the cardinal points as it is related to the duration of exposure, age of the plant, previous history and such externalities. Generally, it is the air temperature or the ambient temperature that affects the crop in several ways.

A-Temperature Periodicity:

Diurnal variation in air temperature is important as it influences photorespiration. The total heat units accumulated during the growth phase of plants influence the physiology, reproduction and maturity of crops. Deviation from normal temperatures or day/night periodicity around reproductive stage influences the seed yield and seed quality. Invariably, short day conditions at pod filling or grain filling stage negatively affect the seed weight and the physico-chemical quality of the seed. In leguminous crops, periodicity pattern influences the root behavior, nodulation patterns and total biomass production. Any temperature deviation due to global weather change is likely to affect the growth and physiology of plants in more than one way.

B- Temperature-Induced Male Sterility:

Hybrid rice has tremendously contributed to the productivity gain of rice in several parts of Asia. Production of hybrid rice seed can be simplified by the availability of two line hybrids. Researchers have been successful in identifying rice lines that carry the *tms* genes, which show complete male sterility and 100% of the pollens turn out to be sterile when exposed to 35.5/23.1°C temperature periodicity at the critical growth stage (i.e., 1–2 week after panicle initiation) (Lopez et al. 2003). This temperature periodicity induced genetic male sterility in rice has opened up new opportunities to produce rice hybrid seeds at an affordable price and at the same time provide productivity gain to the growers.

C- High Temperature and Heat Stress:

The sudden increase in ambient maximum temperature, in a matter of few days, by 5–7°C with corresponding increase in the minimum temperature, creates ‘heat stress’ on plants. The normal physiology of the plant gets affected and plant maturity is accelerated. In some cases, plants shed leaf/flower/fruit or dry-up non productive tillers and even become sterile to overcome the unprecedented stress. In practical agriculture, such heat stress inflicts enormous crop losses. Due to global weather change, the frequency of heat stress is predicted to increase in different parts of the world.

Rates of photosynthesis and respiration increase with an increase in temperature until a threshold maximum photosynthesis level is achieved. Generally, it is around 22–24°C and remains that way, up to 30–32°C. In rice, it was found that grain yields declined if mean seasonal temperature increased above 33°C (Fig. 1). Surpassing the high temperature peak, various enzymes get inactivated, decreasing the photosynthetic efficiency. The high temperature coupled with high respiration and evaporation pushes the plant to permanent wilting when the temperature exceeds 46°C. The extent of crop loss inflicted by heat stress can ruin the income for poor farmers in heat prone areas. In many cases, there may be adequate soil moisture butthe negative water balance created by heat stress lead to withering of plants in a matter of few days. Under the natural habitat, plants have been exposed to more than one stress at a time; consequently they have evolved strategies against a combination of stresses by responding to them in different ways. Often high temperature, high transpiration rate and high light intensity occur together affecting the plant productivity (Wardlaw and Wrigley 1994).

Short periods of very high temperature (>35°C) are of common occurrence in many wheat-growing areas of the world. Such sudden exposure to heat stress affects the yield and quality of the wheat grain (Fig. 2). Maturing kernel is highly sensitive to heat stress at milk and dough stages of grain development. The kernel becomes progressively less sensitive as the grain hardens. Reduction in kernel weight results primarily due to the shortening of the grain filling duration than due to the reduction in the rate of grain filling. The grain filling is seriously impaired and translocation processes get affected due to early senescence of the leaf and ear, and the reduction in chlorophyll content adversely affects photosynthesis. Since the photosynthetic source is affected and the sink duration is reduced, filling of the kernel is poor, resulting in small grain size having less grain weight. Under such situations, alternate sugar sources, stored as stem reserves, get mobilized so as to fill the kernel. It has been well demonstrated in spring wheat cultivars that comparable genotypes differ in grain shriveling under drought and heat stress conditions. This genotypic variation in the mobilization of stored stem reserves to support grain filling is an important consideration in selecting wheat lines for heat tolerance. Also, it is widely acknowledged that in wheat, under heat stress situations, kernel number per spike is a reliable measure for heat tolerance (Shipler and Blum 1990).

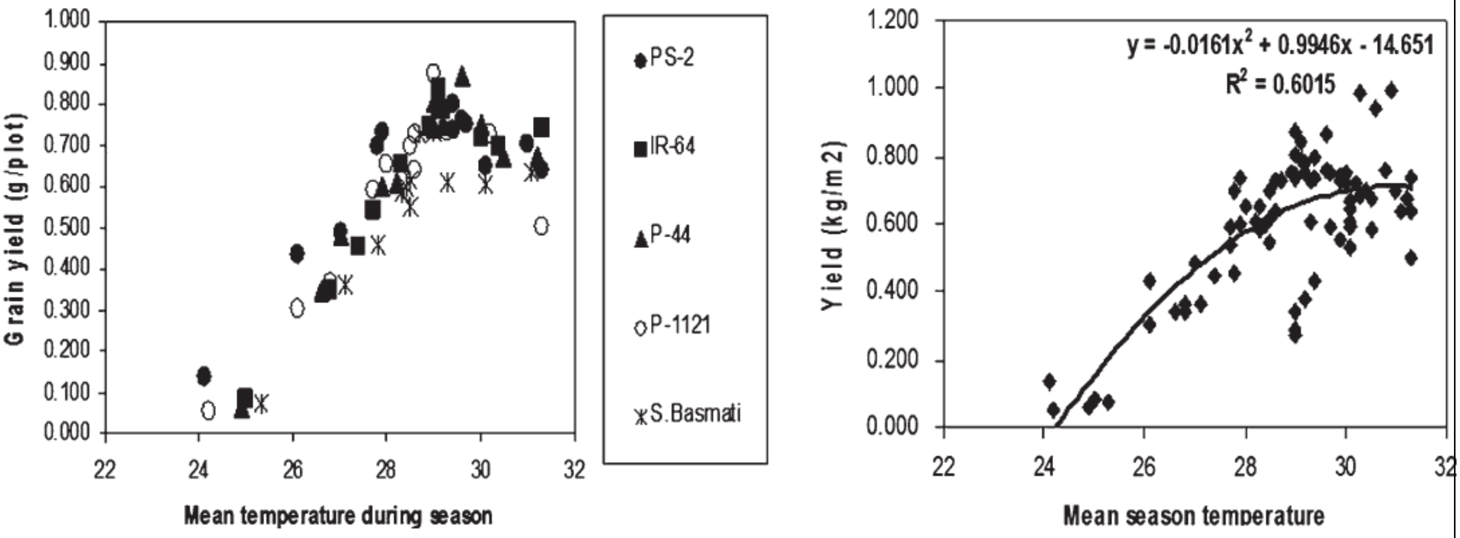

Fig. 1. Relationship of mean season temperature with grain yield of rice cultivars. Mean season temperature above 33°C and below 27°C drastically reduced rice yields both in aromatic and non-aromatic cultivars (Shantha Nagarajan, IARI, New Delhi).

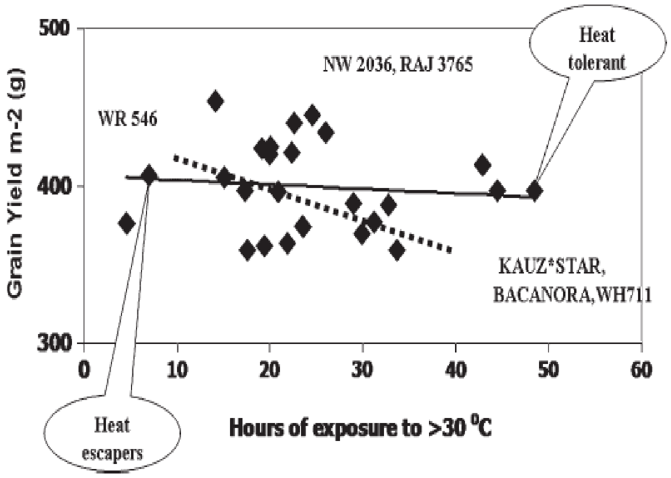

Fig. 2. Effect of high temperature on grain yield in diverse bread wheat genotypes. Twenty-five genotypes were field grown in six locations and were exposed to different temperature regimes (J. Rane, Directorate of Wheat Research, Karnal).

D- Impact on Quality of the Harvest:

High temperature during seed development is associated with a reduction in total oil yield. Under field conditions the negative effect of high temperature gets amplified if there is also a moisture stress. Both temperature and moisture stress together influence the yield of oil in *Brassica* by interfering with seed growth and development. At elevated temperatures, with high night temperatures, a marked reduction in the percentage of linoleic acid occurs, apparently due to desaturase enzymes that are essential for the conversion of oleic to linoleic acid. It is now well recognized that reduced yields and altered oil composition occur in sunflower crop that matures under high temperature conditions. Whole ranges of metabolic changes that occur due to abnormal temperature cycle adversely affect the biosynthesis of fatty acids in sunflower (Harris et al. 1978). High maximum temperature negatively influences the yield of spring wheat affecting the number of productive tillers per square meter, grain weight, grains per spike and quality of the grain protein. And in cotton, both yield and fiber quality gets affected by noncardinal temperature regimes. In aromatic and non-aromatic rice cultivars, elevated temperatures, during grain filling period, decrease the amylase content of the grain (Fig. 3).

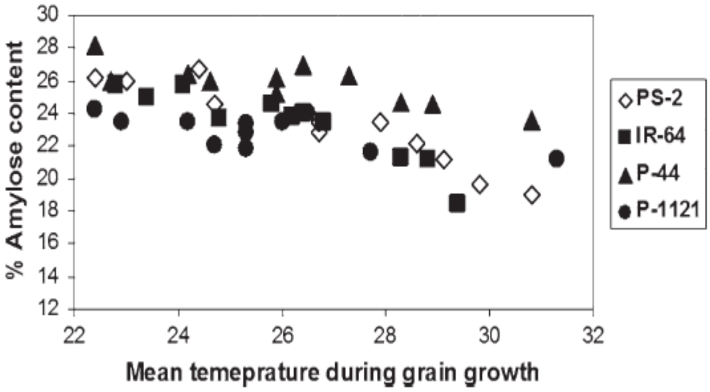

Fig. 3. Effect of mean temperature, during grain-growth period, on amylase content in rice cultivars. Amylase content decreased at the rate of 0.44% per degree rise in temperature in these cultivars (Shantha Nagarajan, IARI, New Delhi).

4-Physiological responses to high temperature:

4-1 High temperature limits to optimal plant performance

Plants can experience wide fluctuations of temperature on a daily or seasonal basis. It is to be expected, therefore, that plants have evolved mechanisms through which cellular activity could be maintained at varying temperatures. These mechanisms have not been fully defined (Patterson & Graham, 1987). It has been estimated that the optimal thermal range for any plant is about 108C wide (Mahan et al., 1995). Exposure to temperatures outside this optimal range, though not necessarily lethal, can be considered stressful. The actual upper temperature limits for survival, which for temperate plant species is between 408C and 558C, depending on the length of exposure (Klueva et al., 2001), act to limit plant distribution and the area available for agriculture.

Plants show differential sensitivity to high temperature depending on the severity, duration and developmental timing of the stress. This makes it difficult to estimate the damage done to crops by heat stress. The connection between plant water status and temperature also complicates analysis of the relative of contribution of heat and drought stress under field conditions (Carlson, 1990). However, for maize, the best single variable for estimating yield was reported to be the extent to which the daily maximum temperature exceeded 328C during pollination and seed fill (Thompson, 1975; Dale, 1983). Similarly, the highest yields of soybean have been correlated with the coolest reproductive season temperatures (Martineau et al., 1979), and optimal temperature for high yield in cereal crops has been determined to be 20-308C (Keeling et al., 1993). Not only moderate midday heat, but also high temperatures at night are damaging, leading to increases in carbon loss by respiration, decreased yield, alterations in timing of flowering, and even inhibition of flower bud development (Hall, 1990). These relatively mild high temperatures contrast with situations in which plants are challenged by severe stress temperatures, such as in the semiarid tropics where cereal grains can experience soil surface temperatures of 558C (Peacock et al., 1993). In closed canopy maize fields in the midwestern USA leaf temperatures can be over 408C, while developing pea seeds in Idaho have been recorded to have temperatures up to 688C (Hawthorn et al., 1966). Altogether, it seems likely that many plants experience some form of heat stress during their life cycle.

4-2 Heat sensitivity of photosynthesis

The fact that heat stress limits photosynthetic output is well documented, and photosynthesis declines at temperatures well below those lethal to the plant. However, the mechanism by which this occurs remains controversial. Current data preclude distinguishing whether the decline in photosynthesis at elevated temperatures occurs by a common mechanism or a diversity of mechanisms. Numerous components of the photosynthetic apparatus display heat lability, but it has been difficult to determine which one is rate limiting under conditions of heat stress. It has long been proposed that PSII is the most heat-sensitive component of the photosynthetic apparatus. Other parameters implicated as weak links during heat stress include components that facilitate CO2 transfer from the intercellular space to the chloroplast (Bernacchi et al., 2002), photosynthetic electron transport (Wise et al., 2004) and loss of ribulose bisphosphate (RuBP) regeneration capacity (Wise et al., 2004).

Recently, Salvucci and Crafts-Brandner (2004) have argued that the heat lability of various photosynthetic components is secondary to the failure of cells to maintain RuBP carboxylase/oxygenase (Rubisco) in an optimally activated state.Under conditions of heat stressRubisco activity declines as a consequence of the association of catalytic ‘misfire products’ at the active site rather than temperature-induced enzyme inactivation. It is the well-characterized temperature sensitivity of Rubsico activase that precludes adequate reactivation of these dead-end complexes during periods of heat stress. Interestingly, in wheat and cotton leaves specific isoforms of activase accumulate during heat stress (Law & Crafts-Brandner, 2001; Law et al., 2001), which may add stability to the multisubunit chaperone-like holoenzyme. Arguing against a role for Rubisco activase as a limiting factor in photosynthetic output during heat stress, Wise et al. (2004) report that Rubisco activity in field-grown cotton remains sufficient during heat stress to process levels of RuBP supplied to the enzyme, and hence maintain upstream photosynthetic processes. Clearly, more work will be required to sort out the factors that limit photosynthetic output during heat stress. Finally, it should be noted that an alternate function for Rubisco activase was suggested by Rokka et al. (2001) as a consequence of their finding that the enzyme was reported to relocate to thylakoid membranes under conditions of heat stress, where it appears to associate with thylakoidbound polysomes. Whether it acts as a chaperone at this location has not yet been explored.

Interest in the consequences of global warming has led to analysis of the influence of CO2 levels on the heat sensitivity of photosynthesis, with both negative and positive consequences documented. For example, the activation state of Rubisco declines with rising CO2 concentrations, with the elevated CO2 stimulating increases in ATP consumption that reduce ATP/ADP ratios, and thus possibly inhibit Rubisco activase (Crafts-Brandner & Salvucci, 2000). This effect would compound photosynthetic losses caused by the heat sensitivity of the enzyme. In contrast, a protective role for CO2 was reported by Taub et al. (2000). Their results showed that leaves of Cucumis sativus and several other species grown in an atmosphere enriched to 750 ppm CO2 retained significantly higher photosynthetic rates (measured as PSII activity or CO2 uptake) after a heat shock at 408C. The heat treatments in these experiments were performed in the dark, thus minimizing the possibly confounding effects of photoinhibition. Although mechanisms for this example of thermoprotection have not been evaluated experimentally, the authors point out that total osmolyte concentrations are known to increase in leaves grown at elevated CO2 levels, thus suggesting a role for compatible solutes in the process.

4-3 Heat sensitivity of reproduction

In addition to the studies cited above concerning effects of chronic high temperature on crop yield, numerous studies document that successful fertilization and seed fill are more sensitive to high temperature than vegetative growth. Unfortunately, reduced fertility and seed fill at high temperature cannot be clearly pinpointed to a defect in a single function, but most likely varies with the type of heat stress and the plant species. Loss of fertility could result from problems in male meiosis, pollen germination, pollen tube growth, or megagametophyte defects among other factors. Likewise, effects on flower production, grain set, endosperm division, source photosynthesis, and assimilate transport and partitioning can all contribute to ultimate seed yield and weight. Even recent studies are still only trying to define the heat-sensitive processes in different plant species (Commuri & Jones, 2001; Kim et al., 2001; Sato et al., 2002; Cross et al., 2003; Hurkman et al., 2003; Zahedi et al., 2003; Young et al., 2004; Kobata & Uemuki, 2004).

Perhaps the most progress at the molecular level has been made in an examination of potential factors limiting starch production in wheat grain at high temperatures. Hurkman et al. (2003) observed transcript levels of starch biosynthetic enzymes comparing 24/178C to 37/288C and 37/178C stress regimes. Although transcript levels of three isoforms of starch synthase were dramatically lowered by the heat treatment, this effect was not mirrored in the rate of starch accumulation. The overall time of grain-fill was severely shortened, however, and the type of starch granule was altered. Heat effects on wheat starch synthase were also reported by Zahedi et al. (2003) who concluded that temperature differences in starch synthase efficiency were correlated with differences in the temperature sensitivity of grain fill between two cultivars. However, the complexity of the reproductive process is obviously consistent with multiple gene effects.

In nature, different plant species, populations and even individuals may employ very different strategies to optimize growth and reproduction in the face of high temperature stress. Plants have evolved morphological, life history, physiological and cellular strategies not only to cope with temperature, but also to avoid high temperature damage. To date, the most successful strategies for enhancing agriculture in high temperature environments has primarily involved avoidance mechanisms, most often altering the timing of reproduction to achieve yield gains in hot climates (Mahan et al., 1995; Slafer, 2003). Further advances in our understanding of responses to heat and our ability to manipulate heat tolerance will greatly benefit from application of genomics and proteomics techniques coupled with additional genetic analysis.

5-The Mitigation of Heat Stress:

5-1 Mitigation of stress by crop management:

A-Management methods at sowing :

In subtropical zones, cool-season annuals such as lettuce may be sown in the late summer to produce a crop during the fall. The soil can be so hot during the late summer that it reduces the maximum germination that is achieved. Germination of lettuce seed can be inhibited by temperatures of 250 to 330C occurring during a short period of 7 to 12 hours after the seed has begun to imbibe water. The incomplete emergence problem can be overcome by sowing the lettuce seed into dry beds during the day and then sprinkle irrigating the beds during the late afternoon. Sprinkling cools the soil in the seed zone by evaporation, and the seeds imbibe water during the cool conditions of the evening and night enabling most of them to germinate. Another potential solution to this problem is “seed priming” which involves placing the seed in an osmotic solution for several days at moderate temperatures and then drying them. During the priming the seed goes through the initial temperature-sensitive stages of germination with the osmoticum reducing water uptake and preventing radical emergence. Primed seed also has some disadvantages in that it often has a shorter shelf life and is more expensive than normal seed.

In tropical zones, inadequate plant emergence and establishment can limit the productivity of several warm-season annual crops. The soil surface can become very hot. For crops with small seed that are sown shallow, such as sorghum and pearl millet, seed zone temperatures can exceed 450C in some cases and substantially reduce emergence independently of drought effects. Hot soils retard hypocotyl elongation of cowpea and this can have a detrimental effect on emergence, which is aggravated by deep sowing of seeds. Consequently, when soils are hot, seed of cowpea must be sown at a depth that is neither too deep and thus constrain hypocotyl emergence nor too shallow and be too close to the very hot surface.

B-Choice of sowing date:

In temperate or subtropical climatic zones, which have seasonal variations in temperature, sowing date can be varied to increase the probability that annual crop species will escape stressfully high temperatures during subsequent sensitive stages of development. For example, sowing dates can be chosen so that reproductive stages that are particularly sensitive to heat do not occur during periods when stressfully hot weather is most likely to occur. In some subtropical zones the weather can be chilling in early spring and become progressively warmer reaching very hot conditions in the middle of the summer. In these zones warm-season annuals, such as cotton, cowpea and maize that are sown earlier in the spring tend to flower earlier and have a higher probability of escaping hot summer weather during heat-sensitive stages of reproductive development. The earliest dates that sowing should be done depends on the extent of chilling tolerance during germination and emergence of the species and cultivar. Genotypic differences in chilling tolerance during emergence have been detected in cowpea. The chilling tolerance was associated with a dominant effect due to the presence of a specific dehydrin protein in the seed and an independent and additive effective associated with slow electrolyte leakage from seed under chilling conditions (Ismail et al. 1997, 1999). Our subsequent research demonstrated that it is possible to combine chilling tolerance during emergence with heat tolerance during reproductive development in cowpea using conventional hybridization.

D-Cultivars, irrigation and other management methods:

Perennial crop species and cultivars should be chosen that are adapted to the high temperatures likely to occur in the specific location. For both perennial and annual crop species, a degree of escape of high leaf temperatures can be achieved by insuring that maximum transpiration rates are maintained since evaporative cooling can result in leaf temperatures being up to about 80C cooler for rapidly transpiring plants compared with slowly transpiring plants. Plants transpire at maximum rates if their root zones have high levels of soil water and adequate aeration.

High temperature and intense direct solar radiation can cause damage to fruit (e.g. citrus or tomato) and reduce their marketing quality. This can be avoided if fruit is shaded by foliage. Extent of fruit shading by leaves can be manipulated by the choice of cultivars, irrigation methods and fertilizer management methods, and plant training and pruning procedures. Damage to tree trunk cambium by high temperatures can be avoided by spraying the bark of exposed trunks and branches with a reflective white coating.

5-2 The Mitigation of Heat Stress by Plant Resistance:

A-The Nature of Resistance to Heat:

Genetic resistance to heat is defined as where a genotype is more productive than another genotype in environments where heat stress occurs. This should be distinguished from heat tolerance, which is 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.

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

$$Y = Yp (1 - S \times D)$$

Where D = (1 - X/Xp) and X and Xp are the mean yields of all cultivars under stressed and optimal conditions, respectively. Algebraic manipulation shows that:

$$S = (1 - Y/Yp)/D = (Yp - Y)/(Yp \times D)$$

Since D is constant for a particular trial, S is a measure of the yield decrease due to the stress relative to the potential yield with a low value of S being desirable. Thus S is the inverse of heat tolerance.

The problem with using S as a measure of adaptation to the stress is that there are cases where S has been positively correlated with Yp in that cultivars whose yield was affected little by the stress also had very low yield potential. This means that the cultivars with low S also may have had low stress resistance (Y) and would not be useful for farmers. The correlation between S and Yp also indicates that it may not be possible or easy to combine the desirable features associated with a low S and high yield potential. However, there may be cases where the desirable features associated with low S can be combined with high yield potential. I will provide two examples to show where low S in a genotype may or may not be useful for breeding.

Many landraces of cereals and grain legumes are competitive and have substantial leaf area and photosynthetic source capability but produce relatively few seed in all environments. An example of this is the guineense sorghums that may be found in West Africa. These landraces have low yield potential but when subjected to a late stress due to heat (or drought) that reduces leaf photosynthesis and accelerates leaf senescence they still fill the few grains that had been set. Thus they exhibit little reduction in yield and a low value of S. Breeding to increase the ratio of their reproductive sink to their photosynthetic source could increase the yield potential of the landraces (Yp). But their sensitivity to stress (S) also probably would increase such that little gain may be achieved in their heat resistance (Y).

In contrast, consider cases where heat stress mainly damages reproductive development and particular genotypes tolerate this stress. The stress-tolerant genotypes would have a low S value that may be independent of traits conferring yield potential, such that combining both sets of traits can increase heat resistance. This has been the case with breeding heat-resistant cowpea cultivars using reproductive-stage heat tolerance that is described in the next section. Consequently, the heat sensitivity index S and various heat-tolerance traits must be used with caution, especially for cases where genotypic values for S are positively correlated with yield potential and S depends on traits that influence yield potential.

Greater heat tolerance is defined as being where a specific plant process is damaged less by high tissue temperature and can involve constitutive effects or require acclimation. 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 also 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 heat-shock proteins, 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 types of mechanisms: as molecular chaperones, and by targeting proteins for degradation. As an example of chaperone activity, it has been shown that a specific small heat-shock protein cooperates with other heat-shock proteins to reactivate a heat-denatured protein (Lee and Vierling 2000). Heat-shock proteins do not appear to be the only mechanism whereby plants differ in heat tolerance. For example, genotypes of cowpea have been bred that have substantial differences in heat tolerance during reproductive development but they produced the same set of heat-shock proteins in their leaves when subjected to moderately high temperatures.

For crops that produce fruit and/or seed, including cereals and grain legumes, it is useful to examine whether high temperatures damage the photosynthetic source more than the reproductive sink. In essence we are asking which of these processes is more limiting under hot conditions because enhancing the heat tolerance of this process could increase resistance to heat. Recall that a heat-resistant cultivar is defined as one that has higher productivity than other cultivars when grown in environments where heat stress occurs.

Photosynthetic sources and reproductive sinks, however, may not always be independent factors in adaptation. For spring wheat growing in hot irrigated environments, cultivar differences in grain yield have been positively associated with photosynthetic carbon dioxide fixation rate (Reynolds et al. 1994). Even stronger positive associations were observed between grain yield and stomatal conductance suggesting that more open stomata may be responsible for the higher photosynthetic rates through facilitating the diffusion of carbon dioxide into leaves and reducing leaf temperature bringing it closer to the optimum for photosynthesis. Also, cultivar differences in grain yield of spring wheat growing in a hot irrigated environment have been positively correlated with kernel number per spike (Shpiler and Blum 1991). Processes that determine kernel number per spike may be linked to photosynthesis. Fischer (1985) established that wheat cultivar variation in kernels per m2 was positively correlated with spike dry weight at anthesis and the ratio of solar radiation to temperature for the 30-day period prior to anthesis. Consequently, heat stress effects on photosynthesis can reduce both the photosynthetic source and the magnitude of the reproductive sink making it difficult to determine overall effects on the ratio of the photosynthetic source to the reproductive sink.

Also, photosynthetic capacity and stomatal behavior may be influenced by the extent of the reproductive sink for photosynthate through complex long-term feedback effects. For example, Pima cotton cultivars with greater boll yields under hot irrigated conditions also have higher stomatal conductance and greater carbon dioxide assimilation rates (Cornish et al. 1991, Lu et al. 1994, 1998). Plants that have higher photosynthetic capacity often have higher maximal stomatal conductance and the mechanism for this long-term regulation is unknown (Hall 2001). Explanations for the mechanisms whereby the Pima cottons are heat resistant are complex. The heat-resistant cotton cultivars were bred by selecting for ability to set more bolls on lower nodes under hot, irrigated conditions and not for stomatal or photosynthetic properties (reviewed by Hall 1992). Possible causes for the higher photosynthetic rates of the heat-resistant cotton cultivars include the following. More open stomata enhance the diffusion of carbon dioxide into the leaves. Cooler leaves operate closer to the optimum for photosynthesis. Slower senescence of leaves could enhance photosynthesis. Positive feedback effects on stomata or components of leaf photosynthesis may occur due to the stronger sink strength that results from the increased fruiting.

The sensitivity of photosynthesis and photosystem II to heat may be due to detrimental effects of high temperature on chloroplast membranes. Murukami et al. (2000) developed transgenic tobacco 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. The transgenic plants also had greater photosynthesis and grew better than wild-type plants in hot but highly artificial environments. The studies are preliminary in that rigorous tests would include evaluating responses of the transgenic and wild type plants in more natural hot environments and determining the whole-plant mechanisms of any effects on photosynthesis and growth. Highly artificial environments can result in artifacts that do not occur in nature.

Clones of Irish potato have been bred with differences in resistance to heat, in terms of tuber yield (reviewed by Hall 1992). Under hot conditions several processes are inhibited that influence tuber production: the rate of photosynthesis, induction to tuberize and tuberization. Controlled-environment studies demonstrated that these processes are influenced differently by root and shoot temperatures (Reynolds and Ewing 1989). High soil temperature inhibited tuber development and growth under either hot or more optimal shoot temperatures. In contrast, high shoot temperatures caused leaf rolling and accelerated leaf senescence and reduced the induction to tuberize under either hot or more optimal root-zone temperatures. This example, illustrates the importance of considering both root-zone and shoot-zone temperatures when developing techniques for screening for heat tolerance and developing management methods for hot environments.

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 about 10 cm is buffered, and does not heat up as much or cool down 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.

Management practices can influence soil temperatures. For example, compare the effects of frequent sprinkler irrigation and frequent drip irrigation on Irish potato grown on beds in hot environments. Overhead sprinkling will cool the beds more than will drip irrigation, and cooler beds may enhance tuber development and growth while effects on plant water status may be similar for the two systems of management.

For cowpea, high temperatures have greater detrimental effects on reproductive development and grain yield than they do on biomass production (Fig.3) and presumably photosynthesis. Consequently, breeding to enhance heat tolerance during reproductive development could enhance heat resistance. Cowpea genotypes have been discovered that differ in heat tolerance during reproductive development (Ehlers and Hall 1996) and genetic studies have elucidated the inheritance of this complex trait. Heat-tolerance during early floral bud development and ability to produce flowers was shown to be consistent with the effect of a single recessive gene and have very high heritability (Hall 1993). In contrast, heat-tolerance during pod set in cowpea was shown to be consistent with the effect of a single dominant gene but with strong environmental effects and low narrow-sense and realized heritabilities of 0.26 (Marfo and Hall 1992). For some other species, such as tomato, high temperatures may influence several aspects of reproduction involving both the anther and the stigma and the inheritance of heat tolerance for fruit set probably is more complex than it is for cowpea (reviewed by Hall 1992).

Embryo abortion also is a complex character that is influenced by many stresses, and plant pod-load and age. The discovery that two cowpea genotypes do not exhibit reductions in number of seeds per pod under high night temperatures, even with a substantial pod load (Ehlers and Hall 1998), indicates there may be an opportunity for genetic and breeding studies of heat tolerance during embryo development. Genetic studies demonstrated that heat-induced seed coat browning is consistent with the effect of a single dominant gene that is not linked to the gene conferring heat tolerance during floral bud development (Patel and Hall 1988).

Heat tolerance during reproductive development of cowpea is consistent with the presence of a set of genes that operate in the following developmental sequence. They determine the number of floral buds that develop and produce flowers, the number of these flowers that produce pods, the number of embryos that develop and produce seed, and the quality of the seed that are produced.

Several reproductive processes are particularly sensitive to high night temperatures but some may be sensitive to or aggravated by high day temperatures. In addition, for cowpea, there were greater effects of heat stress on both flower production and pod set under long days compared with short days. This indicates that heat stress may be more damaging to cowpea in subtropical than tropical zones and this has been confirmed in both glasshouse studies (Ehlers and Hall 1998) and field studies.

In some cases, plant breeding can be used to counteract the detrimental heat-induced acceleration of reproductive development. For indeterminate crops, such as most grain legume cultivars, cotton and tomato, the length of the reproductive period can be changed by modifying plant habit and the progression of production of vegetative nodes, branches and reproductive nodes. For example, once reproductive buds have been initiated, a few cowpea genotypes have the ability to produce more vegetative nodes on the main stem alternating with reproductive nodes (Ehlers and Hall 1996). This trait slows down overall reproductive development and may be advantageous in tropical environments with high night temperature.

For determinate crops, such as rice, sorghum and wheat, the progression of vegetative and reproductive structures is not very plastic and the rapid reproductive development caused by high night temperatures substantially reduces their grain yield potential. Where the overall reproductive stage is short, the opportunity for the fixation of photosynthate and its translocation to developing grain also is short. Enhanced translocation to grain of stored photosynthate fixed prior to anthesis may provide a heat-tolerance mechanism for determinate crops that are subjected to heat stress during grain filling. Wheat often experiences heat and drought stress during grain filling when grown in hotter wheat production zones such as may be found in India and the United States. These stresses can substantially reduce the photosynthetic source during grain filling by both accelerating leaf senescence and causing damage to photosynthesis. Enhanced mobilization of stem reserves may be an effective mechanism of tolerance to late season stresses such as heat and drought, especially for determinate crops.

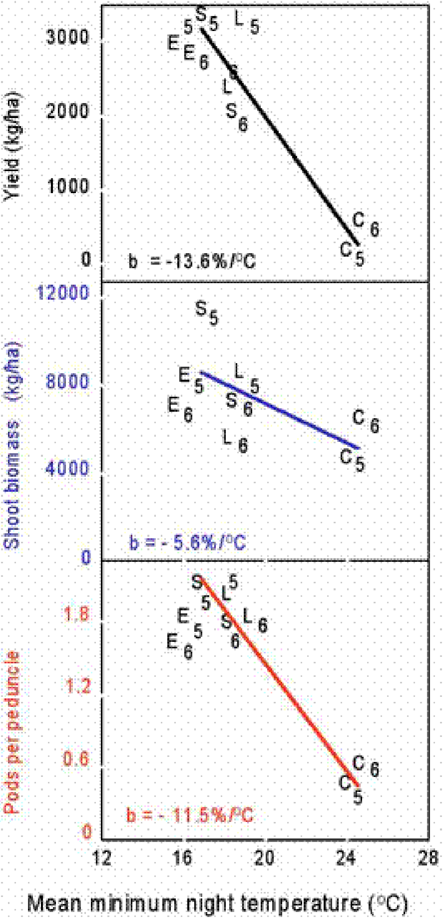

Fig.3. Plant production of heat-susceptible cowpea lines grown in different fields with contrasting thermal regimes (data from Ismail and Hall 1998)

B-Methods of Breeding for Resistance to Heat:

Photograph 1. A heat-tolerant cowpea, 518-2 (right), that is producing many flowers in a hot field environment where a heat-sensitive plant, cultivar CB5 (left), is producing fewer flowers.

Photograph 2. A cowpea line with heat tolerance, H36 (right), that is abundantly producing pods in a hot field environment where a heat-sensitive cultivar, CB5 (left), is producing few pods

Photograph 3. Cowpea lines with similar genetic background growing in a hot field environment that either have (right) or do not have (left) a set of heat-tolerance genes.

The traditional method for breeding for heat resistance is to grow advanced lines in a hot target production environment and select those lines that have greater yields than current cultivars (this provides a direct measure of heat resistance). This approach is more effective with crop species that can be efficiently yield-tested in small plots, such as wheat, than crops such as cowpea that require larger plots and are more difficult to harvest. This direct approach also is more effective in environments where heat is the only major stress. The presence of other stresses makes the evaluation of heat resistance very difficult. For example, insect pests such as lygus bugs and flower thrips can cause damage to developing flower buds of cowpea that appears similar to the damage caused by high night temperatures. Some slow progress may have been made in enhancing the heat resistance of cowpea in West Africa, however, by breeding programs that selected based upon grain yield in hot target production environments (Ehlers and Hall 1998).

A more efficient approach has been developed for breeding for heat resistance that involves early generation selection for specific traits that confer heat tolerance during reproductive development. The first step in this approach is to discover accessions that have heat-tolerance traits. When searching for useful accessions, a wide range of materials should be evaluated including those that evolved or were developed in cool as well as hot environments. Two cowpea accessions were discovered to have heat tolerance during reproductive development that came from a hot tropical zone in Africa (Warrag and Hall 1983). However, a cowpea breeding line developed for the very cool conditions of Minnesota (MN 13), which was not exposed to heat during its selection, also has heat tolerance during reproductive development. This unexpected finding may be due to associations that are present between reproductive-stage heat tolerance and extreme earliness (Ehlers and Hall 1996). We have speculated that this association may be due to heat susceptibility being caused by the presence of certain phytochromes that suppress or slow down floral development in hot conditions (Ahmed et al. 1993b). The association between extreme earliness and heat tolerance during reproductive development has been observed in other species. Some early tomato cultivars developed for cool environments in Canada and Russia have heat tolerance during fruit set, and some chilling-tolerant snap beans also have heat tolerance (reviewed by Hall 1992).

For some crop species, methods have been developed based on selection for heat-tolerance traits in extremely hot environments that are more effective than selection solely based on yield in hot target production environments. An example of breeding for resistance to heat in cowpea is described that has been shown to be very effective. Emphasis was placed on incorporating heat tolerance during reproductive development. Very hot field and glasshouse environments were used for screening for reproductive-stage heat tolerance. The hot field nursery was achieved by sowing a set of cowpea genotypes that have similar earliness (they initiate floral buds at the same time) in the Coachella Valley of California during the hot season. Often sowing was done about the 20th of June and resulted in an environment where the plants experienced minimum and maximum 24-hour air temperatures of 230 to 270C and 420 to 500C, respectively, for the three-week period beginning one week prior to the start of flowering. In this environment, heat-tolerant day-neutral genotypes begin flowering about 32 days after sowing. The plants also experience long days (14.5 hours) and sunny skies, and are subjected to optimal irrigation, fertilizer application and pest management practices. Plants are selected that produce many early flowers, and have high pod set producing about four pods per peduncle on the first five reproductive nodes on the main stem, well-filled pods and adequate grain quality. In most years many plants can be effectively screened using this field nursery.

Most parts of the world do not have field nurseries with the consistently high night temperatures but otherwise optimal conditions experienced in Coachella Valley in the early summer. Consequently, we also have developed a glasshouse environment for screening cowpea for reproductive-stage heat tolerance. The plants are subjected to minimum and maximum 24-hour air temperatures of 270 and 360C, respectively, and sunny long-day conditions. This glasshouse environment is extremely effective for screening for reproductive-stage heat tolerance but only a few hundred plants can be grown in it compared with the thousands of plants that can be screened in our large field nurseries. The key to the success of the glasshouse nursery is the use of high night temperature rather than high day temperature. One advantage of using a hot glasshouse compared with most hot field conditions is that air temperatures are relatively stable from day to day and over weeks. Consequently, genotypes that begin flowering at different times can be screened reliably. In contrast the summer Coachella Valley environment only is effective for screening genotypes that begin flowering at about the same time because temperatures vary substantially from day to day and exhibit seasonal changes.

Diverse sets of several hundred early flowering day-neutral cowpea accessions have been screened and three were detected with ability to produce flowers and set pods under hot conditions in the field. The heat-tolerant accessions have many undesirable agronomic traits so it was necessary to cross them with commercial cultivars. We have shown that heat tolerance during early flower development can be incorporated and virtually fixed by a single selection for ability to produce flowers in the F2 or a subsequent generation, consistent with it being conferred by a single recessive gene with high heritability. During the F2 generation, we select plants that produce many flowers and have high pod set and adequate numbers of seeds per pod and seed size and no heat-induced seed coat browning (Photograph 1).

We only can directly screen for heat tolerance under long days in the summer so we have used the fall and winter seasons to advance generations once or twice in an optimal-temperature glasshouse using single-seed or single-plant decent. During the summer we then screen the F4 or F5 lines for heat tolerance. Most of the lines that were selected during the F2 generation have heat tolerance during early flower development in subsequent generations and produce many flowers. In the advanced generations, we emphasize selecting lines and then single plants with uniformly high pod set, adequate numbers of seeds per pod and seed size, and no seed coat browning (Photograph 2).

At least two cycles of family selection are needed to incorporate heat tolerance during pod set, which is consistent with it having dominant gene inheritance and a low heritability.

Six pairs of lines were developed (for example Photographs 2 and 3) that either have or do not have a set of heat-tolerance genes in similar genetic backgrounds. These pairs of lines were evaluated in eight field environments with average night temperatures ranging from cool to very hot but otherwise similar near optimal conditions (Ismail and Hall 1998). The heat-susceptible lines, which included a commercial cultivar, exhibited a 13.5 % decrease in grain yield per 0C increase in average minimum night temperature above 16.50C for the three week period starting one week prior to first flowering (Fig.3). The heat-tolerant lines had similar grain yields under cooler night temperatures but 50 % greater grain yield and numbers of pods per peduncle than the heat-susceptible lines with average minimum night temperatures of 210C (Fig.4).

Minimum night temperatures greater than 210C occur in several commercial production zones (Nielsen and Hall 1985a). Advanced lines are then evaluated in multi-location trials conducted in commercial fields and experiment stations in the target production environment. Lines are selected that have consistently high yield, adequate grain quality and other agronomic traits such as resistance to lodging. One of the heat-tolerant lines from the study of Ismail and Hall (1998) that performed well in the multi-location trials now has been released as the cowpea cultivar “California Blackeye 27" (Ehlers et al. 2000). It should be noted that heat tolerance by itself will not justify release of a new cultivar, the cultivar must have greater grain yield than current cultivars when grown in the target production environment (i.e. greater heat resistance is needed). Farmers often only will accept a new cultivar that has been shown to substantially enhance yields or profits. “California Blackeye 27" has greater grain yields when conditions are hot at flowering and it also has greater grain yields in some fields due to it having greater resistance to specific pests and diseases than the older cultivars (Ehlers et al. 2000).

When breeding to incorporate heat tolerance or any other trait it is important to evaluate potential negative effects of the trait. In hot and also more moderate temperature environments, the reproductive-stage heat-tolerance genes cause cowpea to be more compact and dwarfed due to their internodes being shorter. At a minimum night temperature of 180C, the heat-susceptible cowpea lines had 50 % longer main stems, and at 220C they had 50 % more vegetative biomass than the heat-tolerant lines (Fig.5 and Photographs 1, 2 and 3).

Heat-tolerant semidwarf cowpea lines were compared with standard-height cowpea cultivars under different row spacing (Ismail and Hall 2000). Heat-tolerant semidwarf cowpea lines were less effective than standard-height cultivars at the wide row spacing of 102 cm used by some farmers, more effective with the widely used 76 cm row spacing, and even more effective with a narrow row spacing of 51 cm than standard-height cultivars. Natural selection likely would not favor this type of heat tolerance in that plants with the compact plant habit are not very competitive. In tomato, cultivars with heat-tolerance during reproductive development may tend to be more compact and exhibit less coverage of fruit by leaves, which can enhance damage to the fruit surface and internal tissues caused by excessive solar radiation and temperature. The compactness of the heat-resistant cowpea and tomato cultivars may be due to their greater and earlier partitioning of carbohydrate to fruits, which thereby restricts their vegetative growth compared with heat-susceptible cultivars. The heat-tolerance gene that enhances pod set in cowpea appears to have major effects on plant development.

Screening for the extent of flowering and fruit set in hot conditions can be effective with several crop species, including several grain legumes, tomato and cotton, but some breeders do not have suitable very hot field environments, and hot glasshouse screening can be expensive. Consequently, scientists have tried to develop more efficient indirect screening procedures.

Considerable research effort has been devoted to using slow electrolyte leakage from leaf disks that have been subject to high temperatures as an indication of cell membrane thermostability (MT, or CMS) and heat tolerance (reviewed by Blum 1988 and Hall 1992).

The yield-forming processes that are linked with MT have not been clearly identified. However, for spring and winter wheat, MT was associated with heat tolerance during grain filling (Shanahan et al. 1990, Saadala et al. 1990a, Reynolds et al. 1994) and it may -be possible to obtain useful data from seedling screens (Saadala et al. 1990b). Seedling screens can be very effective because many plants can be screened and selected plants can be crossed.

Positive associations between MT and grain yield under heat stress have been reported for two spring wheat populations (Blum et al. 2001). One population consisted of 98 F8 random recombinant inbred lines (RILs) between a heat-resistant cultivar, Danbata, and a heat-sensitive cultivar, Nacozari. Grain yield was measured for plants growing in the summer at Bet Dagan in Israel. This environment imposed a substantial heat stress and grain yield was only 53 % of that of the same plants growing in the winter at Bet Dagan. The MT was measured on leaves from the same RILs growing in a growth chamber at optimal temperatures and then heat hardened for one day prior to measuring electrolyte leakage from leaf segments. The grain yield of Nacozari was about 100 g m-2 whereas that of Danbata was much higher at 250 g m-2. Grain yields of the RILs varied from about 50 to 300 g m-2. The MT of Nacozari was 31 % whereas that of Danbata was 72 % and the values for the RILs ranged from 22 to 76 %. There was a fairly high and significant positive correlation across the RILs between biomass ($r=0.60$ $p<0.01$) or grain yield ($r=0.53$ $p<0.01$) measured in the summer and MT. No such correlation was seen for winter production of biomass or grain. The other population consisted of 49 spring wheat F7 breeding lines from 10 different crosses randomly selected from the wheat breeding program at Bet Dagan. Similar methods were used to evaluate these lines as was used with the RILs. Grain yield of the 49 breeding lines ranged from 267 to 370 g m-2 in the hot summer environment. The MT measured with growth chamber plants ranged from 66 to 99 %. There was a significant positive correlation ($r=0.56$ $p<0.01$) across lines between MT and grain yield under heat stress. The authors pointed out that the associations were strong but not perfect and that MT should not be used as the exclusive selection criterion. They suggested MT might be a valuable supplemental criterion in final breeding stages or as a rough selection tool in early stages of breeding programs to reduce a large population into the most likely heat-resistant core.

There has been some work on MT for enhancing heat tolerance of other crops (Blum 1988, Hall 1992). For cowpea, electrolyte leakage of leaf disks was negatively associated with reproductive-stage heat tolerance (Ismail and Hall 1999). Subsequent genetic selection experiments by Thiaw and Hall (2004) confirmed that leaf electrolyte leakage under heat stress was negatively correlated with heat tolerance for pod set in cowpea. The leaf-electrolyte-leakage (LEL) protocol that he used consisted of subjecting leaf discs to 46oC for 6 hours in aerated water and then measuring electrical conductivity of the solution followed by boiling the leaf discs and then measuring the electrical conductivity of the solution again. The percentage 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 tissue, and four measurements of electrolyte leakage are used in calculating MT. Heat-hardening does not appear to be necessary for cowpea in that Thiaw and Hall (2004) and Ismail and Hall (1999) observed useful genotypic differences in LEL with plants grown in a range of different environments. An advantage of the LEL method used by Thiaw (2003) over the MT 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 acclimating plants. Also, only two measurements of electrolyte leakage are needed with the LEL method so that more plants can be evaluated than with the MT method, which requires four measurements.

Thiaw and hall (2004) selected four populations from the same cross between heat-resistant and heat-susceptible parents that have similar genetic background: those with slow LEL and those with fast LEL, and those with high pod set in hot conditions and those with low pod set in hot conditions. The association between pod set and LEL was strong in that lines selected for slow LEL had high pod set, and lines selected for high pod set had slow LEL. The realized heritability when using slow LEL to indirectly select for heat tolerance during pod set was significantly greater than zero but small, similar to the realized heritability for direct selection for pod set of 0.26 observed by Marfo and Hall (1992). The LEL protocol we used has an advantage over direct selection in that it can be conducted in the off season with plants grown in moderate temperatures. We now propose 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.

Heat tolerance in spring wheat and Pima cotton has been associated with greater stomatal conductance, which can be rapidly detected in plots by a low canopy temperature compared with air temperature using an infrared thermometer (Reynolds et al 1994, Lu et al. 1994 and 1998). However, key tests have not yet been reported for any species that demonstrate whether selecting in segregating populations based on canopy temperature differences confers some heat resistance. Since measurement of canopy temperature differences requires plots of similar genotypes it could only be practiced in relatively advanced generations. This is unfortunate because much progress can be made if selection can be effectively initiated in the first segregating generation using single plants. Also the genotypic differences in canopy temperature that have been reported are relatively small in relation to the errors encountered in these data. This approach probably may not be effective with grain legumes that exhibit diurnal leaf movements because this can increase errors due to the sensor detecting the far infrared radiation emitted from the soil surface. In addition there are theoretical limits to the extent that stomatal conductance can be increased by selection and enhance crop performance.

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 photosystem II. Equipment is available that permits rapid field measurement of the Fv/Fm parameter which provides an estimate of the damage to photosystem II. 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 resistance. It should be noted that when determining whether a selection method is effective it also is necessary to determine the efficiency of the method: the costs of the selection procedure in relation to the gains that are made compared with other selection procedures.

In extreme conditions, heat-resistance may depend upon the ability of plants to survive hot environments. The maximum emergence of sorghum and pearl millet seedlings can be substantially reduced by hot soil conditions in tropical Africa and India. Studying heat tolerance during emergence is difficult under field conditions due to the extreme variability in microclimates that is encountered at the soil surface and interactions with variations in soil water status. A laboratory technique has been developed for screeningseedling emergence at different controlled soil temperatures which uses infra-red lamps to simulate the heating effects of sunlight and can subject emerging plumules of sorghum and pearl millet to high soil temperatures but without water stress (Soman and Peacock 1985).

In plant breeding it is necessary to take a long term view and consider the environmental and socio-economic conditions likely to be present in future years (Hall and Ziska 2000). Climatic conditions are changing, such as the progressive increases in atmospheric carbon dioxide concentration that are occurring everywhere and will tend to make photosynthesis of C3 plants more effective. Plant photosynthetic systems may require modifications through plant breeding so that they can take full advantage of the elevated atmospheric [CO2]. Also, maintaining a balance between carbohydrate sources and sinks could require selecting plants with greater reproductive sinks (Hall and Ziska 2000). Breeding to maintain a balance will be particularly important for environments and species where stresses, such as high temperatures, cause greater damage to the reproductive sink than the photosynthetic source. The genes for reproductive-stage heat tolerance in cowpea enhance sink strength and harvest index (Ismail and Hall 1998, 2000). Studies in controlled environments indicate these heat-tolerance genes may also enhance responsiveness to elevated atmospheric [CO2] under moderate as well as high night temperatures (Ahmed et al. 1993a).

Advances in biotechnology may make possible some new approaches for breeding for heat resistance. Apomixis could provide resistance to stresses, such as heat, that damage reproductive development, since the seed are produced from maternal tissues and do not require meiosis or fertilization. A type of apomixis would be needed that does not require fertilization of polar nuclei for endosperm development. Through genetic engineering it may be possible to insert the cassette of genes needed to confer facultative apomixis (Jefferson 1993). Facultative apomixis also would provide many other benefits to plant breeding and farmers. These benefits include making hybrid cultivars with seeds that breed true to type. This would make possible the use of hybrid cultivars in many species where currently it is not economically feasible due to the current high cost of producing hybrid seed in relation to the amount of seed that is needed per unit area sown. An additional benefit to farmers would be that they could use their own hybrid seed for several years, which would reduce their seed costs and be of particular benefit for poor farmers.

The literature contains relatively little information on breeding for heat resistance. Some commercial companies have been active in this area but have not published their results. This is unfortunate since their experience with breeding for heat resistance could guide future breeders. Many advanced institutions are located in temperate zones where resistance to cold is more important than resistance to heat. Also, the limited research on heat tolerance conducted in these advanced institutions often has emphasized heat-shock proteins but has not yet led to any methods for breeding for resistance to heat that is based on this information. Breeding for resistance to heat deserves a higher priority than it has been given in the past.

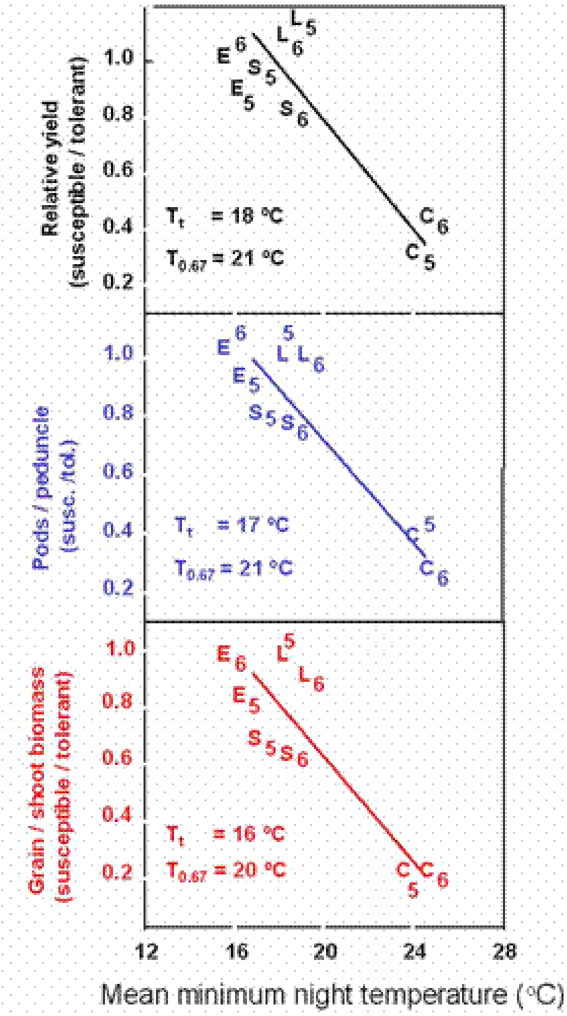

Fig.4. Relative plant production of heat-susceptible and heat-tolerant pairs of cowpea lines grown in different fields with contrasting thermal regimes (data from Ismail and Hall 1998).

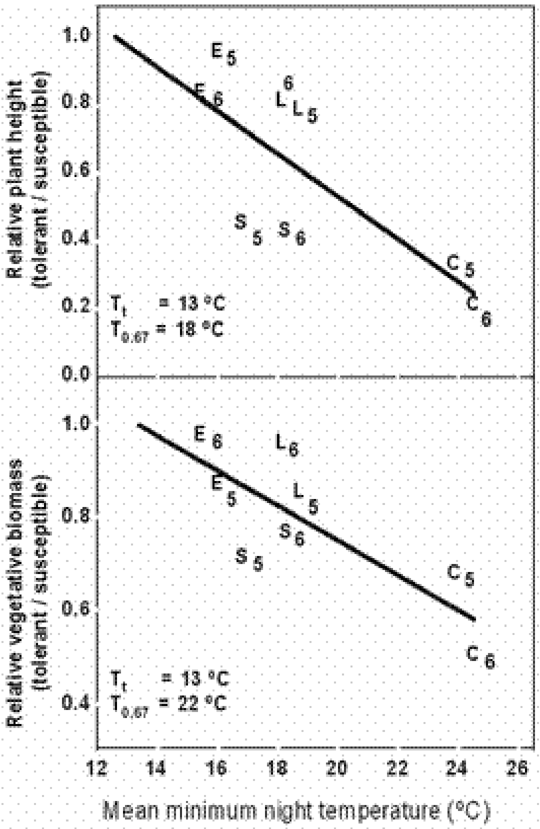

Fig.5. Relative plant height and vegetative biomass of heat-tolerant and heat-susceptible pairs of cowpea lines grown in different fields with contrasting thermal regimes (data from Ismail and Hall 1998)

6- Inhibition of photosynthesis by heat stress: the activation state of Rubisco as a limiting factor in photosynthesis

Michael E. Salvucci* and Steven J. Crafts-Brandner

Abstract

Although the catalytic activity of Rubisco increases with temperature, the low affinity of the enzyme for CO2 and its dual nature as an oxygenase limit the possible increase in net photosynthesis with temperature. For cotton, comparisons of measured rates of net photosynthesis with predicted rates that take into account limitations imposed by the kinetic properties of Rubisco indicate that direct inhibition of photosynthesis occurs at temperatures higher than about 30_C. Inhibition of photosynthesis by moderate heat stress (i.e. 30–42_C) is generally attributed to reduced rates of RuBP regeneration caused by disruption of electron transport activity, and specifically inactivation of the oxygen evolving enzymes of photosystem II. However, measurements of chlorophyll fluorescence and metabolite levels at air-levels of CO2 indicate that electron transport activity is not limiting at temperatures that inhibit CO2 fixation. Instead, recent evidence shows that inhibition of net photosynthesis correlates with a decrease in the activation state of Rubisco in both C3 and C4 plants and that this decrease in the amount of active Rubisco can fully account for the temperature response of net photosynthesis. Biochemically, the decrease in Rubisco activation can be attributed to: (1) more rapid de-activation of Rubisco caused by a faster rate of dead-end product formation; and (2) slower re-activation of Rubisco by activase. The net result is that as temperature increases activase becomes less effective in keeping Rubisco catalytically competent. In this opinionated review, we discuss how these processes limit photosynthetic performance under moderate heat stress.

7- Expression of dehydrins under heat stress and their relationship with water relations of sugarcane leaves

A. Wahid[1] ✉ and T. J. Close[2]

Abstract

The heat stress-induced dehydrin proteins (DHNs) expression and their relationship with the water relations of sugarcane (Saccharum officinarum L.) leaves were studied. Sugarcane seedlings were subjected to heat stress (day/night temperature of 40/35 °C) under relative humidity 60/65 % to avoid aerial desiccation and determinations made at 4, 12, 24, 36, 48, 60 and 72 h. The leaves showed a sharp decline in the water and osmotic potentials, and relative water content during first 12 h of heat stress, but a regain in their values in 24 h. The pressure potential (ψp) decreased initially but increased later and approached control leaves. The increase in ψp was tightly correlated to the accumulation of free proline, glycinebetaine and soluble sugars, indicating their possible involvement in the osmotic adjustment under heat stress. Immunological detection revealed the expression of three DHNs with an apparent molecular mass of 21, 23 and 27 kDa under heat stress (48 to 72 h) and their expression was independent of the changes in the water relations of leaves.

8- Heat stress effects on morpho-physiological characters of Indian mustard (Brassica juncea L.)

J. S. Chauhan, M. L. Meena, Maheshkumar Saini, D.R. Meena,

Maharaj Singh, S. S. Meena and K. H. Singh

ABSTRACT

Effects of heat (high temperature) stress during terminal stage were investigated on plant height, primary branches/plant, siliquae on main shoot, seeds/siliqua, 1000-seed weight, seed yield, oil and protein content, leaf area index (60 DAS), specific leaf weight (80 DAS), crop growth rate (40-60 DAS), chlorophyll stability index (60 DAS) and harvest index of 22 advanced breeding lines/varieties of Indian mustard (Brassica juncea L.) during 2008-09. The genotypes were grown in randomized complete block design with three replications in two environments, viz., E1 (9th November sowing) and E2 (25th November sowing). Of the 45 days prior to physiological maturity, crop under E2 was exposed to higher mean daily temperature differential of 0.9-5.60C for 28 days. Genotypic differences were significant for all the characters except protein content and chlorophyll stability index. Environment effects were highly significant for all the moropho-physiological characters investigated. Genotypes x environment interactions were significant only for 1000-seed weight, leaf area index and crop growth rate. Leaf area index, specific leaf weight, crop growth rate, chlorophyll stability index and harvest index were drastically reduced under E2 by up to 49.4%, 52.1%, 76.2%, 54.2% and 28.9% respectively. The highest reduction in seed yield and its components ranged from 22.2% for seeds/siliqua to 69.2% for seed yield/plant. Four terminal high temperature tolerant genotypes as indicated by their low HIS for seed yield were BPR 538-10 (0.33), NRCDR 2 (0.44), RH 0216 (0.57) and NPJ 112 (0.58). Genotypes BPR 2, BPR 141-B-205-43 and BPR 540-6 having tolerance to high temperature for multiple characters were identified for utilization in the breeding programme.

9- Yield Components of Wheat Grown under High Temperature Stress during Reproductive Growth

L.R. Gibsona and G.M. Paulsenb

Abstract

High temperature is a major determinant of wheat (Triticum aestivum L.) development and growth, decreasing yields by 3 to 5% per 1°C increase above 15°C in plants under controlled conditions. Even greater yield differences have been reported between favorable and unfavorable temperature conditions in the field. The objective of this study was to identify the yield components of the hard red winter wheat cultivar Karl 92 that are affected by controlled high temperature during maturation of intact plants under simulated field populations. Plants at a final density of 144 m2 were grown in the greenhouse until anthesis and transferred to growth chambers for temperature treatment. Day/night temperatures of 20/20, 25/20, 30/20, and 35/20°C were imposed from 10 and 15 d after anthesis until ripeness in two experiments, and temperatures of 25/20, 30/20, and 35/20°C were applied from 20 d after anthesis until ripeness in a third experiment. Grain yield was reduced by 78%, kernel number was reduced by 63%, and kernel weight was reduced by 29% at 35/20°C compared with 20/20°C from 10 d after anthesis until ripeness. The yield loss from high temperature applied during this period was much greater than for previous controlled-environment studies. Kernel numbers in treatments applied during early reproductive growth in ourstudy were as sensitive to high temperature as wheat plants in previous field studies. High temperature applied 15 d after anthesis until ripening reduced grain yield 18%. Since kernel number was set by this time, the loss was exclusively due to decreased kernel weight. High temperature imposed from 20 d after anthesis decreased kernel weight by 18%.

10- Growth and yield response of rice under heat stress during vegetative, reproductive, and ripening growth phases

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Abstract

The rise in atmospheric temperature causes detrimental effects on growth, yield, and quality of the rice crop by affecting its phenology, physiology, and yield components (Singh 2001, Sheehy et al 2005, Peng et al 2004). The sensitivity of rice to high temperature varies with growth phase, an increase in day/night

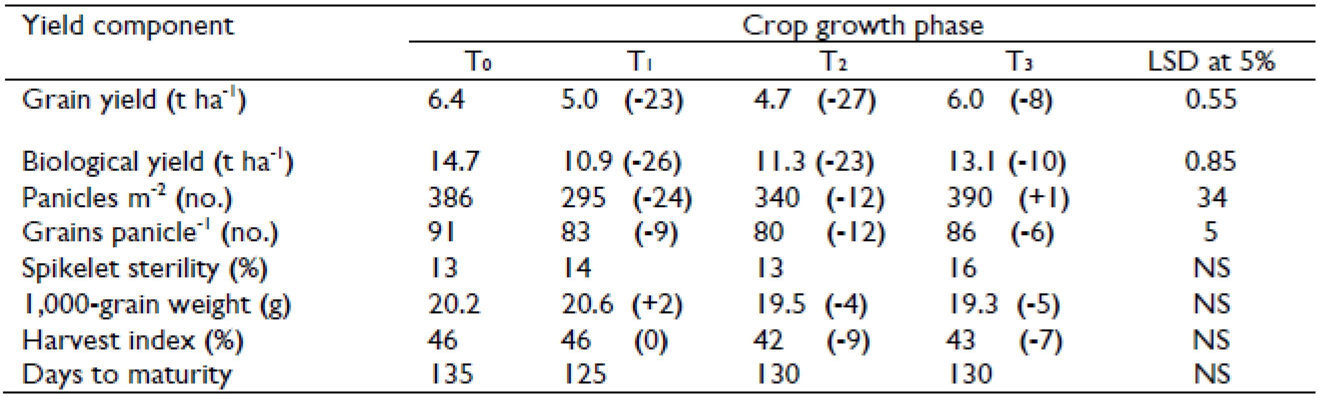
temperature, and genotype (Yoshida 1981, Singh 2001, Peng et al 2004). The unusual rise in atmospheric temperature during different growth phases differentially affects rice growth and productivity. The quantitative assessment of such type of climatic variability on indica rice is meager. Keeping in view the significance of climatic variability on the growth and yield of the rice crop, a field experiment was conducted using rice variety Pusa 44 to assess the effects of high temperature during vegetative, reproductive, and ripening growth phases on its growth, yield, and yield components. Thirty-day-old seedlings of Pusa 44 were transplanted in a rice field at the research farm of the Indian Agricultural Research Institute, New Delhi, during the 2006 wet season. Transplanting of seedlings was done at 20 × 20-cm spacing with three to four seedlings per hill. Normal agronomic practices were followed throughout the crop-growing season. Based on known phonological characteristics of this variety, the rice crop was subjected to high-temperature stress during its vegetative (T1: seedling establishment to panicle initiation), reproductive (T2: panicle initiation to flowering), and ripening growth phase (T3: flowering to maturity) by covering the plants in the field with a portable chamber (2.0 × 2.0 × 2.0 m, made of aluminum frame, and covered with 150-μ-thick transparent (90%) PVC sheet). The control plants (T0) in the field were partially covered with a similar type of chamber to provide a light intensity similar to that used on the treated plants, without increasing the inside-chamber temperature. The field experiment was conducted in a randomized block design with five replications. The maximum and minimum temperatures of both the control and fully covered plants were measured using a maximum/minimum temperature thermometer throughout the crop-growing period. Weekly mean values were calculated during the stress treatment. The temperature inside the chambers was raised by 2–3 °C above ambient by covering the chamber to varying extents (Table 1).

Table 1. Weekly mean temperature during the crop-growing season of Pusa 44.

Month/period	Weekly mean temperature (°C)	
	Partially closed chamber	Closed chamber
July		
1st wk	32.0	34.5
2nd wk	31.5	34.2
3rd wk	30.8	33.1
4th wk	30.2	32.6
August		
1st wk	30.0	32.4
2nd wk	29.5	32.0
3rd wk	29.0	31.5
4th wk	28.5	31.0
September		
1st wk	28.0	30.2
2nd wk	27.5	29.0
3rd wk	27.0	29.0
4th wk	26.8	28.8
October		
1st wk	25.5	27.6
2nd wk	24.0	26.0
3rd wk	23.0	25.0
4th wk	21.5	23.3

High-temperature stress (+2.5 °C) during the vegetative and reproductive growth phases caused greater and almost equal reduction in biomass (23% and 26%) and grain yield (23% and 27%) as compared with that during the ripening growth phase, which showed 8% and 7% reduction in biomass and grain yield, respectively. Among yield components, the number of panicles m-2 and grains panicle-1 showed greater sensitivity to high-temperature stress, whereas 1,000- grain weight was least affected by the same level of heat stress. The marked reduction in grain yield of rice under high-temperature stress during vegetative growth was mainly attributed to the significant reduction in the number of panicles m-2 (24%), followed by the number of grains panicle-1 (9%). The 1000- grain weight increased to a lesser extent (2%). The reduction in grain yield by high-temperature stress during the reproductive growth phase was caused by a significant decrease in the number of panicles m-2 (12%) and number of grains panicle-1 (12%) and the marginal reduction in 1,000-grain weight (4%). However, the relatively low reduction in grain yield (8%) due to heat stress during ripening was probably caused by the small reduction in 1,000-grain weight (5%) and the number of grains panicle-1 (6%), probably the consequence of a greater respiratory loss of assimilates in the panicles (Table 2).

Table 2. Growth and yield response of Pusa 44 to high temperature during various growth phases.



Yield component	Crop growth phase				
	T_0	T_1	T_2	T_3	LSD at 5%
Grain yield (t ha^{-1})	6.4	5.0 (-23)	4.7 (-27)	6.0 (-8)	0.55
Biological yield (t ha^{-1})	14.7	10.9 (-26)	11.3 (-23)	13.1 (-10)	0.85
Panicles m^{-2} (no.)	386	295 (-24)	340 (-12)	390 (+1)	34
Grains panicle^{-1} (no.)	91	83 (-9)	80 (-12)	86 (-6)	5
Spikelet sterility (%)	13	14	13	16	NS
1,000-grain weight (g)	20.2	20.6 (+2)	19.5 (-4)	19.3 (-5)	NS
Harvest index (%)	46	46 (0)	42 (-9)	43 (-7)	NS
Days to maturity	135	125	130	130	NS

T_0: normal ambient from vegetative stage to maturity; T_1: high temperature (ambient +2.5 °C) during vegetative phase; T_2: high temperature (ambient + 2.3 °C) during reproductive phase; T_3: high temperature (ambient +2.0 °C) during ripening phase. Data presented in parentheses are percent increase (+) or decrease (-) over control values.

Compared with crops grown under normal conditions, those exposed to heat stress during their vegetative and reproductive growth phases had the development of their sink potential impaired—i.e., number of panicles m-2 and number of spikelets panicle-1—but the stress did not increase spikelet sterility. However, heat stress during the grain-filling period did not show any detrimental effects on sink development (number of panicles m-2) but rather impaired sink potential realization by reducing the number of grains panicle-1. Research should thus focus on screening rice germplasm for a higher number of spikelets panicle-1 with low tiller mortality in order to develop high-yielding rice cultivars for warmer conditions.

11- References

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