

CHAPTER 10

Heat Tolerance



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Wheat is the most widely grown cereal in temperate environments, and is also cultivated in many tropical cropping systems, where it is often grown as the winter season crop in rotation with a number of other crops—for example, with maize in Africa, rice in Asia, and soybean in Latin America (Figure 1). Among the numerous advantages of cultivating wheat in this niche are that it is stress tolerant, relatively high yielding, and easy to transport and store.

There are also disadvantages linked to growing wheat in tropical areas; foremost among them are the different types of high temperature stress that

affect the crop. Perhaps the greatest challenge to understanding the physiological problems associated with heat stress is to encompass the diversity of hot environments all over the world (Figure 2). Continual heat stress affects approximately 7 million ha of wheat in developing countries, while terminal heat stress is a problem in 40% of temperate environments, which cover 36 million ha. Continual heat stress is defined by a mean daily temperature of over 17.5°C in the coolest month of the season (Fischer and Byerlee, 1991), and over 50 countries (importing more than 20 million tons of wheat per year) experience this type of stress throughout the wheat cycle.

When consulted, representatives of national agricultural research systems (NARSs) from the major wheat-growing regions in the developing world identified heat stress as one of their top research priorities (CIMMYT, 1995).

CIMMYT/NARS Collaboration on Heat Tolerance

Breeding efforts by a number of national wheat breeding programs has resulted in the release of germplasm adapted to warm growing environments, such as in Egypt and Sudan (AbdElShafi and Ageeb, 1994), India (Tandon, 1994),

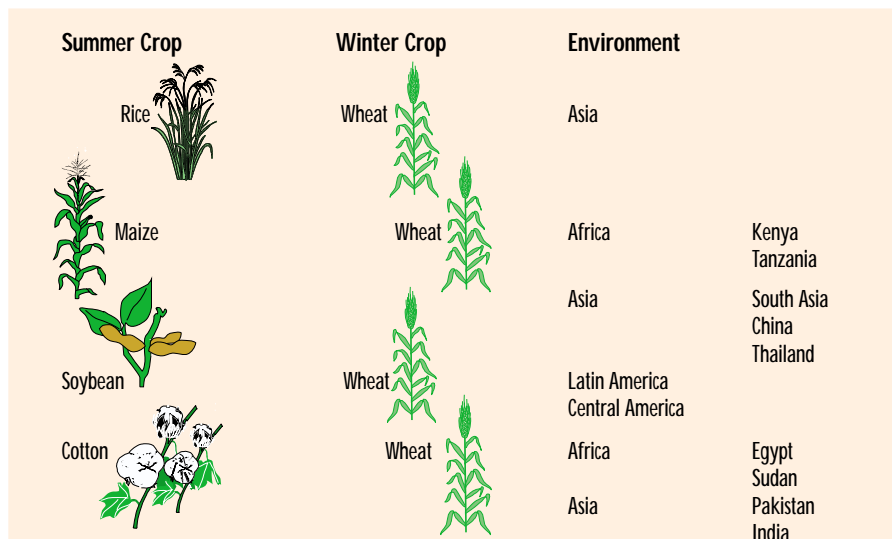


Figure 1. Wheat in tropical cropping systems.

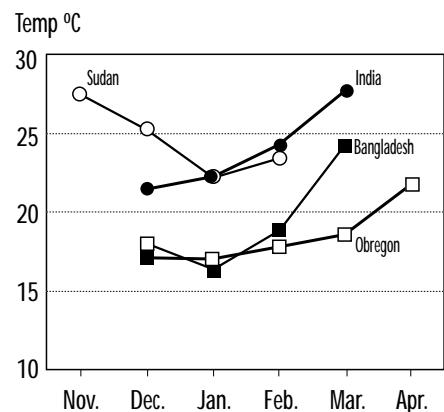


Figure 2. Typical average temperatures during the wheat cropping cycle for three types of hot environments (Wad Medani, Sudan; Dharwad, India; Dinajpur, Bangladesh) and one temperate environment (Ciudad Obregon, Mexico).

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Bangladesh (Razzaque et al., 1994), and Uruguay (Pedretti and Kohli, 1991). CIMMYT has been actively involved in many of these regions (Kohli et al., 1991; Ortiz-Ferrara et al., 1994). Collaboration between CIMMYT and NARS on physiological aspects of heat tolerance in wheat started in 1990, with the establishment of a network involving wheat scientists in Bangladesh, Brazil, Egypt, India, Nigeria, Sudan, and Thailand.

Collaborative experiments conducted by network scientists were named the International Heat Stress Genotype Experiment (IHSGE) (Reynolds et al., 1992; 1994; 1997; 1998; Reynolds, 1994). The IHSGE was grown in wheat-growing areas classified by CIMMYT as heat stressed, i.e., CIMMYT mega-environment 5 (ME5). The main objectives of the IHSGE were to establish the degree of genotype by environment interaction (G×E) in ME5, evaluate potential physiological screening techniques by observing genetic diversity for traits and their association with heat tolerance, and improve our understanding of the physiological and genetic basis of heat tolerance.

There were three main outcomes of the study. First, cluster analyses of over 40 hot site×year combinations indicated that most interaction between sites and genotypes was accounted for by relative humidity (RH). Hence low RH sites (e.g., Sudan, Mexico, and India) and high RH sites (e.g., Bangladesh and Brazil) showed less G×E within RH groups than when comparison was done across RH groups (Reynolds et al., 1998; Vargas et al., 1998). This kind of analysis indicates that breeding for these two broad environments should be undertaken as separate objectives. Second, data collected on IHSGE lines in the low RH sites showed consistent association between yield and a number of morphological traits (Table 1). Third, physiological data collected in Mexico showed that several parameters were associated with performance at international low RH sites (Table 2).

The information emanating from the IHSGE may be useful in establishing indirect selection criteria for heat tolerance. The application of some of these traits to breeding will be discussed in subsequent sections, but first we will present a brief review of some of the physiological traits associated with heat stress.

Table 1. Genetic correlations between morphological traits and wheat yields for 10 varieties averaged over 16 low relative humidity environments in ME5, IHSGE 1990-94.

| Trait | Genetic correlation |
|---------------------------------|---------------------|
| Final biomass (above ground) | 0.88** |
| Grains/m ² | 0.77** |
| Grains/spike | 0.67* |
| Harvest index | 0.51 |
| Kernel weight | -0.10 |
| Spikes/m ² | 0.0 |
| Days to anthesis | 0.83** |
| Days to maturity | 0.81** |
| Plant height | 0.20 |
| % ground cover (anthesis) | 0.67* |
| Biomass at anthesis | 0.35 |
| Plant dry weight (5-leaf stage) | -0.45 |
| % ground cover (5-leaf stage) | -0.30 |
| Plants/m ² | -0.15 |

* Denotes significance at ≤ 0.05 , ** significance at ≤ 0.01 .

Table 2. Genetic correlations (R_g) for physiological parameters measured in Tlaltizapan, Mexico, and wheat yields for 10 varieties averaged over 16 low relative humidity environments, IHSGE 1990-94.

| Physiological trait | R(g) |
|---------------------------------|--------|
| Canopy temperature depression | 0.86** |
| Membrane thermostability | 0.81** |
| Leaf chlorophyll (grainfilling) | 0.72** |
| Leaf conductance (heading) | 0.63* |
| Photosynthesis (heading) | 0.63* |

* Denotes significance at ≤ 0.05 , ** significance at ≤ 0.01 .

Physiological Traits Associated with Heat Tolerance

Genetic diversity for heat tolerance in cultivated wheat is well established (Midmore et al., 1984; Rawson, 1986; Wardlaw et al., 1989; Al-Khatib and Paulsen, 1990; Reynolds et al., 1994). Photo-assimilation is more likely to be yield-limiting under heat stress than in temperate environments, especially as stress typically intensifies during grainfilling, when demand for assimilates is greatest. This is borne out by the observation that under stress, total above-ground biomass typically shows a stronger association with yield than with partitioning, i.e., harvest index (Table 1); the situation is usually reversed under temperate conditions.

Hence traits affecting radiation use efficiency (such as early ground cover, stay-green, and photosynthetic rate) could be expected to be important under heat stress. Although early ground cover seems to be important in an agronomic context (Rawson, 1988; Badaruddin et al., 1999), variation in this trait among genotypes does not seem to be associated with heat tolerance (Table 1). The stay-green trait has been used widely in breeding for heat tolerance, partly as an indicator of disease resistance (Kohli et al., 1991). Physiological evidence indicates that loss of chlorophyll during grainfilling is associated with reduced yield in the field (Reynolds et al., 1994). Studies in controlled environments have revealed genetic variability in photosynthetic rate among wheat cultivars when exposed to high temperatures (Wardlaw et al., 1980; Blum, 1986).

Such differences in photosynthesis under heat stress have been shown to be associated with a loss of chlorophyll and a change in the a:b chlorophyll ratio due to premature leaf senescence (Al-Khatib and Paulsen, 1984; Harding et al., 1990). Studies at CIMMYT comparing 16 diverse semi-dwarf wheats demonstrated genetic variability for photosynthetic rate under heat-stressed field conditions

(Reynolds et al., 2000). In addition, both canopy temperature depression (CTD) and flag-leaf stomatal conductance, as well as photosynthetic rate, were highly correlated with field performance at a number of international locations (Reynolds et al., 1994). Besides being a function of stomatal conductance (Amani et al., 1996), CTD itself is a mechanism of heat escape, as suggested, for example, by Cornish et al. (1991) in cotton.

Conductometric measurement of solute leakage from cells was used in several studies to estimate heat damage to the plasma membranes. Genetic variation in membrane thermostability (MT) has been inferred using conductometric measurements in various field-grown crops, including spring wheat (Blum and Ebercon, 1981). Shanahan et al. (1990) obtained a significant increase in yield of spring wheat in hot locations by selection of membrane-thermostable lines, as determined by measurements on flag leaves at anthesis. By applying the MT test on winter wheat seedlings, Saadalla et al. (1990) found a high correlation in MT between seedlings and flag leaves at anthesis for genotypes grown under controlled environmental conditions. Measurements of MT of 16 spring wheat cultivars were compared internationally with performance at several heat-stressed locations. Variation in MT of both field-acclimated flag leaves and seedlings grown in controlled conditions was associated with heat tolerance in warm wheat-growing regions (Reynolds et al., 1994). Other studies have confirmed genetic variation of these materials and indicated high heritability for the trait (Fokar et al., 1998).

Although the physiological basis for the association of MT with heat tolerance has not been determined, plasma membranes are known to be more heat tolerant than the photosynthetic thylakoid membranes, for example (Berry and Bjorkman, 1980). While loss of membrane integrity may be the cause of ion leakage from the cell, this phenomenon could also be caused by

thermally induced inhibition of membrane-bound enzymes responsible for maintaining chemical gradients in the cell. Direct evidence for a biochemical limitation to heat tolerance in wheat comes from studies of the enzymes involved in grainfilling, specifically soluble starch synthase, which is deactivated at high temperatures (Keeling et al., 1994). If conversion of sucrose to starch is a limitation to yield under heat stress, this would explain the increased levels of carbohydrates in vegetative tissue of wheat observed when grainfilling was limited by heat stress (Spiertz, 1978).

Several other processes are clearly affected by high temperatures, but not discussed in depth here, since either genetic variation has not been shown to be associated with performance, or they do not lend themselves to simple screening. There is some evidence that meiosis is adversely affected at high temperatures (Saini et al., 1983). Respiration costs are higher as temperature increases, leading eventually to carbon starvation because assimilation cannot keep pace with respiratory losses (Levitt, 1980). However, this apparently wasteful process would seem unavoidable, at least in current germplasm, as evidenced by positive associations observed between dark respiration at high temperatures and heat tolerance of sorghum lines (Gerik and Eastin, 1985). On the other hand, high rates of dark respiration in grains may be severely detrimental to yield (Wardlaw et al., 1980).

Heat shock proteins are synthesized at very high rates under high temperature stress and are thought to have a protective role under stress; nonetheless, their role in determining genetic differences in heat tolerance has not been established. Chlorophyll fluorescence may be more promising as a screening trait, given that associations between heat tolerance and lower fluorescence signals have been reported in a number of crops, including wheat (Moffat et al., 1990). Although screening protocols are yet to be thoroughly

evaluated, preliminary evidence with CIMMYT lines has indicated that fluorescence parameters may lend themselves to screening for heat tolerance (Balota et al., 1996).

While there is still no definitive picture of the physiological basis of reduced growth rates under heat stress, many drought-adaptive traits may be useful under heat stress. Examples would include leaf glaucousness to reduce the heat load, awn photosynthesis when high temperatures reduce assimilation rate of the leaves, and early escape from heat stress. Heat stress is almost certainly a component of drought stress, since one of the principal effects of drought is to reduce evaporative cooling from the plant surface. Nonetheless, not all traits conferring heat tolerance are also associated with genetic variability for drought tolerance, a good example being membrane thermostability (Blum, 1988). In addition, wheat germplasm that typically performs well under heat stress is not necessarily useful under drought (S. Rajaram, pers. comm.).

Physiological Approaches to Breeding for Heat Tolerance

Different physiological mechanisms may contribute to heat tolerance in the field—for example, heat tolerant metabolism as indicated by higher photosynthetic rates, stay-green, and membrane thermostability, or heat avoidance as indicated by canopy temperature depression. Breeding programs may measure such traits to assist in the selection of heat tolerant parents, segregating generations, or advanced lines (Figure 3). Based on field data collected in the IHSGE, a number of physiological traits that had been presented in the literature were evaluated as potential selection criteria (Table 3). While useful as indicators, these conclusions are by no means definitive for two important reasons.

For one thing, the results cannot be extrapolated with any certainty to environments outside the test site. Also, the data were for the most part measured on unrelated fixed lines and as such do not necessarily imply that selection for these traits would result in genetic gains in yield among the progeny of a cross. To establish the potential genetic gains associated with indirect selection criteria, similar experiments need to be conducted with randomly derived sister lines using a number of relevant crosses and heritability of traits established, as outlined in the introduction of this book.

Evidence for applying three traits (namely, canopy temperature depression, leaf conductance, and membrane thermostability) in selecting for heat tolerance is presented in the following sections; sufficient evidence has been collected on these traits to suggest their potential as breeding tools. Nonetheless, if these techniques have not been evaluated in a given breeding environment, they should first be evaluated, as outlined in chapter one, before being applied to mainstream breeding operations.

Canopy temperature depression

As discussed earlier, experimental data have shown a clear association of CTD with yield in both warm and temperate environments. CTD shows high genetic correlation with yield and high values of proportion of direct response to selection (Reynolds et al., 1998), indicating that the trait is heritable and therefore amenable to early generation selection. Since an integrated CTD value can be measured almost instantaneously on scores of plants in a small breeding plot (thus reducing error normally associated with traits measured on individual plants), work has been conducted to evaluate its potential as an indirect selection criterion for genetic gains in yield. CTD is affected by many physiological factors, which makes it a powerful

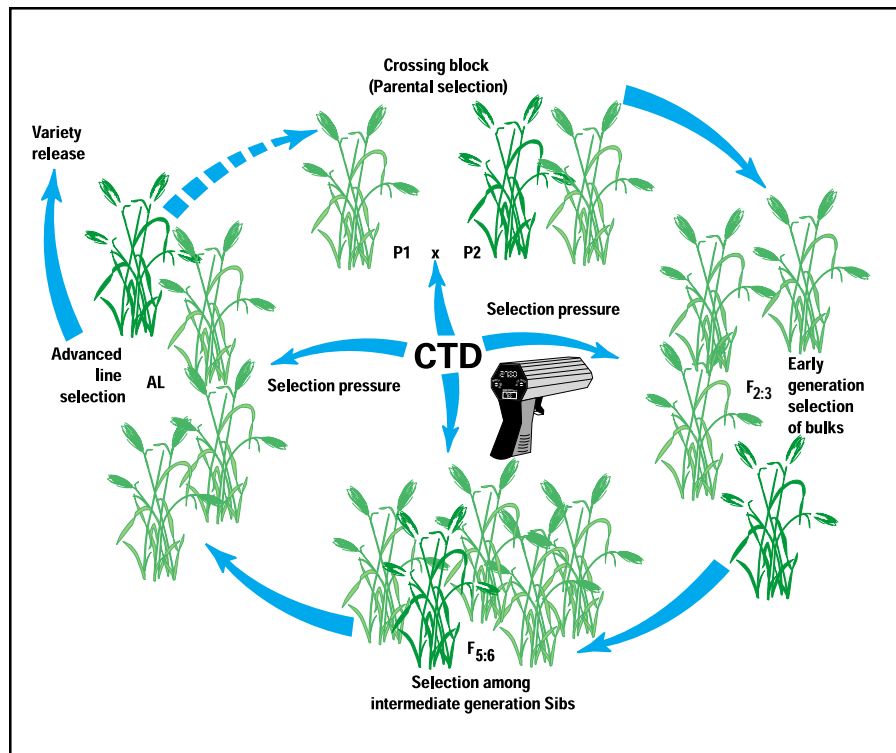


Figure 3. Potential use of canopy temperature depression in a breeding program.

Table 3. Summary of heat stress mechanisms previously reported for wheat and their association with yield in the IHSGE.

| Reported heat stress mechanism | Accounting for genetic variation in yield in IHSGE |
|--|--|
| Accelerated development (Midmore et al., 1984) | Yes, lateness associated with higher yield in many environments |
| Stand establishment (Rawson, 1988) | No, poor correlation with early growth |
| Evaporative cooling (Idso et al., 1984) | Yes, strong correlation of CTD with yield |
| Inhibition of meiosis (Saini et al., 1983; Zeng et al., 1985) | No, sterility not observed. Grain:spikelet ratio not correlated with yield |
| Sensitive growth phase (Fischer, 1985; Shpiler and Blum, 1991) | Partial least squares analysis confirmed spike growth sensitivity, especially to high night temperatures (Vargas et al., 1988) |
| Photosynthesis/chlorosis (Al-Khatib and Paulsen, 1990; Shpiler and Blum, 1991) | Yes, high association of photosynthesis and stay-green with yield in field plots |
| Thylakoid thermostability (Moffatt et al., 1990) | Preliminary data on IHSGE lines confirms association of chlorophyll fluorescence with yield (Balota et al., 1996) |
| Membrane thermostability (MT) (Shanahan et al., 1990) | Yes, MT measured on seedlings and flag leaves associated with yield at several sites |
| Inhibition of starch synthase (Bhullar and Jenner, 1986; Rijven, 1986) | No clear evidence, but yield not associated with TGW |

integrative trait, but its use may be limited by its sensitivity to environmental factors (Figure 4).

Factors affecting expression of CTD.

Leaf temperatures are depressed below air temperature when water evaporates from their surface. One of the factors determining evapotranspiration is stomatal conductance, which itself is regulated by the rate of carbon fixation. To maintain high rates of photosynthesis, a genotype must have an effective vascular system for transpiration of water, as well as for transport of nutrients and assimilates. Since CTD is directly or indirectly affected by a number of physiological processes, it is a good indicator of a genotype’s fitness in a given environment. CTD also seems to be affected by the ability of a genotype to partition assimilates to yield, indicated by the fact that CTD frequently shows a better association with yield and grain number than it does with total above-ground biomass (Table 4).

For a given genotype, CTD is a function of a number of environmental factors (Figure 4), principally soil water status, air temperature, relative humidity, and incident radiation. The trait is best expressed at high vapor pressure deficit

conditions associated with low relative humidity and warm air temperature (Amani et al., 1996). For these reasons, CTD is not a useful selection trait in generally cool and/or humid conditions, and is quite sensitive to environmental fluxes. Therefore, it is important to measure the trait when it is best expressed—that is, on warm, relatively still, cloudless days. Some environmental flux during the measurement period is inevitable, but correcting data against reference plots, spatial designs, use of replication, and repetition of data collection during the crop cycle can compensate for this.

When measuring CTD, care should be taken to view the plot so as to avoid including soil temperature. If a plot is sown in rows, it is best to stand to one side of it so that the thermometer is pointed at an angle to the rows. If ground cover is low (e.g., leaf area index of less than 2-3), it is best to point the thermometer at a low angle to the horizontal to minimize the likelihood of viewing soil (Figure 5).

Association of CTD with performance. Measurements of CTD made on 23 wheat lines at CIMMYT’s subtropical experiment station (Tlaltizapan,

Mexico) showed a high correlation with yield measured on the same plots (Figure 6). Sixteen of the same cultivars were yield tested at a number of hot wheat-growing regions internationally, and their performance compared with CTD measurements made in Mexico (Table 5). In some cases, CTD was associated with over 50% of yield variability of the same lines at sites in Brazil, Sudan, India, and Egypt, clearly indicating the promise of CTD as an indirect selection criterion for yield.

In subsequent work, crosses were made between parents contrasting in CTD to generate homozygous sister lines. These were evaluated for both CTD and yield in warm and temperate environments. Populations of randomly derived F₅ sister lines from two crosses showed a clear association of CTD with yield potential in both warm and temperate environments (Figure 7; Table 6), with CTD explaining up to 50% of yield variation.

While heritability of CTD has not been thoroughly evaluated, preliminary data suggest moderate heritability values for the trait. When comparing traits measured on F_{2,5} bulks with subsequent yields in F_{5,7} lines, performance was

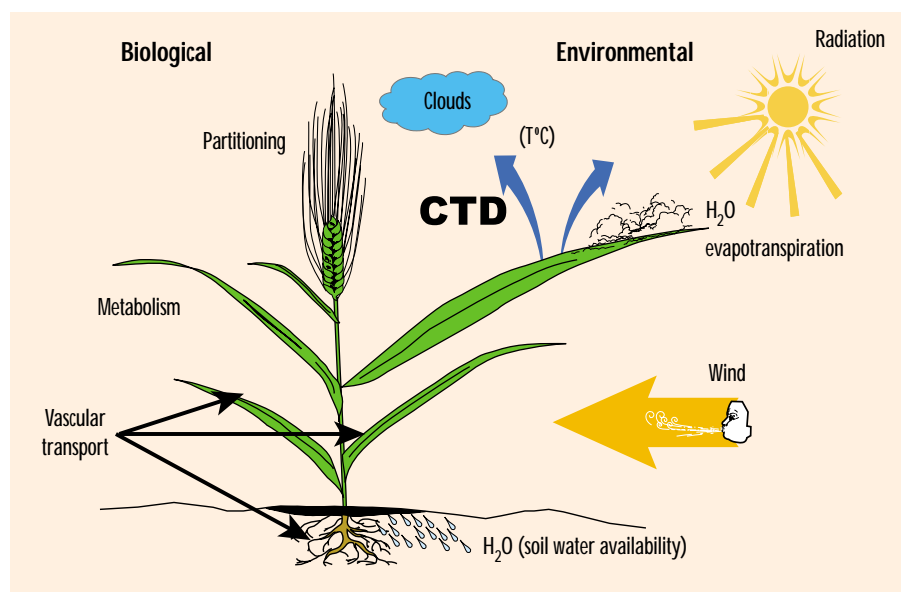


Figure 4. Factors affecting canopy temperature depression (CTD) in plants.

Table 4. Association of CTD with traits of 60 advanced lines, Ciudad Obregon (Marchsown), Mexico, 1995.

| Trait | Correlation coefficient with CTD |
|------------------------|----------------------------------|
| Yield | 0.60** |
| Biomass | 0.40** |
| Harvest index | 0.14 |
| Kernel weight | -0.32* |
| Grains m ⁻² | 0.62** |
| Spikes/m ² | 0.33* |
| Grains/spike | 0.40** |
| Days to maturity | 0.10 |
| Days to flowering | 0.42** |
| Height | 0.10 |

* Denotes significance at ≤ 0.05, ** significance at ≤ 0.01.

better predicted by CTD than it was by yield, when both were measured on bulks (Reynolds et al., 1997).

CTD as an efficient means of evaluating advanced lines. In addition to the work on early and intermediate generation breeding lines, experiments were also conducted at CIMMYT with advanced lines to assess the power of

CTD as a tool for predicting performance (Reynolds et al., 1997; 1998). Sixty advanced lines (ALs) of diverse genetic backgrounds were selected for superior performance under hot conditions using late sowings in Ciudad Obregon, Mexico. The 60 ALs were multiplied and grown as replicated yield trials in the 1995-96 spring wheat

cycle at 15 warm environments: 4 in Mexico, 4 in Sudan, 3 in Bangladesh, 3 in India, and 1 in Nigeria. Physiological traits were measured on yield plots and on smaller 3-row plots in the selection environment, i.e., a March-sown trial in Obregon. Yield and CTD in the selection environment were compared with performance of ALs averaged

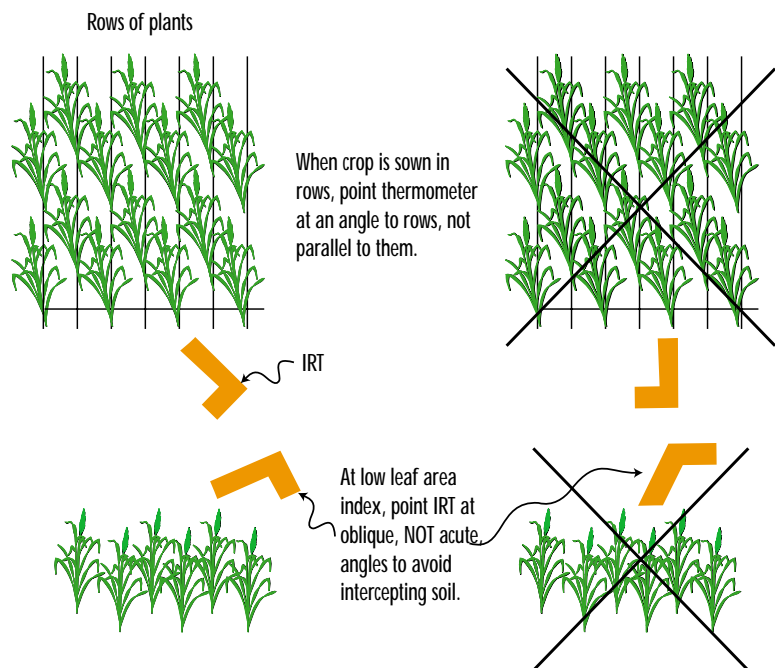


Figure 5. How to view a plot to avoid including soil temperature when measuring canopy temperature depression with an infrared thermometer (IRT).

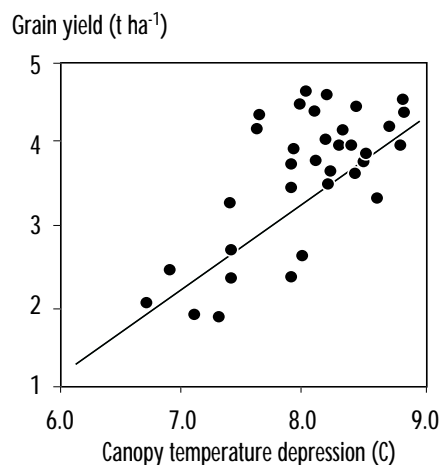


Figure 7. Regression of yield on CTD measured after heading for 40 recombinant inbred lines from a cross between lines contrasting in heat tolerance (Seri 82* Siete Cerros 66), Tlaltizapan, Mexico, 1995-96. Source: Reynolds et al. (1998).

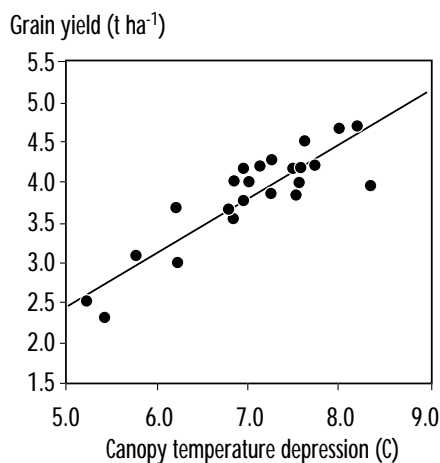


Figure 6. Relationship of mean grain yield to mean CTD for 23 genotypes, averaged over two sowings, Tlaltizapan, Mexico, 1992-93.

Source: Amani et al. (1996).

Table 5. Correlation coefficients between yield, averaged over two cycles at six locations of the IHSGE (1990-92), and CTD of 16 wheat lines measured at different stages of development, December and February sowings, Tlaltizapan, Mexico, 1992-93.

| Location | CTD December | | | CTD February | | |
|---------------------|--------------|----------|---------------|--------------|----------|---------------|
| | Pre-anthesis | Anthesis | Post-anthesis | Pre-anthesis | Anthesis | Post-anthesis |
| Brazil | 0.45 | 0.60* | 0.50* | 0.68** | 0.52* | 0.68** |
| Egypt | 0.73** | 0.91** | 0.91* | 0.82** | 0.79** | 0.78** |
| India | 0.33 | 0.56* | 0.62** | 0.60** | 0.37 | 0.64** |
| Sudan | 0.71** | 0.91** | 0.88** | 0.77** | 0.75** | 0.71** |
| Tlaltizapan | 0.66** | 0.84** | 0.78** | 0.50* | 0.53* | 0.43 |
| Average correlation | 0.58 | 0.76 | 0.74 | 0.67 | 0.59 | 0.65 |

* Denotes significance at ≤ 0.05 , ** significance at ≤ 0.01 . Source: Reynolds et al. 1994.

across the 15 environments. CTD measured in the selection environment explained at least as much of the variability in performance across all warm sites as yield itself (Table 7).

In this study, several other physiological and morphological traits were evaluated along with CTD. While some also showed significant association with yield (e.g., leaf chlorophyll, leaf conductance, spike number, biomass, and flowering date), no other single trait was consistently as well associated with performance as CTD (Reynolds et al., 1997; 1998). Data also indicated that CTD measured in 3-row plots was as good a predictor of yield as CTD measured in yield plots, suggesting that the technique would be amenable to selection in smaller plots.

Stomatal conductance

Canopy temperature depression is highly suitable for selecting physiologically superior lines in warm, low relative humidity environments where high evaporative demand leads to leaf cooling of up to 10 °C below ambient temperatures. This permits differences among genotypes to be detected relatively easily using infrared thermometry. However, such differences cannot be detected in high relative humidity environments because the effect of evaporative cooling of leaves is negligible. Nonetheless, leaves maintain

their stomata open to permit the uptake of CO₂, and differences in the rate of CO₂ fixation may lead to differences in leaf conductance that can be measured using a porometer.

Porometry can be used to screen individual plants, unlike CTD, which can only be estimated on a canopy. The heritability of stomatal conductance is reasonably high, with reported values typically in the range of 0.5 to 0.8 (Vilhelmsen et al., 2001; Rebetzke, pers. comm.); genetic correlation with yield is also high (Table 2). Plants can be assessed for leaf conductance using a viscous flow porometer that is newly available on the market (Thermoline and CSIRO, Australia). This instrument can give a relative measure of stomatal conductance in a few seconds (Rebetzke et al., 1996), making it possible to identify physiologically superior genotypes from within bulks.

For reliable results, more than one reading of stomatal conductance should be taken per plot or per plant. Single-leaf readings always have associated errors that may be caused by environmental fluxes, leaf position, and the fact that leaves may show diurnal and cyclical patterns in stomatal behavior. When crops are irrigated, it is best to take measurements shortly after irrigation to avoid effects of soil heterogeneity that may affect water availability. It is advisable in

preliminary studies to measure leaf conductance at different times of day and during different stages of the crop cycle to ascertain when differences between genotypes are best expressed.

Since CTD and leaf conductance show an association with each other and with yield (Amani et al., 1996), the possibility of combining selection for both traits is attractive. For example, CTD could be used to select among early generation bulks that are heterogeneous and may still be segregating. Porometry can be used to identify the best genotypes from among the plants making up the bulk (Figure 8). Work in Mexico where leaf conductance was measured on individual plants in a F2:5 bulk indicated the utility of this approach (Figure 9; Gutiérrez-Rodríguez et al., 2000).

Membrane thermostability

Although resistance to high temperatures involves several complex tolerance and avoidance mechanisms, the membrane is thought to be a site of primary physiological injury by heat (Blum, 1988), and measurement of solute leakage from tissue can be used to estimate damage to membranes. Since membrane thermostability is reasonably heritable (Fokar et al., 1998) and shows high genetic correlation with yield (Table 2), it has potential application in breeding, but does require a laboratory methodology to make measurements.

Laboratory methodology. Membrane thermostability (MT) can be measured on leaf tissue taken at almost any phenological stage, from 10-day-old seedlings to grainfilling. Plants must be heat-acclimated either *in situ* if growing conditions are warm enough, or by putting them in a controlled environment for 48 hours at approximately 35/15°C max/min. At least four leaves should be sampled per plot to ensure that tissue is representative, and 10 or more if the

Table 6. Association of CTD with yield potential of homozygous sister lines from two crosses, sown in warm (1995-96) and temperate environments (1996-97).

| Site | Correlation coefficient of CTD with yield | |
|----------------------------|---|---------------------|
| | Cross 1 | Cross 2 |
| | Seri 82* Siete Cerros | Seri 82* Fang 60 |
| Tlaltizapan (warm) | 0.64** | 0.39* |
| Ciudad Obregon (warm) | - | 0.55** |
| Ciudad Obregon (temperate) | 0.64** | 0.51** |

* Denotes significance at ≤ 0.05, ** significance at ≤ 0.01.

Table 7. Phenotypic correlations between mean yield of 60 advanced lines at international sites and CTD and yield measured in Ciudad Obregon (March-sown), Mexico, 1995-96.

| Trait | Average yield | |
|----------------|---------------|--------|
| | n=11† | n=15 |
| Yield | 0.62** | 0.59** |
| CTD 3-row plot | 0.66** | 0.56** |
| CTD 5-row plot | 0.65** | 0.58** |

** Denotes significance at ≤ 0.01.

† 11 locations with least G*E determined by cluster analysis for crossover interaction.

plot contains segregating lines or lines that are genetically heterogeneous. Leaves should be randomly collected and placed with their cut ends immersed in water in stoppered glass jars. All jars should be placed in a cold box for transportation from the field to the laboratory.

In the laboratory, the middle portions of leaves can be isolated, quickly washed with de-ionized water, and completely re-hydrated by keeping them in de-ionized water overnight in a refrigerator. To measure MT, 1-cm sections of each leaf can be cut for both the control and heat-shock treatments. To measure MT on seedlings, fungicide-treated seed should be germinated on moistened paper and grown in an environmental growth chamber at 10-20 °C. The oldest leaves of 10-day-old seedlings can be used; however, seedlings must be acclimated before measuring MT. For this purpose, approximately 10 seedlings are placed in a covered water bath with their roots immersed in water maintained at 35°C for 48 h.

Once acclimated, plant material (flag leaves or seedlings) should be washed with de-ionized water and divided into vials containing 17 mL de-ionized water. Half of the vials are maintained

at 46.5°C (flag leaves) or 49°C (seedlings) for 60 min in a water bath. The second set of vials is used as controls and maintained at room temperature for the same time periods. After the treatment periods, the heat-treated and control samples are held at 6°C overnight. A first conductometric reading is made at 25°C and a second (also at 25°C) after autoclaving for 20 min at 120°C and 0.10 MPa. MT is expressed as relative injury (RI) using the following:

$$RI\% = (1 - (1 - T_1/T_2) / (1 - C_1/C_2)) \times 100,$$

where T is treatment, C is control, and 1 and 2 refer to the first and second readings of conductance, i.e., before and after autoclaving.

Measuring MT on seedlings vs flag leaves. At CIMMYT experiments were conducted on 16 lines of the IHSGE using both seedlings and flag leaves (Reynolds et al., 1994). The MT trait was favorably correlated with yield in a number of heat stressed international environments, using both methodologies (Table 8). When comparing MT for seedlings versus field-grown flag leaves, there was a significant positive correlation ($r^2 = 0.67$, $n = 16$) indicating that the MT determined at the two

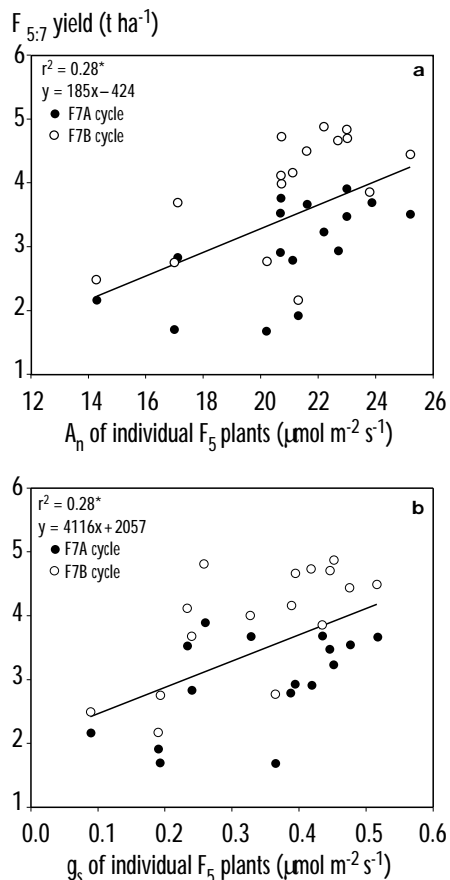


Figure 9. (a) Relationship between $F_{5:7}$ grain yield and leaf photosynthesis rate (A_n) of individual F_5 plants. (b) Relationship between $F_{5:7}$ grain yield and stomatal conductance (g_s) of individual F_5 plants. * significant at $p = 0.05$.

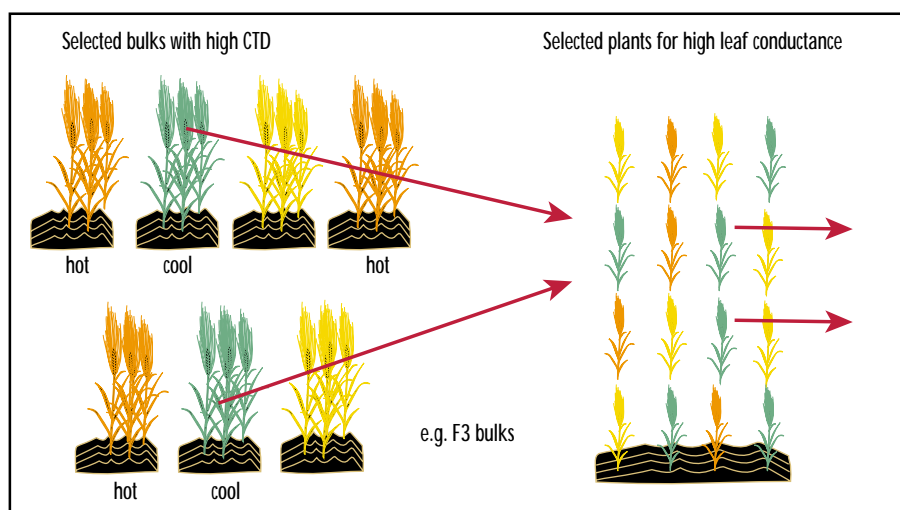


Figure 8. Using canopy temperature depression (CTD) and leaf conductance in early generation selection.

Table 8. Spearman correlation coefficients between yield, averaged over two cycles at each of six locations of the IHSGE (1990-92), and membrane relative injury of 16 wheat genotypes measured using two different methods.

| Heat-stressed location | Flag leaf (field grown) | Seedlings (chamber grown) |
|------------------------|-------------------------|---------------------------|
| Taltizapan Dec. | -0.65** | -0.40 |
| Taltizapan Feb. | -0.31 | -0.01 |
| Brazil | -0.59* | -0.57* |
| Egypt | -0.69** | -0.64** |
| India | -0.66** | -0.57* |
| Sudan | -0.69** | -0.58* |
| Average correlation | -0.60 | -0.46 |

* and ** refer to $P < 0.05$ and $P < 0.01$, respectively.

development stages was well associated. These data support the idea that using seedlings raised under artificial conditions for screening MT may be a viable alternative to using field-grown tissue. The use of seedlings is preferable logistically because the conditions of plant acclimation can be controlled, which is not possible in the field. The importance of this point is illustrated indirectly by the data.

Using the seedling procedure, the three repetitions of the experiment were measured for MT on three subsequent days. While the interaction of genotype with repetition was not significant, the main effect of repetition (i.e., day of experiment) was highly significant (data not shown). Even under controlled conditions, unintentional discrepancies either in procedure or day-to-day variability of conditions influenced absolute values of MT. Since it would not be practical for a breeding program to assess MT on all the germplasm of interest in one experimental run, a methodology involving controlled conditions would seem preferable.

Another advantage of using seedlings rather than more mature tissue is that MT is unlikely to be affected by phenology at such an early stage of development. In these experiments there was a range in anthesis and maturity dates among the genotypes. Instead of measuring MT on the precise date of anthesis for each genotype, MT values were measured on all flag leaves on the same calendar date and subsequently adjusted using the number of days between measurement of MT and anthesis as a covariate.

Genetic Diversity for Heat Tolerance Traits

While genetic diversity for heat tolerance has been shown to exist among conventional wheat cultivars (Rawson, 1986; Wardlaw et al., 1989; Al-Khatib and Paulsen, 1990; Reynolds

et al., 1994), progress would be limited if new sources of genetic diversity were not exploited. Materials that could be exploited fall into two broad categories: landraces that can be used directly in conventional breeding efforts and wild species with compatible genomes from which genes can be introduced into cultivated wheats using wide crossing approaches.

Genetic diversity for heat tolerance has been shown to exist in wild *Triticum* and *Aegilops* species by Edhaie and Waines (1992), who tested accessions from Afghanistan, Iran, Iraq, Israel, Jordan, Syria, Lebanon, Turkey, and the USSR. Interestingly, all of the heat tolerant accessions came from only three regions: eastern Israel, western Jordan, and southwestern Syria. The authors suggest that a search among the bread and durum wheat landraces from these regions may provide genotypes with a high degree of heat tolerance that could be incorporated into modern wheat backgrounds.

Some work has been conducted to identify new sources of heat tolerance traits among accessions in the CIMMYT wheat genebank. For example, high leaf chlorophyll content has been identified in Mexican landrace collections where the best genotypes showed substantially greater leaf chlorophyll concentration than the check Seri-M82. While high leaf chlorophyll content does not guarantee heat tolerance, the stay-green trait has been associated with heat tolerance in fixed lines (Reynolds et al., 2000), and high chlorophyll was associated with heat tolerance of sister lines in some wheat crosses (Reynolds et al., 1997).

High stomatal conductance (which may permit leaf cooling through evapotranspiration) has started to be examined in accessions from CIMMYT's genebank collections, under heat stressed conditions. For reasons discussed earlier, measuring stomatal conductance as an indication of heat tolerance/escape is more suitable than measuring CTD, since it can be evaluated relatively easily on individual plants, a necessary efficiency when

screening very large numbers of accessions from a germplasm bank. Apart from identifying genetic diversity for the trait, preliminary work also indicated reasonable levels of broad-sense and realized heritability (60-75%) for the trait (Vilhelmsen et al., 2001).

Molecular approaches may be helpful for identifying useful genetic diversity expressed in the progeny of wide crosses. Genetic diversity from wheat wild relatives has already been exploited through wide crossing to introduce disease resistance (e.g., Villareal et al., 1995). Potential exists for identifying the loci encoding other quantitatively inherited traits associated with abiotic stress tolerance using QTL analysis in mapping of delayed backcross generations (Tanksley and Nelson, 1996).

Agronomic Strategies for Ameliorating the Effects of Heat Stress

Optimal crop growth requires a non-limiting supply of water, nutrients, and radiation; as temperatures rise, the demand for growth resources increases due to higher rates of metabolism, development, and evapotranspiration (Rawson, 1988). When growth resources are limited by heat stress, the size of plant organs such as leaves, tillers, and spikes is reduced (Fischer, 1984). The apparent sensitivity of metabolic processes to heat stress in the field (Reynolds et al., 1998; 2000), coupled with the reduced length of life cycle at high temperature (Midmore et al., 1984), explains why grain yield is strongly associated with total plant biomass in hot environments. These interactions make crop management practices critical to sustaining wheat yields in warm environments.

A few studies have shown the benefits of specific management practices under stress. For example, the application of farmyard manure (FYM) has been reported to improve soil physical and

chemical conditions, and to help conserve soil moisture (Sattar and Gaur, 1989; Gill and Meelu, 1982; Tran-Thuc-Son et al., 1995). A one-time application of FYM (10-15 t ha⁻¹) increased wheat yields for up to three successive crop cycles, when applied in conjunction with inorganic N fertilizers, and for up to four years with the addition of P fertilizers under hot and humid conditions in Bangladesh (Mian et al., 1985). Under high-temperature conditions, volatilization of N fertilizers such as NH₃ is more likely, and further decreases wheat yields compared with the application of equivalent N in organic forms such as FYM (Tran-Thuc-Son et al., 1995).

Straw mulch is another agronomic input with the potential to ameliorate stress by reducing evaporation of soil moisture and increasing infiltration rate (Lal, 1975). Straw mulch has also been reported to lower soil temperature (Benoit and Kirkhoun, 1963) and to impede seedling emergence, a negative effect (Chopra and Chaudhary, 1980). Surface soil temperatures can exceed air temperature by 10 to 15°C if the soil surface is bare and radiation intensity is high; straw mulch in such conditions may increase seedling emergence and survival (Fischer, 1984). Given that wheat growth under warm conditions is highly sensitive to management, judicious combinations of management practices could substantially benefit performance by improving crop establishment and the availability of water and nutrients during subsequent growth stages.

A collaborative study was conducted by CIMMYT and the national wheat research programs of Sudan and Bangladesh to provide information from warm environments on the response of wheat to management factors such as mulching and application of FYM, and to elevated levels of inorganic fertilizer and increased irrigation frequency (Badaruddin et al., 1999). The research was conducted to determine whether modifications to recommended crop

management practices could significantly improve grain yield. Control treatments represented recommended practices and gave yields of 3.6 t ha⁻¹, averaged across all environments. Considering main effects, FYM (10 t ha⁻¹) gave the highest yield response (14%), and approximately equivalent levels of NPK the lowest (5.5%), suggesting that organic fertilizer provided growth factors in addition to nutrient content. Mulch and extra irrigation increased yield in the hot, low relative humidity environments (i.e., Sudan and Mexico), but not in Bangladesh, which is hot and humid.

In Mexico, extra inputs were more beneficial under hotter, spring-sown conditions than in winter sowings. Comparison of heat tolerant (Glennson 81) and heat sensitive (Pavon 76) genotypes showed that the heat tolerant genotype was generally more responsive to additional inputs. Improved performance in response to inputs was generally associated with better stand establishment and with significant increases in plant height, grain m⁻², and above-ground biomass; in Mexico it was also related to higher canopy temperature depression and light interception.

These results clearly indicate that wheat yields in warm environments can be raised significantly by modifying agronomic practices. Overall, the application of animal manure had the largest and most consistent effect on yield. Some of the benefits associated with extra organic matter may also be provided by practicing residue retention and reduced tillage. Such integrated approaches to crop and soil management in abiotically stressed environments are becoming increasingly relevant in light of diminishing water supplies in many agro-ecosystems.

This study did not attempt to analyze the economic basis of management factors, only to establish their biological value. Nonetheless, data indicate that recommended levels of fertilizer, whether organic or otherwise, were not generally sufficient to meet crop

requirements. Average yield responses to NPK and FYM at a given site were as much as 17% and 24%, respectively, suggesting that in hot regions even economic yields might be improved through better crop nutrition.

The economic basis of increasing irrigation frequency is more complex for two reasons. First, irrigation schemes such as the one in the Gezira of central Sudan lack the flexibility to permit farmers to irrigate at will. Water is usually available only at set times in a given area as water is passed systematically through the whole irrigation scheme. Second, water availability is declining in many regions of the world, so the expectation of raising economic returns through increased irrigation may not be fulfilled if water prices rise dramatically. As mentioned previously, it may be possible to obtain the benefits of mulching and, perhaps, increase soil organic matter through a combination of residue retention and reduced tillage practices. Nonetheless, significant investment will be required on the part of national agricultural research systems and their governments, or agricultural development agencies sponsored by industrialized countries, if such practices are to become a reality in the developing world.

Conclusions

While patterns of heat stress may vary widely between wheat growing regions, a major factor explaining genotype by environment interaction has been shown to be relative humidity (RH). In low RH environments, lack of physiological heat tolerance is the major yield constraint, while in high RH environments, disease pressure may be an additional and possibly more serious limitation. Canopy temperature depression seems to be a potentially powerful indirect selection criterion in low RH environments, while stomatal conductance and membrane thermostability may be applied in all hot environments. However, genetic gains to

selection should be tested in any new environment using locally adapted germplasm (as outlined in the introductory chapter) before the use of physiological traits as indirect selection criteria is incorporated into mainstream breeding.

Where germplasm collections are available, accessions from abiotically stressed regions should be screened for heat tolerance characteristics as a means of introducing new sources of genetic diversity into the breeding program. In addition to genetic improvement, agronomic strategies (such as residue retention to lower soil surface temperatures and increase soil organic matter) are also a means of increasing productivity in warm environments.

References

- AbdElShafi, A.M., and O.A.A. Ageeb. 1994. Breeding strategy for developing heat-tolerant wheat varieties adapted to upper Egypt and Sudan. In: D.A. Saunders and G.P. Hettel (eds.). *Wheat in Heat Stressed Environments: Irrigated, Dry Areas and Rice Farming Systems*. Proceedings of the International Conference, Wheat in Hot, Dry, Irrigated Environments. Mexico, D.F.: CIMMYT.
- Al Khatib, K., and G.M. Paulsen. 1984. Mode of high temperature injury to wheat during grain development. *Plant Physiol.* 61:363-368.
- Al-Khatib, K., and G.M. Paulsen. 1990. Photosynthesis and productivity during high temperature stress of wheat cultivars from major world regions. *Crop Sci.* 30:1127-1132.
- Amani, I., R.A. Fischer, and M.P. Reynolds. 1996. Evaluation of canopy temperature as a screening tool for heat tolerance in spring wheat. *J. Agron. Crop Sci.* 176:119-129.
- Badaruddin, M., M.P. Reynolds, and O.A.A. Ageeb. 1999. Wheat management in warm environments: effect of organic and inorganic fertilizers, irrigation frequency, and mulching. *Agronomy J.* 91.
- Balota, M., D. Rees, and M.P. Reynolds. 1996. Chlorophyll fluorescence parameters associated with spring wheat yield under hot, dry, irrigated conditions. Proceedings of the International Drought Stress Congress. Belgrade.
- Benoit, G.R., and R.J. Kirkhoun. 1963. The effect of soil surface conditions on evaporation of soil water. *Soil Sci. Soc. Am J.* 27:495-498.
- Berry, J.A., and O. Bjorkman. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Ann. Rev. Plant Physiol.* 31:491.
- Bhullar, S.S., and C.F. Jenner. 1986. Effects of temperature on the conversion of sucrose to starch in the developing wheat endosperm. *Aust. J. Plant Physiol.* 13:605-615.
- Blum, A. 1986. The effect of heat stress on wheat leaf and ear photosynthesis. *J. Experimental Botany* 37:111-118.
- Blum, A. 1988. *Plant Breeding for Stress Environment*. CRC Press, Inc., Boca Raton, Florida.
- Blum, A., and A. Ebercon. 1981. Cell membrane stability as a measure of drought and heat tolerance in wheat. *Crop Sci.* 21:43-47.
- Chopra, U.K., and T.N. Chaudhary. 1980. Effect of soil temperature alternation by soil covers on seedling emergence of wheat (*Triticum aestivum* L.) sown on two dates. *Plant Soil* 57(1):125-129.
- CIMMYT. 1995. CIMMYT/NARS Consultancy on ME1 Bread Wheat Breeding. Wheat Special Report No. 38. Mexico, D.F.
- Cornish, K., J.W. Radin, E.L. Turcotte, Z.-M Lu, and E. Zeiger. 1991. Enhanced photosynthesis and g_s of pima cotton (*Gossypium barbadense* L.) bred for increased yield. *Plant Physiol.* 97:484-489.
- Edhaie, B., and Waines, J.G. 1992. Heat resistance in wild *Triticum* and *Aegilops*. *J. Genetics and Breeding* 46:221-228.
- Fischer, R.A. 1984. Physiological limitations to producing wheat in semi-tropical and tropical environments and possible selection criteria. In: *Wheats for More Tropical Environments*. A Proceedings of the International Symposium. Mexico, D.F.: CIMMYT. pp. 209-230.
- Fischer, R.A. 1985. Number of kernels in wheat crops and the influence of solar radiation and temperature. *J. Agric. Sci. (Cambridge)* 105:447-61.
- Fischer, R.A., and D.B. Byerlee. 1991. Trends of wheat production in the warmer areas: Major issues and economic considerations. In: D.A. Saunders (ed.). *Wheat for Nontraditional, Warm Areas*. Mexico, D.F.: CIMMYT. pp. 3-27.
- Fokar, M., H.T. Nguyen, and A. Blum. 1998. Heat tolerance in spring wheat. I. Genetic variability and heritability of cellular thermotolerance. *Euphytica* 104:1-8.
- Gerik, T.J., and J.D. Eastin. 1985. Temperature effects on dark respiration among diverse sorghum genotypes. *Crop Sci.* 25:957-961.
- Gill, H.S., and O.P. Meelu. 1982. Studies on the substitution of inorganic fertilizers with organic manure and their effect on soil fertility in rice-wheat rotation. *Fertilizer Res. (Netherlands)*. 3(4):303-314.
- Gutiérrez-Rodríguez, M., M.P. Reynolds, and A. Larqué-Saavedra. 2000. Photosynthesis of wheat in a warm, irrigated environment. II: Traits associated with genetic gains in yield. *Field Crop Res.* 66:51-62.
- Harding, S.A., J.A. Guikema, and G.M. Paulsen. 1990. Photosynthetic decline from high temperature stress during maturation of wheat. I. Interaction with senescence process. *Plant Physiol.* 92:648-653.
- Idso, S.B., R.J. Reginato, K.L. Clairson, and M.G. Anderson. 1984. On the stability of stress baselines. *Agric. Forest Meteorol.* 32:177-182.
- Keeling, P.L., R. Banisadr, L. Barone, B.P. Wasserman, and A. Singletary. 1994. Effect of temperature on enzymes in the pathway of starch biosynthesis in developing maize and wheat grain. *Aust. J. Plant Physiol.* 21:807-827.
- Kohli, M.M., C.E. Mann, and S. Rajaram. 1991. Global status and recent progress in breeding wheat for the warmer areas. In: D.A. Saunders (ed.). *Wheat for Nontraditional, Warm Areas*. Mexico, D.F.: CIMMYT. pp 96-112.
- Lal, R. 1975. Role of mulching techniques in tropical soil and water management. IITA Tech. Bull. I. Ibadan, Nigeria.
- Levitt, J. 1980. Response of plants to environmental stresses. Chilling, Freezing and High Temperature Stresses. I. Academic Press New York. 497 p.
- Mian, M.I.A., M.A. Rouf, M.A. Rashid, M.A. Mazid, and M. Equb. 1985. Residual effects of triple super phosphate (TSP) and farmyard manure (FYM) under renewed application of urea on the yield of crops and some chemical properties of soil. *Bangladesh J. Agric. Sci.* 10(2):99-109.
- Midmore, D.J., P.M. Cartwright, and R.A. Fischer. 1984. Wheat in tropical environments. II. *Crop Growth and Grain yield*. *Field Crops Res.* 8:207-227.
- Moffat, J.M., G. Sears, T.S. Cox, and G.M. Paulsen. 1990. Wheat high temperature tolerance during reproductive growth. I. Evaluation by chlorophyll fluorescence. *Crop Sci.* 30:881-885.
- Ortiz-Ferrara, G., S. Rajaram, and M.G. Mosaad. 1994. Breeding strategies for improving wheat in heat-stressed environments. In: D.A. Saunders and G.P. Hettel (eds.). *Wheat in Heat Stressed Environments: Irrigated, Dry Areas and Rice Farming Systems*. Proceedings of the International Conference, Wheat in Hot, Dry, Irrigated Environments. Mexico, D.F.: CIMMYT.

- Pedretti, R.R., and M.M. Kohli. 1991. Wheat production in Paraguay: Trends, major constraints, and potential. In: D.A. Saunders (ed.). *Wheat for Nontraditional, Warm Areas*. Mexico, D.F.: CIMMYT.
- Rawson, H.M. 1988. Effect of high temperatures on the development and yield of wheat and practices to reduce deleterious effects. p. 44-62. In: A.R. Klatt (ed.). *Wheat Production Constraints in Tropical Environments*. Mexico, D.F.: CIMMYT.
- Rawson, H.N. 1986. High temperature-tolerant wheat: A description of variation and a search for some limitations to productivity. *Wild Crops Res.* 14:197-212.
- Razzaque, M.A., A.B.S. Hossain, S.M. Ahmed, A.K. Sarkar, M. Rahman, C.D. Barma, and R. Amin. 1994. Wheat breeding strategies in the rice farming system of Bangladesh. In: D.A. Saunders and G.P. Hettel (eds.). *Wheat in Heat Stressed Environments: Irrigated, Dry Areas and Rice Farming Systems*. Proceedings of the International Conference, Wheat in Hot, Dry, Irrigated Environments. Mexico, D.F.: CIMMYT.
- Rebetzke, G.J., A.G. Condon, and R.A. Richards. 1996. Rapid screening of leaf conductance in segregating wheat populations. In: R.A. Richards, C.W. Wrigley, H.M. Rawson, J.L. Davidson, and R.I.S. Brettell (eds.). *Proc. Eighth Assembly, Wheat Breeding Society of Australia*. pp. 130-134.
- Reynolds, M.P. 1994. Summary of data from the 1st and 2nd International Heat Stress Genotype Experiment. In: D.A. Saunders and G.P. Hettel (eds.). *Wheat in Heat Stressed Environments: Irrigated, Dry Areas and Rice Farming Systems*. Proceedings of the International Conference, Wheat in Hot, Dry, Irrigated Environments. Mexico, D.F.: CIMMYT.
- Reynolds, M.P., E. Acevedo, O.A.A. Ageeb, S. Ahmed, M. Balota, L.J.B. Carvalho, R.A. Fischer, E. Ghanem, R.R. Hanchinal, C. Mann, L. Okuyama, L.B. Olugbemi, G. Ortiz-Ferrara, M.A. Razzaque, and J.P. Tandon. 1992. Results of the First International Heat Stress Genotypes Experiment. *Wheat Special Report No. 14*. Mexico, D.F.: CIMMYT.
- Reynolds, M.P., M. Balota, M.I.B. Delgado, I. Amani, and R.A. Fischer. 1994. Physiological and morphological traits associated with spring wheat yield under hot, irrigated conditions. *Aust. J. Plant Physiol.* 21:717-30.
- Reynolds, M.P., M.I. Delgado, M. Gutiérrez-Rodríguez, and A. Larqué-Saavedra. 2000. Photosynthesis of wheat in a warm, irrigated environment. I: Genetic diversity and crop productivity. *Field Crops Res.* 66:37-50.
- Reynolds, M.P., R.P. Singh, A. Ibrahim, O.A.A. Ageeb, A. Larqué-Saavedra, and J.S. Quick. 1998. Evaluating physiological traits to complement empirical selection for wheat in warm environments. *Euphytica* 100:84-95.
- Reynolds, M.P., S. Nagarajan, M.A. Razzaque, and O.A.A. Ageeb (eds.). 1997. Using canopy temperature depression to select for yield potential of wheat in heat-stressed environments. *Wheat Special Report No. 42*. Mexico, D.F.: CIMMYT.
- Rijven, A.H.G. 1986. Heat inactivation of starch synthase in wheat endosperm. *Plant Physiol.* 81:448-453.
- Saadalla, M.M., J.F. Shanahan, and J.S. Quick. 1990. Heat tolerance in winter wheat. I. Hardening and genetic effects on membrane thermostability. *Crop Sci.* 30:1243-1247.
- Saini, H.S., M. Sedgley, and D. Aspinall. 1983. Effect of heat stress during floral development of pollen tube growth and ovary anatomy in wheat (*Triticum aestivum* L.) *Aust. J. Plant Physiol.* 10:137-144.
- Sattar, M.A., and A.C. Gaur. 1989. Effect of VA-mycorrhiza and phosphate dissolving microorganism on the yield and phosphorus uptake of wheat (*Triticum vulgare*) in Bangladesh. *Bangladesh J. Agric. Res.* 14(3):233-239.
- Shanahan, J.F., I.B. Edwards, J.S. Quick, and R.J. Fenwick. 1990. Membrane thermostability and heat tolerance of spring wheat. *Crop Sci.* 30:247-251.
- Shpiler, L., and A. Blum. 1991. Heat tolerance for yield and its components in different wheat cultivars. *Euphytica* 51:257-263.
- Spiertz, J.H.J. 1978. Grain production and assimilate utilization of wheat in relation to cultivar characteristics, climatic factors and nitrogen supply. *Versl. Land-bouwkund, Onderz* 881:1-35.
- Tandon, J.P. 1994. Wheat cultivation, research organization, and production technology in the hot dry regions of India. In: D.A. Saunders and G.P. Hettel (eds.). *Wheat in Heat Stressed Environments: Irrigated, Dry Areas and Rice Farming Systems*. Proceedings of the International Conference, Wheat in Hot, Dry, Irrigated Environments. Mexico, D.F.: CIMMYT.
- Tanskley, S.D., and J.C. Nelson. 1996. Advanced back-cross QTL analysis: A method for the simultaneous discovery and transfer of valuable QTLs from unadapted germplasm into elite breeding lines. *Theor. Appl. Genet.* 92:191-203.
- Tran-Thuc-Son, U. Singh, J.L. Padilla, and R.J. Buresh. 1995. Management of urea and degraded soils of Red River Delta (Vietnam): Effect of growing season and cultural practice. p. 161-175. In G.L. Denning and Vo-Tong-Xuan (eds.). *Vietnam and IRRI, A Partnership in Rice Research*. Proceedings of a Conference. Los Baños, Laguna (Phil.). IRRI.
- Vargas, M., Crossa, J., Sayre, K.D., Reynolds, M.P., Ramírez, M.E., and Talbot, M. 1998. Interpreting genotypes by environment interaction in wheat by partial least square regression. *Crop Sci.* 38:679-689.
- Vilhelmsen, A.L., M.P. Reynolds, B. Skovmand, D. Mohan, K.N. Ruwali, S. Nagarajan, and O. Stoelen. 2001. Genetic diversity and heritability of heat tolerance traits in wheat. *Wheat Special Report* (in preparation).
- Villareal, R.L., G. Fuentes-Davila, and A. Mujeeb-Kazi. 1995. Synthetic hexaploids x *Triticum aestivum* advanced derivatives resistant to Karnal bunt (*Tilletia indica* Mitra). *Cereal Res. Com.* 27:127-132.
- Wardlaw, I.F., I.A. Dawson, P. Munibi, and R. Fewster. 1989. The tolerance of wheat to high temperatures during reproductive growth. I Survey procedures and general response patterns. *Aust. J. Agric. Res.* 40:1-13.
- Wardlaw, J.F., I. Sofield, and P.M. Cartwright. 1980. Factors limiting the rate of dry matter accumulation in the grain of wheat grown at high temperature. *Aust. J. Plant Physiol.* 7:387-400.
- Zeng, Z.R., J.M. Morgan, and R.W. King. 1985. Regulation of grain number in wheat: Genotypic difference and responses to applied Abscisic acid and to high temperature. *Aust. J. Plant Physiol.* 12:609-619.