

Wheat Special Report No. 30

**Genetic Diversity for Photosynthesis
in Wheat under Heat-stressed Environments
and Its Relationship to Productivity**

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Contents

iii	Preface
iii	Abstract
1	Introduction
1	Materials and Methods
1	Test materials
1	Growing conditions
2	Measurements
2	Photosynthesis
2	Dark respiration
2	Chlorophyll evaluation
2	Results
2	Main effects
4	Genotypic responses
6	Discussion
8	Mechanisms associated with genetic variation in heat tolerance
9	Potential selection criteria for heat tolerance
12	References
14	Appendix 1. Analysis of variance for photosynthetic rates of 16 wheat genotypes in a randomized complete block design, Tlaltizapan, Mexico, 1991-92.
15	List of Wheat Special Reports

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Preface

This wheat special report provides additional physiological knowledge for breeders who are working to break yield potential barriers in wheat. The research discussed here shows that the photosynthetic rate of wheat genotypes grown under high-temperature field conditions varies greatly and is significantly associated with grain yield. The associations we have found between net photosynthesis, stomatal conductance, canopy temperature, chlorophyll content, plant development and grain yield are contributing significantly to our understanding of the mechanisms that determine potential productivity in superior germplasm under hot conditions. The stay green (maintenance of leaf chlorophyll) and cool canopy temperature traits are reinforced for the production of high yielding genotypes in hot environments.

I would like to acknowledge the collaboration of our colleagues at Colegio de Postgraduados, Chapingo, Mexico: Miguel I. Delgado, Alfonso Larqué-Saavedra, and Tomás Nava S., who served as co-authors of this report.

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Abstract

Genetic variation in photosynthetic rate, stomatal conductance, leaf chlorophyll content, and dark respiration was studied in 16 wheat genotypes (*Triticum aestivum* L.) grown under high-temperature field conditions in central Mexico. Measurements were made on flag leaves in full sun light, at three different stages of plant development, and at different times of the day. Two experiments were conducted with sowing dates in December 1991 and March 1992, and the results compared with the grain yields of the experimental plots on which measurements were made. Photosynthetic rate was fairly stable during the day between 10:00 and 14:00, and across experiments, despite differences in leaf temperature of up to 4°C. However, rates of photosynthesis fell noticeably at successively later stages of plant development, and showed a strong interaction with genotype. For both planting dates, there was a clear association among the parameters photosynthetic rate, stomatal conductance, leaf temperature, and chlorophyll content, and all of these parameters were correlated significantly with grain yield. Photosynthetic rate in the post-anthesis period was strongly associated with chlorophyll loss after anthesis, which suggests that genetic variability in the onset of senescence may be an important variable determining the yield of wheat in hot environments.

Introduction

The productivity of wheat, a temperate crop, decreases under high temperature conditions. The principal cause is the acceleration of the rate of plant development (Midmore 1982). Physiological studies have also shown that increased temperatures result in premature plant senescence and shorten the period of photosynthetic activity (Al-khatib and Paulsen 1984). Consequently, grain weight will be low due to reduced grain-filling (Wardlaw et al. 1980). Nonetheless, it is apparent that some common wheat genotypes are heat tolerant (Midmore et al. 1982, Rawson 1986). Genetic variability among wheat varieties has been demonstrated for traits such as maintenance of high photosynthetic rate, high grain weight, and high harvest index when exposed to high temperatures under controlled conditions (Blum 1986, Al-khatib and Paulsen 1990). Increased dark respiration as a result of heat stress may also contribute to poor grain-filling (Wardlaw et al. 1980).

It is well established that high temperatures can affect many of the processes involved in photosynthesis (Berry and Bjorkman 1980). However, the physiological mechanisms, which are causal in determining the relative performance of varieties in heat-stressed environments, are not well documented, despite the interest in using physiological traits as selection criteria in crop breeding programs (Hall 1992). Studies attempting to establish a relationship between photosynthetic metabolism and differences in crop productivity among genotypes are few, and most have been conducted under controlled conditions (Wells et al. 1982, 1986; Blum 1986, Al-khatib and Paulsen 1990; Cornish et al. 1991, Sasaki and Ishii 1992). In wheat, differences in photosynthesis among genotypes 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). These mechanisms have also been shown to be related to heat tolerance in different genotypes of *Solanum* species (Reynolds et al. 1990).

The objective of the present study was to determine if genotypic differences in photosynthesis and dark respiration are causally related to yield potential of wheat under heat-stressed field conditions. Photosynthesis and dark respiration were measured on the flag leaves of 16 varieties grown in field plots that had been established as part of an international experiment to evaluate the response of wheat yields to hot climates (Reynolds 1994). The parameters--photosynthetic rate, leaf chlorophyll content, stomatal conductance, leaf temperature, and grain yield--were well correlated among one another. The results suggest that the relative heat tolerance of the varieties studied was causally related to their photosynthetic capacity and that the principal mechanism involved was the ability to maintain leaf chlorophyll content during grain-filling.

Materials and Methods

Test materials

Test materials used in this study were 16 wheat genotypes (*Triticum aestivum* L.) selected on the basis of recommendations by researchers working on wheat in warmer environments. These materials represent wide variation for yield under high temperature conditions and have been tested in a number of countries (Reynolds et al. 1990) as part of a collaborative project of CIMMYT.

Growing conditions

The study was conducted under field conditions at Tlaltizapan in the State of Morelos, Mexico, located at 18° 41'N and 941 masl. The climate is subhumid, warm, and characterized by summer rains. The wheat varieties were sown in 5- x 1.5-m yield plots,

in a randomized complete block design, and in a conventional planting arrangement so that yield could be estimated at maturity. All genotypes were planted on two sowing dates in December 1991 and March 1992. The average maximum, average minimum, and mean temperatures for each crop cycle were 32, 11, and 21°C for Expt. 1, and 36, 16, and 26°C for Expt. 2, respectively. The experiments were conducted under good irrigation, high fertility, favorable temperatures, and good weed and insect control.

Measurements

Photosynthesis--Photosynthesis was measured under field conditions using an infrared gas analyzer (IRGA, LCA-2 ADC) on flag leaves positioned at right angles to incident solar radiation. Photosynthesis was measured at three growth stages: booting (10 days before anthesis), anthesis, and grain-filling (two weeks after anthesis). Due to differences in the genotypes' phenologic development, measurements were timed based on an average growth stage so that all genotypes were evaluated on the same date. The exact phenologic stage of each genotype was recorded and used in data analysis as a covariable to check for the possible confounding effects of growth stage. At each growth stage, photosynthetic measurements were taken at four different times of the day. At each time, measurements were made on two leaves of all 16 genotypes in the shortest time possible to reduce the potentially confounding effects caused by daytime photosynthetic rhythms and the accompanying changes in temperature, light, and humidity. The procedure was repeated over three days, with one replication assessed each day. Measurements were taken at 10:00, 11:00, 12:00, and 13:00 in Expt. 1 and at 10:00, 11:00, 15:00, and 16:00 in Expt. 2. Stomatal conductance (gs), leaf temperature (Lt), and photosynthetic photon flow density were recorded at the same time as photosynthesis using the LCA-2.

Dark respiration--Dark respiration was estimated using the ACD infrared gas analyzer (model LCA-2) in a gas exchange chamber (Parkinson chamber) covered with a black lid to keep the light out. The rate of CO₂ evolution was recorded after 5 minutes of dark adaptation. It was found in preliminary measurements that the rate of CO₂ evolution stabilized after approximately 3 to 4 minutes of dark adaptation. Evolution of CO₂ was recorded once during the day, on one repetition of all 16 genotypes, with one of the flag leaves that was used to measure photosynthesis. Rates were measured between 15:00 and 17:00 in Expt. 1 and between 13:00 and 15:00 in Expt. 2.

Chlorophyll evaluation--After all measurements in the field were complete, the leaves used were separated from the plants, placed on moist filter paper, wrapped in aluminum foil, and taken to the laboratory in a cooler. Six disks of 11 mm diameter were cut from each leaf; three of them were placed in a drying oven to estimate dry weight. Chlorophyll was extracted from the other three disks by crushing them in a mortar with 80% acetone and a pinch of calcium carbonate. The extract was centrifuged at 3500 rpm for 7 minutes. The supernatant was made up to a known volume and absorbance was measured at 663 and 645 nm in an ultraviolet spectrophotometer. Chlorophyll a, chlorophyll b, and total chlorophyll were estimated using equations of Harborne (1973).

Results

Main effects

The mean net photosynthetic rates (A), incident photosynthetically active radiation (PAR), and leaf temperatures measured at different times of day for 16 genotypes (average for 3 growth stages) are presented for both sowing dates in **Table 1**. In Expt. 1, the differences in mean rates of photosynthesis when measured at different times of the

Table 1. Rate of net photosynthesis (A), photosynthetically active radiation (PAR), and leaf temperature (Lt) at different times of day. The values are averages for flag leaves of 16 wheat genotypes at three growth stages grown at Tlaltizapan, Mexico, 1991-92.

Experiment 1	10:00	11:00	12:00	13:00	LSD	SE
A (mg of CO ₂ /dm ² /h)	32.21	31.22	31.87	32.22	1.86	0.322
PAR (μmol/m ² /s)	1316	1426	1450	1371	60.7	10.77
Lt (°C)	29.36	31.46	32.69	33.30	0.46	0.106

Experiment 2	10:00	11:00	15:00	16:00	LSD	SE
A (mg of CO ₂ /dm ² /h)	31.16	34.96	28.28	24.78	1.97	0.34
PAR (μmol/m ² /s)	1137	1243	1070	871	42.6	9.90
Lt (°C)	31.78	33.69	36.60	36.56	0.37	0.109

Mean total chlorophyll was 4.48 mg/dm² for Expt. 1 and 4.86 mg/dm² for Expt. 2.

LSD is the least significant difference ($\alpha = 0.05$).

Table 2. Variation of photosynthetic rate (mg of CO₂/dm²/h) among 16 different wheat genotypes evaluated at three growth stages using two sowing dates (Expts. 1 and 2). Maximum, minimum, and average rates are shown.

	Growth stage					
	Booting		Anthesis		Post-anthesis	
	Expt. 1	Expt. 2	Expt. 1	Expt. 2	Expt. 1	Expt. 2
Maximum	42.3	36.6	36.9	35.1	31.6	35.6
Minimum	32.5	27.7	27.9	25.3	17.3	20.7
Mean	38.4	32.5	32.9	30.3	25.4	28.6
LSD	4.61	4.19	4.13	3.93	4.30	4.38
SE	0.388	0.633	0.365	0.493	0.431	0.629

LSD is the least significant difference ($\alpha = 0.05$).

day were very small despite the fact that there was a 4°C rise in leaf temperature, and a noticeable diurnal rhythm in light intensity. For the March trial (Expt. 2), measurements were made later into the afternoon than in Expt. 1 and the net photosynthetic rates and PAR were found to be progressively lower at 1500 and 1600 hours than they were in the morning, while leaf temperatures were several degrees hotter. The analyses of variance for net photosynthetic rates showed significant differences ($P < 0.01$) among all factors under study, i.e., time of day, genotype and growth stage, and also for sowing date when a combined analysis was made (**Appendix 1**). The mean rates of photosynthesis, as well as the maximum and minimum values measured among genotypes, at each stage of development for both sowing dates are presented in **Table 2**. The highest photosynthetic rates were recorded at booting and were 42.3 and 36.6 mg of CO₂/dm²/h for Expts. 1 and 2, respectively. There was significant variation in net photosynthetic rates among genotypes, with a difference of approximately 10 mg CO₂/dm²/h between the maximum and minimum rates of genotypes. Greater variation was found at the third growth stage. The mean net photosynthetic rates decreased in each successive sampling stage and were higher for Expt. 1 than Expt. 2.

Other parameters measured at the same time as photosynthetic rate are summarized in **Table 3**. The differences in photosynthesis at different growth stages were paralleled by similar differences in stomatal conductance, which was measured at the same time. The total chlorophyll content of flag leaves fell after anthesis in both experiments, but was generally higher in Expt. 2. The chlorophyll a:b ratio decreased in each successive sampling stage in both experiments, and was not significantly different between experiments. Dark respiration did not differ between the first two growth stages measured, but declined in the third in both experiments. In the second experiment, dark respiration rates were significantly higher than in the first. Average leaf temperatures during the measurement of dark respiration were for the booting, anthesis, and post-anthesis stages, respectively, 27.6, 30.2, and 32.7°C for Expt. 1, and 34.1, 35.8, and 34.8°C for Expt. 2.

Genotypic responses

In presenting data involving genotypic variability in this study, it was important to consider the interaction between the treatment factors and the genotypes. Analysis of variance showed that the statistical interaction between genotypes and the other factors, time of day and sowing date, were not statistically significant (**Appendix 1**). There was, however, a statistically significant interaction between genotype and growth stage, which is discussed later. (None of the three-way interactions between factors were significant for either experiment, nor was the four-way interaction of the combined analysis, including both sowing dates). Since there was no interaction between genotype and the time of day at which measurements were made, correlations were made with values of photosynthesis at 10:00 and 11:00. In the analysis of covariance, where the covariate was the number of days between the date of the measurements and the date of anthesis for each variety, the covariate was not statistically significant for any of the parameters analyzed. This indicated that the relative phenology of the genotypes was not a confounding influence on the absolute values of the parameters measured. The correlation coefficients between grain yield and the physiological variables evaluated in this study are presented in **Table 4**. There was a significant positive correlation between grain yield and net photosynthetic rate at all three growth stages, for both sowing dates. The mean net photosynthesis of all six sampling dates showed a highly significant ($P < 0.01$), positive correlation ($r = 0.729$) with grain yield. However, when photosynthesis was adjusted for leaf chlorophyll content, there was no clear relationship with yield.

Stomatal conductance measured in the flag leaf at the same time as photosynthesis was significantly correlated with grain yield, in both experiments. Total chlorophyll content

Table 3. Average gas exchange and chlorophyll content of 16 wheat genotypes measured at four different times of the day. Measurements were taken at three growth stages in 2 sowing dates (Expts. 1 and 2).

	Net photo-synthesis	Yield/ mg CHL	Stomatal conductance	Chloro- phyll	Chl a:b	Dark resp.
Experiment 1						
Booting	38.4	8.323	0.678	4.64	3.58	6.4
Anthesis	32.9	6.765	0.586	4.90	3.34	6.3
Post-anthesis	25.4	6.225	0.317	3.90	3.22	4.3
LSD	0.187	0.394	0.035	0.21	0.10	0.98
SE	0.459	0.097	0.013	0.049	0.023	0.22
Experiment 2						
Heading	32.5	7.17	0.365	5.13	3.64	10.4
Anthesis	30.3	6.736	0.429	5.19	3.50	9.3
Post-anthesis	28.6	7.073	0.285	4.25	3.38	5.8
LSD	1.564	0.499	0.033	0.23	0.13	1.21
SE	0.403	0.103	0.010	0.054	0.027	0.31

A = mg CO₂dm⁻²h⁻¹; Rc = mol CO₂ mol photons⁻¹; Rs = mg CO₂g⁻¹; gs = mols m⁻²s⁻¹; Chl = mg g⁻¹.

Table 4. Correlation coefficients obtained by relating wheat grain yield to physiological variables measured on the different genotypes at each phenologic stage for 2 sowing dates (Expts. 1 and 2).

	Net photo-synthesis	Quantum yield	Stomatal conductance	Chloro- phyll	Chl a:b	Dark resp.
Experiment 1						
Booting	0.667**	0.008	0.820**	0.125	-0.252	0.304
Anthesis	0.566*	0.519*	0.787**	0.161	0.028	-0.281
Post-anthesis	0.614*	0.628*	0.783**	0.525*	0.015	-0.293
Mean	0.716**	0.489*	0.880**	0.379	0.094	-0.120
Experiment 2						
Booting	0.614*	0.745**	0.631**	-0.008	-0.077	-0.121
Anthesis	0.488*	0.467	0.360	0.016	0.067	-0.634*
Post-anthesis	0.563*	0.646**	0.613*	0.682*	0.085	-0.124
Mean	0.644**	0.696**	0.580*	0.361	-0.012	-0.312
General mean	0.729**	0.664**	0.820**	0.469	-0.136	-0.277

*, ** indicate significance at $\alpha = 0.05$ and $\alpha = 0.01$, respectively.

in the flag leaf was related to yield when measured post-anthesis, with correlation coefficients of 0.525 ($P < 0.05$) and 0.682 ($P < 0.01$) for Expts. 1 and 2, respectively. Coefficients were non-significant at the earlier growth stages. The change in the chlorophyll a:b chlorophyll ratio was not associated with grain yield, as indicated by the low correlation coefficients (Table 4). Dark respiration rates showed a negative but generally nonsignificant correlation with grain yield.

Using the mean values across treatments and experiments for each genotype, **Table 5** presents the correlation between all variables measured. From this, it is clear that the variables grain yield, net photosynthesis, stomatal conductance, leaf temperature, and leaf chlorophyll content were all significantly associated among one another.

Discussion

This study demonstrated a large degree of genotypic variability in net photosynthesis, stomatal conductance and rate of leaf chlorophyll loss among 16 wheat varieties when grown under high temperature field conditions. There have been relatively few published studies which have examined the genotypic variability of photosynthesis in wheat, and none on genotypes growing under field conditions. In the controlled environment, genotypic variability of the photosynthetic rate of wheat grown under high temperatures has been reported (Blum 1986, Al-khatib and Paulsen 1990). Genotypic variation in photosynthetic capacity has also been observed in other species such as cotton (Wells et al. 1986, Cornish et al. 1991, Peng and Krieg 1991), potato (Reynolds et al. 1990); rice (Sasaki and Ishii 1992), sorghum (Kidambi et al. 1990), and soybean (Wells et al. 1986). This study demonstrated a clear correlation between the yield of field grown plots and rate of photosynthesis, stomatal conductance (**Figure 1**), and chlorophyll loss (**Figure 2**) measured during the growth cycle. Photosynthetic rates were seen to decline with the advance in developmental stage (Table 2), while diurnal changes in leaf temperature had apparently no effect (Table 1). When photosynthesis per unit of chlorophyll was calculated, differences in rate between developmental stage were negligible (Table 3) and the correlation between yield of genotypes and their photosynthetic rate disappeared (Table 4). These observations suggest that photosynthetic metabolism is relatively heat stable across the range of temperatures and genotypes studied, while genetic diversity in the rate of the onset of senescence may be a causal factor in determining yield potential in hot environments.

Before further discussion of the mechanisms that may help to explain the observed genotypic differences in heat tolerance, it is worth reviewing the conditions under which measurements were taken. Light levels in all measurements taken in Expt. 1 were close to saturation for photosynthesis ($> 1300 \mu\text{mol m}^{-2} \text{s}^{-1}$), judging from the observed relationship between photosynthesis and light intensity (PvI) (**Figure 3**). While the mean leaf temperature became progressively higher between 10:00 and 14:00, this did not apparently affect net photosynthesis (Table 1). In Expt. 2, measurements were made later into the afternoon (15:00 to 17:00). Photosynthetic rates measured in the morning did not differ greatly between experiments, despite the fact that the mean leaf temperature was 2°C higher in the second experiment. Measurements made in the afternoon (15:00 to 17:00) had lower net photosynthetic rates than those in the morning and coincided with leaf temperatures which were 3 to 4°C higher. The decrease in photosynthesis was most probably a result of low levels of light rather than a temperature effect since light level for these measurements (Table 1) were not saturating. This is apparent from the PvI curve (Figure 3) and, when the rates were adjusted for incident light (Table 1), their values were quite similar to those occurring in the morning. Both net photosynthesis and stomatal conductance are known to be a function of the daytime rhythm of PAR (Gerber and Dawson 1990; Cornish et al. 1991, Girma and Krieg 1992). It can be concluded that

Table 5. Correlation matrix showing correlation coefficients between net photosynthesis (PS), photosynthetic rate per unit of chlorophyll (PS/CHL), stomatal conductance (GS), leaf temperature (LT), leaf chlorophyll content (CHL), chlorophyll a:b ratio (A:B), dark respiration (RSP), and grain yield (YLD), for 16 genotypes of wheat using the means from three stages of development in Expts. 1 and 2.

	PS	PS/CHL	GS	LT	CHL	A:B	RSP	YLD
PS	1.0							
PS/CHL	0.353	1.0						
GS	0.864**	0.229	1.0					
LT	0.722**	-0.239	-0.683**	1.0				
CHL	0.604**	-0.519*	0.631**	-0.456	1.0			
A:B	-0.314	0.531*	-0.494*	0.397	-0.772*	1.0		
RSP	-0.139	-0.068	-0.280	0.166	-0.124	0.289	1.0	
YLD	0.729	0.265	0.820**	-0.457	0.469	-0.137	-0.295	1.0

*, ** indicate significance at $\alpha = 0.05$ and $\alpha = 0.01$, respectively.

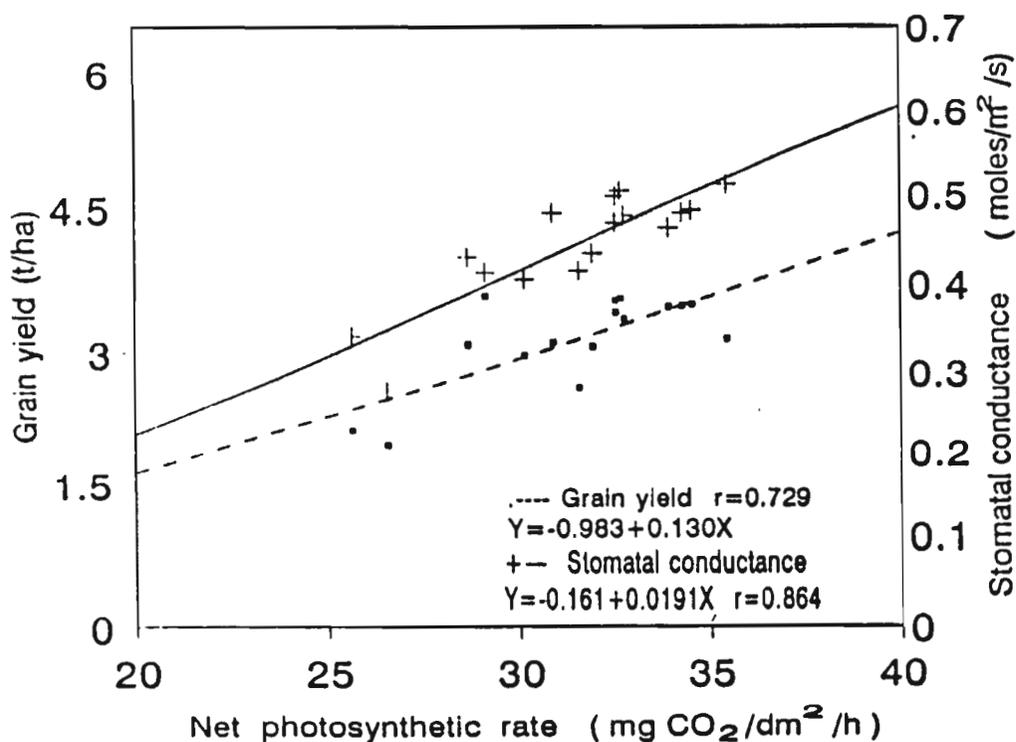


Figure 1. Regression of grain yield and stomatal conductance of 16 wheat genotypes on rate of flag leaf photosynthesis averaged over three stages of plant development and two sowing dates (Expts. 1 and 2), Tlaltizapan, Mexico, 1991-92.

photosynthetic capacity was probably quite stable during the day, with rates of carbon fixation depending more on incident radiation than leaf temperature itself.

Mechanisms associated with genetic variation in heat tolerance

Midmore et al. (1982) reported that the main effect of high temperature on wheat is to accelerate phenologic development, which seems to be associated with premature leaf senescence (Al-khatib and Paulsen 1984, Harding et al. 1990). In this study, the change in flag leaf chlorophyll content from anthesis to post-anthesis (Expt. 1) and from booting to post-anthesis (Expt. 2) showed a strong negative correlation to grain yield and photosynthetic rate (Figure 2). This suggests that sensitive genotypes experience an early loss of chlorophyll, causing a reduction in photosynthesis and grain yield, while the more tolerant genotypes maintain leaf chlorophyll for a longer period. Total chlorophyll content of the flag leaves during post-anthesis showed a significant direct correlation to photosynthetic rate for both Expt. 1 ($r = 0.872$, $P < 0.01$) and Expt. 2 ($r = 0.810$, $P < 0.01$). Early chlorophyll loss would appear to be a causal factor in reducing photosynthesis and grain yield under temperature stress, especially in heat-sensitive genotypes. While there was a preferential decline in chlorophyll a over chlorophyll b, as evidenced by the decline in a:b ratios over time (Table 3), the value of the a:b ratio itself was not correlated with yield of the genotypes (Table 4). Further support for the idea that a causal mechanism of heat stress was accelerated senescence, and the associated loss of chlorophyll, came from the observed interaction between genotypes and growth stages for photosynthetic rate (Figure 4). When rate of photosynthesis for genotypes at each stage of development was plotted against the mean rate of photosynthesis over all 3 stages of development (Figure 4), the gradient of the fitted slope became steeper at successive growth stages. The increase in gradient of the slope indicated that the more heat-sensitive genotypes become progressively less capable of photosynthesis over time in comparison to the more heat tolerant varieties.

A highly significant positive correlation was found between stomatal conductance and grain yield in this study (Figure 1). Cornish et al. (1991) reported that in cotton the highest yielding genotypes in their study showed higher photosynthetic rates and greater stomatal conductance. The positive correlation between conductance and grain yield was to be expected considering that this variable is closely linked to the photosynthetic rate (Cornish et al. 1991). This fact may help to explain another mechanism that could potentially have conferred heat tolerance, since there was a significant positive correlation between stomatal conductance and leaf temperature of genotypes in this study (Table 5). Previous studies conducted in the experimental environment have shown that crop canopy temperatures as much as 10°C below air temperature are possible, and that afternoon leaf-canopy temperatures were significantly correlated with yield of the 16 genotypes (Reynolds 1994). Further studies showed a significant relationship between stomatal conductance and evaporative cooling of the leaf surface (Balota et al. 1993). A positive correlation between leaf temperature and stomatal conductance has been found in cotton genotypes with different levels of productivity indicating that genotypes bred for increased yield had higher stomatal conductances and maintain lower leaf temperatures than older varieties (Zeiger, pers. comm.).

The rate CO₂ evolution of dark adapted leaves was measured during the day, between photosynthesis measurements, in order to obtain an estimate of dark respiration rates in photosynthetic tissue (Decker 1955). Although the average values for dark respiration across genotypes were significantly higher in the second experiment than the first, and lower in the post-anthesis growth stage than the earlier stages in both experiments, there was no apparent relationship between dark respiration rates and ambient or leaf temperatures, nor was there any indication that evolution of CO₂ measured in this way

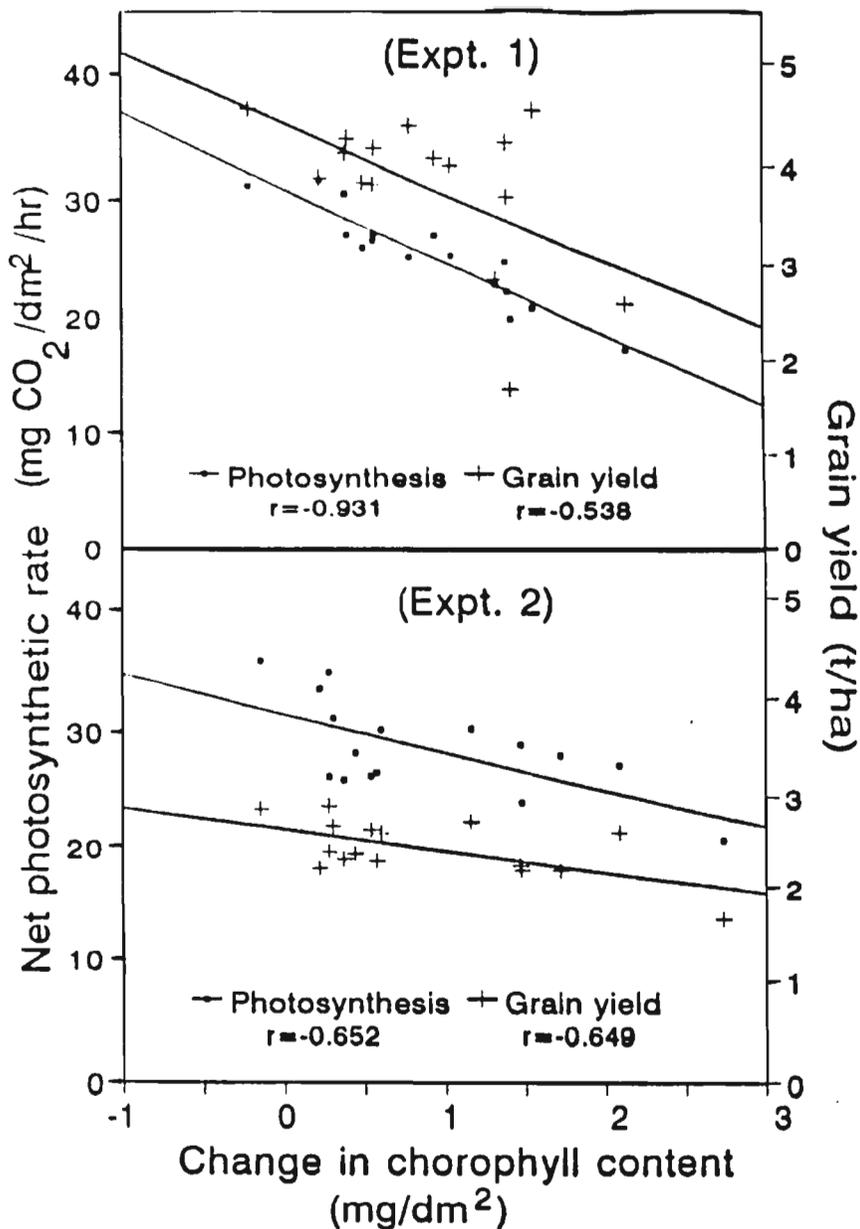


Figure 2. Regression of grain yield and net photosynthesis for 16 wheat genotypes on the change in chlorophyll content from anthesis to post-anthesis in Expt. 1, and from booting to post-anthesis in Expt. 2. Each point represents a genotype and is the average of three measurements and four sampling times (r is the correlation coefficient).

was related to genetic differences in heat tolerance (Table 4). Grain respiration may be more important in grain dry weight reduction (Wardlaw et al. 1980).

Potential selection criteria for heat tolerance

In theory, the variation in a genotypes' photosynthetic rate at high temperature could be used as a selection criterion for heat tolerance provided there is a positive correlation between the photosynthetic rate and productivity. Despite the fact that dry matter production is generally highly correlated with net photosynthetic rate (Zelitch, 1982), it

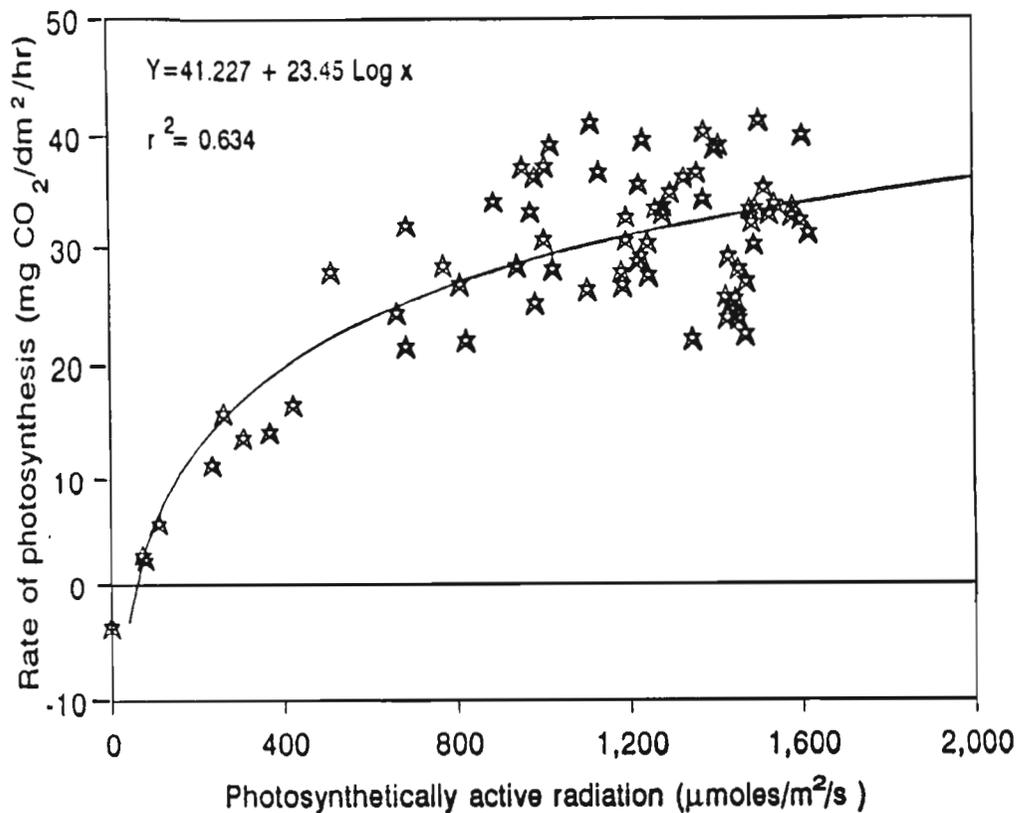


Figure 3. Regression of rate of photosynthesis of wheat flag leaves on incident photosynthetically active radiation (PAR). Each point represents the mean of 16 genotypes measured in different repetitions (3), different developmental stages (3), and different times of day (4), in Expts. 1 and 2, Tlaltizapan, Mexico, 1991-92.

has been stated by Gifford (1987) that, after years of work aimed at demonstrating positive correlations between photosynthesis and yield, no new variety has ever been selected based on the conscious incorporation of a yield-enhancing photosynthetic attribute. One possible explanation may be the fact that, before adopting a new screening trait, most breeders require evidence of a good correlation between the trait of interest and the performance of a random population in relevant field environments. While other studies have not provided such information, this work was conducted with 16 genotypes that were simultaneously being evaluated for their performance in seven international hot, wheat growing environments, including the experimental site (Reynolds 1994). Rate of photosynthesis was favorably correlated with yield in five of the seven environments. Another reason why photosynthetic traits may not be popular in breeding programs is likely to be the fact that photosynthesis is not a simple parameter to measure and is therefore not amenable to the screening of large numbers of progeny. Nonetheless, the results of this study do support two potential criteria for screening for heat tolerant germplasm, namely leaf chlorophyll content, and leaf temperature at least in hot, dry environments. Leaf chlorophyll content measured during grain-filling was significantly correlated with yield (Table 4), and the relationships between chlorophyll loss during the growth cycle and photosynthetic rate and yield (Figure 2) suggest a causal relationship with heat tolerance. Chlorophyll content, or stay green as it is often referred to, is a

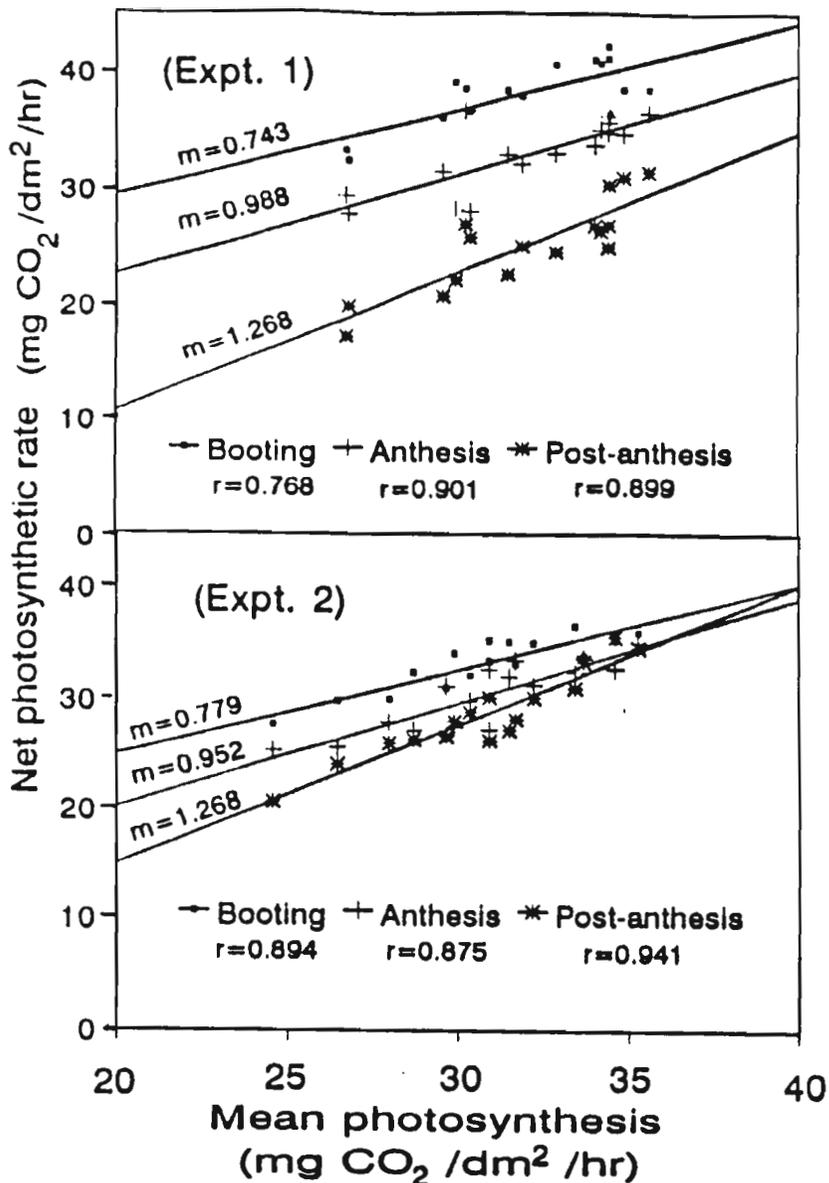


Figure 4. Regression of net photosynthetic rate at three growth stages on the average value of photosynthesis over the three stages for 16 wheat genotypes planted in December (Expt. 1) and March (Expt. 2). Each point represents a genotype and is the mean of three replications and four sampling times throughout the day (r is the correlation coefficient and m is the gradient of the fitted slope).

selection criterion that is already used to select for heat tolerance in CIMMYT's breeding work (Kohli et al. 1991). It is a characteristic that is very easy to estimate visually, and can be measured rapidly with a self-calibrating chlorophyll meter. Leaf temperature, which also correlated with photosynthetic rate and stomatal conductance as well as yield (Table 5), can be measured rapidly using an infrared thermometer, which integrates the temperature of the leaf canopy. Canopy temperature has already been shown to correlate with yield in the experimental environment (Reynolds 1994), and further work has established that genotypic differences in the trait are best expressed in the afternoon, when vapor pressure deficits are highest (Balota et al. 1993).

This study showed that the photosynthetic rate of wheat genotypes grown under high temperature field conditions varies greatly and is significantly associated with grain yield. The associations found between net photosynthesis, stomatal conductance, chlorophyll content, plant development and grain yield, contribute significantly to our understanding of the mechanisms determining potential productivity in superior germplasm under hot conditions.

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Appendix 1. Analysis of variance for photosynthetic rates of 16 wheat genotypes in a randomized complete block design, Tlaltizapan, Mexico, 1991-92.

Source of variation Pr>F***	Degrees of freedom	Pr>F*	Pr>F**
Genotypes (G) 0.0001	15	0.0001	0.0001
Date (D) 0.0001	1	0.0017	
Stage (S) 0.0001	2	0.0001	0.0001
Time (T) 0.0001	1	0.0005	0.2489
D*G	15	0.5640	
D*S	2	0.0001	
D*T	1	0.0001	
D*S*G	30	0.7137	
D*S*T	15	0.7069	
S*G 0.2854	30	0.0189	0.0001
S*T 0.0001	2	0.2642	0.0002
G*T 0.7344	15	0.3621	0.9413
S*G*T 0.4701	30	0.9861	0.9995
D*S*G*T	30	0.9825	

* Analyzed using two planting dates and two sampling times (10:00 and 11:00).

** Expt. 1 with four sampling times (10:00, 11:00, 12:00, and 13:00).

*** Expt. 2 with four sampling times (10:00, 11:00, 15:00 and 16:00).

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