



Genotypic differences in utilization of assimilate sources during maturation of wheat under chronic heat and heat shock stresses

Utilization of assimilate sources by wheat under heat stresses

J. Yang¹, R.G. Sears¹, B.S. Gill² & G.M. Paulsen^{1,*}

Departments of Agronomy¹ and Plant Pathology², Kansas State University, Manhattan, KS 66506-5501 U.S.A.
(*Author for correspondence: E-mail: gmpaul@ksu.edu)

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Summary

Heat stress from chronic, prolonged exposure up to 32 °C or heat shock from brief exposure to 33 °C and above alters the source of assimilates for grain growth of wheat (*Triticum aestivum* L.). Our objectives were to identify genotypes that resist chronic heat stress and heat shock and to determine the relative contributions of photosynthesis and stem reserves to grain filling under both conditions. Twenty-eight genotypes were grown in controlled environments at 20/15 and 30/25 °C day/night in light and darkness during maturation in the first experiment, and six genotypes were grown in light at the same temperatures and at 40/35 °C followed by 20/15 or 30/25 °C in the second experiment. Heat susceptibility indices (HSI) were calculated from grain yields of the genotypes in both experiments. The ratio of chlorophyll variable fluorescence to maximum fluorescence (Fv/Fm), a measure of the stability of photosynthesis, and carbohydrate reserves in the stems were measured in the second experiment. Photosynthesis provided 63 and 65% of assimilates in the grain at 20/15 and 30/25 °C, respectively, but both stable photosynthesis in some genotypes and high content of reserves in other genotypes were associated with low susceptibility to stress. The Fv/Fm ratio was decreased by heat shock and returned to normal values in tolerant genotypes when the treatment was followed by 20/15 °C but not 30/25 °C. Grain yield was highly correlated among 20/15, 30/25, and 40/35 °C followed by 20/15 °C treatments, suggesting that similar plant traits were involved. We conclude that assimilates from either stable photosynthesis or high reserve levels provided for high grain yields during heat stress. Combining the two traits could improve heat tolerance of wheat but might not be feasible if other traits are impeded.

Abbreviations: Fv/Fm – ratio of chlorophyll variable fluorescence to maximum fluorescence;
HSI – heat susceptibility index; WSC – water-soluble carbohydrates.

Introduction

High temperature during maturation constrains productivity of wheat in many regions (Reynolds et al., 1994; Wardlaw & Wrigley, 1994; Porter & Gawith, 1999). Yields are reduced 3 to 4% per 1 °C above the optimum of 15 to 20 °C for grain-filling (Chowdhury & Wardlaw, 1978). Normal high temperature of 30 to 40 °C in affected regions may decrease harvests by 50% or more every year (Paulsen, 1994).

Stress by high temperature occurs either as chronic exposure to prolonged, moderately high temperatures up to 32 °C or as heat-shock from rapid but relatively brief exposure to 33 °C and above (Paulsen, 1994; Savin et al., 1997). Most research has focused on determining plant responses and identifying genotypes that resist chronic stress (Wardlaw et al., 1989b; Savin et al., 1997). Less is known about the effects of heat shock, although its importance is indicated by the special designations given to the combination of elevated temperature, low humidity, and high wind velocity that

often occurs where wheat is grown. These weather conditions include the *Sirocco* in North Africa, the *Larrechi* in Spain, the *Sukhovei* in Russia, and the *Gan Re Feng* in China (Paulsen, 1994).

Assimilates for growth of grain come from current photosynthesis and reserve carbohydrates in stems (Hunt, 1979; Kühbauch & Thome, 1989; Hossain et al., 1990; Blum, 1998). Injury to wheat from high temperature during maturation alters the relative contributions of the two sources to grain-filling. Photosynthesis provides 90 to 95% of the carbohydrates in wheat grain under optimum temperature conditions (Evans et al., 1975). However, high temperature directly damages the photosynthetic apparatus and reduces the rate and duration of assimilation (Paulsen, 1994). Depending on the reduction in photosynthesis, stress may increase the contribution of stem reserves from 6 to 100% of the mass of grain (Blum, 1998).

Genotypes of wheat differ considerably in effects of temperature on photosynthesis and utilization of reserves for filling of grain. In a range of cultivars from different regions, the rate of photosynthesis fell 11 to 32% and the duration of activity declined 0 to 40% when the temperatures were increased from 22 to 32 °C (Al-Khatib & Paulsen, 1990). The contribution of stem reserves to grain filling varied nearly 5-fold between resistant and susceptible cultivars under control and stress conditions (Blum et al., 1994). High carbohydrate concentration, large stem mass, rapid senescence, and extensive remobilization favored grain-filling from reserves but were antithetical to high yields in favorable environments (Blum, 1998).

Many regions need wheat cultivars that are capable of high yields when the weather is beneficial but produce stable yields when conditions are adverse. The objectives of these experiments were to identify genotypes that have high yield potential in both favorable and high temperature environments and to determine the relative contributions of current photosynthesis and stem reserves under both conditions. The responses of a range of genotypes representing adapted cultivars and lines of known resistance to chronic high temperature and heat-shock were investigated.

Table 1. Sources and seasonal adaptation of 28 bread wheat genotypes evaluated for contributions of photosynthesis and stem reserves to grain yield at 20/15 and 30/25 °C in light and darkness

Genotype	Source	Adaptation
Ventnor	Australia	Winter
Debeira	Sudan	Spring
Newton	USA	Winter
Trigo 3	Philippines	Spring
Xiao Yie 6	China	Winter
Len	USA	Spring
Trigo 1	Philippines	Spring
Seri 82	Mexico	Spring
Glennson 81	Mexico	Spring
Kanchan	Bangladesh	Spring
TAM 105	USA	Winter
Pavon 76	Mexico	Spring
Genaro 81	Mexico	Spring
Siete Cerros 66	Mexico	Spring
Anza 87	Sudan	Spring
Nesser	Jordan	Spring
Chisholm	USA	Winter
Banks	Australia	Spring
Fang 60	Thailand	Winter
Bacanora	Mexico	Spring
Daws	USA	Winter
Nacozari	Mexico	Spring
Sonora 64	Mexico	Spring
CIANO 79	Mexico	Spring
IP4	Burma	Spring
Chinese Spring	China	Spring
Sturdy	USA	Winter
Karl 92	USA	Winter

Materials and methods

Experiment I – Genotypic susceptibility to chronic heat stress in relation to assimilates

Twenty-eight genotypes of spring and winter wheat were selected to represent different regions of the world (Table 1). Several genotypes exhibited extreme differences in high-temperature tolerance in previous studies (Wardlaw et al., 1989a, 1998b; Al-Khatib & Paulsen, 1990; Moffatt et al., 1990a, 1990b), and the others were entries from broad geographical areas in the International Wheat and Maize Improvement Center (CIMMYT) International Heat Stress Genotype Experiment (IHSGE) (Reynolds et al., 1994). All of the genotypes were semidwarf except Trigo 1, Trigo 3,

and Chinese Spring, which were tall. Mean heights were 63.2 cm for semidwarf genotypes and 95.3 cm for tall genotypes.

Seeds of the 28 genotypes were germinated on moistened filter paper in Petri dishes at 25 °C until the seedling radicals were visible. The seedlings were vernalized at 5 °C for 6 weeks and transplanted into 12 × 15-cm pots containing equal volumes of loam soil, sand, and peat moss. Each pot held two seedlings. The medium was fertilized (Peters Professional Fertilizer, W.R. Grace and Co., Fogelsville, PA) to supply 100 mg N, 43 mg P, and 83 mg K per pot at transplanting, jointing, and early anthesis. Imidacloprid and propiconazole were applied to the plants at recommended rates to control insects and fungal diseases, respectively. One seedling was removed from each pot after the early jointing stage.

The plants were grown until 10 days after anthesis in controlled environment chambers (Model PGW-36, Conviron, Pemsina, ND) set at 20/15 °C day/night, 50/70% relative humidity, 16-hour photoperiod, and illumination of 420 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the top of the leaves. The spike of the primary culm of each plant was labeled when the first anthers were extruded, which was considered the date of anthesis, and only the primary culm was used for measuring yield to avoid confounding from differences in developmental stages among tillers.

Differential temperature and light treatment regimes were imposed on the plants at 10 days after anthesis. The regimes were Treatment 1 (Control), 20/15 °C and 16-hour photoperiod of 420 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Treatment 2, 20/15 °C and continuous darkness; Treatment 3, 30/25 °C and 16-hour photoperiod of 420 $\mu\text{mol m}^{-2} \text{s}^{-1}$; and Treatment 4, 30/25 °C and continuous darkness. The genotypes were arranged in randomized complete block designs within each regime, and the genotype-treatment combinations were replicated three times.

The pots containing the plants were placed in shallow saucers, which were filled daily with water to prevent moisture deficiency. When plants reached physiological maturity as indicated by chlorosis of the glumes, water was withheld and the grain was ripened at 30 °C for 2 weeks. The grain was then threshed manually from the primary spikes and weighed.

Heat susceptibility indices for grain yield of each genotype were calculated as $\text{HSI} = [(1 - Y/Y_p)/D]$, where Y = yield at 30/20 °C, Y_p = yield at 20/15 °C, D = stress intensity = $1 - X/X_p$, X = mean Y of all genotypes, and X_p = mean Y_p of all genotypes (Fischer

& Maurer, 1978). Separate HSI values were calculated for grain yield in light, yield in light minus yield in darkness, and yield in darkness to approximate total susceptibility to high temperature and the relative susceptibility of the proportions of grain yield that result from photosynthesis and reserves, respectively. The results are only approximate, since darkening the plants might overestimate the contribution of stem reserves to assimilate accumulation in light (Blum, 1998). Genotypes were considered highly tolerant at $\text{HSI} \leq 0.500$, moderately tolerant at $\text{HSI} > 0.500$ to ≤ 1.000 , and susceptible at $\text{HSI} > 1.000$ (Khanna-Chopra & Viswanathan, 1999). Phenotypic relationships among the parameters were measured by Spearman rank correlation analysis.

Experiment II – Genotypic susceptibility to chronic heat stress and heat shock in relation to assimilates

Six genotypes that differed in HSI and grain yield in light at 30/25 °C in Experiment I were selected to investigate responses to heat shock. Seeds of the genotypes, Ventnor, Karl 92, Debeira, Sonora, Trigo 3, and Chinese Spring, were germinated, and the plants were vernalized at 5 °C and grown at 20/15 °C until 10 days after anthesis as described in Experiment I.

At 10 days after anthesis, the plants were subjected to four treatments: Treatment 1 (Control), 20/15 °C, 16/8 hour day/night; Treatment 2, 30/25 °C, 16/8 hour day/night; Treatment 3, 40/35 °C, 16/8 hour day/night for 3 days followed by 20/15 °C, 16/8 hour day/night until maturity; and Treatment 4, 40/35 °C, 16/8 hour day/night for 3 days followed by 30/25 °C, 16/8 hour day/night until maturity. The treatments represented optimum temperature, chronic heat stress, heat shock followed by optimum temperature, and heat shock followed by chronic heat stress, respectively. The genotypes and temperature treatments were arranged in randomized complete block designs and replicated three times. The plants were grown to maturity in the same controlled environment chambers with the same light, humidity, and watering regimes as described in Experiment I.

The ratio of chlorophyll variable fluorescence to maximum fluorescence (F_v/F_m), an indicator of the stability of the photosynthetic apparatus to high temperature (Moffatt et al., 1990b), was measured immediately before the treatments were imposed, immediately after the heat shock treatments ended, and 3 days after the treatments ended (10, 13, and 16 days after anthesis). Measurements were taken 3 to 4 cm

Table 2. Grain yield and heat susceptibility index (HSI) of 28 bread wheat genotypes grown at 20/15 and 30/25 °C under 16/8-hour day/night (light) and under darkness. Values of HSI from yield in light, light minus darkness, and darkness approximate relative susceptibility to high temperature of assimilates from photosynthesis plus stem reserves, photosynthesis, and stem reserves, respectively

Genotype	Grain yield				HSI		
	Light		Darkness		Light	Light – darkness	Darkness
	20/15 °C	30/25 °C	20/15 °C	30/25 °C			
	(g/spike)						
Ventnor	1.742	1.562	0.662	0.395	0.375	-0.372	1.494
Debeira	1.787	1.595	0.431	0.356	0.396	0.402	0.642
Newton	1.627	1.417	0.599	0.568	0.456	0.808	0.189
Trigo 3	1.775	1.530	0.985	0.722	0.495	-0.106	0.988
Xiao Yie 6	1.413	1.191	0.756	0.706	0.572	1.216	0.245
Len	1.397	0.991	0.184	0.195	0.596	1.595	-0.212
Trigo 1	1.361	1.100	0.686	0.486	0.677	0.421	1.078
Seri 82	1.361	1.019	0.592	0.523	0.679	1.647	0.432
Glennson 81	1.135	0.921	0.455	0.421	0.682	1.228	0.278
Kanchan	1.051	0.843	0.351	0.321	0.719	1.179	0.316
TAM 105	1.309	1.045	0.386	0.292	0.727	0.853	0.908
Pavon 76	1.198	0.947	0.321	0.195	0.743	0.662	1.453
Genaro 81	1.496	1.160	0.673	0.524	0.810	1.053	0.820
Siete Cerros 66	1.223	0.942	0.187	0.168	0.829	1.171	0.384
Anza 87	1.450	1.123	0.693	0.519	0.829	0.937	0.931
Nesser	1.367	1.110	0.608	0.498	0.899	0.898	0.672
Chisholm	1.355	1.012	0.500	0.392	0.924	1.274	0.803
Banks	1.444	1.028	0.692	0.347	1.028	0.440	1.845
Fang 60	1.379	0.983	0.415	0.210	1.050	0.919	1.829
Bacanora	1.451	1.209	0.192	0.284	1.058	1.233	-1.787
Daws	1.291	0.909	0.323	0.273	1.058	1.590	0.574
Nacozari	1.460	1.020	0.675	0.598	1.081	2.148	0.420
Sonora 64	1.202	0.822	0.299	0.134	1.140	1.104	2.045
CIANO 79	1.505	1.022	0.491	0.451	1.156	2.029	0.300
IP4	1.452	0.980	0.748	0.365	1.167	0.589	1.896
Chinese Spring	1.272	0.851	0.597	0.196	1.190	0.140	2.486
Sturdy	1.607	1.028	0.598	0.214	1.288	0.898	2.377
Karl 92	1.456	0.892	0.518	0.325	1.393	1.834	1.380
Mean	1.413	1.080	0.522	0.381	0.858	0.992	0.885
LSD _{0.05}	0.452	0.203	0.124	0.078	0.099	0.214	0.268

from the base of the abaxial surface of flag leaves with a Plant Efficiency Analyzer (Hansatech Instruments, Ltd., King's Lynn, UK). Primary stems of the plants were sampled on the dates that chlorophyll fluorescence was measured and at maturity for determining water-soluble carbohydrates. The samples were dried at 80 °C for 48 hours, weighed, and ground to 0.5-mm size. Water-soluble carbohydrates were extracted as described by Nalewaja & Smith (1963) and assayed by the procedure of Dubois et al. (1956).

Water was withheld from the plants at physiological maturity and the grain was ripened for 2 weeks, threshed, and weighed. Heat susceptibility indices were calculated from yields of the primary stems for genotypes subjected to the chronic stress and heat-shock treatments relative to the control treatment (Fischer & Maurer, 1978).

Table 3. Spearman (phenotypic) correlation coefficients among grain yields at 20/15 and 30/25 °C in light and darkness and heat susceptibility indices (HSI) for grain assimilates from photosynthesis plus stem reserves (Total), photosynthesis, and stem reserves of 28 bread wheat genotypes

Variable	Yield 20/15 light	Yield 30/25 light	Yield 20/15 Dark	Yield 30/25 Dark	HSI Total	HSI Photosynthesis	HSI Reserves
	r						
Yield 20/15 Light	1.000	0.848**	0.514*	0.425*	-0.267	-0.356	0.029
Yield 30/25 Light		1.000	0.414*	0.519*	-0.671**	-0.523*	-0.208
Yield 20/15 Dark			1.000	0.760**	-0.122	-0.386	0.352
Yield 30/25 Dark				1.000	-0.410	-0.008	-0.277
HSI Total					1.000	0.406	0.338
HSI Photosynthesis						1.000	-0.444*
HSI Reserves							1.000

*, ** significant at $P = 0.05$ and 0.01 , respectively.

Statistical procedures

Data were analyzed by general linear model (GLM) procedures, and means were compared by LSD at $\alpha = 0.05$. Spearman correlation analyses of the parameters were conducted where appropriate. All statistical procedures were performed with SAS (1995).

Results

Responses to chronic heat stress

Grain yield of all 28 genotypes averaged 1.413 g at 20/15 °C and 1.080 g at 30/25 °C under 16/8 hour day/night, a reduction of 23% with high temperature (Table 2). Yields of four genotypes – Debeira, Trigo 3, Ventnor, and Newton – exceeded the others in both regimes. Darkness reduced mean yields to 0.522 g at 20/15 °C and 0.381 g at 30/25 °C, or more than 60% compared with yields in light at the same temperatures. Yields of Trigo 3 and Xiao Yie 6 were superior to most of the other genotypes in darkness.

Values of HSI for grain yield in light ranged from 0.375 to 1.393 (Table 2). Only four genotypes – Ventnor, Debeira, Newton, and Trigo 3 – produced high yields in light, had $HSI < 0.500$, and were considered to be highly tolerant of high temperature. Eleven genotypes were rated as susceptible. Values of HSI for grain yield in light minus grain yield in darkness, an estimate of the susceptibility of photosynthesis to high temperature, were extremely low in Ventnor and Trigo 3 and were high in Karl 92 and Nacozari. When the plants matured in darkness and depended on stem re-

serves for yield, HSI was low in Bacanora and was high in Sturdy and Chinese Spring.

A highly significant correlation ($r = 0.848^{**}$) between yields in light at 20/15 and 30/25 °C suggested that similar features were involved in productivity of the 28 genotypes under the two regimes (Table 3). Yields in light at 20/15 °C were not related to HSI, but yields in light at 30/25 °C were correlated inversely with total HSI for photosynthesis. Although yields in light at 30/25 °C were not associated with HSI for reserves, their highly positive correlations with yields in darkness at both temperatures implied that reserves were important.

Responses to chronic heat stress and heat shock

Ratios of Fv/Fm indicated that stability of the photosynthetic apparatus of the six genotypes differed in responses to chronic heat stress but not to heat shock (Table 4). Little change occurred in any of the genotypes at 20/25 °C between 10 and 16 days after anthesis. At 30/25 °C, however, values were nearly constant in Ventnor and Debeira but were significantly lower in the other genotypes after 6 days of treatment. Heat shock of 40/35 °C imposed between 10 and 13 days after anthesis lowered the ratios in all six cultivars immediately after the treatment ended. After three additional days (16 days after anthesis), the ratios returned to their former levels in Ventnor and Debeira but not in the other genotypes when the plants were held at 25/15 °C. When the plants were subjected to chronic stress of 30/25 °C after the heat shock treatment, Fv/Fm ratios remained low in all the genotypes.

Table 4. Ratio of chlorophyll variable fluorescence to maximum fluorescence (Fv/Fm) of six bread wheat genotypes before temperature treatments at 10 days after anthesis (10 DAA), after treatment at 20/15 or 30/25 °C for 6 days (16DAA), after treatment at 40/35 °C for 3 days (13DAA), and after treatment at 40/35 °C for 3 days followed by 20/15 or 30/25 °C for 3 days (16DAA)

Genotypes	10 DAA	16 DAA		13 DAA	40/35 16 DAA	
	(Before treatment)	20/15	30/25	40/35	20/15	30/25
	Fv/Fm					
Ventnor	0.73	0.70	0.70	0.62	0.69	0.63
Debeira	0.74	0.73	0.73	0.63	0.72	0.60
Trigo 3	0.71	0.72	0.65	0.59	0.61	0.61
Sonora 64	0.73	0.74	0.67	0.61	0.60	0.61
Chinese spring	0.71	0.70	0.64	0.60	0.59	0.58
Karl 92	0.70	0.69	0.63	0.60	0.63	0.59
Mean	0.72	0.71	0.67	0.61	0.64	0.60
LSD _{0.05}	ns	0.04	0.04	ns	0.07	ns

Table 5. Water-soluble carbohydrate concentrations in stems of six bread wheat genotypes before treatments at 10 days after anthesis (10 DAA), after treatment at 20/15 or 30/25 °C for 6 days (16 DAA), after treatment at 40/35 °C treatment for 3 days (13 DAA), after treatment at 40/35 °C for 3 days followed by 20/15 or 30/25 °C for 3 days (16 DAA), and at maturity for all treatments

Genotype	Before treatment 10 DAA	16 DAA		13 DAA	40/35 16 DAA		Maturity			
		20/15	30/25	40/35	20/15	30/25	20/15	30/25	40/35	
(mg/g)										
Ventnor	193	281	212	173	154	155	37	41	38	101
Debeira	124	179	148	110	112	120	26	29	32	59
Trigo 3	217	273	183	201	158	164	28	35	42	89
Sonora 64	152	230	162	131	122	123	40	34	31	86
Chinese Spring	152	183	120	150	132	140	31	27	30	90
Karl 92	157	210	150	142	125	131	33	32	36	92
Mean	166	226	162	151	134	139	33	33	35	86
LSD _{0.05}	21	18	17	20	23	15	6	7	9	10

Reserve carbohydrates were high in Trigo 3 and low in Debeira relative to the other genotypes when temperature treatments were imposed at 10 days after anthesis (Table 5). The concentration continued to increase in all genotypes at 20/15 °C until 16 days after anthesis. However, growth at 30/25 °C slowed the increase of reserve carbohydrates in Ventnor, Debeira, and Sonora and slightly decreased the concentration in Trigo 3, Chinese Spring, and Karl 92. Heat shock at 40/35 °C for 3 days decreased reserves in most genotypes immediately after the treatment ended at 13 days after anthesis. Holding the plants at 20/15 or 30/25 °C

for 3 days after the 40/35 °C treatment reduced levels an additional amount in all genotypes except Debeira. At maturity, reserve concentrations were low in all genotypes except in plants that were subjected to heat shock followed by 30/25 °C, which were substantially higher than in the other regimes.

Grain yields differed considerably among genotypes and temperature treatments (Table 6). Three genotypes – Ventnor, Debeira, and Trigo 3 – yielded high relative to the other genotypes at 20/15 and 30/25 °C. Heat shock of 40/35 °C followed by 20/15 °C reduced productivity of all genotypes, but yields of the same

Table 6. Grain yield and heat susceptibility index (HSI) of six bread wheat genotypes grown at 20/15, 30/25, and 40/35 followed by 20/15 or 30/25 °C during maturation

Genotype	Grain yield			HSI			
	20/15	30/25	40/35	30/25	40/35		
			20/15		30/25	20/15	30/25
	(g/spike)						
Ventnor	1.84	1.65	1.45	0.70	0.426	0.800	1.081
Debeira	1.85	1.58	1.26	0.67	0.602	1.204	1.113
Trigo 3	1.87	1.62	1.52	0.86	0.551	0.706	0.942
Sonora 64	1.37	0.89	0.90	0.70	1.444	1.295	0.853
Chinese Spring	1.55	0.87	1.13	0.63	1.808	1.023	1.035
Karl 92	1.46	0.92	1.05	0.68	1.525	1.060	0.932
Mean	1.66	1.26	1.22	0.71	1.06	1.01	0.99
LSD _{0.05}	0.22	0.49	0.17	0.11	0.365	0.231	0.124

three genotypes exceeded the others. However, heat shock followed by 30/25 °C greatly diminished differences among the six genotypes, and only Trigo 3 yielded more than the others.

Values of HSI at 30/25 °C relative to 20/15 °C were higher but followed the same pattern as described in the first experiment (Table 6). The three genotypes Ventnor, Debeira, and Trigo 3, that yielded high at both temperatures had low HSI ratings. Treatment at 40/35 followed by 20/15 °C raised HSI values of the three genotypes, particularly Debeira, but lowered the HSI ratings of Sonora 64, Chinese Spring, and Karl 92. High temperature of 30/25 °C following heat shock increased HSI of the genotypes that were tolerant or moderately tolerant at 30/25 °C alone and decreased HSI of the others. Values only ranged from 0.853 for Sonora to 1.113 for Debeira.

Grain yields of the six genotypes correlated significantly among all treatments except 20/15 °C and 40/35 °C followed by 30/25 °C (Table 7). None of the yields were related to Fv/Fm (data not shown). However, correlations between yields and the content of carbohydrate reserves at 10 days after anthesis increased from 0.395 (ns) to 0.796** as the severity of the treatments increased from the control to the 40/35 °C followed by 30/25 °C treatment. A similar but less distinct trend was evident in the relationship between grain yields and the amounts of reserve carbohydrates used between 10 days after anthesis and maturity. Those correlations ranged from 0.498* at 20/15 °C, 0.390 (ns) at 30/25 °C, 0.642* at 40/35 °C followed by 20/15 °C, to 0.936** at 40/35 °C followed by 30/25 °C. Yields at 30/25 °C and 40/35 °C followed

by 20/15 °C were correlated negatively with HSI values at the same treatments, -0.983^{**} , and -0.860^{**} , respectively. Values of HSI at 30/25 °C and 40/35 °C followed by 20/15 °C were also correlated negatively with the content of reserve carbohydrates at 10 days after anthesis and the amount of reserves used between 10 days after anthesis and maturity. Positive correlations between HSI at 40/35 °C followed by 30/25 °C and grain yields under the other treatments were noted as well.

Discussion

The relative importance of assimilates from photosynthesis and reserves for grain growth of wheat was estimable from yield of plants grown in light and darkness during maturation. Although the caveat that the contribution from reserves might be overestimated should be considered (Blum, 1998), the effect appeared to be minor. Mean yields of the 28 genotypes of 1.413 and 0.522 g/spike in light and darkness, respectively, at 20/15 °C indicated that 63% of the grain mass was from photosynthesis and 37% from reserves. The share from photosynthesis was similar to that reported in other studies and to the mean decrease in yield from defoliating plants (Borrell et al., 1993; Fokar et al., 1998).

High temperature greatly reduced the photosynthetic rate of wheat (Al-Khatib & Paulsen, 1990), but it had little effect on the relative sources of assimilates for grain growth. Mean yields of the 28 genotypes of 1.080 and 0.381 g/spike in light and darkness, respectively, at 30/25 °C showed that 65% was from pho-

Table 7. Spearman (phenotypic) correlation coefficients among grain yields at 20/15, 30/25, 40/35 followed by 20/15, and 40/35 followed by 30/25 °C; water soluble carbohydrate (WSC) content at 10 days after anthesis (10DAA); WSC used between 10 DAA and maturity for each treatment; and heat susceptibility index (HSI) of grain yield for each stress treatment relative to the 20/15 °C treatment of six bread wheat genotypes. Water soluble carbohydrate used was calculated as the difference in total content in plants between 10 DAA and maturity

Variable	Yield 20/15	Yield 30/25	Yield 40/35- 20/15	Yield 40/35- 30/25	WSC 10 DAA	WSC 20/15	WSC 30/25	WSC 40/35- 20/15	WSC 40/35- 30/25	HSI 30/25	HSI 40/35- 20/15	HSI 40/35- 30/25
Yield 20/15	1.000	0.958**	0.935**	0.448	0.395	0.498*	0.382	0.356	0.621*	-0.891**	-0.627*	0.683*
Yield 30/25		1.000	0.891**	0.521*	0.431*	0.501*	0.390	0.390	0.654*	-0.983**	-0.564*	0.557*
Yield 40/35–20/15			1.000	0.597*	0.675*	0.752**	0.668*	0.642*	0.800*	-0.821**	-0.860**	0.514*
Yield 40/35–30/25				1.000	0.796**	0.829**	0.802**	0.777**	0.936**	-0.544*	-0.627*	-0.340
WSC 10 DAA					1.000	0.987**	0.992**	0.996**	0.912**	-0.479*	-0.930**	-0.125
WSC 20/15						1.000	0.991**	0.978**	0.947**	-0.372	-0.901**	-0.215
WSC 30/25							1.000	0.991**	0.913**	-0.388	-0.875**	-0.230
WSC 40/35–20/15								1.000	0.896**	-0.643*	-0.836**	-0.095
WSC 40/35–30/25									1.000	-0.431*	-0.982**	0.207
HSI 30/25										1.000	0.502*	-0.452*
HSI 40/35–20/15											1.000	-0.196
HSI 40/35–30/25												1.000

*, ** significant at $P = 0.05$ and 0.01 , respectively.

tosynthesis and 35% from reserves, nearly the same as at the lower temperature. The lower rate of photosynthesis was apparently matched by the increased respiratory loss of reserves at high temperature, which was indicated by the mean decrease in yield in darkness from 0.522 to 0.381 g/spike between 20/15 and 30/25 °C. Since the relative contributions of photosynthesis and reserves to grain growth are a genetically controlled constitutive trait (Blum, 1998), temperature would be expected to have little effect.

The mean contributions of photosynthesis and reserves to grain yield obscured considerable differences among the 28 genotypes. The proportion of assimilates from photosynthesis ranged from 24% for Trigo 3 and Xiao Yie 6 to 87% for both Len and Bacanora at 20/15 °C. At 30/25 °C, the proportion ranged from 41% for Xiao Yie 6 and Nacozari to 80% or greater for Len, Siete Cerros 66, and Sonora 64. The variation, while typical, was greater than the range reported in other studies that had fewer genotypes (Wardlaw et al., 1989a, 1989b; Moffatt et al., 1990a, 1990b; Reynolds et al., 1994).

Low susceptibility to high temperature came from sustained contributions of either photosynthesis or reserves to grain growth. Among the four genotypes that had low HSI values and were rated tolerant to high temperature, the share of assimilates from photosynthesis ranged from 45 and 53% for Trigo 3 to 76 and 78% for Debeira at 20/15 and 30/25 °C, respectively.

The variation in the proportion of assimilates from the two sources in Experiment I was explained by the content of carbohydrates measured in the stems of the plants at the onset of the treatments in Experiment II. The high content of reserves in Trigo 3 likely reduced dependence on photosynthesis for assimilates, whereas the low level in Debeira made photosynthesis critical for grain growth. The importance of reserves to low HSI values was further shown by their significant correlations in Experiment II. Tall stature may have complemented the contribution of stem reserves to low HSI (Blum, 1998). However, the range in HSI values among semidwarf and tall genotypes indicated that plant height was not a critical factor.

Many effects of heat shock at 40/35 °C followed by 20/15 °C were similar to those of prolonged, chronic stress at 30/25 °C. Most of the genotypes that performed well at 30/25 °C had superior yield, low HSI values, and similar correlations with other variables at 40/35 °C followed by 20/15 °C. The Fv/Fm ratios suggested that returning the plants to the favorable conditions enabled the photosynthetic system to recover from any injury that occurred during the heat shock, particularly in Ventnor and Debeira, the genotypes that depended most on current assimilates for grain growth. However, the effects of heat shock followed by high temperature of 30/25 °C were quite different. No recovery of photosynthesis was evident in Ventnor and Debeira. Instead, high correlation coef-

ficients of yields with contents of carbohydrate at 10 days after anthesis and the amount of carbohydrate used until maturation suggested that reserves were very important. A similar treatment of 40 °C in barley for 5 days halted grain growth, possibly by irreversibly inactivating enzymes involved in starch synthesis (Savin et al., 1997).

High correlations between yield of plants grown at 20/25 and 30/25 °C in Experiment I suggested that resistance to high temperature was unlikely to impose a penalty on performance under favorable conditions. The results also implied that similar traits were involved in productivity in the two environments. The close relationship might be expected of genotypes that were developed primarily for unfavorable conditions in Asia, Australia, and North America. However, it was unlike the contrary association between yield potential and resistance to drought and defoliation found in other studies (Blum, 1998). Significant correlations between yields at 20/15 °C and 40/35 °C followed by 25/15 °C also indicated that resistance to brief heat shock did not penalize yield potential. However, some of the relationships expressed by plants grown at 40/35 °C followed by 30/25 °C were worrisome, particularly the positive correlations between HSI values and yields of plants grown under the other regimes. The positive correlations implied that resistance to the most severe conditions might be incompatible with yield potential under favorable or moderately unfavorable conditions.

Several implications for improving wheat for high-temperature regimes were evident. Apparently, the source of assimilates, whether from photosynthesis or reserves, for grain-filling was not critical. Either stable photosynthesis, as in Ventnor, or a high level of reserves, as in Trigo 3, at the onset of stress supported high yields. Combining the two traits into one genotype would be desirable but might not be possible. Photosynthesis might be inhibited by high levels of reserves (Wardlaw, 1993), and the slow senescence that is needed for a steady rate of photosynthesis might deter mobilization of reserve carbohydrates for export to grain (Blum, 1998). Whatever the source of assimilates, however, it is essential that enzymes involved in incorporating carbohydrates into starch in the grain are stable at high temperature (Wardlaw & Wrigley, 1994). Combining a steady source of assimilates with a stable system for their utilization might be the most effective means of improving productivity.

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