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Growth and senescence characteristics associated with tolerance of wheat-alien amphiploids to high temperature under controlled conditions

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Summary

Tolerance of wheat (*Triticum aestivum* L.) to high temperature might be improved by introducing alien genes from amphiploids. Our objectives were to determine responses of synthetic hexaploid and octaploid amphiploid wheats to high temperature and evaluate their potential usefulness for developing improved cultivars. Thirty synthetic hexaploids from durum wheat (*T. turgidum* L.) × *Aegilops tauschii* Cos. accessions and four octaploid amphiploids from Chinese Spring wheat × different grasses were grown at 20/15 and 30/25 °C day/night during maturation. Tolerance was ascertained by two measures of senescence, leaf chlorophyll content and grain filling duration, plus grain yield and its components. Leaf chlorophyll was measured after 10 and 15 days of treatment, and grain yield was determined at maturity to calculate the heat susceptibility index (HSI), a gauge of the reduction in yield at high temperature of each line relative to all other lines. Chlorophyll content, grain filling duration, yield, and kernel weight were highly negatively correlated with HSI of the hexaploid amphiploids at 30/25 °C, but grain yield was positively correlated with HSI at 20/15 °C. The hexaploid lines might be useful for improving wheat for regions where stress from high temperature occurs frequently. Chlorophyll content and grain filling duration also were highly negatively correlated with HSI of the octaploid lines, but they would be less directly useful for improving wheat because the kernel number was reduced greatly due to unbalanced meiotic chromosomal segregation.

Abbreviations: GLM – general linear model; HSI – heat susceptibility index; LSD – least significant difference

Introduction

Genetic incorporation of heat tolerance is the most efficient way to improve productivity of wheat in high-temperature environments (Fischer & Byerlee, 1991; Ferara et al., 1994; Wardlaw & Wrigley, 1994). Genetic variation in heat tolerance was identified in domestic wheat (Wardlaw et al., 1989a, 1989b; Al-Khatib & Paulsen, 1990; Ferrara et al., 1994; Reynolds et al., 1994; Hede et al., 1999) and its wild relatives (Damania & Tahir, 1993; Waines, 1994; Sun & Xu, 1998). Grasses with the D genome had a higher survival rate in hot summer temperature than grasses with only the A or B(S) genome (Ehdaie & Waines, 1992).

Yield and/or its components are used widely as indicators of tolerance of wheat to late heat stress (Wardlaw et al., 1989a, 1989b; Reynolds et al., 1994; Khanna-Chopra & Viswanathan, 1999). However, determining yield parameters is costly in both time and resources (Reynolds et al., 1994; Hede et al., 1999), and results are questionable when the criteria are applied to primitive genotypes that perform poorly because of genetic and physiological defects (Waines, 1994; Rajaram et al., 1997; Hede et al., 1999).

Senescence, characterized by chlorosis of leaves and early maturity of grain, is a primary response of wheat to high temperature (Blum, 1988; Al-Khatib & Paulsen, 1990; Wardlaw & Wrigley, 1994). Loss of chlorophyll decreases leaf area duration, and early

Table 1. Synthetic hexaploid wheats from CIMMYT used for investigation of senescence and high temperature tolerance, identifier and origin of their *Ae. tauschii* parents, and pedigree of their durum parents

Hexaploid	*Ae. tauschii* parent		Durum parent pedigree
	Identifier	Origin	
TA4041	TA2371	Uzbekistan	Geta
TA4043	TA2385	Pakistan	Yav 2/Tez's'
TA4044	TA2389	Afghanistan	Duergand
TA4045	TA2397	Afghanistan	Chen's'
TA4047	TA2415	Afghanistan	Gr's'/Boy's'
TA4048	TA2423	Afghanistan	Sca's'
TA4049	TA2426	Afghanistan	Altar 84/Ao's'
TA4050	TA2430	Afghanistan	Gr's'/Boy's'
TA4051	TA2434	Afghanistan	Altar 84/Ao's'
TA4053	TA2452	Iran	Chen's'
TA4055	TA2456	Iran	Gr's'/Boy's'
TA4056	TA2463	Iran	Altar 84/Ao's'
TA4059	TA2471	Iran	68111/Rubgy//Ward
TA4063	TA2477	Iran	Rabi's'//Gs's'/Cr's'
TA4064	TA2481	Iran	133812; 133813
TA4066	TA2528	Iran	68112/Ward
TA4069	TA2528	Iran	Chen's'
TA4072	TA1693	Turkmenistan	68111/Rubgy//Ward/Stil's'
TA4073	TA1695	Japan	Yar's'
TA4075	TA2378	Iran	Yar's'
TA4077	TA2422	Afghanistan	Ceta's' Wp122
TA4078	TA2436	Afghanistan	Yuk
TA4080	TA2451	Iran	68111//Rugby/Ward/3/Fg's'/4/Rabi's'
TA4081	TA2455	Iran	68111//Rugby/Ward/3/Fg's'/4/Rabi's'
TA4082	TA2457	Iran	Sba81/Cr's'//Cit's'/3/Chi's'/4/Pal's'
TA4085	TA2473	Iran	68111//Rugby/Ward/3/Fg's'/4/Rabt's'
TA4087	TA2487	Iran	Rabi's'//Gs's'/Cr's'
TA4089	TA2524	Iran	68111//Rugby/Ward/3/Fg's'/4/Rabi's'
TA4093	TA2556	Afghanistan	Ceta's' Wp122
TA4094	TA2459	Iran	Laru's'

maturity shortens the grain filling duration (Noodén, 1980; Camp et al., 1982; Benbella & Paulsen, 1998). Because of the close relationship between photosynthesis and productivity of wheat, a reduction in either leaf area duration or grain filling duration greatly decreases yield (Simpson, 1968; Noodèn, 1980; Rawson et al., 1983). Reynolds et al. (1994) suggested that a sustained chlorophyll level during maturation was an efficient indicator of heat tolerance in wheat cultivars. Hede et al. (1999) found a significant correlation between leaf chlorophyll content and kernel weight in 2,255 Mexican landraces and pointed out the reliability of chlorophyll level in indicating heat tolerance in primitive wheats.

Considerable differences in heat tolerance among genotypes of wheat and its wild relatives have not lead to substantial improvement of new cultivars (Wardlaw et al., 1989a, 1989b; Al-Khatib & Paulsen, 1990; Reynolds et al., 1994; Waines, 1994; Sun & Xu, 1998). The slow progress might be attributed to the significant tolerance that already exists in cultivars that are adapted to stressful environments and the difficulty of identifying markedly superior genotypes (Paulsen, 1994). Additional sources of tolerance might occur among the physiological, morphological,

Table 2. Analyses of variance for chlorophyll content (Chl), grain filling duration (GFD), grain yield (GY), kernel number (KN), and kernel weight (KW) of 30 hexaploid amphiploid and four octaploid amphiploid wheats under control (15/20 °C) and high-temperatrue stress (25/30 °C) conditions

Source	Mean squares					
	df	Chl	GFD	GY	KN	KW
Hexaploids						
Genotypes (G)	29	26,615**	25,508**	0,051**	24,653**	26,090**
Temperatures (T)	1	34891,873**	9364,349**	30,324**	2,450	34891,873**
G × T	29	40,478**	18,824**	0,057**	5,800	40,478**
Error	120	3,757	2,520	0,019	4,084	4,932
Octaploids						
Genotypes (G)	3	5,310*	5,014	0,002*	0,930	1,962
Temperatures (T)	1	1096,201**	2057,202**	0,048**	2,041	178,215**
G × T	3	25,036**	12,813	0,001	1,375	3,749
Error	16	1,671	7,981	0,001	4,250	4,668

*, ** Significant at 0.05 and 0.01 levels of probability, respectively.

and genetic changes from polyploidization (Siddiqui, 1976; Mears, 1979; Tal, 1979; Jiang et al., 1994; Mujeeb-Kazi, 1995; Rajaram et al., 1997). Synthetic hexaploids formed by crossing durum wheat with *Ae. tauschii* accessions and octaploid amphiploids derived from hybridization of cv. Chinese Spring are available (Driscoll & Sears, 1971; Dvořák & Sosulski, 1974; Dvořák, 1975; Feldman, 1975; Hart & Tuleen, 1983; Friebe et al., 1993, 1995; Mujeeb-Kazi, 1995). These genetic stocks are bridges for introducing alien genes into wheat cultivars and are valuable for genetic investigation of many traits (Siddiqui, 1976; Jiang et al., 1994; Rajaram et al., 1997). The objectives of this investigation were to characterize senescence and yield responses of synthetic hexaploid and octaploid amphiploid wheats to controlled high temperature stress and to evaluate their potential use for improvement of wheat in stressful environments.

Materials and methods

Germplasm

Thirty hexaploid amphiploids from CIMMYT that were used in the first study and their identification and parents are shown in Table 1. The four octaploid amphiploids in the second study were products of hybridization and chromosome-doubling between hexaploid Chinese Spring (*Triticum aesticum* L.) and *Aegilops logissima* by Feldman (1975), Hart & Tuleen (1983), and Friebe et al. (1993); *Ae. searsii* by Friebe et al. (1995); *Secale cereale* by Driscoll & Sears (1971); and *Agropyron elongatum* (*Thinopyrum elongatum*) by Dvořák & Sosulski (1974) and Dvořák (1975). The hard red spring wheat cultivar Len was included as a check with the octaploid genotypes.

Plant growth

Seeds of the genetic stocks were germinated on moistened filter paper in Petri dishes at 25 °C until the radicals appeared. The seedlings were vernalized at 5 °C for 6 weeks and transplanted into a mixture of soil: sand: peat moss (1:1:1 v:v:v) in 12 × 15-cm pots. Each pot held two seedlings. The pots were placed randomly in controlled environment chambers (PGW-36, Conviron, Pembina, ND) set at 20/15 °C day/night, 50/70% relative humidity, 16-h photoperiod, and illumination of 420 μmol m^{-2} s^{-1}. Fertilizer (0.5 g) (Peters Professional Plant Food, W.R. Grace & Co., Fogelsville, PA) to supply 100 mg N, 43 mg P, and 83 mg K was applied to each pot at transplant, jointing, and early anthesis stages of wheat development. After jointing, one seedling was removed from each pot, and the remaining seedling was grown to anthesis.

The spike on the primary tiller of each plant was labeled when the first anthers appeared. After 10 days, one-half of the plants were moved randomly to controlled environment chambers set at 30/25 °C day/night with all other conditions the same as before. The remaining plants were maintained at 20/15 °C as controls. The plants were watered daily from shallow saucers containing the pots to prevent moisture deficiency and were re-randomized weekly within each replication in the controlled environment chambers.

Table 3. Flag leaf chlorophyll content after 10 days of treatment and grain filling duration to maturity of 30 synthetic hexaploid wheats under control (20/15 °C) and high-temperature stress (30/25 °C) conditions

Hexaploid	Chlorophyll content (SPAD units)		Grain filling duration (Days)	
	Control	Stress	Control	Stress
TA4041	60.5	53.8	28.2	18.7
TA4043	53.2	39.3	30.1	18.8
TA4044	55.8	46.3	28.3	17.9
TA4045	62.3	51.7	29.0	17.8
TA4047	56.1	41.8	29.4	18.0
TA4048	60.4	48.9	29.4	16.1
TA4049	61.4	38.0	30.1	10.6
TA4050	58.1	45.9	29.3	18.5
TA4051	61.4	43.4	28.1	16.1
TA4053	61.3	49.4	28.7	13.2
TA4055	61.2	55.0	26.9	12.2
TA4056	58.5	38.1	27.5	17.1
TA4059	60.3	42.7	27.9	17.9
TA4063	59.2	45.0	31.0	15.8
TA4064	60.5	50.5	29.1	16.4
TA4066	61.5	44.3	26.8	14.7
TA4069	61.3	37.4	30.5	13.2
TA4072	61.5	44.9	26.9	14.3
TA4073	60.8	47.7	29.4	16.9
TA4075	57.3	43.5	26.8	12.2
TA4077	60.5	43.6	25.4	11.0
TA4078	57.2	41.8	28.4	13.0
TA4080	58.3	46.3	28.4	17.3
TA4081	58.9	37.7	29.4	8.1
TA4082	62.2	46.6	30.7	11.0
TA4085	56.9	37.2	28.4	12.7
TA4087	62.9	47.8	26.9	7.4
TA4089	59.7	45.2	28.9	8.2
TA4093	62.5	40.0	27.8	8.7
TA4094	63.5	45.2	29.5	9.3
$\text{LSD}_{0.05}$	4.5	3.1	3.3	1.3

When the spike of the primary tiller reached physiological maturity as indicated by chlorosis of the glumes, water was withheld and the plants were kept at 30 °C for two weeks for the grain to ripen.

Parameters measured

Chlorophyll content was measured 10 days after the differential temperature treatments were applied to the hexaploid wheats (Study 1) and 15 days after they were applied to the octaploid wheats (Study 2). Six readings were taken along the length of the flag leaves of control and treated plants with a portable chlorophyll meter (SPAD-502, Minolta Camera Co., Ltd., Tokyo, Japan). Grain filling duration of the genotypes was defined as the interval between 10 days after anthesis and physiological maturity of the primary spike.

The primary spikes of all plants were harvested after two weeks of ripening, the grain was threshed manually, and the kernels were counted and weighed. A heat susceptibility index (HSI) was calculated by the formula of Fischer & Maurer (1978): $\text{HSI} = (1\text{-}Y/Yp)/D$, where Y = yield of the primary spike at 30/25 °C, Y_p = mean yield of the primary spike at 20/15 °C, D = stress intensity = $1\text{-}X/X_p$, X = mean Y of all genotypes, and X_p = mean Y_p of all genotypes. The genotypes were rated as highly tolerant ($\text{HSI} \leq 0.50$), moderately tolerant ($0.50 < \text{HSI} \leq 1.00$), or susceptible ($\text{HSI} > 1.00$) to high temperature (Fischer & Maurer, 1978; Khanna-Chopra & Viswanathan, 1999).

Experimental design and statistical analyses

Genotypes and temperature treatments were arranged in completely randomized designs and replicated three times. All data were subjected to an F-test by 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 by SAS (1995).

Results

Senescence characteristics of synthetic hexaploids and octaploids

Chlorophyll content of flag leaves and grain filling duration differed significantly among the 30 hexaploid amphiploid wheats and between the two temperature regimes (Tables 2 and 3). High temperature decreased both parameters but markedly extended the range among the genotypes. Variation increased from 10.3 to 17.8 chlorophyll units and from 5.6 to 11.4 days of grain filling between 20/15 and 30/25 °C, respectively. The extended range reflected substantial differences in susceptibility of the genotypes to high temperature. Whereas chlorophyll content decreased 6.7 units and grain filling 9.5 days in TA4041, the same parameters fell 23.4 units and 19.1 days, respectively, in TA4049.

The octaploid genotypes responded like the synthetic hexaploids but appeared to be more tolerant than

Table 4. Flag leaf chlorophyll content after 15 days of treatment and grain filling duration to maturity of Len and Chinese Spring and its octaploid progeny under control (20/15 °C) and high-temperature stress (30/25 °C) conditions

Genotype	Chlorophyll content (SPAN units)		Grain filling duration (Days)	
	Control	Stress	Control	Stress
Len	62.0	25.1	30.9	17.2
Chinese Spring (C.S.)	59.2	Chlorotic	34.7	15.8
C.S./*Ae. longissima*	64.9	48.1	41.3	19.8
C.S./*Ae. searsii*	64.0	50.1	41.5	21.9
C.S./*Secale cereale*	63.3	47.2	39.7	20.4
C.S./*Ag. elongatum*	61.6	53.1	37.0	22.7
$LSD_{0.05}$	2.9	4.2	NS	NS

the check cultivar Len and the parent line Chinese Spring (Tables 2 and 4). Chlorophyll content was slightly higher in most of the octaploids than in the two other genotypes at 20/15 °C but was markedly higher after 15 days at 30/25 °C. The grain filling duration was considerably longer in the amphiploids than in Len and Chinese Spring but did not differ among the octaploid lines.

Yields and HSI of synthetic hexaploids and octaploids

Grain yields of the 30 hexaploid wheats differed within the two temperature regimes, and mean yields of all the genotypes decreased from 1.51 to 0.69 g/spike between 20/15 and 30/25 °C (Tables 2 and 5). Stress also reduced the range in yields among the genotypes from 1.15 to 1.73 g/spike under control conditions to 0.52 to 0.86 g/spike at 30/25 °C. A significant genotype × temperature interaction indicated that yields of the genotypes responded differently to the two regimes. Only five hexaploid genotypes (TA4041, TA4045, TA4048, TA4053, TA4055) had HSI ratings of 1.00 or less and were considered moderately tolerant to high temperature.

Kernel numbers differed among the 30 hexaploid wheats (Tables 2 and 5). However, the number already was established when the treatments were applied, and temperature had no effect. Kernel weights also differed among the genotypes, and the mean value declined from 55.6 to 27.9 mg between the two temperature treatments. The magnitude of the reduction in kernel weight varied among the genotypes and ranged from 15.6 mg for TA4041 to 35.3 mg for TA4094.

Grain yields of the octaploid lines were similar within the two regimes, but the means decreased from 0.36 to 0.26 g/spike between the low and high temperatures (Table 6). Yields of the spring wheat cultivar Len and parent Chinese Spring greatly exceeded those of the octaploids. Values of HSI were nearly similar for the octaploids and Len, which were rated as moderately tolerant compared with the susceptible Chinese Spring. Neither kernel number nor kernel weight differed among the four octaploids under either regime. All the octaploids set fewer kernels than the two check cultivars, and temperature had no effect. The weight of the kernels also was lower for the octaploids than for the check cultivars, and mean values decreased significantly at the high temperature.

Correlations of plant traits with heat susceptibility indices

Both measures of senescence of plants grown at high temperature, leaf chlorophyll content and grain-filling duration, were correlated negatively with HSI of the hexaploid lines (Table 6). However, neither parameter of plants grown at 20/15 °C was correlated with HSI values. The grain yield of hexaploid plants at 30/25 °C varied inversely with HSI, whereas the yield at 20/15 °C was correlated positively with HSI at $P = 0.076$. Kernel number was unrelated to HSI in either regime, but kernel weight was correlated positively with HSI at 20/15 °C and correlated negatively at 30/25 °C.

In the octaploid lines, both chlorophyll content and grain-filling duration were correlated positively with HSI at 20/15 °C but negatively with HSI at 30/25 °C

Table 5. Grain yield, heat susceptibility index (HSI), and yield components at maturity of 30 synthetic hexaploid wheats under control (20/15 °C) and high-temperature stress (30/25 °C) conditions

Hexaploid	Grain yield (g/spike)		HSI	Kernel number (no/spike)		Kernel weight (mg/kernel)	
	Control	Stress		Control	Stress	Control	Stress
TA4041	1.32	0.84	0.82	24.1	24.2	50.6	35.0
TA4043	1.61	0.60	1.42	23.6	25.6	49.1	29.8
TA4044	1.65	0.67	1.36	25.2	25.6	52.0	33.5
TA4045	1.25	0.76	0.89	23.6	26.0	54.7	31.2
TA4047	1.42	0.72	1.12	24.1	22.7	54.4	35.2
TA4048	1.40	0.81	0.95	20.2	23.0	52.5	27.9
TA4049	1.73	0.63	1.44	22.7	25.1	54.3	28.9
TA4050	1.49	0.62	1.34	22.8	22.4	57.5	32.3
TA4051	1.24	0.52	1.34	24.4	21.7	57.4	34.3
TA4053	1.42	0.80	1.00	27.9	26.5	51.8	28.9
TA4055	1.42	0.86	0.90	20.3	22.1	56.6	26.6
TA4056	1.58	0.59	1.43	25.3	22.1	56.2	32.8
TA4059	1.48	0.65	1.28	27.0	26.9	58.3	28.9
TA4063	1.60	0.73	1.24	25.9	24.4	57.1	29.8
TA4064	1.15	0.64	1.01	23.6	22.7	58.2	28.9
TA4066	1.71	0.78	1.24	25.2	25.1	54.3	25.9
TA4069	1.48	0.62	1.32	27.9	25.6	53.5	27.7
TA4072	1.73	0.69	1.36	25.2	24.4	56.6	26.7
TA4073	1.57	0.77	1.17	27.9	27.2	54.4	25.5
TA4075	1.51	0.74	1.16	25.2	24.4	54.1	25.5
TA4077	1.66	0.66	1.38	19.9	22.2	57.6	23.2
TA4078	1.62	0.71	1.28	23.9	24.7	57.5	25.0
TA4080	1.54	0.73	1.21	25.9	24.2	58.7	27.5
TA4081	1.65	0.69	1.32	27.9	27.2	57.1	25.5
TA4082	1.55	0.65	1.32	26.4	26.3	58.2	25.1
TA4085	1.66	0.62	1.43	25.2	24.4	58.7	24.7
TA4087	1.24	0.59	1.20	27.0	26.8	56.8	23.2
TA4089	1.33	0.72	1.04	25.9	26.3	56.3	22.3
TA4093	1.72	0.56	1.54	28.1	26.9	56.8	23.6
TA4094	1.48	0.66	1.27	28.5	27.2	55.8	20.5
$\text{LSD}_{0.05}$	0.28	0.13	0.11	3.1	1.2	3.2	1.2

(Table 6). Grain yield was associated positively with HSI at 30/25 °C but not at 20/15 °C. Neither of the yield components was related to HSI at either temperature.

Discussion

Significant variation in leaf chlorophyll content and grain filling duration and their high correlation with HSI of the amphiploids demonstrated the importance of senescence in high-temperature responses of wheat (Paulsen, 1994; Reynolds et al., 1994; Hede et al., 1999). Leaf chlorophyll content undoubtedly reflected the capacity for photosynthesis, the major source of assimilates for growth of grain (Evans et al., 1975; Al-Khatib & Paulsen, 1990), and grain filling duration indicated the period for incorporating the assimilates into kernels (Wardlaw et al., 1989a, 1989b; Wardlaw & Wrigley, 1994). Both traits must be as constant as possible to stabilize yields in high-temperature regimes (Ferrara et al., 1994; Slafer & Rawson 1994; Khanna-Chopra & Viswanathan, 1999).

Table 6. Grain yield, heat susceptibility index (HSI), and yield components at maturity of Len and Chinese Spring wheat and its octaploid progeny under control (20/15 °C) and high-temperature stress (30/25 °C) conditions

Genotype	Grain yield (g/spike)		HSI	Kernel number (no/spike)		Kernel weight (mg/kernel)	
	Control	Stress		Control	Stress	Control	Stress
Len	1.57	1.16	0.795	37.5	36.5	41.9	31.7
Chinese Spring (C.S.)	1.57	0.85	1.384	32.5	32.1	48.2	26.4
C.S./*Ae. longissima*	0.36	0.26	0.810	11.2	10.5	32.3	25.2
C.S./*Ae. searsii*	0.32	0.24	0.792	11.0	9.0	29.4	26.5
C.S./*Secale cereale*	0.36	0.27	0.823	12.0	10.2	30.4	26.0
C.S./*Ag. elongatum*	0.37	0.28	0.758	12.0	11.5	31.1	24.3
$LSD_{0.05}$	0.06	0.05	0.031	NS	NS	NS	NS

Table 7. Spearman correlation coefficients of flag leaf chlorophyll content, grain filling duration, grain yield, kernel number, and kernel weight with heat susceptibility indices of 30 wheat synthetic hexaploids and four octaploid amphiploids under control (20/15 °C) and high-temperature stress (30/25 °C) conditions

Variable	Treatment	HSI	
		Hexaploids	Octaploids
		- r -	
Chlorophyll content	Control	–0.087(0.653)	0.718(<0.01)
	Stress	–0.751(<0.01)	–0.998(<0.01)
Grain filling duration	Control	–0.216(0.356)	0.665(<0.01)
	Stress	–0.742(<0.01)	–0.894(<0.01)
Grain yield	Control	0.471(0.076)	0.043(0.547)
	Stress	–0.881(<0.01)	0.526(<0.05)
Kernel number	Control	0.249(0.162)	–0.167(0.362)
	Stress	0.355(0.153)	–0.459(0.058)
Kernel weight	Control	0.604(<0.01)	–0.106(0.492)
	Stress	–0.958(<0.01)	–0.305(0.210)

Yield and its components are used widely as criteria for heat tolerance of wheat (Wardlaw et al., 1989a; Reynolds et al., 1994; Khana-Chopra & Viswanathan, 1999). Although they are expensive to obtain (Hede et al., 1999), they are the ultimate measures of productivity in stressful environments and highly applicable for comparing cultivars (Reynolds et al., 1994; Hede et al., 1999). However, yield is less useful for contrasting amphiploids derived from wide hybridization, which suffer partial sterility from unbalanced chromosomal segregation during meiosis (Siddiqui, 1976; Jiang et al., 1994; Rajaram et al., 1997). The low kernel number that resulted from sterility was partially compensated by a high kernel weight in the hexaploid amphiploids but not in the octaploid amphiploids. The combination of low kernel number and low kernel weight in the latter greatly depressed the yield and obscured any differences among the lines. Senescence was more appropriate than yield for identifying tolerance to high temperature in the octaploid amphiploids.

Genotypes that had HSI values between 0.50 and 1.00 were considered to be moderately tolerant to high temperature (Khanna-Chopra & Viswanathan, 1999). Traits shared by the synthetic hexaploids that had low HSI ratings indicated some characteristics that were important for productivity under high-temperature conditions. High chlorophyll content of all five low-HSI lines compared with most of their high-HSI counterparts demonstrated that continued viability of leaves was essential for grain growth at high temperature (Simpson, 1968; Rawson et al., 1983). The highly negative correlation between grain filling duration and HSI substantiated the importance of prolonged activity, but the brief grain-filling period of two low-HSI lines, TA4053 and TA4055, under high temperature suggested that a high rate of filling might compensate, at least in part, for the disadvantage (Wardlaw & Wrigley, 1994). Conversely, although kernel number correlated poorly with HSI, it was noteworthy that none of the low-HSI lines aborted kernels under high temperatures (Paulsen, 1994).

Kernel weight, the only yield component that wasn't set when the treatments were imposed, was most important. The extraordinarily high kernel weight at 20/15 °C suggested that synthetic hexaploids might be useful for improving the most conserved of all yield components under high-yield conditions (Frederick & Bauer, 1999). However, the positive correlation between kernel weight of the control plants and HSI implied that lines selected for the trait might be susceptible to stress. The importance of kernel weight to yield under stress conditions was indicated amply by its highly negative correlation with HSI in plants grown at 30/25 °C. The close association reflected the marked effect of high temperature during maturation on kernel growth (Wardlaw et al., 1989b; Al-Khatib & Paulsen, 1990; Reynolds et al., 1994). Lines like TA4041 that had high kernel weight at 20/15 °C and a minimal reduction at 30/25 °C would be most useful for developing improved cultivars. However, the significant genotype × temperature interaction indicated that many lines would not express high kernel weight under both regimes.

The significant genotype × temperature interaction for gain yield and the positive, nearly significant phenotypic correlation (0.471) between HSI and grain yield of the hexaploids under control conditions are of some concern. Low HSI values, such as for TA4041, TA4045, and TA4055, came from relatively high yields under stress conditions and moderate yields under control conditions. High HSI values, such as in TA4093, TA4044, TA4056 and TA4085, on the other hand, usually resulted from low yields under stress conditions and high yields under control conditions. The dichotomy between tolerance to stress and yield under favorable conditions was typical (Blum, 1988; Ferrara et al., 1994). It suggested that HSI values should be considered with other traits, and that less emphasis should be given to HSI when stress occurs infrequently instead of regularly.

The value of the octaploid amphiploids for improving resistance of wheat to high temperature stress is questionable. Some worth was indicated by the relatively small decline in chlorophyll and kernel weight and the low HSI of the lines compared with their Chinese Spring parent. However, the low kernel number at 20/15 °C suggested that the yield potential was low under the best conditions because of the unbalanced segregation that occurs in the lines (Siddiqui, 1976; Jiang et al., 1994; Rajaram et al., 1997). In contrast to the highly conserved kernel weight, increased kernel number per plant or area correlated highly with yield and was mostly responsible for improved productivity of modern cultivars (Frederick & Bauer, 1999). The low kernel number of the octaploid amphiploids would seriously compromise their use in wheat improvement.

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