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Wheat Cultivars Adapted to Post-Heading High Temperature Stress

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With 5 figures and 4 tables

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Abstract

The existence of genetic variation in wheat for tolerance to high temperature stress has been reported but cultivars released for a particular production system often are not characterized. The objective of this study was to identify and describe the characteristics of wheat cultivars adapted to production systems with risks of high temperature during the post-heading period. Fifteen diverse wheat cultivars and one unreleased genotype were evaluated at the Texas A&M University Agricultural Research and Extension Center, Uvalde, TX, during two seasons characterized by daily maximum temperatures as high as 36 °C. Measurements during both seasons included days to heading, days to physiological maturity and grain yield. Large and significant ($P < 0.05$) grain yield differences were measured among cultivars within each season. Yield varied between 2979 and 4671 kg ha^{-1} in the first season and between 1916 and 5200 kg ha^{-1} in the second season. Late planting in the second season delayed heading date resulting in the post-heading period to coincide with periods of high temperatures. Cultivars that headed early, in general, yielded better than cultivars that headed later within each season with yield reduction of 35.3 kg ha^{-1} in the first season and 91.0 kg ha^{-1} in the second season for every 1 day delay in heading after mid-March. Early-heading cultivars outperformed later-heading cultivars because of two distinct advantages: the early-heading cultivars had longer post-heading and, therefore, longer grain filling period than the later-heading cultivars. In addition, early-heading cultivars completed a greater fraction of the grain filling earlier in the season when air temperatures were lower and generally more favourable. The advantage of earlier-heading cultivars was also manifested in the amount of green leaves retained to anthesis. Earlier-heading cultivars produced fewer total leaves per tiller but retained more green leaves and lost fewer leaves to senescence at anthesis than later-heading cultivars. The results suggest that early heading is an important and effective single trait defining wheat cultivars adapted to production systems prone to high temperature stress during the post-heading period.

Key words: grain filling — heading — heat stress — leaf senescence — winter wheat

Introduction

Wheat (*Triticum aestivum* L.) is produced worldwide under largely temperate but also under tropical and subtropical temperatures. This distribution implies the crop is versatile and adapted to various growing conditions. However, it has been known that high temperatures during the post-heading stages detrimentally affect its yield (Wiegand and Cuellar 1981, Wardlaw and Wrigley 1994) and sometimes grain quality (Blumenthal et al. 1993, Stone et al. 1997, Gibson et al. 1998). Mean temperatures that exceed 15 °C are considered beyond the optimum for wheat (Wiegand and Cuellar 1981, Wardlaw et al. 1989) and are known to reduce yield by as much as 10–15 % (Wardlaw and Wrigley 1994). Wheat in the USA often experiences temperatures that exceed 30 °C during the critical stages of heading and grain filling. This is particularly true in the southern parts of the wheat-growing regions. Variation for tolerance to high temperature stress among genotypes has been reported in wheat (Wardlaw et al. 1989, Al-Khatib and Paulsen 1990, Viswanathan and Khanna-Chopra 2001, Tahir and Nakata 2005). Al-Khatib and Paulsen (1990) found that the grain yield of cultivars they considered tolerant to high temperature was affected little by the same temperature that decreased grain yield of susceptible cultivars by >40 %. They

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associated the better performance of tolerant cultivars with longer duration of photosynthesis, larger kernels and higher harvest index. Tahir and Nakata (2005) increased maximum temperature from 30 to 38 °C during the reproductive growth phase of 18 wheat genotypes under controlled environment and found the reduction in mainstem grain weight to vary between 20 % and 44 %. Variation among genotypes with duration of grain filling, grain weight and grain number per spike under high temperature stress are also reported (Wardlaw et al. 1989, Viswanathan and Khanna-Chopra 2001).

Wheat cultivars adapted to a certain production system are often developed based on overall yield performance, disease resistance and grain quality. The basis of their adaptation to high temperature and drought often is not evaluated at the time of their development. Cultivar registration descriptions rarely mention adaptation to temperature or drought. The objective of this study was to identify and describe the characteristics of old and newer wheat cultivars adapted to production systems with significant risks of high temperature during the post-heading period.

Materials and Methods

The study was conducted at the Texas A&M University Agricultural Research and Extension Center, Uvalde, Texas, in the USA (29°13′N, 99°45′W; 279 m elevation) in a Uvalde silty clay loam soil (fine-silty, mixed, hyperthermic Aridic Calciustolls) in the 1993–1994 and 1994–1995 wheat growing seasons, which will be referred to as season 1 and season 2, respectively. For each season, 16 wheat genotypes were tested under five irrigation regimes. The genotypes included 11 hard red winter (HRW) cultivars and one unreleased HRW experimental line, three soft red winter (SRW) cultivars, and one hard red spring (HRS) cultivar (Table 1). Year of cultivar release ranged from 1963 to 1995. The genotypes for this study were selected out of variety trials conducted at the Research Center for several years. Many of the cultivars were a representative sample of those grown or sold within about 240 km of the Research Center. Some of the genotypes which showed reasonable yield performance in previous tests were chosen to represent a wider range of maturity dates. Irrigation regimes included 0 %, 25 %, 50 %, 75 % and 100 % replacement of estimated potential evapotranspiration. Irrigation, when needed, was applied using a linear-move low pressure system with drop nozzles of different sizes to deliver the desired amounts of water to the respective irrigation treatment.

Table 1: Heading, grain yield and grain characteristics of wheat cultivars grown in south-western Texas, USA, in season 1. Each value is an average of three replications and five irrigation regimes

Cultivar	Year released	Days to heading	Days to physiological maturity	Post-heading duration (days)	Grain yield (kg ha^{-1})	Grain growth rate (g m^{-2} day^{-1})	1000-kernel weight (g)	Kernel per head	
								n	wt (g)
Sturdy^1	1966	100.2	134.1	33.9	2979	8.8	23.9	27.2	0.687
Mit^1	1980	75.9	114.4	38.5	3481	9.0	31.5	23.4	0.774
TAM 107^1	1984	94.7	130.0	35.3	3515	10.0	24.7	25.7	0.736
TAM 200^1	1986	83.3	121.1	37.8	4311	11.4	22.2	26.4	0.637
Collin^1	1986	75.1	115.4	40.3	4032	10.0	29.9	27.8	0.868
Pioneer 2180^1	1987	102.9	137.1	34.2	3416	10.0	24.5	26.9	0.696
TAM 201^1	1987	81.5	118.6	37.1	4182	11.3	28.9	24.2	0.699
Pioneer 2163^1	1989	109.4	137.0	27.6	3199	11.6	22.0	31.0	0.728
TAM 202^1	1992	86.1	126.8	40.7	4168	10.2	23.2	31.0	0.787
TAM 300^1	1993	102.3	133.4	31.1	2998	9.6	22.8	24.3	0.595
RSI 220^1	1995	102.3	134.6	32.4	3294	10.2	27.4	33.1	0.996
TX87U7003$^{(NR)}$	NR	75.2	115.5	40.3	4649	11.5	28.8	29.8	0.938
Florida 302^2	1988	84.1	119.7	35.5	4579	12.9	31.3	36.6	1.216
Pioneer 2548^2	1991	95.3	130.8	35.5	4671	13.2	25.4	37.6	1.035
Coker 9835^2	1993	79.5	118.0	38.5	4566	11.9	26.0	32.6	0.891
Nadadores 63^3	1963	88.3	123.4	35.1	3098	8.8	23.1	34.4	0.825
Means	–	89.8	125.6	35.9	3821	10.5	26.0	29.5	0.819
LSD$_{0.05}$	–	1.35	1.28	1.5	437	1.11	2.22	2.48	0.108
CV (%)	–	2.1	1.4	5.8	15.8	14.6	11.8	11.6	18.3

NR, unreleased experimental line.
[1] Hard red winter.
[2] Soft red winter.
[3] Hard red spring.

The test was conducted in a randomized complete block design with a split-plot arrangement of treatments in three blocks. Irrigation treatments were applied to main plots and genotypes were planted to subplots. Each subplot consisted of seven 4.57-m long rows spaced 0.15 m apart. The genotypes were planted on 19 November 1993 and 8 December 1994 in moist seedbed at 355 seed m^{-2}. Urea (46-0-0 N-P-K) as the source of nitrogen and triple superphosphate (0-46-0 N-P-K) as the source of phosphorus were broadcast and incorporated before bedding each year to supply 101 kg N ha^{-1} and 67 kg P_2O_5 ha^{-1}.

Measurements taken during both seasons included days to heading, days to physiological maturity and grain yield. The amount of senescent and non-senescent leaves and aboveground biomass was also quantified in season 2. Heading was determined by visually inspecting each subplot three to four times a week starting at the first appearance of heads and recording approximate percent of plants that had fully emerged spikes. Days to heading is presented as the number of days counting from 1 January up to the date of 50 % heading each season, which was estimated by interpolation when 50 % heading did not occur on the same day of inspection. The same approach was used for physiological maturity, whole-plant senescence being the criteria used as an indicator of physiological maturity. The number of days between days to 50 % heading and physiological maturity will be referred to as the post-heading period. This period approximates the grain filling duration but post-heading period is used throughout this article because it reflects the period starting with the 50 % heading until maturity better than the grain filling period.

The amount of senescent and non-senescent leaves and aboveground biomass was determined at or shortly after anthesis on the 0 and 100 % ET replacement irrigation treatments. All tillers from two 0.5-m middle drills (0.15 m^2) were cut just aboveground. Senescent and non-senescent leaves from 10-tiller subsamples were separated, counted, dried at 70 °C to constant weight and weighed. A leaf was considered senescent if the majority (approximately >75 %) of its area had lost chlorophyll as visually estimated. A dead leaf was counted as senescent leaf. The bulk tillers were counted and dried at 70 °C and weighed without separating into the different plant parts.

Grain yield was determined by harvesting entire plots with a small plot combine. Daily weather data were recorded at a weather station located at the experiment station.

The data were subjected to statistical analysis using the GLM procedures of SAS (SAS Institute, Inc. 1996) as a split-plot design. The main effects of irrigation and cultivars were compared using the least significant difference (LSD) test. The relationships of grain yield and post-heading period with earliness measured as days to heading were evaluated using simple regression analysis. All differences identified as significant were tested at $P < 0.05$ unless specified otherwise.

Results and Discussion

Differences among cultivars in grain yield were large and significant within each season. Yield in season 1 varied between 4671 kg ha^{-1} for the SRW cultivar Pioneer 2548 and 2979 kg ha^{-1} for the

Table 2: Heading, grain yield and grain characteristics of wheat cultivars grown in south-western Texas, USA, in season 2. Each value is an average of three replications and five irrigation regimes

Cultivar	Days to heading	Days to physiological maturity	Post-heading duration (days)	Grain yield (kg ha^{-1})	Grain growth rate (g m^{-2} day^{-1})	1000 kernel weight (g)	Kernel per head	
							n	wt (g)
Sturdy	107.3	135.7	28.4	2656	9.4	23.7	25.0	0.619
Mit	88.4	124.3	35.8	4649	13.0	30.8	26.4	0.855
TAM 107	105.8	134.7	29.0	1916	6.6	22.3	21.1	0.502
TAM 200	96.0	128.9	32.9	3579	10.9	24.2	26.2	0.671
Collin	84.6	125.1	40.4	4070	10.1	28.6	28.4	0.926
Pioneer 2180	114.9	141.3	26.4	2054	7.8	21.3	25.6	0.624
TAM 201	93.2	127.8	34.6	4110	11.9	32.0	24.2	0.822
Pioneer 2163	120.5	141.2	20.7	2112	10.2	17.2	22.7	0.458
TAM 202	98.2	132.6	34.4	4279	12.4	26.6	28.8	0.732
TAM 300	108.9	136.7	27.8	3195	11.5	24.4	23.6	0.608
RSI 220	110.5	139.9	29.4	3379	11.5	28.3	32.4	0.929
TX87U7003	85.1	122.3	37.2	5144	13.8	28.4	33.0	0.947
Florida 302	96.7	128.8	32.1	3741	11.6	31.0	28.4	1.046
Pioneer 2548	103.7	134.1	30.4	3858	12.7	23.3	38.6	0.923
Coker 9835	91.8	126.4	34.6	5200	15.0	30.0	33.7	1.070
Nadadores 63	94.1	129.1	35.0	3795	10.8	28.9	29.2	0.913
Mean	100.0	131.8	31.8	3609	11.2	26.3	28.0	0.790
$LSD_{0.05}$	0.73	0.64	0.9	498	1.77	1.97	3.13	0.131
CV (%)	1.0	0.68	3.9	19.1	21.8	10.4	15.5	22.9

HRW cultivar Sturdy (Table 1). Yield in season 2 varied between 5200 kg ha^{-1} for the SRW cultivar Coker 9865 and 1916 kg ha^{-1} for the HRW cultivar TAM 107 (Table 2). TX87U7003, classed as a HRW experimental line on preliminary mixing and baking data at the time of the experiment, was the highest yielding among all entries when yield was averaged across the two seasons. However, this experimental line has not been released as a cultivar as its milling qualities were subsequently found to be similar to SRW cultivars and its mixing, baking and kernel characteristics were closer to HRW cultivars.

Irrigation did not significantly affect any of the measurements in season 1 because rain received between 1 January and 31 May during this season (492 mm) exceeded the 463 mm calculated ET. Only one irrigation was necessary during the entire season. Season 2 which received only 223 mm of rain between 1 January and 31 May was much drier than season 1. The plots in season 2 were irrigated on five dates between 10 February and 25 April with a total of 0, 36, 52, 79 and 110 mm for the 0 %, 25 %, 50 %, 75 % and 100 % ET replacement treatments respectively. Irrigation in season 2 had a small but significant effect on days to heading and maturity, grain yield and certain grain characteristics. Lack of irrigation (0 % ET replacement) in season 2 shortened days to heading by 1.2 days, days to physiological maturity by 2.2 days, and post-heading duration by 1.0 day and reduced grain yield by 422 kg ha^{-1}. Interactions between irrigation and cultivars were not significant for all measurements but days to maturity in season 2. Days to maturity of Florida 302 and TAM 200 was essentially unaffected by irrigation while those of Mit, Coker 9835, Collins, Pioneer 2548 and TAM 300 were shortened by >3 days due to lack of irrigation. Lack of irrigation shortened days to maturity of the other cultivars by ≤ 3 days.

Subsequent discussions of heat adaptation of the cultivars will be based largely on data pooled across irrigation treatments as irrigation did not affect any of the measurements in season 1 and only had a small effect on some of the measurements in season 2 with no significant interaction between cultivars and irrigation other than days to maturity as presented above.

Mean air temperature effect on yield

Grain yield was affected by mean ambient temperature averaged across the post-heading period of each cultivar. Grain yield was significantly and adversely affected by increasing mean temperature during the post-heading period (Fig. 1). Yield decreased by an average of 287 kg ha^{-1} in season 1 and 488 kg ha^{-1} in season 2 for every 1 °C increase in mean temperature during the post-heading period.

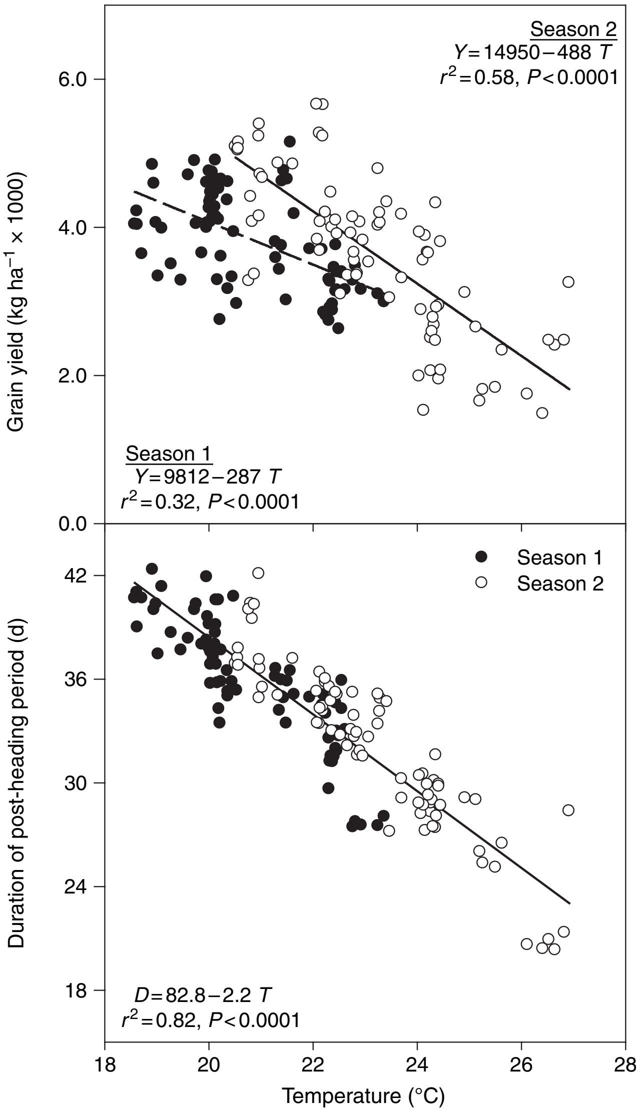

Fig. 1: Relationship of daily mean temperature averaged across the post-heading period (T) with duration of post-heading period (D) and grain yield (Y) of wheat in south-western Texas, USA

The adverse effect of rising temperature on yield may be largely due to its effect on the duration of the post-heading period. Increasing temperature during both seasons had a drastic shortening effect on the post-heading period (Fig. 1). An increase of 1 °C in mean temperature shortened the post-heading period by 2.2 days when data for both seasons were combined. This is considerably less than the decrease of 3.1 days per 1 °C increase in mean daily temperature reported by Wiegand and Cuellar (1981) from their field study of several winter and spring wheat cultivars. Wiegand and Cuellar (1981) also reviewed and summarized previous work and showed a shortening effect of temperature on grain filling duration ranging between 2.4 and 6.1 days per 1 °C increase in temperature. This makes the finding of 2.2 day decrease in the duration of post-heading period per 1 °C increase in mean daily temperature in this research to be the smallest value reported which may be attributed to cultivar differences. It is possible the cultivars used in this study, many of which were released in the 1980s and 1990s, were better adapted to heat stress and, therefore, may be less affected by temperature rise than those studied or cited in the review by Wiegand and Cuellar (1981).

Relationship between yield and earliness to heading

Cultivars widely varied in days to heading, with 34 and 36 day differences between the earliest and the latest-heading cultivars in season 1 and season 2 respectively. The HRW cultivars Collin, Mit, and the experimental line TX87U7003 were among the earliest heading both seasons. Collin was the earliest during both seasons, reaching 50 % heading on 16 March in season 1 and on 25 March in season 2 (Tables 1 and 2). The latest heading cultivar was Pioneer 2163 which reached 50 % heading on 19 April in season 1 and on 30 April in season 2.

Cultivars that headed early in general yielded better than cultivars that headed later within each season. Regression analysis showed a relatively strong association between grain yield and earliness to heading. For each season, grain yield decreased significantly ($P < 0.0001$) with increasingly delayed heading. Grain yield decreased by 35.3 kg ha^{-1} in season 1 and by 91.0 kg ha^{-1} in season 2 for every 1 day delay in heading after mid-March ($Y = 3996 - 35.3D$, $r^2 = 0.35$, $P < 0.0001$ in season 1 and $Y = 12730 - 91.0D$, $r^2 = 0.70$, $P < 0.0001$, where Y = yield in kg ha^{-1}, D = days to heading beginning January 1).

Collin and TX87U7003, two of the earliest heading genotypes, were among the highest yielding HRW genotypes during both seasons. The HRW cultivar TAM 201, which headed within 8 days after Collin and TX87U7003, also performed well in both seasons. Mit, which was one of the earliest heading cultivars, performed well in season 2 but not in season 1. The poor performance of Mit in season 1 despite its earliness is attributed to lodging that affected this cultivar throughout much of the season starting the third week of February. Pioneer 2163, which headed later than Collin by 34 days in season 1 and by 36 days in season 2, was among the lowest yielding cultivars. Sturdy and TAM 107, two relatively old HRW cultivars that headed 20–25 days later than Collin, were also among the poor yielding cultivars in both seasons. Contrary to these results, Moffatt et al. (1990) found both Sturdy and TAM 107 to be the highest yielding cultivars among six entries. They tested the heat tolerance of these entries and reported that TAM 107 and Sturdy, which they considered as adapted to the southern Great Plains, produced the highest yield, along with an ‘unadapted’ genotype from the People’s Republic of China, which headed the earliest. However, their test was conducted in Kansas, a markedly different wheat-growing environment than south-western Texas.

The early-heading cultivars had two distinct advantages over the later-heading cultivars. First, early-heading cultivars had longer post-heading period and therefore longer grain filling period than later-heading cultivars. Regression analysis showed a strong association between duration of post-heading period and earliness to heading during both seasons (Fig. 2). In season 1, Collin which headed the earliest during both seasons had the longest post-heading period of 40 days. The post-heading period was as short as 28 days in season 1 and 21 days in season 2 for the latest heading cultivar, Pioneer 2163. A rise in air temperature towards the end of the season hastened the senescence of Pioneer 2163 and the other late-heading cultivars resulting in such drastically shortened post-heading period and reduced grain yield. This effect may be seen when ranges in days to heading and maturity are compared: the difference in days to heading between the earliest and latest cultivars was 34–36 days while the difference in maturity was only 19–23 days. This smaller difference in days to physiological maturity may simply be attributed to premature senescence of the late-heading cultivars due to late-season rise in temperature.

High temperature during the grain filling period has been reported to accelerate senescence (Al-Khatib and Paulsen 1984), shorten the grain filling duration (Marcellos and Single 1972, Wiegand and Cuellar 1981, Vos 1985) and cause yield reductions. Spiertz and Vos (1985) stated that the rate and duration of grain growth are strongly governed by temperature. A rise in temperature

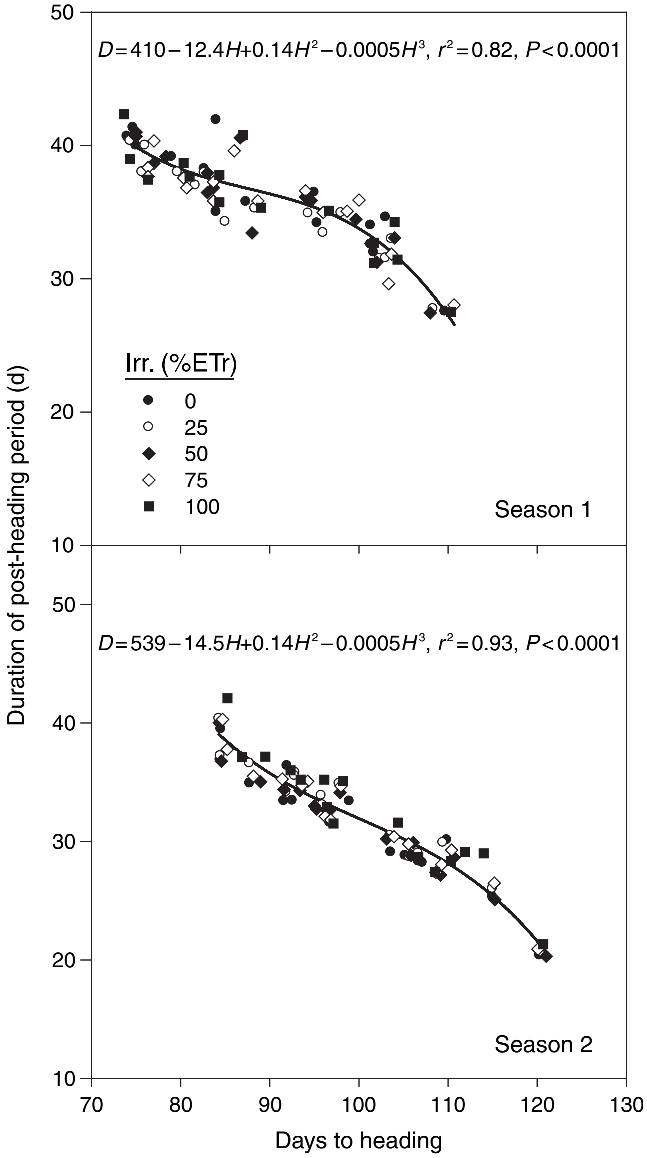

Fig. 2: Relationship between the duration of post-heading period (D) and days to heading (H) of wheat cultivars grown in south-western Texas, USA. Each data point is an average of three replications. (%ETr = percentage of estimated evapotranspiration replaced by irrigation)

enhances the rate of carbohydrate and nitrogen accumulation but shortens the duration. Spiertz and Vos (1985) showed a relationship between duration and temperature under controlled environment condition as $1/D = 0.0016T - 0.0096$, where D = duration (days) and T = temperature (°C).

In this study in south-western Texas, accelerated senescence due to late-season rise in temperature is considered to be a major cause for the poor performance of the late-heading cultivars. Increasing daily mean temperature averaged across the post heading period of each cultivar in season 2 resulted in accelerated leaf senescence (Fig. 3) and in a significant linear decrease of grain yield and the duration of post-heading period (Fig. 1). Based on controlled-environment research, Al-Khatib and Paulsen (1984) reported results similar to ours. However, other than some general observations that support these findings, our research seems to be the first to relate and show that increasing mean temperature averaged across the post-heading period drastically increases leaf senescence of field-grown wheat.

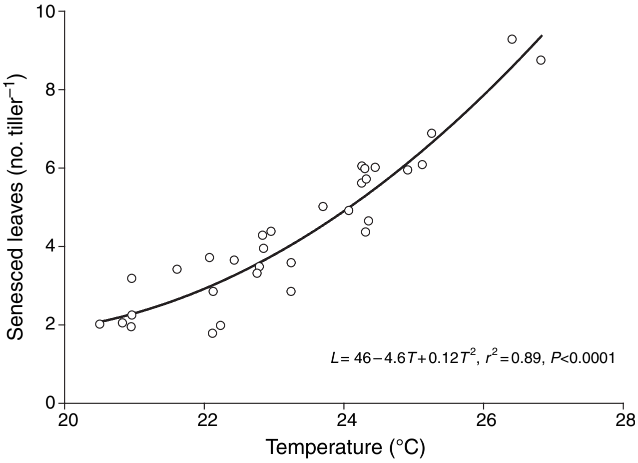

Fig. 3: Relationship between the amount of senesced wheat leaves (L) and daily mean temperature (T) averaged across the post-heading period in season 2 in south-western Texas, USA. Each data point is an average of three replications

The second advantage of early heading is that a greater fraction of grain filling occurs when air temperatures are lower and generally more favourable for wheat. Wheat grain yield is significantly and detrimentally affected by average temperatures that exceed 15 °C during the grain filling period (Chowdhury and Wardlaw 1978, Wiegand and Cuellar 1981). Exposures to very high temperatures for as short as 1 day during the reproductive stages can reduce grain growth by as much as 14 % in certain heat-sensitive varieties (Stone and Nicolas 1998). In our study under south-western Texas conditions, mean air temperature during both seasons steadily increased from about 15 °C in early March, when many of the cultivars headed, to as high as 29 °C towards the end of May when all cultivars reached physiological maturity (Fig. 4). The number of days with maximum air temperature exceeding 25 or 30 °C also increased from March to May (Table 3). This implies cultivars that headed early within this period were exposed to less high temperature stress than cultivars that headed

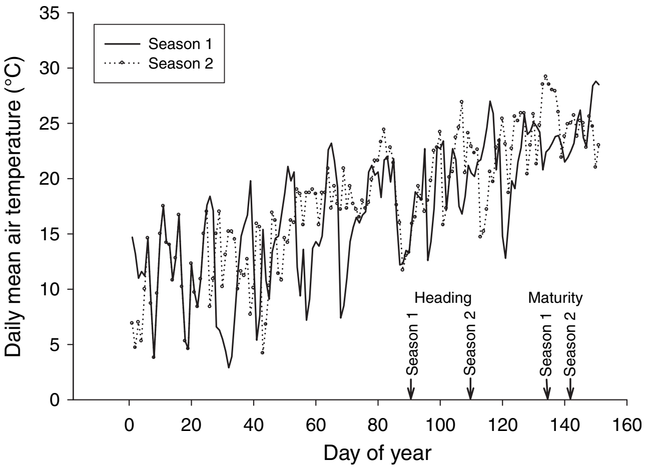

Fig. 4: Daily mean air temperature during wheat growth stages after January 1 in south-western Texas, USA. Down arrows show dates of heading and physiological maturity of earliest cultivars

Table 3: Number of days with daily maximum air temperature exceeding 25 or 30 °C during wheat heading and grain filling stages in south-western Texas, USA

Season	Month	Days with maximum air temperature	
		> 25 °C (days)	> 30 °C (days)
Season 1	March	11	2
	April	20	6
	May	26	8
Season 2	March	17	7
	April	20	8
	May	28	19

later. For example, in season 1, daily maximum temperature exceeded 30 °C essentially only on 1 of the 40-day post-heading period of TX87U7003, which reached 50 % heading on 16 March in season 1. Pioneer 2163, which reached 50 % heading on 19 April in season 1, experienced daily maximum temperatures that exceeded 30 °C on six of its 28-day post-heading period.

The advantage of earlier-heading cultivars is also manifested in the amount of green leaves retained to anthesis. Earlier-heading cultivars in season 2 had fewer total leaves per tiller but retained more green leaves to anthesis than later-heading cultivars (Table 4). The two best yielding genotypes, Coker 9835 and TX87U7003, retained ≥4.0 green leaves per tiller at anthesis, while the two worst yielding cultivars, TAM 107 and Pioneer 2163, retained only about 1.7 green leaves per tiller. The later-heading cultivars produced more total leaves and tended to produce greater amount of aboveground biomass at anthesis. But this tendency did not translate to grain yield, because the later-heading cultivars lost a greater fraction of their leaves to senescence by anthesis. Regardless of irrigation, senescence had a strong association with days to heading (Fig. 5) suggesting that the poor performance of late-heading cultivars is associated, at least in part, with accelerated leaf senescence. Figure 5 shows that grain yield decreases drastically with increasing amount of senesced leaves. Although there seemed to be a tendency for number of tillers to decrease with delayed heading (Tables 2 and 4), tiller number was not significantly ($P < 0.05$) correlated with days to heading ($r^2 = 0.10$, $P = 0.08$) or grain yield ($r^2 = 0.10$, $P = 0.08$).

Early heading, which has been used as a general selection criterion for many years, has been an overlooked trait for selecting wheat genotypes particularly adapted to environments with high temperature stress. An early test in India (Chinoy 1947) confirmed previous general observations that early wheat genotypes do better than later genotypes by avoiding late-season high temperatures. But, in general, early heading as a desirable trait in wheat adapted to environments characterized by late-season rise in temperature is not well documented and received only a rare cursory mention in the literature. Recently, certain traits have been evaluated as selection criteria for wheat genotypes tolerant to heat stress. Shpiler and Blum (1991) evaluated yield components of 21 wheat cultivars and consider kernel number per spike to reasonably estimate heat tolerance. Reynolds et al. (2001) reviewed previous work where physiological traits were evaluated as selection criteria and listed chlorophyll retention during grain filling, membrane thermostability, enzyme stability, chlorophyll fluorescence and canopy temperature depression as potential traits that may be related to high temperature adaptation. Early heading was not mentioned in the review. To the contrary, Reynolds et al. (2001) cited 'lateness' to be '…associated with high yields in many environments.' Hunt et al. (1991) also consider '…late anthesis date…' in combination with a short filling period and rapid grain growth as plausible selection criteria for wheat. Unlike these arguments, the results from this research demonstrate earlier-heading cultivars perform better than later-heading cultivars under south-western Texas growing conditions. Therefore, the effectiveness of programmes that use physiological or biochemical traits to develop heat-tolerant germplasm for environments

Table 4: Amount of green and senesced leaves of wheat cultivars at or shortly after anthesis in south-western Texas, USA, in season 2. Each value is an average of three replications and two irrigation regimes

Cultivar	Green leaves (n per tiller)	Senesced leaves (n per tiller) (%)	Tillers (n m^{-2})	Total aboveground DW (g m^{-2})
Sturdy	2.3	5.8 (71.7)	537	989
Mit	3.2	3.3 (50.5)	584	791
TAM 107	1.6	6.0 (78.6)	574	771
TAM 200	2.2	3.9 (63.9)	713	835
Collin	3.6	2.0 (36.0)	627	707
Pioneer 2180	2.2	6.5 (75.3)	571	1018
TAM 201	2.5	3.7 (60.1)	717	874
Pioneer 2163	1.7	9.0 (84.4)	556	888
TAM 202	3.2	3.2 (49.6)	635	845
TAM 300	2.8	4.9 (63.7)	632	1090
RSI 220	3.5	5.8 (62.8)	436	1191
TX87U7003	4.0	2.1 (34.7)	654	752
Florida 302	2.0	4.2 (67.6)	447	790
Pioneer 2548	3.1	4.8 (60.7)	478	905
Coker 9835	4.3	1.9 (29.8)	598	814
Nadadores 63	2.7	3.1 (52.9)	507	951
Mean	2.8	4.4 (58.9)	579	888
$LSD_{0.05}$	0.43	0.43 (5.7)	83.8	114.9
CV (%)	13.4	10.5 (8.4)	12.5	11.2

similar to that of south-western Texas may greatly be enhanced by making earliness an integral component of the programme.

Season effect

The adverse effect of high temperature during the post-heading stages on grain was evident to some degree when grain yields of the two seasons were compared. Due to delayed planting, both 50 % heading and physiological maturity occurred later in season 2 than in season 1. As a result, there were more days with high temperatures during the overall post-heading period in season 2 than in season 1. There were more days with maximum temperatures that exceeded 25 and 30 °C in season 2 than in season 1 (Table 3). It is likely the occurrence of the post-heading period during periods of higher temperatures resulted in lower average grain yield in season 2 than in season 1 (Tables 1 and 2). Grain yield averaged across all cultivars decreased from 3821 kg ha^{-1} in season 1 to 3609 kg ha^{-1} in season 2, a decrease of 5.6 %. The post-heading period was shorter by an average of 4 days, which was 11.1 % shorter in season 2 than in season 1. The smaller difference in average yield (5.6 %) relative to the difference in post-heading period (11.1 %) between season 1 and season 2 may be explained by the increase in grain filling rate from 10.5 g m^{-2} day^{-1} in season 1 to 11.2 g m^{-2} day^{-1} in season 2 (Tables 1 and 2). This increase in grain filling rate may be attributed to the higher temperature in season 2 than in season 1. However, the increase in grain filling rate was not large enough to fully compensate for the shorter post-heading period which resulted in similar 1000-kernel weights in both seasons (Tables 1 and 2). Vos (1985) showed that an increase of average temperature from 16 to 22 °C shortened the duration of grain growth from > 55 to 40 days. This shortened duration was severe enough to result in smaller grains despite an increase in the rate of grain growth.

Delayed heading and the resulting high temperatures during the post-heading period in season 2 affected some cultivars more than others. The HRW cultivars were more affected than the SRW or HRS cultivars. TAM 107, a cultivar developed in the High Plains of Texas, was the most affected, its yield dropping from 3515 kg ha^{-1} in season 1 to only 1916 kg ha^{-1}, a decrease of 46 %. The post-heading period of TAM 107 decreased by 6.3 days and the grain filling rate decreased from 10.0 g m^{-2} day^{-1} in season 1 to only 6.6 g m^{-2} day^{-1} in season 2. The two HRW Pioneer cultivars in the test were also among the most affected, their post-heading period

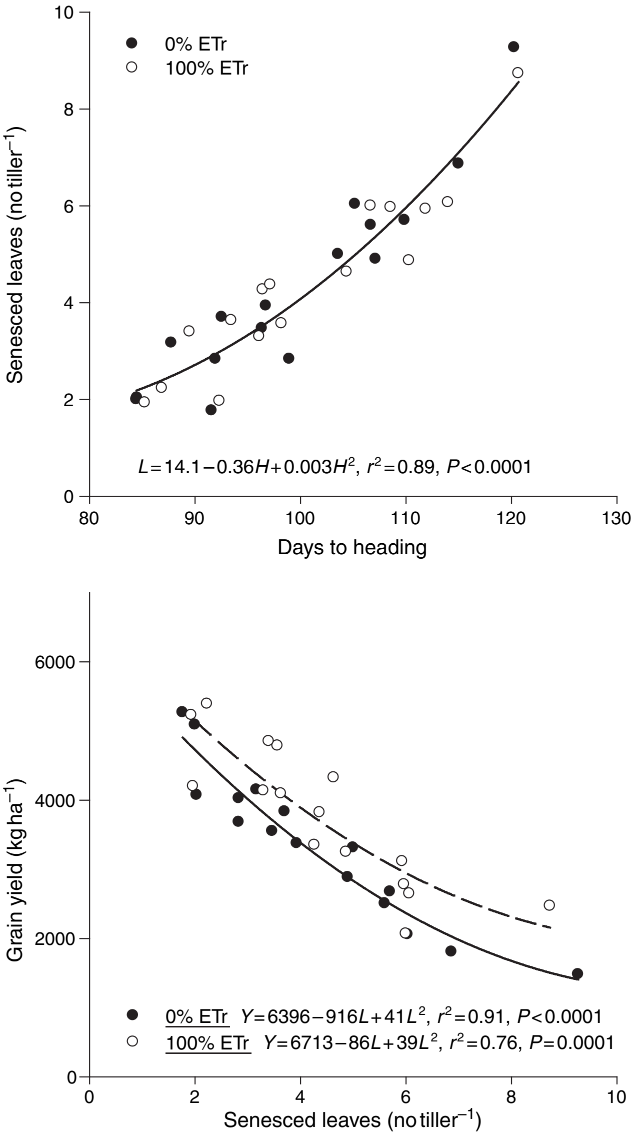

Fig. 5: Association of the amount of senesced leaves (L) with earliness to heading (H) and grain yield (Y) of wheat cultivars grown in south-western Texas, USA, in season 2. Each data point is an average of three replications (%ETr = percentage of estimated evapotranspiration replaced by irrigation)

decreasing by 7–8 days and their yield decreasing by 1087 or 1362 kg ha^{-1} in season 2 compared with season 1. Collin, the earliest heading cultivar during both seasons, was essentially unaffected by season differences.

Despite the higher temperatures during post-heading and shorter post-heading period in season 2 than in season 1, a few of the cultivars performed better in season 2 than in season 1. Nadadores 63, which is a relatively old day-length-sensitive HRS cultivar developed by CYMMIT in Mexico, produced 22.5 % more grain in season 2 than in season 1. Unlike nearly all other cultivars, the post-heading period of Nadadores 63 was not affected by the season differences. Coker 9835, a SRW cultivar, and the experimental line TX87U7003, also yielded better in season 2 than in season 1. It is possible cultivars such as Nadadores 63, that performed better in season 2 than in season 1, may have certain adaptive traits to high temperatures. Mit, a HRW cultivar developed at the Research Center in south-western Texas, yielded 1168 kg ha^{-1} (34 %) more grain in season 2 than in season 1. The poor yield performance of Mit in season 1 relative to its yield in season 2 may be due to lodging that affected this cultivar in particular. The lodging problem on Mit plots started during the third week of February and lasted throughout much of the remainder of the season. Mit therefore may not have specific adaptive traits other than its early heading which make it perform better under more adverse growing conditions such as the second season in this study.

Conclusion

These results suggest that early heading is an important and most effective single trait of wheat cultivars adapted to production systems prone to high temperature stress during the post-heading period. Early heading allows wheat to complete all or a greater fraction of its grain filling period during favourable temperatures and avoid the late-season rise of temperature that has been known to detrimentally affect grain yield and quality. Cultivars with this trait plus a reasonable grain growth rate and duration of grain filling should potentially be the cultivars of choice for production in regions characterized by rapid temperature rise late in the wheat growing season. Such cultivars should also be chosen for late planting or other situations where the wheat crop may mature during periods of high temperatures.

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