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Full Length Research Paper

Effects of kernel weight and source-limitation on wheat grain yield under heat stress

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High temperature in terminal growth stages is a major stress of wheat productivity in South-west Iran, as well as in other Mediterranean environments and the long-term spring temperatures trend to increase. Determination of affecting factors or traits helps to improve the yield potential of wheat. The effects of heat stress during and post anthesis for physiologic, phenologic and agronomic traits was evaluated in ten bread wheat genotypes. The research was conducted under field condition in two different dates under less and more heated environments (two different sowing times). Also, source levels were manipulated through 50% spikelet removal at anthesis to evaluate cultivar source/sink limitations to kernel growth. The results depicted that grain yield, kernel number per spike and 1000 kernel weight were reduced by 24.1%, 9.2% and 23.7% in warmer environment, respectively. Hence, kernel weight was more suited for heat stress screening than other traits evaluated in this study. Thus, wheat genotypes that are able to maintain high individual kernel weight despite heat stress may possess a high level of heat tolerance. Furthermore, results indicated that the poor grain filling could mainly be attributed not to sink-limited conditions, but to source-limited conditions.

Key words: Heat, stress intensity, tolerance, sink-source limitation.

INTRODUCTION

Global warming as a result of climate change negatively affects wheat grain yield, which potentially increases food insecurity and poverty (Ortiz et al., 2008). Kosina et al. (2007) estimated its effect on an area of up to 58.7 million hectares of wheat-grown area in sample countries (57.3 of entire wheat area in surveyed countries) by heat. Average estimated yield loss due to extreme temperature varies between 14.7 to 31.3%, depending on the region. The total estimated loss (aggregated 19 sample countries) amounts to 21 million ton (Kosina et al., 2007). The major treat identified by respondents was terminal heat stress during anthesis and grain filling period, which accelerate maturity and significantly reduces grain size, weight and yield. The heat-stressed environments are divided into separate agroecozones within their respective mega-environment to better target wheat breeding. They are splinted according to high or low relative humidity; example humid sites in Bangladesh, lowland Bolivia, Brazil, Eastern India, Terai of Nepal, Paraguay, Thailand or Uganda, and dry sites in Egypt, central and peninsular India, Nigeria, Sudan, Syria (Lillemo et al., 2005) or Iran.

Many regions need wheat cultivars that are capable of high yields when the weather is beneficial but produce stable yields when conditions are adverse. These genotypes should have high yield potential in both favorable and high temperature environments (Yang et al., 2002a; Ahmed et al., 2011a, b). On the other hand, late harvesting of previous crops like rice or maize, plant machine deficiency or continual rainfall caused late planting in many regions that has coincided reproductive stage of crop with high temperature. High temperature stress during reproductive development is particularly detrimental, with post-anthesis heat stress resulting in a reduction in both individual kernel weight and kernel number (Ahmed et al., 2011a, b; Hays et al., 2007; Plaut et al., 2004; Tashiro and Wardlaw, 1990a; Wardlaw and Wrigley, 1994). Although, varieties that show improved yield stability under heat stress have been identified (Hays et al., 2007, b; Yang et al., 2002b), the quantitative

Table 1. Name and pedigree of genotypes used for drought tolerance assessment.

S/N	Parentage	Origin
1	BHRIKUTINL623-0NPL	CIMMYT
2	FRTL /2*PIFED CMSS96M05650M-040Y-050M-050SY-040SY-030M-27SY-010M-0Y-0SY	CIMMYT
3	CN079//PF70354/MUS/3/PASTOR/4/BABAX CMSS97M02936T-040Y-030M-040SY-030M-040SY-26M-0Y	CIMMYT
4	SKAUZ/BAV92//PASTOR CMSS97Y06166T-040M-8Y-010M-010SY-010M-8SY-010M-0Y-0SY	CIMMYT
5	CS/TH.SC//3*PVN/3/MIRLO/BUC/4/MILAN/5/TILHICMSS97M04005T-040Y-020Y-030M-020Y-040M-28Y-1M-0Y	CIMMYT
6	CS/TH.SC//3*PVN/3/MIRLO/BUC/4/MILAN/5/TILHICMSS97M04005T-040Y-020Y-030M-020Y-040M-28Y-3M-0Y	CIMMYT
7	HAMAM-4 ICW92-0477-1AP-1AP-4AP-1AP-0AP	ICARDA
8	CHEN/AEGILOPSSQUARROSA(TAUS)//BCN/3/VEE#7/BOW/4/PASTOR CMSS93 B01854T- 040Y-8Y-010M-010Y-010M-10Y-0M-4KBY-0KBY-0M-0HTY	CIMMYT
9	CHAMRAN	Iran
10	KOUHDASHT	Iran

nature of heat tolerance and unpredictability of heat stress in the field makes it particularly difficult for breeders to effectively select for the trait. Hence, to develop heat tolerant lines, selection should be made on the basis of yield, grain weight and grain number per spike. High temperature effects on yield and grain weight had also been reported by Ahmed et al. (2010a, b, c), Bluementhal et al. (1995), Wardlaw et al. (2002) and Mian et al. (2007).

A number of morphological and physiological traits have been found to be associated with yield potential in hot environments. According to Al-Khatib and Paulsen (1984), high temperature results in premature plant senescence and shortening of the period of photosynthetic activity. Grain yield depends on the number of grains per unit area (sink) and the availability of assimilates (source) to fill these grains (Zhang et al., 2010). When some spikelets are removed before grain filling, there are differential responses in final kernel mass. Some cultivar differences resulted from sink limitations for nonresponsive cultivars and from source limitations for responsive cultivars. The kernel growth rate of responsive cultivars increased and resulted in higher final mass of individual kernels (Slafer and Savin, 1994; Ahmed et al., 2010a, b). A detailed understanding of the heat tolerance, as well as the use of the proper germplasm will facilitate the development of heat tolerant cultivars. Potential parents are characterized for a range of physiological traits, thereby allowing plant breeders to combine these traits in a strategic manner in crosses

The objectives of this study were: (1) to assess the impact of heat stress during and post anthesis on phenologic periods, plant height and yield components; (2) to determine source/sink limitation in considered genotypes in different environments; (3) to evaluate the response of some wheat genotypes facing high temperatures during and after anthesis under field conditions to find out sources of heat tolerance in bread wheat germplasm for utilization in the breeding program.

MATERIALS AND METHODS

A field study was carried out in 2010 to 2011 season, at a field (with silty clay loam soil) near the experimental fields of Gachsaran Agricultural Research Station (30° 20´N, 50°50´E, 710 m a.s.l) that is located in the southwest Iran. Trials involved ten bread wheat genotypes including two common cultivars (Chamran and Kouhdasht) (Table 1). They were chosen by their selection history and are mostly based on CIMMYT germplasm. They were planted at two sowing dates: normal sowing in 27th November 2010, and late sowing in 7th February 2011. The second sowing was used to expose the crops to more heat, but realistic field combinations during and post-anthesis temperatures.

Plot size of 6.3 m^2 consisting of six rows, 17.5 cm apart and 6 m long were distributed on a randomized complete block design for each sowing date. Crop management was optimal in terms of fertilization, irrigation, weed and pest control to avoid drought and biotic stresses. So, they were considered as less and more heated environments (E1 and E2). Yield components were calculated using standard protocols (Sayre et al., 1997). Days to anthesis was determined when 50% of the spikes had half florets with anther extrusion (Zadocks 65, Zadok et al., 1974) starting from sowing date; and days to maturity were recorded when 50% of the spikes showed total loss of green color. Grain filling duration was recorded as the difference between days to maturity and days to anthesis.

Data on early growth vigor, plant height, spike length, peduncle length, flag leaf extrusion, spikes per m^2, grains per spike, grain yield, kernel length, thousand kernel weight and hectoliter were recorded and analyzed statistically by Fisher's method of analysis of variance.

Table 2. Analysis of variance of different traits for 10 bread wheat genotypes.

SOV	EGV	DHE	GFP	DMA	PLH	SL	PED	FLEX	SM^{-2}	KPS	GYD	KL	TKW	TW
E1														
Replication	0.6416	0.7	6.1	2.4666	22.9743	2.4836	15.2676	7.2863	7435.56	32.1709	423899.9	0.0933	1.5103	5.2633
Genotype	1.4555**	12.2666**	12.044**	32.3333**	90.8023^{ns}	4.6916**	34.8890^{ns}	9.6690^{ns}	15673.4**	63.2431*	1689405.82**	1.0248**	29.7312**	2.0910**
Error	0.2139	2.1259	3.044	2.2074	42.2891	1.1873	20.8943	15.1181	2529.641	29.3948	366327.1	0.237	3.4473	0.6405
E2														
Replication	0.9666	8.025	2.766	20.0916	190.4186	2.6836	121.368	49.2196	0.8575	175.2562	253694.3	2.5466	0.84	3.9226
Genotype	0.6944**	5.5805^{ns}	4.055^{ns}	9.4694**	81.3018**	4.8890^{ns}	97.6555^{ns}	50.847**	1.2024**	77.5673*	736677.9**	7.5804**	24.561***	4.2516^{ns}
Error	0.1055	2.8027	3.5815	2.9064	19.5468	5.697	51.6694	7.6026	0.3675	31.9921	176625.5	1.7222	6.155	3.115

EGV, Early growth vigor; DHE, days to heading; GFP, grain filling period; DMA, days to maturity; PLH, plant height; SL, spike length; PED, peduncle; FLEX, flag leaf extrusion; SM^{-2}, spike per square meter; KPS, kernel per spike; GYD, grain yield; KL, kernel length; TKW, thousand kernel weight; TW, test weight; *and **: Significant at 0.05 and 0.01 probability levels, respectively; E1: less heated environment; E2: more heated environment.

Throughout the crop cycle, the dates of doubled ridge, anthesis and physiological maturity were recorded according to the Zadoks scale (Zadok et al., 1974). Furthermore, to study source-sink relationship at anthesis, 40 main spikes per plot selected and in half of them all the spikelets along one side of the spike were removed. After calculation of mean grain weight in removal and intact spikelets, source limitation (SL) was calculated based on the equation (Ma et al., 1996): S.L. = (a/b - 1)*100, where a and b represent grain weight in removal spikelets and intact spikelets, respectively.

Source limitation under heat condition in comparism with potential kernel weight under less heated conditions (S´.L´) for each genotype was calculated based on following equation: S´.L´.= (a´/b´-1)*100, where a´ and b´ represent grain weight for removal spikelets treatment and intact spikelets treatment under less and more heated conditions, respectively. Heat susceptibility indices for grain yield of each genotype were calculated as HSI = [(1-Y/Yp)/D], where Y is the variable at time of planting; Yp is the variable at late sowing; D is the stress intensity = 1- X/Xp; X is the mean Y of all genotypes and Xp is the mean Yp of all genotypes (Fischer and Maurer, 1978).

RESULTS

Analysis of variance showed significant differences between heated and less heated treatments for early growth vigor, days to maturity, spikes per square meter kernels per spike, 1000-kernel weight, kernel length and grain yield. The genotypes had significant difference for days to heading, grain filling period, spike length and test weight only in less heated conditions vs. for plant height and flag leaf extrusion under more heat conditions (Table 2). The highest stress intensity among phenologic stages was assigned to grain filling period, followed by days to maturity and days to heading. In view of yield components, kernel weight decreased much more than kernel number. However, grain yield as final product of different physiological and biochemical processes was affected by heat stress intensity (Table 3). Comparison between less and high-temperature field environments showed 24.1% difference in wheat yield. Kernel number and weight were reduced by 9.2% and 23.7%, respectively in comparison with wheat grown under E1 and E2 conditions. Moreover, temperature difference between double ridge to anthesis and between anthesis to maturity in E1 and E2 were 4.6 and 2.1°C, respectively.

The number of days between heading to maturity was reduced by 7.1 days for each degree centigrade increase in mean temperature. On the other hand, grain filling rate was increased from 0.9 to1 mg/day in comparison with wheat grown under E1 and E2 conditions. In the present study, kernel numbers reduced nearly 2.2% per 1°C increase in mean temperature from double ridge to anthesis. Gibson and Paulsen (1999) reported that kernel numbers reduce by 63%, at 35/20°C compared with 20/20°C from 10 days after anthesis until ripeness. The reduction in thousand kernel weight was 14.9% per degree centigrade increase in mean temperature from anthesis to maturity under more heat stress comparing with less heated condition. Increasing kernel growth rate cannot compensate this reduction. Acevedo et al. (1991) report 4% reduction in grain weight for each degree centigrade increase in mean air temperature during grain-filling. Obtained results based on stepwise regression (Table 4) showed thousand kernel weight was the most important yield component that remained in final equation.

Table 3. Average of different traits in two adverse environments and their stress intensity.

Trait	EGV (1-5)	DHE (days)	GFP (days)	DMA (days)	PLH (cm)	SL (cm)	PED (cm)	FLEX (cm)	SM^{-2} (no.)	KPS (no.)	GYD (kg/ha)	KL (cm)	TKW (g)	TW (kg/100 L)
E1	3.7	114.1	50	164	92.3	11.5	36.5	28.1	413.7	52	5344.7	14.3	45.8	80
E2	3.8	94.5	34.2	128.7	81.6	10.3	29.7	22.3	414.8	47.2	4056.6	13.7	34.9	78.7
SI	1.7	23.7	4.7	24.1	9.2	0.7	20.9	18.6	10.5	11.6	21.5	314	17.2	-0.7

This trait justifies 37.5 percent of total variation of grain yield. To determine whether the poor grain filling was due to source-limited or sink-limited conditions, the present study examined the responses of genotypes to spikelet-removal (SR) treatment at anthesis. The removal of half of the spikelets on the main stem increased significantly ($P<0.05$) kernel weight of the remaining grains, which were 6.1 and 7.6 mg in high and less heated conditions, respectively. Obtained results showed that maximum source limitation (SL) in E1 belonged to G2 followed by G8 and the least SL specified to G5, G9 and G10, respectively while, the highest SR belonged to G8 followed by G9, G10, and G5 had the least SR under more heated conditions, respectively (Table 5). Average of SR in E1 was only 0.8% more than E2. However, source limitation in more heated conditions compare to potential kernel weight in less heated conditions (S´.L´) (grain weight for intact spikelets of main stem in heat conditions to grain weight for SR treatment in more favorable condition) was 53.4%. Hence, all cultivars showed increase in individual kernel weight under two different conditions and classified as responsive cultivars. Removal of spikelets at anthesis from main stems decreased kernel number and induced a range of compensatory growth responses for the remaining kernels on the main stem.

Furthermore, heat tolerance was estimated for grain yield and 1000 kW by the "Heat Susceptibility index" (S) which scales the reduction in cultivar performance from less to more heated conditions relative to the respective mean reduction over all cultivars. Figure 1 indicates reasonable genotypic heat tolerance in terms of grain yield and thousand kernel weight. There was a clear difference between heat tolerance for G2, G5, G6, G7 and G10 with other genotypes based on grain yield. Meanwhile, G2, G5, G7, G9 and G10 showed the least susceptibility for thousand kernel weight.

DISCUSSION

Proper environment and genotypes can improve yield formation, suggesting that wheat growth is closely related to optimum temperature. However, this can only be achieved by crop if it is sown at a proper environment because gradual rise in temperature can cause a decrease in production. Mean temperature data in current cropping season showed 0.1 to 2.2°C difference compared with long term data (Table 6).

In most parts of Iran, particularly the south west region, yield and its components suffer due to heat stress under natural and late planting like as really conditions in this research. Thus, obtained results have agreement with usual wheat production damage that has occurred every year. Some genotypes showed improved yield stability under heat stress. But, quantitative nature of heat tolerance and unpredictability of heat stress in the field makes it particularly difficult for breeders to effectively select for the trait. Furthermore, as shown by Ortiz-Ferrara et al. (1994), yield *per se* is a reliable but also an expensive indicator of heat tolerance due to the high cost associated with conducting yield trials. Based on obtained results, wheat cultivars capable of maintaining high 1000-kernel weight under heat stress appeared to possess higher tolerance to warm environments according to previous results (Ahmed et al., 2011a, b; Hays et al., 2007; Plaut et al., 2004; Reynolds et al., 1994; Tashiro and Wardlaw, 1990a; Wardlaw and Wrigley, 1994).

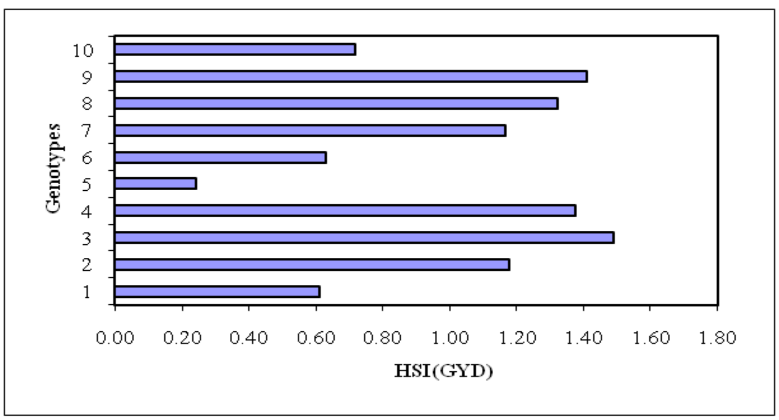
As the mean daily temperatures rose, the productivity of wheat decreases partly because accelerated crop development rate reduces crop duration. In this research, grain filling period in two different environments occurred in April and May and grain filling period was reduced about 15 days in more heated environment. High temperature reduced grain weight via reduced grain growth duration not grain growth rate, hence grain weight was low due to reduced grain-filling period. On the other hand, increasing temperature decreases grain size due to high respiration rate which reduces grain weight because of forced grain development (Gribsin and Paulsen, 1999; Stone and Nicolas, 1984; Tashiro and Wardlaw, 1990b). Consequently, maintaining optimum kernel weight under heat stress is a measure of heat tolerance. Similar findings had been reported by many authors (Tyagi et al., 2003; Singha et al., 2006). In

Table 4. The results of stepwise regression analysis on grain yield.

Traits entered to model	Regression coefficient	Standard error	Partial R^2	Model R^2	F	P
TKW	60.574	17.678	0.375	0.375	11.74	0.001
KPS	183.285	44.156	0.193	0.568	17.229	0
SM^{-2}	-5.058	1.389	0.043	0.611	13.27	0
TW	13.634	5.544	0.029	0.64	6.074	0.016

Table 5. Source limitation (SL) in two different environments and source limitation under heat condition in compared with potential kernel weight in normal conditions (S´.L´).

S/N	SL (E1)	SL (E2)	S´.L´
1	16.0^{b}	20.8^{bc}	55.7^{a}
2	26.6^{a}	16.9^{c}	51.3^{ab}
3	20.1^{ab}	25.5^{b}	54.4^{ab}
4	12.6^{bc}	18.7^{c}	48.2^{b}
5	9.6^{c}	13.4^{cd}	51.2^{ab}
6	16.7^{b}	13.6^{cd}	55.7^{a}
7	12.4^{bc}	16.0^{c}	56.6^{a}
8	21.7^{ab}	36.3^{a}	56.0^{a}
9	16.2^{b}	7.9^{d}	51.9^{ab}
10	16.8^{b}	8.0^{d}	52.5^{ab}



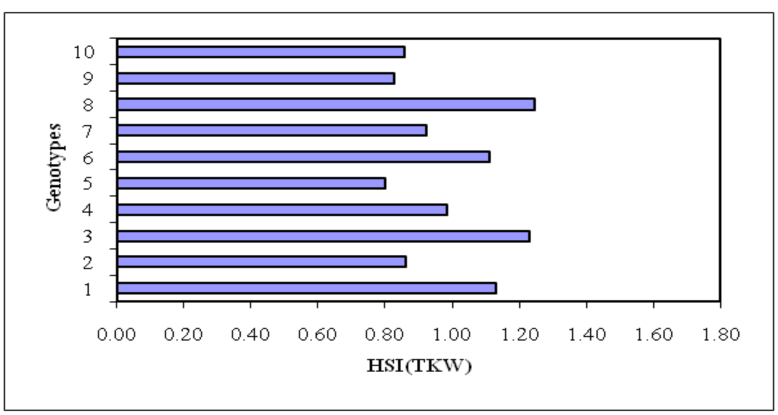


Figure 1. The distribution of different wheat cultivars with respect to mean heat susceptibility index for grain yield and thousand kernel weight.

Table 6. Monthly mean temperature in cropping season in current year and long term.

Parameter	November	December	January	February	March	April	May
2010 to 2011	20.8	14.7	12.0	11.2	14.9	19.3	27.3
Long term	18.6	13.2	10.7	11.3	14.7	18.6	25.4

varieties showed different response for grain weight with temperature after anthesis. Since wheat is a temperate crop, its productivity decreases under higher temperatures. Wheat has as an optimal daytime growing temperature during reproductive development of 15°C and for every 1°C above this optimum, a reduction in yield of 3 to 4% has been observed (Wardlaw et al., 1989). Exposure to higher than optimal temperatures reduces yield and decreases quality of cereals (Ahmed et al., 2011a; Fokar et al., 1998; Maestri et al., 2002; Wardlaw et al., 2002). Research in the Yaqui Valley has demonstrated that high wheat yields are strongly associated with low average temperatures (especially low average minimum temperatures; Lobell et al., 2005).

One of the aim of this study was to determine whether wheat yield under irrigation conditions of South-western Iran was limited in common cultivars and some improved genotypes by the size of the sink or by the assimilates available for grain filling. In this research, the weight and growth rate of individual kernels of responsive cultivars were source-limited and source and sink strengths of these cultivars were not balanced. The effect of changes in source-sink relationship on grain growth would imply that the assimilate availability in control plants in this study was insufficient to fully satisfy grain growth requirements. This may that during post-anthesis; grain yield of wheat is either source-limited or co-limited by both source and sink -limited. Enhanced availability of assimilates and differential kernel responses caused by SR indicated that kernel growth of responsive cultivars was initially source-limited and later sink-limited once maximum kernel growth was attained.

Conclusion

This study concludes that most of the wheat genotypes were more affected when exposed to heat stress for long period of time and vice versa. However, the genotypes varied in their ability to tolerate heat stress. Tolerant genotypes can be utilized in breeding programs for development of wheat varieties having heat tolerance at terminal growth stage. It was suggested that the yield of the common wheat cultivars (Chamran and Kouhdasht) were more source than sink-limited and that breeding wheat with a larger source size than in the these common cultivars may raise the yield potential of wheat under irrigation condition of South-western Iran.

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