

Inheritance of Terminal Heat Tolerance in Two Spring Wheat Crosses

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The objective of this study was to develop an understanding about the genetics of terminal heat tolerance in wheat (*Triticum aestivum* L.). The minimum number of genes was assessed using Mendelian and quantitative genetic approach. Two crosses were made between heat tolerant and heat susceptible bread wheat cultivars: NW1014 × HUW468 and HUW234 × HUW468. Heat susceptible HUW468 was common in both the crosses. The F₄, F₅ and F₆ generations were evaluated including F₁ in two different dates of sowing (normal and very late) under field conditions in year 2006–07. The data was recorded for grain fill duration (GFD) and thousand-grain weight (TGW). Based on data of two dates, decline% and heat susceptibility index (HSI) of GFD and TGW were estimated. Heat tolerance in F₁ showed absence of dominance. Estimation of genes using Mendelian approach in F₄, F₅ and F₆ progenies (148–157) of the two crosses suggested that heat tolerance was governed by a minimum of three genes. Quantitative approach also indicated similar number of genes. The distribution of progeny lines in F₄ and F₆ supported the polygene nature of heat tolerance. These genes if mapped by molecular approach can play an important role through marker assisted selection (MAS) for developing improved thermo-tolerant lines of wheat.

Keywords: *Triticum aestivum* L., terminal heat tolerance, inheritance, heat susceptibility index

Introduction

Wheat production in many tropical and subtropical parts of the world is limited by the high temperature (Ortiz et al. 2008). This problem is more acute in India during reproductive stage which is often termed as terminal heat stress (Joshi et al. 2007a). In general, terminal heat stress refers to rise in temperatures (>30°C) at the time of grain development (grain filling duration). According to an estimate, there are currently around 9 million ha of wheat in tropical or subtropical areas (Lillemo et al. 2005) that experience yield losses due

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to high temperature stress in many countries, including Bangladesh, India, Nigeria, Uganda, Sudan and Egypt, which have long traditions of cultivating wheat. However, the current estimates indicate that in India alone, around 13.5 million ha area is heat stressed (Joshi et al. 2007b). This area is likely to expand significantly if current trends and future predictions about global warming continue (Ortiz et al. 2008). Therefore, breeding for high temperature tolerance in wheat is a major objective of wheat improvement programs in South Asian countries, including India, Nepal and Bangladesh.

In wheat, high temperatures (>30°C) after anthesis can decrease the rate of grain-filling (Barakat et al. 2011), while it can also decrease yield if imposed before anthesis (Wardlaw et al. 1989a). Yields are reduced 3–4% per 1°C rise above the optimum of 15–20°C for grain filling (Wardlaw et al. 1989b). Using this factor, most commercially-sown wheat cultivars in India would loss approximately 50% of their yield potential from exposure to 32°C–35°C at the crucial grain formation stage. Therefore, heat stress related traits have received considerable attention particularly, canopy temperature depression (Blum et al. 1982), GFD (Yang et al. 2002; Mason et al. 2010; Paliwal et al. 2012) and yield related traits including TGW (Mason et al. 2010; Pinto et al. 2010; Paliwal et al. 2012).

It is believed that around as much as 51% of Indo Gangetic plain might be reclassified as a heat-stressed, short-season production mega-environment by 2050 (Ortiz et al. 2008). Hence, there is urgent need to understand the genetics and its mode of inheritance of heat tolerance in wheat, which is still in its infancy (Ortiz et al. 2008; Ashraf 2010). This study investigates the inheritance of terminal heat tolerance in wheat in eastern Gangetic plains of India using TGW and GFD as an accessing parameter.

Materials and Methods

This study was carried out at the research farm of the Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, India which is located in the North Eastern Plain Zone (NEPZ) of India. An off-season facility of Indian Agricultural Research Institute (IARI), Wellington, Tamil Nadu, India was used for advancing the generations. Two populations were developed by making cross between heat tolerant genotypes (NW1014 and HUW234) and heat susceptible HUW468. Both HUW234 and NW1014 are recommended for planting under late-sown conditions of the NEPZ while HUW468 for timely-sown conditions (Joshi et al. 2007b).

Development and evaluation of recombinant inbred lines (RILs) for heat tolerance

RILs were developed following the method described by Singh and Rajaram (1991) and Joshi et al. (2004). The cross was made in 2002–2003 and F₁ grown in the off-season (2003). F₂ was grown in 2003–2004 main crop season and F₃ obtained by harvesting random F₂ plants separately. One hundred forty eight and one hundred fifty-seven F₃ progeny lines of the two crosses were grown in 2004–2005. The F₄ was obtained from randomly planted F₃ progeny rows. Half of the F₄ seed was advanced to F₅ during off-season 2006. The remaining half was used to grow F₄ bulk in 2006–2007 main season. Likewise seeds of all plants of F₅ in off season 2006 were bulked to grow F₅ in three replications in

2006–2007 main season. The F₅ progeny lines of the two crosses obtained from off-season 2005 were planted in 2005–2006 main season and one random single plant was taken from each line to obtain F₆. Remaining plants of F₅ of both crosses were bulked to grow a replicated trial in 2006–2007. Following similar approach, F₆ progeny lines were advanced at off-season nursery and F₆ RILs lines bulked for the replicated trial in 2006–2007. Thus, RILs were evaluated in F₄, F₅ and F₆ generations. F₁ of both crosses were evaluated in 2005–2006 and 2006–2007 under normal and very late sowings.

Three (F₄, F₅ and F₆) generations of the two crosses were planted at two different sowing dates (normal = 3rd week of November 2006 considered as control; very late sown = 1st week of January 2007 considered as heat-stressed) in three replications. Each replication consisted of four blocks having 39 lines with a check (HUW468) after every 5th line to serve as covariate in ANOVA analysis. Each RIL was hand sowed using a randomized complete block design in four-row plots of 3 m length and 20 cm spacing between the rows.

Agronomic practices used were as recommended for irrigated and normal fertility (120 kg N; 60 kg P₂O₅ and 40 kg K₂O ha⁻¹) conditions. The fungicide Tilt (propiconazole; [1-{{2-(2,4-dichlorophenyl)-4-propyl-1,3-dioxolan-2-yl}methyl}-1H-1,2,4-triazole]) was applied (625 g a.i./ha) at two growth stages (GS), GS54 and GS69 (Zadoks et al. 1974) to prevent spot blotch and leaf rust, the two most important diseases of wheat in NEPZ of India.

Variables measured

Data were recorded for TGW, date of anthesis (anthers extruding from 75% of the plants per RIL plot) and physiological maturity (complete loss of green color from the glumes of 75% of the plants per RIL plot) for all RILs and parents. The GFD was calculated using the interval between the date of anthesis and physiological maturity. HSITGW of each line was calculated using the following formula (Fischer and Maurer 1978):

$$\text{HSITGW} = [(1 - \text{TGW}_{\text{heat stress}}) / \text{TGW}_{\text{control}}] / D$$

where, $\text{TGW}_{\text{heat stress}}$ = TGW in late sowing; $\text{TGW}_{\text{control}}$ = TGW in normal sowing conditions.

$$D (\text{stress intensity}) = 1 - (X_{\text{heat stress}} / X_{\text{control}})$$

where, $X_{\text{heat stress}}$ = Mean of $\text{TGW}_{\text{heat stress}}$ of all RILs; X_{control} = Mean of $\text{TGW}_{\text{control}}$ of all RILs.

Dec % TGW was calculated by applying following formula:

$$\text{Dec \% TGW} = ((\text{TGW}_{\text{control}} - \text{TGW}_{\text{heat stress}}) / \text{TGW}_{\text{control}}) \times 100$$

Similarly, Dec % and HSI of GFD (HSIGFD) were calculated on each dates of sowing.

Estimation of gene number

Genes for heat tolerance was estimated following χ^2 analysis (Joshi et al. 2004) as well as the quantitative approach in which Wright's (1968) modified formula (Singh et al. 1995) was used. Narrow sense heritability was estimated following Fehr (1987). The minimum number of genes was verified using the modified formula (Singh et al. 1995; Joshi et al. 2004), $n = (GR)^2 / (R \times \sigma^2g)$ where n = minimum number of genes, GR = Genotypic range and σ^2g = Genetic variance and $R = (8/(2-1/2^g))$. GR was estimated by two methods (Singh et al. 1995; Joshi et al. 2004). In the first, GR was the range of line means, while in the second it was multiplication of range and heritability. The second method is more precise since the integration of heritability is expected to reduce the influence of environment (Mullitez and Baker 1995).

Results

Performance of parents, F₁'s and segregating generations

Heat tolerant (HUW234 and NW1014) and susceptible (HUW468) parents differed for decline% and HSI of GFD and TGW (Table S1*). Compared to parents, the decline% and HSI of GFD and TGW (Table S1) of F₁s were intermediate in both the years indicating absence of dominance.

Cross 1: NW1014 × HUW468

The range, population means and LSD of decline% and HSI of F₅ and F₆ are given in Table S2. The heritability estimates for decline% and HSI of GFD and TGW were high and ranged from 0.77–0.80 and 0.75–0.80, respectively. The distribution of F₄ and F₆ progeny rows (Fig. S1a) showed normal distribution and indicated that genes interacted in an additive manner.

The χ^2 values of decline% and HSI of GFD and TGW (Table 1) in F₄, F₅ and F₆ generations showed goodness of fit for three genes. The results of quantitative method (Table 2) also showed that genes controlling heat tolerance were around three. The method II (heritability used) displayed number of genes quite close to that obtained by χ^2 analysis (Table 1).

Cross 2: HUW234 × HUW468

The heritability estimates for decline% and HSI of GFD and TGW were high (Table S2) and ranged from 0.76–0.81 and 0.80–0.84, respectively. The distribution of F₄ and F₆ progeny rows for both decline% and HSI of GFD and TGW (Fig. S1b) showed a normal distribution.

The χ^2 values of decline% and HSI of GFD and TGW (Table 1) in F₄, F₅ and F₆ generations showed goodness of fit for three genes. The quantitative approach also showed three gene controls. Method II showed similar number of genes as obtained by χ^2 analysis (Table 1).

* Further details about the Electronic Supplementary Material (ESM) can be found at the end of the article.

Table 1. Goodness of fit of ratios observed for the decline% and heat susceptibility index (HSI) of grain fill duration (GFD) and thousand-grain weight (TGW) in F₄, F₅ and F₆ generations of the two crosses (NW1014 × HUW468 and HUW234 × HUW468) of spring wheat tested in the eastern Gangetic plains of India

Generation	Traits	Observed ratio			Hypoth. ratio	χ^2 value	P value	Gene No.
		HTPT ^a	Seg ^b	HSPT ^c				
NW1014 × HUW468								
F ₄	Decline% GFD	7	136	5	2:60:2	1.29	0.52	3
	HSIGFD	8	135	5	2:60:2	2.57	0.28	3
F ₅	Decline% GFD	9	133	6	4:56:4	1.24	0.54	3
	HSIGFD	9	132	7	4:56:4	0.61	0.74	3
F ₆	Decline% GFD	13	119	16	8:48:8	2.54	0.28	3
	HSIGFD	13	121	14	8:48:8	3.64	0.16	3
F ₄	Decline% TGW	9	135	4	2:60:2	4.30	0.12	3
	HSITGW	7	133	8	2:60:2	3.89	0.14	3
F ₅	Decline% TGW	14	126	8	4:56:4	2.70	0.28	3
	HSITGW	9	126	13	4:56:4	1.62	0.44	3
F ₆	Decline% TGW	23	109	16	8:48:8	1.46	0.48	3
	HSITGW	14	106	18	8:48:8	1.43	0.49	3
HUW234 × HUW468								
F ₄	Decline% GFD	7	142	8	2:60:2	3.00	0.22	3
	HSIGFD	6	143	8	2:60:2	2.30	0.32	3
F ₅	Decline% GFD	7	136	14	4:56:4	2.60	0.27	3
	HSIGFD	7	136	14	4:56:4	2.60	0.27	3
F ₆	Decline% GFD	14	124	19	8:48:8	1.96	0.37	3
	HSIGFD	13	128	16	8:48:8	3.79	0.15	3
F ₄	Decline% TGW	8	143	6	2:60:2	2.29	0.32	3
	HSITGW	8	143	6	2:60:2	2.29	0.32	3
F ₅	Decline% TGW	12	138	8	4:56:4	0.82	0.66	3
	HSITGW	9	141	7	4:56:4	0.99	0.61	3
F ₆	Decline% TGW	22	119	16	8:48:8	0.97	0.60	3
	HSITGW	20	115	22	8:48:8	0.37	0.83	3

^a Homozygous for tolerant parental type (homozygous for all tolerant alleles); ^b Segregating for levels higher than tolerant parent but less than or equivalent to susceptible parent (homozygous for at least one tolerant allele or heterozygous for at least one locus and homozygous for susceptibility alleles at other loci);

^c Homozygous for susceptible parental type (homozygous, lacking all tolerant alleles)

Discussion

Heat stress is one of the key factors having high potential impacts on crop yield (Barnabas et al. 2008). It is being believed that wheat yield in most tropical and sub-tropical location is expected to decline due to global warming (Ortiz et al. 2008). Hence, breeding for heat tolerance is a high priority for wheat in many countries including south Asia. Some of the current Indian wheat cultivars have reasonable tolerance to higher temperatures and these varieties dominate eastern Gangetic plains, central India and Peninsular zone. However, the trends of global warming (Battisti and Naylor 2009) demand much more effort for enhancing high temperature tolerance in wheat. This can be facilitated if knowledge on ge-

Table 2. Estimate of minimum number of effective genes segregating for heat tolerance in the two spring wheat crosses for decline% and heat susceptibility index (HSI) of thousand-grain weight (TGW) and grain fill duration (GFD) using Wright's (1968) formula modified for F₄, F₅ and F₆ generation of two crosses (NW1014 × HUW468 and HUW234 × HUW468) of spring wheat (Singh et al. 1995)

Generation	No. of Lines	Method I			Method II	
		Decline%	HSI		Decline%	HSI
NW1014 × HUW468						
				GFD		
F ₄	148	6.22	6.66		2.89	3.11
F ₅	148	6.78	6.93		3.12	3.24
F ₆	148	5.21	5.07		3.02	2.93
TGW						
F ₄	148	6.14	5.29		3.37	2.90
F ₅	148	5.75	5.97		2.94	3.03
F ₆	148	4.90	4.99		3.00	3.11
HUW234 × HUW468						
				GFD		
F ₄	157	6.88	6.49		3.33	3.15
F ₅	157	5.87	5.68		3.44	3.25
F ₆	157	5.18	5.33		3.39	3.45
TGW						
F ₄	157	6.04	6.32		3.14	3.28
F ₅	157	5.60	5.16		3.18	2.93
F ₆	157	4.07	4.33		2.89	3.06

Method I = Without heritability; Method II = With heritability

netics of heat tolerance is made known to breeders. Different traits have been used to study heat tolerance. Among them, canopy temperature depression, senescence related traits (stay green), chlorophyll content and yield and its attributive traits are the most investigated ones (Yang et al. 2002; Mason et al. 2010; Paliwal et al. 2012). In this study TGW and GFD were used.

The minimum numbers of gene for heat tolerance was detected by qualitative and quantitative approach. Compared to parents, the F₁'s were of semi-heat tolerant type, indicating additive nature of genes. Since the crosses used involved parents with contrasting heat tolerance as expressed by decline% and HSI of TGW and genes interacted in an additive manner, only extreme homozygotes were expected to display parental type behavior in the segregating generations (Joshi et al. 2007b). Since we recorded observations in all the plants of each of the progeny rows, a genotype other than parental would appear as either segregating or intermediate type and can be easily detected in the population. The test of goodness of fit suggested that the observed distributions for the two crosses could be explained by segregation of genes at around three independent loci for the parameter decline% and HSI of GFD and TGW (Table 1). The quantitative approach followed in F₄, F₅ and F₆ generations also displayed that around three genes control.

This suggests that heat tolerance is polygenic in nature and governed by additive gene action. Yang et al. (2002) reported minimum 1.4 genes with both additive and dominance

effects in F₂ cross population for heat tolerance. Other reports in wheat also showed importance of additive gene action in heat tolerance (Ibrahim and Quick 2001; Dhanda and Munjal 2006).

The distribution of progeny lines in F₄ and F₆ of the two crosses showed a normal distribution for Decline% and HSI of GFD and TGW (Figs S1a and S1b). In both crosses, few lines appeared transgressive suggesting that parents contributed different genes for heat tolerance. Yang et al. (2002) and Saadalla et al. (1990) also reported transgressive segregants and suggested that heat tolerance is not simply inherited. The results of chi-square and quantitative methods as well as the normal distribution in segregating generations support the hypothesis of Blum (1988) and Yang et al. (2002) that heat tolerance is quantitatively inherited.

The broad sense heritability of decline% and HSI of GFD and TGW ranged from 0.72 to 0.80 in the two crosses. The heritability for heat tolerance as intermediate to high has been reported in wheat (Ibrahim and Quick 2001; Yang et al. 2002). The high heritability suggests that good gain from selection can be obtained.

Results of this investigation suggest that heat tolerance is governed by at least three genes with additive gene effect. The additive interaction of only few (three) genes suggest that heat tolerance can be enhanced by growing fairly large segregating population and applying effective selection in the early segregating generations. The high heritability traits like TGW and GFD deserve more attention for evolving better wheat for heat stress environments.

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Electronic Supplementary Material (ESM)

Electronic Supplementary Material (ESM) associated with this article can be found at the website of CRC at <http://www.akademai.com/content/120427/>

Electronic Supplementary *Table S1*. Mean performance of the three parental genotypes and two F_{1s} of the crosses NW1014 × HUW468 and HUW234 × HUW468 for decline% and heat susceptibility index (HSI) of grain fill duration (GFD) and thousand-grain weight (TGW) under heat stressed condition in two years of testing in eastern Gangetic plains of India

Electronic Supplementary *Table S2*. Mean performance of F_5 and F_6 recombinant inbred lines (RILs) of the two crosses of spring wheat (NW1014 × HUW468 and HUW234 × HUW468) for decline% and heat susceptibility index (HSI) of grain fill duration (GFD) and thousand-grain weight (TGW) when tested in the year 2006 at eastern Gangetic plains of India

Electronic Supplementary *Figure S1a*. The distribution of F₄ and F₅ progenies of the wheat cross 'NW1014 × HUW468' for decline% and heat susceptibility index (HSI) of thousand-grain weight (TGW) and grain fill duration (GFD) when tested in eastern Gangetic plains of India

Electronic Supplementary *Figure S1b*. The distribution of F₄ and F₅ progenies of the wheat cross 'HUW234 × HUW468' for decline% and heat susceptibility index (HSI) of thousand-grain weight (TGW) and grain fill duration (GFD) when tested in eastern Gangetic plains of India