



QTL mapping for heat tolerance related traits using backcross inbred lines in wheat (*Triticum aestivum* L.)

Sunil, Harikrishna*, Deepali Upadhyay, Rahul Gajghate, P. Shashikumara, Divya Chouhan, Swetha Singh, V. P. Sunilkumar, B. Manu, Nivedita Sinha, Sanjay Singh, Neelu Jain, G. P. Singh and P. K. Singh

Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi 110 012; ¹ICAR-Indian Institute of Wheat and Barley Research, Karnal

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Abstract

Heat stress is one of the most limiting factors for the production of wheat. Global warming and consequent changes in climate adversely affect wheat plant growth and yield. To elucidate genetic basis and map heat tolerance traits, a set of 134 backcross inbred lines (BILs) derived from the cross between WH730/*2 HD2733 was used. The population was evaluated under late sown (LS) and very late sown (VLS) conditions, by exposing to heat stress during *rabi* season. Positive association of normalized difference vegetation index (NDVI), thousand grain weight (TGW), grain weight per spike (GWS), biomass and grain yield (GY) under both production conditions was observed. However, canopy temperature (CT) and days to heading (DH) showed negative correlation with GY under heat stress. A total of 9 Quantitative trait loci (QTL) were discovered on 7 chromosomes, which includes 4 QTLs in LS and 5 QTLs under VLS condition. Combining the results of these QTLs revealed a major stable QTL for DH (*qDH_ari_5A*) on chromosome 5A with 23% and 26% explaining phenotypic variance under both sowing conditions. QTL for NDVI was detected on chromosome 1B while QTL for SL and GY on chromosome 2A. The identified QTLs in the genomic regions could be targeted for genetic improvement and marker assisted selection for heat tolerance in wheat.

Key words: Wheat, QTL Mapping, Heat tolerance

Introduction

Wheat (*Triticum aestivum* L.) is one of the most important and widely adapted strategic food crops. Heat stress is a major environmental constraint to crop production. Sensitivity to heat stress is a major limitation to growth and productivity of wheat as especially in sub-tropical and dry regions. Episodes of heatwaves in combination with drought are serious

during the anthesis and grain-filling period, which are the most vulnerable stage affecting the final yield (Ortiz et al. 2008). Potential expression of important traits determining yield formation is essential for productive selection in any breeding plan (Sagar et al. 2016). The decline in yield is the outcome of decreased grain weight, early senescence, shriveled grains, reduced starch accumulation, altered starch-lipid composition in grains, lower seed germination and loss of vigor (Balla et al. 2012). To withstand heat stress and yield normal, plants have evolved with special mechanisms to adapt. The dissection of genomic regions associated with heat tolerance through the mapping of QTLs is essential to know the genetic basis of heat tolerance. It helps to understand the association of traits related to heat stress and pave the way for augmenting the wheat productivity under heat stress conditions. Therefore, breeding for tolerance to chronic as well as short term heat stress is a major objective worldwide (Ayeneh et al. 2002; Yang et al. 2002; Nachit et al. 2004; Reynolds et al. 2007; Jain et al. 2014; Reynolds et al. 2016). In view of the facts mentioned above, the present study was undertaken for characterization of morpho-physiological traits in BILs and mapping QTLs associated with heat tolerance related traits for improving heat stress tolerance in wheat.

Materials and methods

Experimental design and materials

In the present study, a set of 134 BILs derived from the cross between HD2733 and WH730 (IC546937, an elite wheat genotype having highly stable yield and

*Corresponding author's e-mail: harikrishna.agri@gmail.com

better adaptability to terminal heat stress) along with parents were sown in α -lattice design under late and very late sown conditions with two replications constituting eight blocks (each block contains 17 test genotypes) in *rabi* 2017. WH730, Experiment was carried out at an experimental farm, Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi. Dhanda et al. (2012) reported earlier that WH730 is a heat stress tolerant genotype which recorded high grain yield and with its low heat susceptibility index, high thermo-tolerance of membrane, high kernel weight and grain number are the important features of this variety. The F_1 seeds were harvested and sown in *rabi* 2012. The F_1 were backcrossed using as male parent to HD2733, and total 134 individuals of BC_1F_1 plants were allowed to self-pollinate and then harvested seeds from each individual plant were allowed to advance up to BC_1F_5 .

Phenotyping and genotyping of BILs population

The population was phenotyped for nine morphophysiological traits namely, days to heading (DH), grain weight per 10 spikes (GWS), spike length (SL), number of spikelets per spike (NSPS), plant biomass (PB), thousand kernels weight (TKW), grain yield (GY), canopy temperature (CT) and normalized difference vegetation index (NDVI) under late sown (LS) and very late sown (VLS) conditions as follows; Parental means described here were the best linear unbiased predictions (BLUP) which were calculated using R package. The physiological traits CT and NDVI were recorded at different stages of the crop growth.

Genomic DNA of parental genotypes and BILs was isolated using CTAB method of Saghai-Marouf et al. (1984). Quantity and quality of genomic DNA were tested on 0.8% agarose gel by using standard DNA ladder. A total of 1350 Simple sequence repeats (SSRs) were screened and 95 of which were identified as polymorphic SSRs, distributed over different chromosomes were used to genotype the entire population. Parents were evaluated for polymorphism using different series of markers (gwm/wms, wmc, barc, cfd and cfa) selected from published SSR maps (Somers et al. 2004; Roder et al. 1998; Kadam et al. 2012; Pestsova et al. 2000; Gupta et al. 2002). Amplification of genomic DNA of parental genotypes and BILs was done with 'BIO RAD T100 Thermal Cycler' using following conditions: Initial denaturation -94°C for 5 min, denaturation -94°C for 1 min, annealing -52°C to 60°C (vary with SSR primers used) for 1 min, extension -72°C for 1 min, 35 cycles from denaturation to extension step, final extension -72°C

for 10 min. PCR products were resolved by using 2.5% horizontal agarose gel electrophoresis. Profiles of polymorphic SSR markers were scored visually by coding HD2733 alleles as "A" whereas WH730 alleles were scored as "B". While heterozygote individuals are scored as "H". Missing bands were scored as 'NA'. GGT2 software was used for graphical genotyping of 134 BILs. The construction of linkage map and QTL mapping was performed using software ICIM v4.0 following the default functions available with software. The LOD threshold value of 2.5 with 1000 permutations was used for declaration of QTL.

Results

Phenotypic performance of BILs

Analysis of variance indicated significant genotypic variance present in the BILs for heat tolerance (Table 1). The phenotypic values for traits under study showed normal distribution pattern. For the nine morphophysiological traits, values of correlation coefficients based on data pooled over LS and VLS conditions are presented in Table 2. Both in the LS and VLS conditions, NDVI was significantly correlated with grain yield and all other traits, except DH, NSPS and SL. The magnitudes of correlation of NDVI with other traits were higher under VLS condition relative to those in the LS condition. NDVI is strongly correlated with TKW under LS (0.61) and VLS (0.67). The regression analysis is performed using yield as an independent variable and all other traits as dependent. Results of regression analysis are presented in (Tables 3a and 3b) for LS and VLS, respectively.

Molecular characterization of BILs population and genetic linkage map construction

A set of 1350 SSR primers were used to detect polymorphism between parental genotypes, out of which 95 SSRs were polymorphic. Per cent polymorphism between the parents is 9.18. The maximum number of polymorphic markers were found on 2A with nine markers while lowest being two on 6D chromosome. The average numbers of markers per chromosome were 4.52. The linkage map developed using 95 polymorphic markers and 134 BILs population was further utilized to analyze the composition of individual BIL using GGT2 software. The genome of BILs is composed of 63.3 per cent of HD2733 whereas 26.2 per cent of WH730 and remaining is 10.4 per cent, constitute the heterozygous and missing values. The linkage map with identified QTLs in WH730/*2 HD2733 BILs were presented in Fig. 1.

Table 1. Analysis of variance for different morpho-physiological traits under late sown and very late sown conditions in Rabi 2016

Trait	Sources	Mean sum of square		Trait	Sources	Mean sum of square		Trait	Sources	Mean sum of square	
		LS	VLS			LS	VLS			LS	VLS
DH	Modal	39.41**	0.0036*	NDVI6	Modal	0.0087**	4.1622	CT6	Modal	3.78**	3.666
	Rep	11.52	0.0014		Rep	0.0189**	3.7202		Rep	293.4**	3.855
	Block	7.85	0.0016		Block	0.0035*	4.179		Block	2.896**	2.176
	treatment	40.10**	0.0044*		treatment	0.0088**	7.5270*		treatment	1.414*	4.041
NDVI2	Modal	0.0023**	0.0098	CT2	Modal	8.58**	7.428	GWS	Modal	17.0**	55065
	Rep	0.0006	0.0045		Rep	639.9**	3.985		Rep	76.8**	66735
	Block	0.0023**	0.0074		Block	14.93**	8.242		Block	4.58*	57447
	treatment	0.002**	0.0143*		treatment	1.568**	12.390*		treatment	16.62**	55489
NDVI3	Modal	0.0042**	0.0103**	CT3	Modal	0.0087**	4.1622	TGW	Modal	56.15**	0.0004*
	Rep	0.0024	0.0080*		Rep	0.0189**	3.7202		Rep	168**	0.0007**
	Block	0.004**	0.0052		Block	0.0035*	4.179		Block	10.2	0.0003
	treatment	0.0037**	0.0106**		treatment	0.0088**	7.5270*		treatment	54.32**	0.0002
NDVI4	Modal	0.0078**	0.0104**	CT4	Modal	8.58**	7.428	GY	Modal	16083**	0.0009**
	Rep	0.0073*	0.0125**		Rep	639.9**	3.985		Rep	55481.**	0.0015**
	Block	0.0044**	0.0037		Block	14.93**	8.242		Block	7955	0.0005
	treatment	0.0076**	0.0063*		treatment	1.568**	12.390*		treatment	14922**	0.0003
NDVI5	Modal	0.0143**	2.682	CT5	Modal	3.060**	5.130*	Biomass	Modal	68409**	26.54
	Rep	0.0056	3.078		Rep	85.50**	2.863		Rep	413220**	29.38
	Block	0.0032	2.807		Block	5.946**	6.215*		Block	42028	30.064
	treatment	0.0151**	4.3060*		treatment	1.531	10.081**		treatment	65213**	10.66

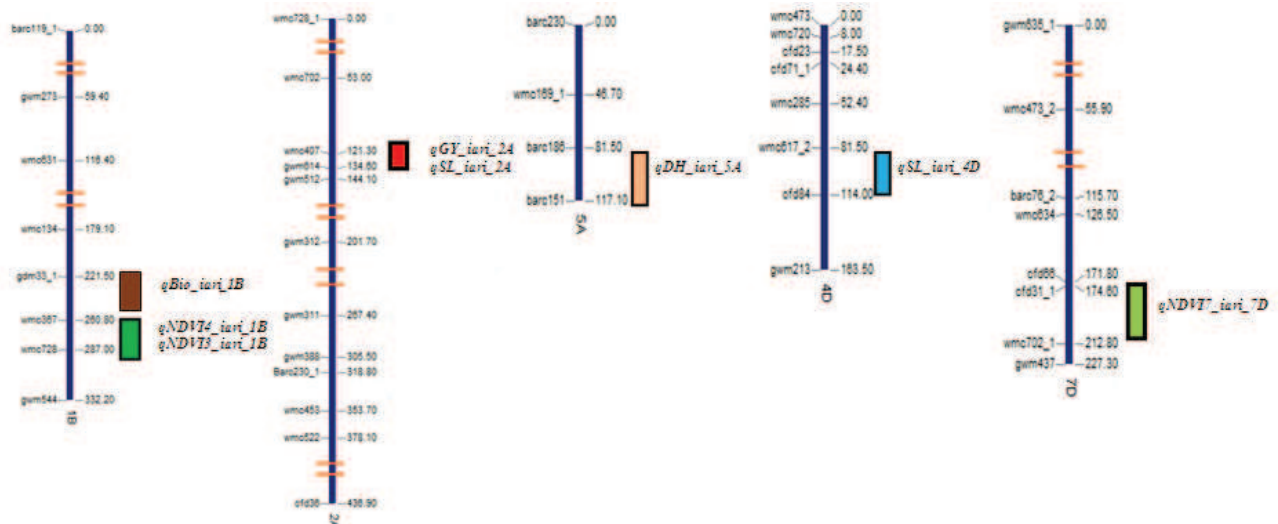


Fig. 1. Genetic linkage map of WH730/2 HD2733 BILs population with identified QTLs

QTL mapping for the heat stress tolerance traits

A total of 9 QTL were detected for five different

agronomic traits using Inclusive Composite Interval Mapping (ICIM) under late sown and very late sown

Table 2(a). Correlation between physiological and yield component traits in BILs population under LS

LS	GY	DH	NDVI	CT	GWS	SL	PS	Biomass	TGW
GY	1								
DH	-0.082	1							
NDVI	0.64**	0.04	1						
CT	-0.34**	0.05	-0.58**	1					
GWS	0.64**	-0.18*	0.62**	-0.41**	1				
SL	-0.08	0.03	-0.04	-0.10	0.11	1			
NSPS	-0.02	0.05	0.14	-0.16	-0.007	0.42**	1		
Biomass	0.64**	-0.02	0.56**	-0.38**	0.46**	-0.03	-0.09	1	
TKW	0.61**	-0.21*	0.55**	-0.36**	0.86**	-0.02	-0.08	0.43**	1

Table 2(b). Correlation between physiological and yield component traits in BILs population under VLS

LS	GY	DH	NDVI	CT	GWS	SL	PS	Biomass	TGW
GY	1								
DH	-0.01	1							
NDVI	0.71**	0.005	1						
CT	-0.57**	0.02	-0.62**	1					
GWS	0.69**	-0.05	0.67**	-0.47**	1				
SL	-0.02	0.02	0.07	-0.07	0.16	1			
NSPS	-0.10	0.16	0.07	-0.007	-0.01	0.31**	1		
Biomass	0.63**	0.11	0.46**	-0.38**	0.35**	0.07	-0.06	1	
TKW	0.67**	-0.11	0.54**	-0.41**	0.82**	0.09	-0.19*	0.24**	1

Table 3(a). Regression analysis using yield as independent variable and all other traits as dependent variable in LS environments in rabi 2016, IARI, New Delhi

Variables	Coefficients	Standard error	t-value	Significance
DH	-0.15	0.70	-0.22	0.83
NDVI	507.32	184.08	2.76	0.01
CT	48.57	33.53	1.45	0.15
GWS	5.72	2.71	2.11	0.04
SL	-12.88	8.59	-1.50	0.14
NSPS	7.62	10.67	0.71	0.48
Biomass	0.26	0.05	5.27	0.00
TGW	1.61	1.45	1.12	0.27

Table 3(b). Regression analysis using yield as independent variable and all other traits as dependent variable in VLS environment in rabi 2016, IARI, New Delhi

Variables	Coefficients	Standard error	t-value	Significance
DH	-0.16	0.56	-0.29	0.77
NDVI	512.09	157.97	3.24	0.00
CT	-60.20	30.91	-1.95	0.05
GWS	2.04	2.73	0.75	0.46
SL	-15.62	5.59	-2.79	0.01
NSPS	1.16	3.75	0.31	0.76
Biomass	0.35	0.05	7.71	0.00
TGW	8.02	1.75	4.60	0.00

conditions (Table 4). These were located on five different chromosomes, 1B, 2A, 4D, 5A and 7D. A minimum of 1 QTL were available each for GY, NDVI, DH, SL and biomass and the maximum of 3 QTLs

were available for NDVI *i.e.*, *qNDVI3_ari_1* and *qNDVI4_ari_1B*, *qNDVI7_ari_7D* under late sown and very late sown conditions, respectively. QTLs were identified both in late sown (4 QTLs) and very late

Table 4. QTLs detected for various physiological and yield component traits in the WH730/*2 HD2733 BILs population

S.No.	Situation	Trait	Chr. No.	Position	Left marker	Right marker	LOD	PVE (%)	Add
1	LS	<i>qDH_iri_5A</i>	5A	116	<i>Xbarc186</i>	<i>Xbarc151</i>	7.11	23.15	2.69
2	LS	<i>qNDVI3_iri_1B</i>	1B	262	<i>Xwmc367</i>	<i>Xwmc728</i>	2.56	8.63	0.005
3	LS	<i>qBio_iri_1B</i>	1B	260	<i>Xgdm33.1</i>	<i>Xwmc367</i>	2.54	8.4	21.8
4	LS	<i>qGY_iri_2A</i>	2A	192	<i>Xgwm388</i>	<i>Xwmc407</i>	3.42	5.37	-38.34
6	VLS	<i>qDH_iri_5A</i>	5A	116	<i>Xbarc151</i>	<i>Xbarc186</i>	8.75	26.42	3.04
7	VLS	<i>qNDVI4_iri_1B</i>	1B	262	<i>Xwmc367</i>	<i>Xwmc728</i>	2.56	8.63	0.005
8	VLS	<i>qNDVI7_iri_7D</i>	7D	176	<i>Xcfd31.1</i>	<i>Xwmc702.1</i>	3.04	10.05	-0.01
9	VLS	<i>qSL_iri_2A</i>	2A	180	<i>Xgwm388</i>	<i>Xwmc407</i>	7.7	10.58	0.27
10	VLS	<i>qSL_iri_4D</i>	4D	94	<i>Xwmc617.2</i>	<i>Xcfd84</i>	5.09	13.29	0.28

Situation: LS (Late sown) and VLS (very late sown), Position of QTL as cM distance from the top of each map., LOD, A LOD threshold of 2.5 was used for declaration of QTL, PVE (%), Phenotypic variance explained by QTL, Additive effect, Positive “additive effect” indicates an increasing effect from HD2733; negative “additive effect” indicates an increasing effect from WH730

sown conditions (5 QTLs). LOD scores for individual QTL ranged from 2.54 to 8.75.

Discussion

Among the several strategies to overcome the problem of climate change in agriculture, development of stress tolerant genotype/varieties utilizing the molecular resources is important and useful strategy. There are several reports on identification of QTLs responsible for stress tolerance in wheat. Majority of the QTL mapping studies in wheat under heat and drought stress conditions involved mapping populations such as RILs (Mason et al. 2010; Pinto et al. 2010; Mason et al. 2011; Paliwal et al. 2012), doubled haploids (Tiwari et al. 2013) and segregating F₂ and F₃ populations (Gupta et al. 2015). The BILs have rarely been used in QTL mapping experiments across crops (Zhang et al. 2015). In present study, significant parental variation was observed for different morpho-physiological traits suggesting ample genetic diversity between the parents. The analysis of variance of different traits showed that most of the traits across the environments considered here were having significant genotypic differences. Phenotypic correlations were estimated using BLUP values of both the environments. DH is used as covariate in BLUP values analysis in order to reduce the variation induced by DH *per se* among the genotypes. The correlations obtained in present study are in agreement with the previous reports under heat stress (Ramya et al. 2015) where early heading and faster grain filling was observed as critical component traits of heat stress tolerance under changing climatic conditions (Tahmasebi et al. 2016). DH was negatively correlated

with GY and its components traits under heat stress.

The NDVI values tend to decrease as the stress and stage of the plant advances whereas CT increased along the stage and stress on the parents. NDVI is robust trait to be used as criteria for evaluation of genotypes for drought and heat tolerance (Harikrishna et al. 2016; Monostori et al. 2016; Manu et al. 2020). Together, ground cover (leaf area) and the leaf greenness of the canopy can be measured by NDVI (Ramya et al. 2016). It provides an indirect measure of leaf health, which is reflected by leaf nitrogen content associated with photosynthetic efficiency. Few researchers used this trait as proxy trait in drought and heat stress breeding programmes (Araus et al. 2008). NDVI has been found to have positive correlation with yield under both late sown and very late sown conditions in the present study. The magnitude of association increased under VLS condition. In the BILs, differences for NDVI became clearer in later stages of crop growth; this signifies the role of NDVI in heat tolerance. CT is negatively associated with yield and its component traits under stress (Sinha et al. 2018). The magnitude of association was strong in VLS. To characterize the mapping populations and genotypes under heat stress, CT has been used earlier (Tiwari et al. 2012; Reynolds et al. 1997). Cooler canopy temperatures associated with optimal root distribution by which roots proliferate at depth under drought or near to surface under hot, irrigated condition thus maintaining cooler canopies (Pinto et al. 2015). The present study also supports this observation as indicated from the correlation and the regression analysis.

The TKW is well known as proxy trait under heat and drought tolerance and serve as component of heat tolerance (Zarei et al. 2013; Mohammadi et al. 2004; Pinto et al. 2015). Correlations between TKW and yield under heat stress is strong and positive. The positive and strong correlation of GWS and TKW with GY implies its significance in heat stress breeding.

Graphical genotyping clearly reflected the genomic composition of individual BIL and population as whole. The results perfectly matched with the hypothesis in which nearly 75% of the genome of individual line was contributed by HD2733. Mapping QTLs in bi-parental populations allowed the identification of chromosome segments controlling traits of agronomic importance with the opportunity to dissect complex traits into component loci (Marza et al. 2006). During the present study, QTL analysis allowed mapping of as many as 9 QTL (VL and VLS conditions) for physiological and yield related traits suggesting that the genetic control of these traits in wheat is polygenic. This was also supported by the continuous distribution in the component traits of heat tolerance. The findings of earlier studies for identification of QTL also suggested complex genetic control of yield and related traits (McIntyre et al. 2010; Pinto et al. 2010; Bennett et al. 2012a; Bennett et al. 2012b; Kadam et al. 2012; Lopes et al. 2012). Use of physiological traits in combination with QTL mapping provides basic understanding and can serve as useful criterion in selection of heat tolerant genotypes. A Major QTL for DH from the chromosome 5A (*qDH_ari_5A*) will be important for wheat improvement for heat stress using MAS, through earliness per se. This QTL was detected both under LS and VLS conditions, suggesting this QTL is more stable and can be used for selection of early genotypes for testing under both conditions. This QTL explained 23-26 per cent of phenotypic variance under LS and VLS conditions however, earlier report on QTL, governing the expression of days to anthesis was associated with Xbarc186, in Seri M82/Babax derived RILs population under heat and drought conditions, which governs early anthesis thereby early maturity explained 6.4 % phenotypic variance (Pinto et al. 2010) in 5A. Zhang et al. (2010) also reported a meta-QTL MQTL4 for yield and related traits in the proximity of Vrn-A1 suggesting the importance of this particular genomic region for traits like days to maturity, GY and other related traits.

The NDVI is an integrative measure of chlorophyll

and total plant biomass, confirmed by a significant positive correlation between NDVIg and Chlg and plant height (Pinto et al. 2016). The QTL *qNDVI3_ari_1B* flanked by markers Xwmc367 and Xwmc728 detected for NDVI3 under LS and NDVI4 under VLS environments was in agreement with a QTL on 1B that explained around 10 % of the phenotypic variance for both rate of senescence and greenness decay reported by Pinto et al. (2016). A QTL *qNDVI7_ari_7D* flanked by cfd31.1 and wmc702.1 on chromosome 7D associated with NDVI at grain filling duration under VLS. Previous studies detected QTL for NDVI on chromosome 7D associated with permanence of greenness under high temperatures (Pinto et al. 2016; Vijayalakshmi et al. 2010; Kumar et al. 2010). Previous studies have documented few QTL for spike length, but none of the studies reported QTLs for spike length on 2A chromosome, suggesting the QTL *qSL_ari_2A*, detected in 2A chromosome flanked by markers Xgwm388-Xwmc407 and with the LOD value 7.7 explaining a phenotypic variance 10.58 %, is putative novel region for spike length under heat stress. Another QTL for SL linked to Xwmc617 in 4D chromosome, the phenotypic variance explained is 13.29 per cent, having the LOD value of 5.09 was also novel to our knowledge. Some previously reported QTL were also confirmed in the present study. The *qGY_ari_2A* is detected in chromosome 2A with a LOD value of 3.4 and phenotypic variance of 5.37. In 2A chromosome, McCartney et al. (2005) reported a QTL for grain yield in DH mapping population derived from RL4452 × 'AC Domain.

Authors Contribution

Conceptualization of research (PKS, GPS NJ); Designing of the experiments (HK); Contribution of experimental materials (PKS); Execution of field/lab experiments and data collection (S, DC, SS, SVP, SK, MB); Analysis of data and interpretation (HK, NJ, SS, RG, DU); Preparation of the manuscript (DU, S, HK, NJ).

Declaration

The authors declare no conflict of interest.

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