



Physiological traits associated with heat tolerance in bread wheat (*Triticum aestivum* L.)

Girish Chandra Pandey · H. M. Mamrutha · Ratan Tiwari · Sindhu Sareen · Shrutkirti Bhatia · Priyanka Siwach · Vinod Tiwari · Indu Sharma

Received: 22 July 2014 / Revised: 15 September 2014 / Accepted: 8 October 2014 / Published online: 23 October 2014
© Prof. H.S. Srivastava Foundation for Science and Society 2014

Abstract Field experiments for evaluating heat tolerance-related physiological traits were conducted for two consecutive years using a mapping population of recombinant inbred lines (RILs) from the cross RAJ4014/WH730. Chlorophyll content (Chl) and chlorophyll fluorescence (CFL) were recorded under timely sown (TS) and late sown (LS) conditions. Late sowing exposes the terminal stage of plants to high temperature stress. Pooled analysis showed that CFL and Chl differed significantly under TS and LS conditions. The mean value of CFL (Fv/Fm) and Chl under both timely and late sown conditions were used as physiological traits for association with markers. Regression analysis revealed significant association of microsatellite markers viz., Xpsp3094 and Xgwm131 with coefficients of determination (R^2) values for CFL (Fv/Fm) and Chl as 12 and 8 %, respectively. The correlation between thousand grain weight (TGW) with Chl and CFL were 14 and 7 % and correlation between grain wt./spike with Chl and CFL were 15 and 8 %, respectively. The genotypes showing tolerance to terminal heat stress as manifested by low heat susceptibility index (HSI=0.43) for thousand grain weight, were also found having very low Chl, HSI (−0.52). These results suggest that these physiological traits may be used as a secondary character for screening heat-tolerant genotypes.

Keywords Chlorophyll content · Chlorophyll fluorescence · Wheat · Heat stress · Microsatellite markers

G. C. Pandey · H. M. Mamrutha · R. Tiwari (✉) · S. Sareen · V. Tiwari · I. Sharma
Directorate of Wheat Research, Karnal 132001, Haryana, India
e-mail: ratantiwari64@gmail.com

S. Bhatia
Department of BT and BI, Jaypee University of Information Technology, Solan 173234, Himachal Pradesh, India

P. Siwach
Chaudhary Devi Lal University, Sirsa 125055, Haryana, India

Abbreviations

Chl	Chlorophyll content
CFL	Chlorophyll fluorescence
TGW	Thousand grain weight
SSR	Simple sequence repeat
RIL	Recombinant inbred lines
Fv/Fm	Variable fluorescence/maximal fluorescence
HSI	Heat susceptibility index
QTLs	Quantitative trait loci
GFD	Grain filling duration
DPA	Days to post anthesis

Introduction

Abiotic stress, especially heat stress, induces complex morpho-physiological phenomenon in plants (Nachit et al. 1998). Temperate cereals are more sensitive to changes in temperature than tropical cereals. Numerous traits identified as responsible for heat tolerance are heritable, additive in nature and display continuous variation; these indicates that there is considerable scope for improvement in heat tolerance (Tuberosa and Salvi 2006). Various physiological traits have been studied to ascertain their contribution to heat tolerance, for example, higher photosynthetic rates, stay-green, chlorophyll content (Chl), chlorophyll fluorescence (CFL), etc. Breeding programmes may include such traits to assist in the selection of heat-tolerant parents, segregating generations or advanced lines.

Evidence indicates that loss of chlorophyll during grain filling is associated with reduced yield in the field (Reynolds et al. 1994). High leaf Chl has been identified in Mexican landrace collections wherein the best genotypes showed substantially greater leaf Chl than the check. High chlorophyll was associated with heat tolerance of sister lines in some wheat crosses (Reynolds et al. 1997). Previous reports

Table 1 Trait characteristics of parental lines

Trait	WH 730	RAJ 4014
Tolerance to terminal heat stress	Tolerant	Sensitive
Grain growth duration	Long	Short
Phenology (heading)	Late	Early
Grain yield under late sown condition	High	Low

revealed controlled environment have genetic variability in photosynthetic rate among wheat cultivars when exposed to high temperatures (Wardlaw et al. 1980; Blum 1986).

Chloroplasts, the site of photosynthetic activity, have membranes carrying pigment molecules such as chlorophyll *a* and *b* and accessory pigments (Emerson and Arnold 1932; Hillier and Babcock 2001). Moffatt et al. (1990), in an experiment with six wheat cultivars in field trials as well as subjected to controlled environment at 37/25 °C, found that variable fluorescence (Fv) and grain yield were negatively correlated under controlled conditions but not under field conditions.

Chlorophyll fluorescence explains the efficiency of photosystem (PS)II and in turn, the photosynthetic efficiency. When photons fall on the leaf surface, it dissipates mainly into two processes: (1) photochemical (charge separation in reaction centres of {PS)II, followed by an electron transport via a set of carriers) in the form of photosynthesis and (2) non-photochemical (i.e. thermal dissipation and Chl fluorescence) in the form of heat and fluorescence. Genotypes having higher CFL were also having higher yield, indicating that CFL can be used in screening for heat-tolerant genotypes. Hede et al. (1999) found a significant correlation between leaf Chl and kernel weight in 2255 Mexican landraces of wheat. Therefore, a visible trait such as leaf Chl may be used along with CFL for screening in breeding programmes.

Molecular markers for traits that contribute to heat tolerance can be used in marker-assisted selection (MAS). traits that could be selected more efficiently, including CFL efficiency (Jiang et al. 2004; Blum and Ebercon 1981), Chl (Li et al. 2006) and canopy temperature (CT) as the ideal physiological selection traits in many ways since measurement is quick, simple and inexpensive (Cossani and Reynolds 2012). Canopy temperature is an ideal trait showing a good genetic association with yield (Saint Pierre et al. 2010). The relationship between yield and stay green trait have been discussed and quantitative trait loci (QTL) have been identified in mapping populations (Kumar et al. 2010; Vijayalakshmi et al. 2010).

Presence of both additive and dominant types of gene action has been reported for membrane thermo-tolerance in wheat (Dhanda and Munjal 2012) as well as QTL and associated simple sequence repeat (SSR) markers (Ciuca and Petcu 2009). The overall impact of MAS on the production and release of heat-tolerant cultivars has not been significant (Tuberosa and Salvi 2006; Ortiz et al. 2008). Much more information is required for a better understanding of the genomic regions in wheat that contribute to variability in physiological traits. This prompted us to study the relationship between CFL and Chl values and heat tolerance in Indian wheat genotypes and to find their association with molecular markers. This will allow breeders to use molecular markers in MAS for enhancing plant performance under heat stress.

Material and methods

Field and sowing conditions

The experiments were conducted in the sandy loam soil at research fields of the Directorate of Wheat Research, Karnal (29 °C 43' N, 76 °C 48' E, 245 m), India. During crop season 2009–2010 and 2010–2011, a total of 112 single-seed descent (SSD)-derived recombinant inbred lines (RILs) from the cross of heat-tolerant WH730 (Kundu et al. 2010) and heat-sensitive RAJ4014 (Anonymous 2011) (Table 1) were evaluated in two replications. Field trials were conducted in randomized complete block design (RCBD) under optimum sowing condition (timely sown, mid-November) and high temperature stress condition (late sown planting, mid-December). The plot area was 1.2 m² and seed rate was 100 kg/ha. Irrigation and fertilizer application were as per recommendation.

Physiological traits

Data recording at different crop growth stages were carried out according to Zadok's scale (Zadoks et al. 1974). The observed physiological traits in the experiment were Chl and CFL. Chlorophyll content was recorded at grain filling (Zadoks 70–85) stage of flag leaves, at 7 and 15 days post anthesis (DPA). It was recorded with chlorophyll metre (CCM-200, Opti-Sciences); the values measured were chlorophyll content index which ranges from 0–99.9.

Table 2 Marker information

Marker	Primer sequences	Ann. Tem. (°C)	Chromosome no.
<i>X psp3094</i>	ACCAGGAGAGATAGTCGTTAGGCTTTGTACACCATGATAGGCTTCC	60	7A
<i>X gwm131</i>	AAT CCC CAC CGA TTC TTC TCAGT TCG TGG GTC TCT GAT GG	60	3B

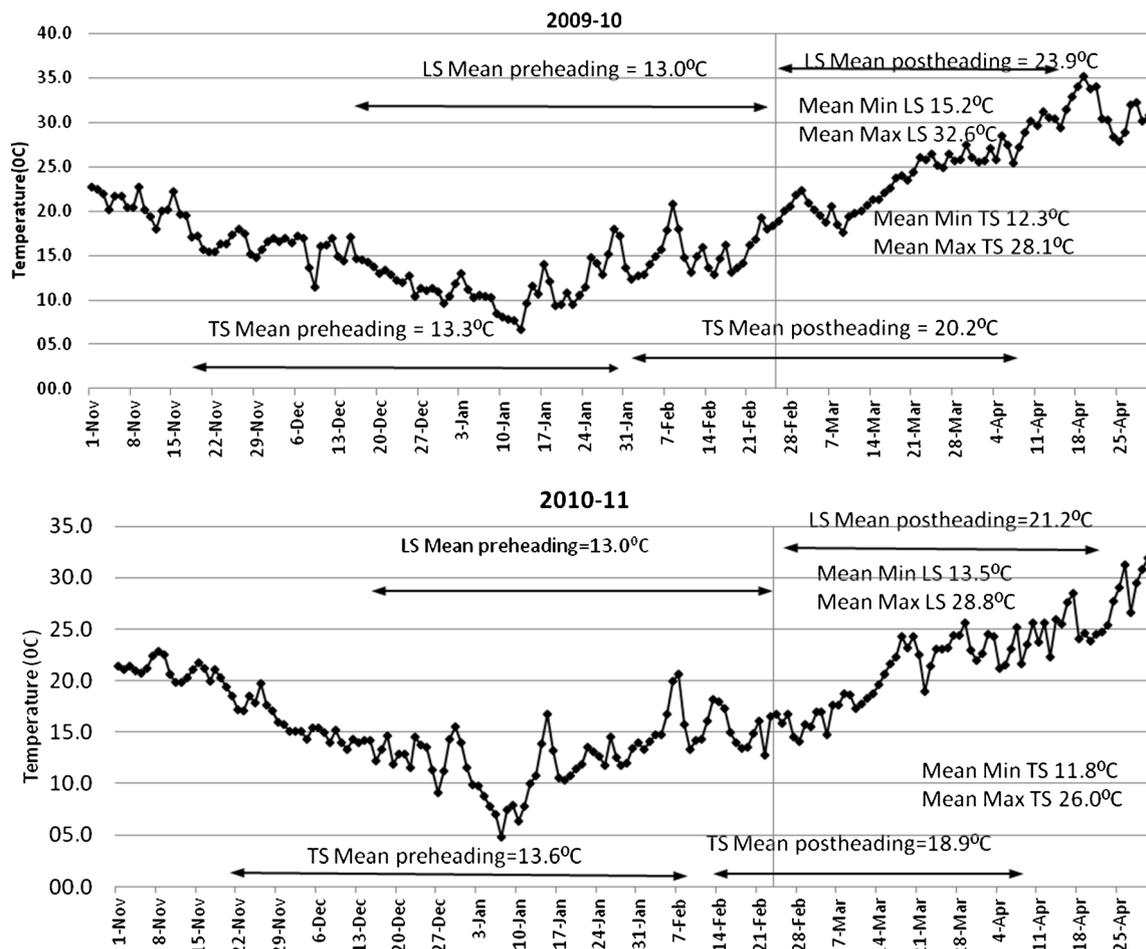


Fig. 1 Mean temperature during pre and post heading periods under timely and late sown conditions are marked by *horizontal arrows*

Chlorophyll fluorescence is one of the traits used extensively in field phenotype after CT and Chl. It is used indirectly for measuring the photosynthetic efficiency of genotypes, mainly in terms of photosystem II (PSII) function. Chlorophyll fluorescence measures $F_v/\text{maximum fluorescence (F}_m\text{)}$ ratio, i.e. immediately after dark adaptation when leaf is exposed to light. The maximum amount of photons used for photochemistry is estimated as ratio of F_v/F_m where, F_v = variable fluorescence and F_m = maximal fluorescence. CFL values were recorded putting clips, which created dark conditions, using a pulse modular fluorometer (Model OS5-FL, Opti-Sciences, Hudson, NH, USA) and was measured on fully expanded flag leaves of each RILs in the timely (optimum) and late sown (stress) condition. The observations were recorded on 7 and 15 DPA. The recordings were carried out as per the user manual. To study the behaviour of RILs, 15 genotypes each selected from tolerant and sensitive category on the basis of heat susceptibility index (HSI) for Chl, CFL and thousand grain weight (TGW) were utilised for explanation considering their mean value *Microsatellite marker analysis*.

Deoxyribonucleic acid was extracted from all RILs along with parents by CTAB method (Saghai-Marooft et al. 1984). A total of 400 microsatellite primers procured from BARC, GWM, WMC, CFA, CFD and GDM sets were used to screen

Table 3 Pooled analysis of variance for chlorophyll content and chlorophyll fluorescence

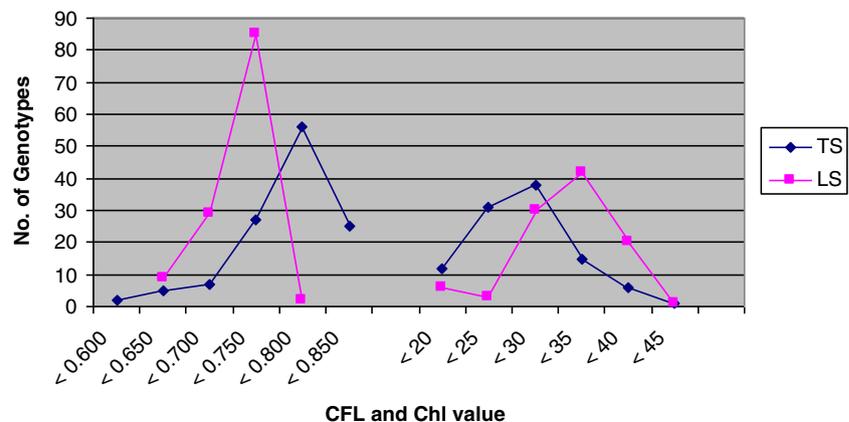
Source of variation	DF	Mean sum of squares		
		CHL1	CHL2	CFL
Years	1	11,295**	97,254**	15.33
Conditions	1	1663.6**	1155.4**	12.46
Genotypes	113	50.36	71.9	7.36
Replications	1	453.55**	1015.5**	14.0
Genotypes × conditions	229	56.94	61.72**	7.36**
Year × conditions	3	32,803**	3380**	14.82
Year × genotype × condition	459	75.57**	265.97**	7.38**
Residual		38.57	45.38	21.56

**Significant at $P \leq 0.01$

Table 4 Variability for Gr. wt./spike in RILs

Genotype	TS	LS	Genotype	TS	LS
RAJ 4014	1.63	1.11	RIL RW 61	2.00	1.64
WH 730	1.92	1.22	RIL RW 62	1.82	1.99
RIL RW 1	1.54	1.27	RIL RW 64	1.93	1.51
RIL RW 2	1.44	0.92	RIL RW 67	1.69	1.58
RIL RW 5	1.51	1.54	RIL RW 71	2.41	2.28
RIL RW 6	1.68	1.27	RIL RW 72	1.23	1.24
RIL RW 7	1.66	2.04	RIL RW 74	2.01	1.29
RIL RW 9	1.64	1.97	RIL RW 92	1.55	1.59
RIL RW 16	1.83	1.93	RIL RW 96	1.87	2.14
RIL RW 17	1.36	1.62	RIL RW 97	1.74	1.68
RIL RW 18	1.48	1.44	RIL RW 101	2.19	1.90
RIL RW 20	2.03	1.29	RIL RW 110	1.83	1.37
RIL RW 22	1.48	1.36	RIL RW 112	1.68	1.77
RIL RW 28	1.76	1.74	RIL RW 114	1.83	1.38
RIL RW 30	1.74	1.47	RIL RW 116	1.44	1.06
RIL RW 39	1.91	1.80	RIL RW 118	1.68	1.89

the parents for allelic variation. The subsets of RILs populations were genotyped with polymorphic marker and significant marker was applied in whole population (Table 2). The PCR was performed in a volume of 25- μ l reaction mix containing (2.5 μ l 10 \times buffer with MgCl₂ mixed, 2 μ l dNTP, 1 μ l primer (F + R), 0.33 μ l Taq polymerase and 1 μ l of template DNA (Merck Bioscience). The reaction mixture was run on a thermocycler (Bio-Rad, USA) by procedure of Roder et al., (1998) with minor modifications. The PCR cycle included an initial denaturation at 94 °C for 4 min followed by 35 cycles of denaturation at 94 °C for 1 min annealing at 50, 55 or 60 °C (depending on the individual microsatellite primer) for 1 min and extension at 72 °C for 1 min followed by 6-min final extension at 72 °C. Amplification products were resolved on 3 % agarose gel (HiMedia laboratories Pvt. Ltd., India) for 30–45 min, visualized by ethidium bromide staining, and photographed using Geldoc system (Syngene Ltd., USA).

Fig. 2 Frequency distribution of CFL and Chl under timely and late sown condition

Statistical analysis

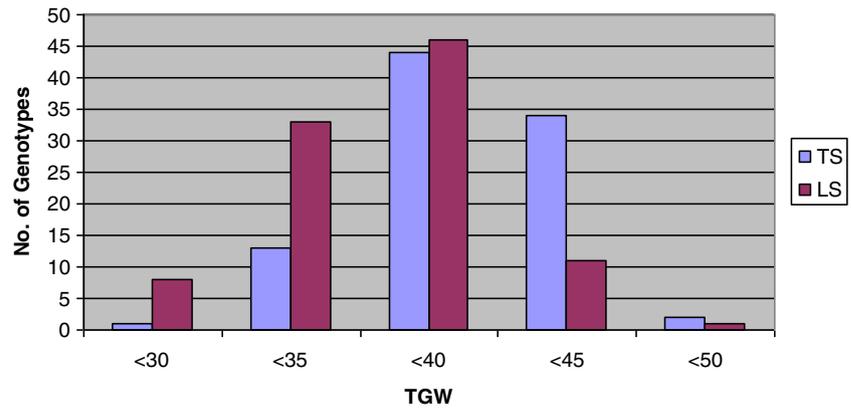
Statistical analyses of all the traits were done using a CROPSTAT (IRRI) computer software programme. ANOVA was performed to determine the effect of genotype, environment and genotype \times environment interaction on the traits across environments (treatment–year combination). Data from both crop seasons was used for pooled analysis of the traits.

Results

The timely sown (TS) and late sown (LS) preheading mean temperature during crop seasons 2009–2010 were 13.3 and 13.0 °C and post heading mean temperature under timely and late sown conditions were 20.2 and 23.9 °C. Mean of minimum and maximum temperature under TS were 12.3 and 28.1 °C and mean of minimum and maximum temperature under LS were 15.2 and 32.6 °C (Fig. 1). During crop season 2010–2011, TS and LS preheading mean temperature during crop seasons were 13.6 and 13.0 °C and post heading mean temperature under timely and late sown conditions were 18.9 and 21.2 °C. Mean of minimum and maximum temperature under TS were 11.8 and 26.0 °C and mean of minimum and maximum temperature under LS were 13.5 and 28.8 °C (Fig. 1).

Analysis of variance revealed that the conditions, replications, genotypes \times conditions, year \times conditions and year \times genotype \times conditions differed significantly for CFL, Chl, (Table 3), grain filling duration (GFD) and thousand grain weight (TGW). Under non stress condition with maximum photon utilization for photochemistry, the ratio of Fv/Fm was 0.79–0.84 (Kate and Giles 2000). The mean of 7 DPA of Fv/Fm was 0.74 and 0.72 for TS and LS, respectively. The mean of 15 DPA of Fv/Fm was 0.71 and 0.72 for TS and LS, respectively. The mean of first-phase Chl was 24.32 and 26.99 and for second-phase Chl was 22.00 and 19.78 for TS and LS, respectively. Average GFD under normal

Fig. 3 Frequency distribution of TGW under timely and late sown condition



and stress conditions were from 37 to 31 days. The average reduction in GFD under stress conditions was 6 days. There was good variability for grain weight/spike (Table 4) and TGW among RILs. The mean of grain weight/spike was 1.75 and 1.43 for TS and LS conditions, respectively, and the mean of TGW was 39.19 and 35.90 for TS and LS conditions, respectively. The correlation between grain weight/spike with Chl and CFL were 15 and 8 %, respectively. Regression analysis revealed significant association with microsatellite markers viz., *Xpsp3094* and *Xgwm131* with coefficients of determination (R^2) values for CFL and Chl were 12 and 8 %, respectively. Molecular markers, associated with CFL and Chl, viz., *Xpsp3094* and *Xgwm131* were distinct in tolerant and sensitive genotypes and were found segregating in the population with their phenotypic contributions 12 and 8 %, respectively.

Table 5 HSI of TGW, Chl and CFL of tolerant and sensitive lines

Tol. RILs TGWHSI	Sen RILs TGWHSI	Tol. RILs ChlHSI	Sen. RILs ChlHSI	Tol. RILs CFLHSI	Sen. RILs CFLHSI
0.39	2.31	0.98	1.54	0.66	2.23
0.76	2.17	0.82	2.75	-0.35	2.51
-0.34	2.67	0.10	1.32	-0.69	1.23
-0.08	1.37	-3.86	2.28	-0.96	3.76
0.85	1.00	-0.16	2.00	0.67	1.27
0.70	1.57	-2.41	2.73	-0.01	2.14
0.40	2.52	-0.78	1.19	0.83	2.21
0.07	1.43	-0.14	6.05	-2.35	2.53
0.20	1.90	-0.80	1.37	-1.54	5.24
0.98	3.21	-0.40	2.00	-0.20	1.29
-0.35	1.69	-0.94	1.56	-0.44	1.19
0.56	2.62	0.12	1.48	-1.30	2.90
0.44	1.24	-0.11	1.43	-1.56	4.04
0.95	2.74	0.23	1.15	-2.02	4.93
0.87	2.56	-0.47	4.08	-2.59	3.04

Discussion

To investigate the relationship between physiological traits and heat stress, a set of 112 RILs were used. The role of CFL and Chl in relation to grain yield under water-stress conditions were recommended for selecting drought and heat-tolerant wheat plants (Blum 1988, 1989; Krause and Weis 1991). In the present study, WH730 (heat tolerant) had higher Chl and CFL than RAJ4014 (heat sensitive), under both normal and high temperature conditions. Similarly, RILs in the experiment also differed significantly for Chl and CFL under optimum (timely sown) and high temperature regime (late sown condition) (Table 3). These results are similar to those of Al-Khatib and Paulsen (1990). The Chl and CFL values in RILs showed continuous variation (Fig. 2) indicating quantitative nature of inheritance.

Among 112 RILs, RIL nos. 12 and 17 under TS as well as RIL nos. 10 and 6 under late sown conditions showed mean CFL and Chl values greater than that of tolerant parent (WH730) indicating presence of transgressive segregants in the population for the respective traits. Recombinant inbred line nos. 60 and 71 were amongst the recombinants as transgressive segregants for more than one trait.

The mean values of these traits (CFL and Chl) along with thousand grain weight (TGW) under optimum (TS) and heat stress conditions (LS) (Fig. 3), were used to estimate the heat susceptibility index (HSI) and calculated by the method suggested by Fischer and Maurer (1978) with the following formula:

$$HSI = (1 - X_h/X) / (1 - Y_h/Y)$$

where X_h and X are the phenotypic means for each genotype under heat stress and control conditions, respectively, and Y_h and Y are the phenotypic means for all the genotypes together under heat stress and control conditions, respectively. Values equal to or less than 1 of HSI and the RILs falling (Table 5) in this category are supposed to be tolerant. Earlier investigation on Chl in wheat, reported (Wang et al. 2008) that an effective strategy of crop plant to increase its biomass production and grain yield is by maintaining a higher Chl. Chl

around flowering time were positively associated with yield in near-isogenic lines (NILs) of wheat (Quarrie et al. (2006)). Leaf Chl in CS X SQ1 DH lines were also significantly positively correlated with grain yield under field conditions (Quarrie et al. 1995). In the present study, similar observation were made wherein out of 112 RILs, 17 RILs had their HSI less than 1 for all three traits viz., CFL, Chl and TGW. The group of genotypes showing tolerance to terminal heat stress by virtue of low HSI (0.43) for thousand grain weight were also found having Chl HSI values less than zero (−0.52) indicating substantial increase in the Chl value under stress. However, contrasting HSI values of 2.07 and 2.19 were observed for TGW and Chl in another set of RILs depicting heat sensitivity. This could be because of the plants of the heat-tolerant genotypic group may try to compensate for yield losses, generally caused due to reduced thousand grain weight under LS (terminal heat stress) conditions, through increased Chl values. Chl has been suggested as a reliable indicator for photosystem II efficiency (Vijayalakshmi et al. 2010) and under stress possibly plants (tolerant ones) try to be more efficient. However, no such compensation was observed in heat-sensitive genotypes. Another observation was that in general, the mean Chl value of LS crop was higher as against Chl value of TS (Fig. 2). Considering CFL, similar observations were made but with low magnitudes viz., HSI for heat-tolerant and sensitive groups were −0.79 and 2.70, respectively.

Besides this, in general, positive association of chlorophyll content with thousand grain weight was observed. The correlation between thousand grain weight (TGW) with Chl and CFL values were 14 and 7 % and correlation between grain weight/spike with Chl and CFL were 15 and 8 %, respectively. Similar results were observed in wheat genotypes subjected to heat stress by Al-Khatib and Paulsen (1990) and in maize under differential water conditions by O'Neill et al. (2004). Therefore, Chl and CFL can be used as a secondary trait for measuring heat tolerance, as suggested by Moffatt et al. (1990). Regression analysis revealed significant association with microsatellite markers viz., *Xpsp3094* and *Xgwm131* with coefficients of determination (R^2) values for CFL and Chl as 12 and 8 %, respectively. The marker (*Xpsp3094*) had been found linked to grain characters in earlier reports as well (Quarrie et al. 2005). The marker-trait association conducted in this study provided preliminary information of genomic regions that may be useful for heat tolerance, but further mapping and validation is necessary before it is further applied for MAS.

Acknowledgments The authors acknowledge the ICAR for financial support for carrying out the work under NPTC: Functional Genomics in wheat project.

References

- Al-Khatib K, Paulsen GM (1990) Photosynthesis and productivity during high temperature stress of wheat genotypes from major world regions. *Crop Sci* 30:1127–1132
- Anonymous (2011) Annual Report 2010–11, Directorate of Wheat Research, Karnal-132001 (India). pp: 18
- Blum A, Ebercon A (1981) Cell membrane stability as a measure of drought and heat tolerance in wheat. *Crop Sci* 21:43–47
- Blum A (1986) The effect of heat stress on wheat leaf and ear photosynthesis. *J Exp Bot* 37:111–118
- Blum A (1988) Plant breeding for stress environments. CRC Press, Boca Raton, p 232
- Blum A, Shpiler L, Golan G, Mayer J (1989) Yield stability and canopy temperature of wheat genotypes under drought stress. *Field Crop Res* 22:289–296
- Ciuca M, Petcu E (2009) SSR markers associated with membrane stability in wheat (*Triticum aestivum* L.). *Rom Agric Res* 26: 21–24
- Cossani CM, Reynolds MP (2012) Physiological traits for improving heat tolerance in wheat. *Plant Physiol* 160:1710–1718
- Dhanda SS, Munjal R (2012) Heat tolerance in relation to acquired thermotolerance for membrane lipids in bread wheat. *Field Crops Res* 135:30–37
- Emerson R, Arnold W (1932) The photochemical reaction in photosynthesis. *J Gen Physiol* 16:191–205
- Fischer RA, Maurer R (1978) Drought resistance in spring wheat cultivars. I. Grain yield responses in spring wheat. *Aust J Agric Sci* 29: 892–912
- Hede A, Skovmand RB, Reynolds MP, Crossa J, Vilhelmsen AL, Stølen O (1999) Evaluating genetic diversity for heat tolerance traits in Mexican wheat landraces. *Genet Resour Crop Evol* 46:37–45
- Hillier W, Babcock GT (2001) Photosynthetic reaction centres. *Plant Physiol* 125:33–37
- Jiang GH, He YQ, Xu CG, Li XH, Zhang Q (2004) The genetic basis of stay-green in rice analyzed in population of dihybrid lines derived from indica by japonica cross. *Theor Appl Genet* 108:688–698
- Kate M, Giles NJ (2000) Chlorophyll fluorescence. *J Exp Bot* 51(345): 659–668
- Krause GH, Weis E (1991) Chlorophyll fluorescence and photosynthesis: the basic. *Annu Rev Plant Physiol Plant Mol Biol* 42:313–349
- Kumar U, Joshi AK, Kumari M, Paliwal R, Kumar S, Röder M (2010) Identification of QTLs for stay green trait in wheat (*Triticum aestivum* L.) in the 'Chirya 3' 3 'Sonalika' population. *Euphy* 174: 437–445
- Kundu S, Singh C, Shoran J, Singh SS (2010) An update on released wheat varieties and registered genetic stocks (*Triticum* L.). Technical Bulletin No.13, Directorate of Wheat Research, Karnal-132001 (India). pp: 34
- Li R, Guo P, Baum M, Grande S, Ceccarelli S (2006) Evaluation of chlorophyll content and fluorescence parameters as indicators of drought tolerance in barley. *Agric Sci China* 5:751–757
- Moffatt JM, Sears G, Cox TS, Paulsen GM (1990) Wheat high temperature tolerance during reproductive growth. I. Evaluation by chlorophyll fluorescence. *Crop Sci* 30:881–885
- Nachit MM, Monneveux P, Araus JL, Sorrells ME (1998) Relationship of dryland productivity and drought tolerance with some molecular markers for possible MAS in durum (*T. turgidum* L. var.durum). *CIHEAM Opt Mediter* 1:203–206
- O'Neill PM, Shanahan JF, Schepers JS, Caldwell B (2004) Agronomic responses of corn hybrids from different areas to deficit and adequate level of water and nitrogen. *Agron J* 96:1660–1667
- Ortiz R, Sayre KD, Govaerts B, Gupta R, Subbarao GV, Ban T, Hodson D, Dixon JM, Ortiz-Monasterio JI, Reynolds M (2008) Climate change: can wheat beat the heat. *Agric Ecosyst Environ* 126:46–58

- Quarrie SA, Steed A, Semikhodski A, Lebreton C, Calestani C, Clarkson DT, Tuberosa R, Sanguineti MC, Melchiorre R, Prioul JL (1995) Identification of quantitative trait loci regulating water- and nitrogen-use efficiency in wheat. In: Proceedings of STRESSNET meeting, Salsomaggiore, Sept 1995. European Commission, Luxembourg, pp 175–180
- Quarrie SA, Steed A, Calestani C, Semikhodskii A, Lebreton C, Chinoy C, Steele N, Pljevljakusic D, Waterman E, Weyen J, Schondelmaier J, Habash DZ, Farmer P, Saker L, Clarkson DT, Abugalieva A, Yessimbekova M, Turuspekov Y, Abugalieva S, Tuberosa R, Sanguineti MC, Hollington PA, Aragues R, Royo A, Dodig D (2005) A high-density genetic map of hexaploid wheat (*Triticum aestivum* L.) from the cross Chinese Spring X SQ1 and its use to compare QTLs for grain yield across a range of environments. *Theor Appl Genet* 110:865–880
- Quarrie SA, Pekic Quarrie S, Radosevic R, Rancic D, Kaminska A, Barnes JD, Leverington M, Ceoloni C, Dodig D (2006) Dissecting a wheat QTL for yield present in a range of environments: from the QTL to candidate genes. *J Exp Bot* 57:2627–2637
- Reynolds MP, Balota M, Delgado MIB, Amani J, Fischer RA (1994) Physiological and morphological traits associated with spring wheat yield under hot, irrigated conditions. *Aust J Plant Physiol* 21: 717–730
- Reynolds MP, Nagarajan S, Razzaque MA, Ageeb OAA (1997) Using canopy temperature depression to select for yield potential of wheat in heat-stressed environments. Wheat Special Report No. 42. Mexico, D.F.: CIMMYT
- Roder MS, Korzun V, Wendehake K, Plaschke J, Tixier M, Leroy P, Ganal MW (1998) A microsatellite map of wheat. *Genet* 149:2007–2023
- Saghai-Marooif MA, Soliman KM, Jorgensen RA, Allard RW (1984) Ribosomal DNA spacer length polymorphisms in barley: Mendelian inheritance, chromosomal location, and population dynamics. *Proc Natl Acad Sci U S A* 81:8014–8018
- Saint Pierre C, Crossa J, Manes Y, Reynolds MP (2010) Gene action of canopy temperature in bread wheat under diverse environments. *Theor Appl Genet* 120:1107–1117
- Tuberosa R, Salvi S (2006) Genomics-based approaches to improve drought tolerance of crops. *Trends Plant Sci* 11(8):405–412
- Vijayalakshmi K, Fritz A, Paulsen G, Bai G, Pandravada S, Gill B (2010) Modeling and mapping QTL for senescence-related traits in winter wheat under high temperature. *Mol Breed* 26:163–175
- Wang FH, Wang GX, Li XY, Huang JL, Zheng JK (2008) Heredity, physiology and mapping of a chlorophyll content gene of rice (*Oryza sativa* L.). *J Plant Physiol* 165:324–330
- Wardlaw IF, Sofield I, Cartwright PM (1980) Factors limiting the rate of dry matter accumulation in the grain of wheat grown at high temperature. *Aust J Plant Physiol* 7:387–400
- Zadoks JC, Chang TT, Konzak CF (1974) A decimal code for the growth stages of cereals. *Weed Res* 14:415–421