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Earliness in wheat: A key to adaptation under terminal and continual high temperature stress in South Asia

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ABSTRACT

High temperatures are a primary concern for wheat production in South Asia. A trial was conducted to evaluate the grain yield performance of high yielding, early maturing heat tolerant CIMMYT wheat lines, developed recently in Mexico for adaptation to high temperature stresses in South Asia. The trial, comprised of 28 entries and two checks, was grown in 13 locations across South Asia and two environments in Mexico. Each location was classified by mega environment (ME); ME1 being the temperate irrigated locations with terminal high temperature stress, and ME5 as warm, tropical, irrigated locations. Grain yield (GY), thousand kernel weight (TKW), days to heading (DH) and plant height (PH) were recorded at each location. Canopy temperature (CT) was also measured at some locations. Significant differences were observed between ME for DH, PH, GY, and TKW. The cooler ME1 locations had a mean DH of 83 days, compared to 68 days mean DH in ME5. The ME1 locations had higher mean GY of 5.26 t/ha and TKW of 41.8 g compared to 3.63 t/ha and 37.4 g, respectively, for ME5. Early heading entries (<79 days, mean DH) performed better across all locations, with GY of 2–11% above the local checks and 40–44 g TKW. Across all locations the top five highest yielding entries had 5–11% higher GY than the local checks. The early maturing CIMMYT check 'Baj' also performed well across all locations. In the Mexico location, CT was associated with GY, thereby suggesting that cooler canopies may contribute to higher GY under normal as well as high temperature stress conditions. Our results suggest that the early maturing, high yielding, and heat tolerant wheat lines developed in Mexico can adapt to the diverse heat stressed areas of South Asia.

1. Introduction

Wheat (*Triticum aestivum* L.) is a primary staple food crop for South Asia; it is grown on nearly 38 million hectares, with a production of 106 million tons (FAO Stat, 2010). As a highly populous region comprising of India, Nepal, Pakistan and Bangladesh, South Asia's demand for wheat is ever increasing, and it is estimated that production increases of 1.5–2% are required if consumption demands are to be met (Chatrath et al., 2007). In South Asia, wheat is grown in temperate irrigated regions and warm tropical rainfed or partially irrigated regions. Breeding efforts have targeted toward increased wheat yield potential but the presence of biotic and abiotic stress factors remain a serious challenge in sustaining high production. Continual and terminal high temperature stresses are the two major constraints to wheat production in South Asia

Abbreviations: CC, chlorophyll content; CT, canopy temperature; DH, days to heading; DM, days to maturity; GY, grain yield; ME, mega environment; PH, Plant height; TKW, thousand kernel weight.

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(Chatrath et al., 2007; Joshi et al., 2007a; Rane et al., 2002). Lobell et al. (2008) estimated yield losses of 3–17% for each degree rise in temperature in northwest India and Pakistan. It is imperative to direct breeding efforts toward developing wheat varieties adapted to warm temperatures.

High temperature stress adversely affects plant physiological processes; limiting plant growth and reducing grain yield (GY). At anthesis, high temperatures may result in pollen and anther sterility and restrict embryo development thereby reducing grain number. High temperature stress after anthesis affects the rate of grain filling, leading to reductions in GY (Al-Khatib and Paulsen, 1984; Tashiro and Wardlaw, 1990; Weigand and Cueller, 1981). In order to adapt to high temperature stress, plants employ various physiological adaptive mechanisms such as earliness, high transpiration rate, cooler canopies, stay-green and reduced photosynthetic rates (Cornish et al., 1991; Reynolds et al., 1998). Early maturity provides an escape mechanism under late incidence of high temperature stress and has been suggested as a good approach for wheat breeding for the Eastern Gangetic Plains, which suffers from terminal high temperature stress (Joshi et al., 2007a). Another important trait is cooler canopy temperatures (CT), which enables plants to maintain physiological functions under elevated temperatures and has been associated with GY under hot irrigated conditions (Kumari et al., 2012; Reynolds et al., 1994). Maintaining high leaf chlorophyll content is also considered a desirable trait as it indicates a low degree of photo inhibition of the photosynthetic apparatus at high temperatures (Ristic et al., 2007; Talebi, 2011). Studies have shown that the ability of plants to maintain leaf chlorophyll content under high temperatures stress is associated with GY and yield components (Ali et al., 2010; Yang et al., 2002). Thus, physiological characterization under high temperature stress may provide a better understanding of the adaptive traits that can be further integrated into breeding programs.

The Cereal Systems Initiative for South Asia (CSISA) is a collaborative project involving CGIAR centers (CIMMYT, IRRI, IFPRI, and ILRI) and national programs in South Asia (Bangladesh, India, Nepal, and Pakistan), which prioritizes the need to improve cereal productivity in South Asia. One of the objectives of the CSISA project is to develop improved bread wheat varieties that feature exceptional heat tolerance and adaptation in South Asia. Our objectives were to determine 1) GY and adaptation of a set of high yielding, early maturing and heat tolerant wheat lines, developed recently in Mexico, by testing them during the 2010–2011 crop season in 13 diverse locations across South Asia and two environments in Mexico; and 2) the effect of temperature on GY in two wheat-growing mega environments (ME). The manuscript also presents the wheat lines and the traits that offer promise to face the challenges of heat stress.

2. Materials and methods

2.1. Multi-location trial

High yielding, early maturing, and heat tolerant entries were identified for inclusion in the trial, 2nd CSISA Heat Tolerance Early Maturity Yield Trial (2nd CSISA HT-EM YT), after testing them for GY during the 2008–2009 and 2009–2010 crop seasons at the CIMMYT research station in Cd. Obregon, Sonora, Mexico. The trial, conducted in 2010–2011, comprised of 28 entries, with one CIMMYT check variety ('Baj') and a local check. The local check was the best locally adapted variety at each location. The trial was sown in 13 locations across India, Pakistan, Bangladesh and Nepal and two environments in Mexico (Table 1). In Mexico the trials were conducted under optimal irrigated conditions at the Norman E. Borlaug Experimental Station (CENEB) in Cd. Obregon, Sonora, sown

Table 1
Location information, mega environments, planting and harvest dates, plot sizes, maximum and minimum temperatures during grain filling and days to heading in the 2nd CSISA HT-EM YT during the 2010–2011 crop season.

Location	Country	ME[a]	Latitude	Longitude	Planting date	Harvest date	Plot area (m^2)	Max. Temp. (°C)[b]	Min. Temp. (°C)[c]	Days to heading
Delhi	India	ME1	28°35′N	77°12′E	15/12/2010	–	6.9	32.5	19.0	–
Gurgaon	India	ME1	28°37′N	77°04′E	10/11/2010	15/04/2011	8.3	32.5	19.0	97
Jalandhar	India	ME1	30°54′N	75°48′E	19/11/2010	–	7.6	30.0	15.0	106
Karnal	India	ME1	29°43′N	75°57′E	19/12/2010	26/04/2011	5.5	31.0	16.5	82
Ludhiana	India	ME1	30°54′N	75°48′E	17/11/2010	29/04/2011	6.2	30.0	15.0	101
Obregon1	Mexico	ME1	27°29′N	109°56′E	21/11/2010	10/05/2011	7.1	29.0	15.0	81
Faisalabad	Pakistan	ME1	31°25′N	73°09′E	29/11/2010	19/05/2011	8.1	30.5	18.0	98
Dinajpur	Bangladesh	ME5	25°38′N	88°41′E	20/12/2010	15/04/2011	4.0	30.0	21.0	68
Indore	India	ME5	22°37′N	75°50′E	12/12/2010	27/04/2011	4.6	35.5	19.0	67
Jalna	India	ME5	19°51′N	75°53′E	26/11/2010	15/04/2011	3.7	36.0	21.0	71
Ugar	India	ME5	16°37′N	70°51′E	22/12/2010	10/04/2011	3.7	35.0	20.5	64
Varanasi	India	ME5	25°26′N	82°98′E	09/12/2010	09/05/2011	3.6	36.5	20.5	76
Vijapur	India	ME5	23°35′N	72°45′E	16/11/2010	23/03/2011	3.5	38.5	23.5	64
Bhairahwa	Nepal	ME5	27°32′N	83°25′E	23/12/2010	03/03/2011	3.0	28.5	20.5	68
Obregon2	Mexico	ME5	27°29′N	109°56′E	21/02/2011	15/06/2011	4.5	32.5	18.0	57

[a] ME – Mega environment.
[b] Max. Temp. – Maximum temperature at grain filling.
[c] Min. Temp. – Minimum temperature at grain filling.

on normal sowing date in last week of November (Obregon1) to determine yield potential and at a late sowing date in last week of February (Obregon2) to evaluate the effects of high temperature stress. Trial management practices were based on standard procedures at each location. The individual locations were also grouped into ME based on the classification system developed by CIMMYT (Table 1). This classification system defines ME1 as an optimally irrigated and highly productive environment where wheat grows in cool temperature but may suffer from terminal heat stress. ME5 regions are warm humid, tropical, or subtropical regions, where continuous high temperatures are a major constraint to wheat production. Mean maximum and minimum temperatures in the ME1 and ME5 locations in India were recorded across the wheat growing season (Table 1; data provided by Dr. M.L. Jat, CIMMYT – India).

2.2. Agronomic and physiological traits

Days to heading (DH) was estimated as the number of days from the date of sowing/first irrigation till 50% of the spikes had emerged from the flag leaf. Days to physiological maturity (DM) was recorded in the Mexico trials and was estimated as the senescence in the peduncles of 50% spikes. Plant height (PH) was also recorded. At maturity, plots were harvested and GY and thousand kernel weight (TKW) were recorded. GY was also expressed as percent over local checks for each entry with the following formula

$$\%\,\text{Grain Yield} = 100 + \left(\frac{(\text{GY}_\text{E} - \text{GY}_\text{LC})}{\text{GY}_\text{LC}}\right) \times 100)$$

Where GY_E is GY of the individual entry and GY_LC is GY of the local check. Canopy temperatures (CT) were measured during the vegetative and grain filling stages in Varanasi, Indore, Dinajpur, Obregon1 and Obregon2. CT was recorded with a handheld infra-red thermometer (Sixth Sense LT 300 Infrared Thermometer, Instrumart, South Burlington, Virginia, USA) in the Mexico locations. Leaf chlorophyll content (CC) was recorded at Varanasi, India, and was measured after heading using a SPAD -502 Minolta (Spectrum Technologies Inc., Plainsfield, IL, USA).

2.3. Statistical analysis

A mixed model analysis was performed to estimate the adjusted means in each environment and across all locations following the MIXED procedure of SAS (2004). Phenotypic correlations were estimated using the CORR procedure in SAS (2004). Broad sense heritability (H) was estimated for each trait in each environment as;

$$H = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2/r}$$

Where, σ_g^2 is the genetic variance σ_e^2 is the residual variance, and r is the number of replicates. The estimate of H for a multi environment trial planted in e environment is

$$H = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_{ge}^2/er + \sigma_e^2/r}$$

where σ_{ge}^2 is genotype by environment interaction variance.

2.3.1. Site regression model (SREG)

The SREG was performed to better understand the genotype main effect and the genotype by environment interaction effect (Crossa and Cornelius, 1997, Crossa et al., 2002).

Briefly, the SREG model is represented by;

$$\bar{y}_{ij} = \mu + \delta_j + \sum_{k=1}^{t} \lambda_k \alpha_{ik} \gamma_{jk} + \bar{\varepsilon}_{ij}$$

Where $\bar{y}_{ij}$ is the empirical mean response of the ith genotype (i = 1,2,. . .,I) in the jth environment (j = 1,2,. . .,J) with n replications, μ is the grand mean of all genotypes and environments, δ_j is the effect of the jth environment, λ_k is the singular value of the kth multiplicative component that is ordered $\lambda_1 \geq \lambda_2 \geq ... \geq \lambda_t$, the α_{ik} are elements of the kth left singular vector of the true interaction and represent genotypic sensitivity to hypothetical environmental factors represented by the kth right singular vector with elements γ_{jk}. The α_{ik} and γ_{jk} satisfy the constraints $\sum_i \alpha_{ik}\alpha_{ik'} = \sum_j \gamma_{jk}\gamma_{jk'} = 0$ for $k \neq k'$ and $\sum_i \alpha_{ik}^2 = \sum_j \gamma_{jk}^2 = 1$.

Biplots of the SREG analysis were constructed to evaluate the yield performance and adaptation of the entries across multiple locations, by depicting the diverse responses of genotypes in locations.

3. Results

3.1. Climate characterization of testing locations

Fig. 1 shows the mean maximum and minimum temperatures in the ME1 and ME5 regions in India during the wheat growing season of 2010–2011. Wheat in South Asia is sown in November/December and harvested in March/April/May, depending on the area. The ME1 regions are cooler at sowing and vegetative stages but the temperatures gradually increase during grain filling and are comparable to the ME5 regions. This trend is similar for both daily maximum and minimum temperatures. Information on latitude and longitude,

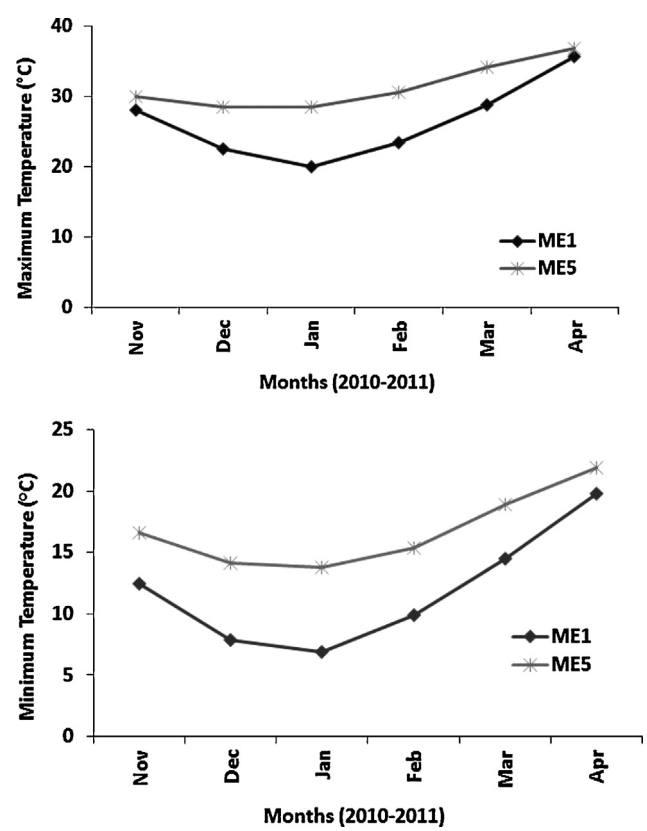

Fig. 1. Maximum and minimum temperatures in the mega environments (ME) in India during the wheat growing season in 2010–2011.

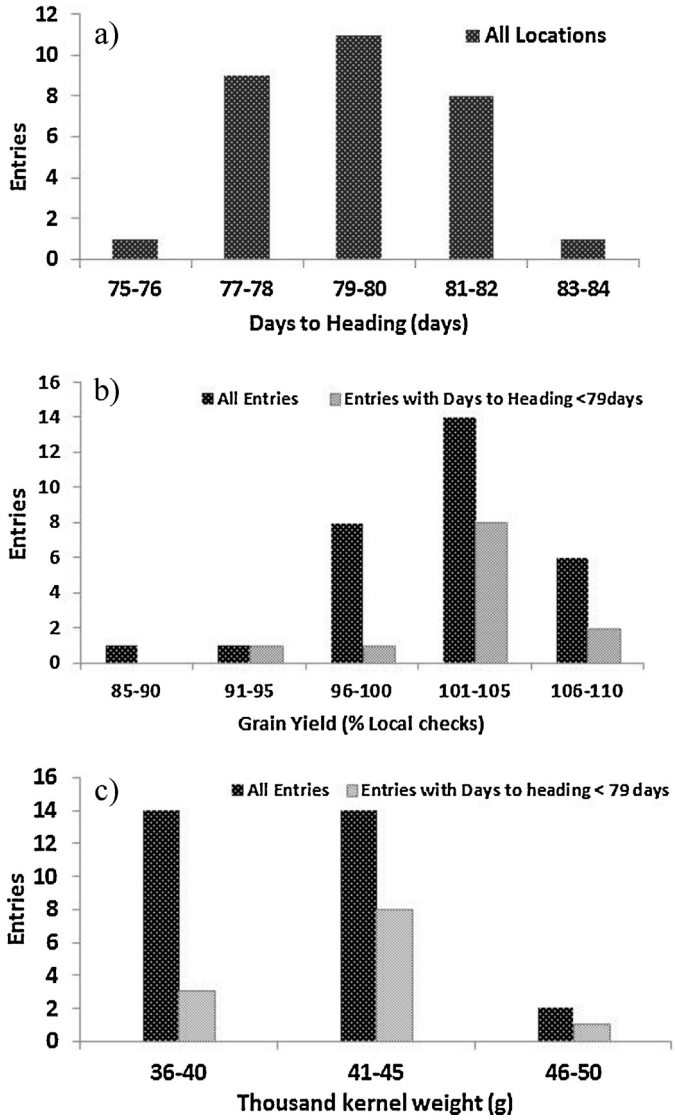

Fig. 2. Days to heading (a), grain yield (b) and thousand kernel weight (c) for the 30 entries in the 2nd CSISA HT-EM YT grown during 2010–2011 crop season across 13 locations in South Asia and 2 environments in Mexico.

mean maximum and minimum temperatures during grain filling stages, planting date, plot sizes, and harvest date for all locations is given in Table 1.

3.2. Days to heading, plant height, grain yield, and thousand kernel weight

For all entries across locations, DH ranged from 76 to 83 days, with a mean of 79 days (Table 2). Mean DH of the local checks was 83 days. Nearly half of the entries in the trial had DH less than 79 days (mean DH of entries) across locations (Fig. 2a). Mean DH for each location is given in Table 1; the DH in the ME5 locations ranged from 57 to 76 days whereas in the ME1 locations it ranged from 81 to 106 days. The mean PH across all locations was 99.7 cm (Table 2). The PH in ME5 (95.4 cm) was significantly lower than ME1 (108.3 cm).

Mean GY across all locations was 4.4 t/ha, while the mean GY in ME1 and ME5 was 5.26 t/ha and 3.63 t/ha, respectively (Table 2). Fig. 3 shows the GY for each entry in the individual ME. A significant reduction in GY was observed for all the entries in ME5. The performance of the entries was also expressed as a percentage over the local checks and 21 entries had a GY of 1–10% above the local checks (Fig. 2B). The CIMMYT check 'Baj' performed well across all locations with a mean GY of 4.5 t/ha (Table 3) and 4% above the grain yield of local checks. Early heading entries performed well across locations; entries with DH <79 days (mean DH of entries) had a GY of 3–10% higher than local checks (Fig. 2b). The top five entries across locations had 7–11% superiority in GY compared to local checks (Table 3). GY accumulation per day (GY/ha/day) was estimated in Cd. Obregon, ME1, ME5 and across locations. Based on DH, the GY/ha/day across locations and in each ME was equal that is 5.5 kg. Due to unavailability of data for maturity at some locations the GY/ha/day based on days to maturity and grain filling duration could not be estimated. Differences were observed for GY/ha/day in the two environments in Cd. Obregon. The heat stressed environment of Obregon2 had GY/ha/day of 6.8, 4.4 and 12.7 kg compared to 8.7, 5.6, and 12.7 for Obregon1 when estimated based on DH, days to maturity and grain filling duration respectively.

Across locations, TKW ranged from 36 to 50 g, with a mean of 40.9 g (Table 2). More than 50% of the entries in the trial had TKW higher than 40 g (Fig. 2c). Mean TKW in the ME1 and ME5 locations was 41.8 g and 36.1 g, respectively (Table 2). Though there was significant reduction of TKW for all entries in ME5, entries with a higher TKW in ME1 maintained a relatively high TKW in ME5 (Fig. 4). Ten entries in the trial with DH <79 days (mean DH of entries) had TKW ranging from 41 to 50 g (Fig. 2c). Three entries (16, 25, and 27) with mean TKW higher than 40 g across all locations were also among the best performing entries (Table 3).

The biplot was constructed to partition the genotype and genotype by environment effect (Fig. 5). The principal component axis 1 (PC1) and principal component axis 2 (PC2) together explained 44% of the variation. Another biplot for locations was constructed to understand the diversity in the locations based on GY (Fig. 5a). The biplot showed that locations had both positive and negative PC1 values. Most locations had positive PC1 values, indicating that the performance of the genotypes was similar across these locations. The locations with negative PC1 values had a disproportional genotype yield difference. The four locations (Obregon2, Varanasi, Vijapur and Ugar) that had negative PC1 values belonged to ME5. For the PC2 axis, locations had both positive and negative values suggesting that some entries may have had positive interaction in some of the environments but negative interactions in others. A few exceptions were noted, such as Varanasi, which had negative PC1 and PC2 values, and Bhairahwa, Dinajpur, Jalna, and Indore, which are classified as ME5 but in this trial were grouped with the ME1 locations.

A biplot focused on the entries was also constructed to evaluate their performance across locations. The entries with PC1 score >0 and PC2 scores near zero were the high yielding stable performing across locations (Fig. 5b). CIMMYT check 'Baj' (entry number 2) had a positive PC1 score, a near zero PC2 score and was one of the high yielding stable performing line across the locations. Entries 4, 8, 11, 16, 25, and 27 had PC1 scores >0 and PC2 scores near zero and were also among the high yielding and stable performing entries in the trial (Table 3).

3.3. Canopy temperatures and chlorophyll content

In Obregon1 and Obregon2, CT showed significant genotypic differences and significant association with the mean GY (ME1, $r = -0.44$, $P < 0.05$ and ME5, $r = -0.46$, $P < 0.05$) in the respective environments (Fig. 6). Entries with cooler canopies had higher GYs in Obregon1 and Obregon2 environments. At the other three locations (Varanasi, Indore, and Dinajpur), CT also had significant genotypic differences but failed to associate with GY in respective locations or across all locations (data not shown). Total CC was measured in Varanasi, India, and ranged from 46 to 53 SPAD units. The

Table 2
Grain yield, days to heading, thousand kernel weight and plant height across locations, and ME1 (7 locations) and ME5 (8 locations) for the 30 entries in the 2nd CSISA HT-EM YT during the 2010–2011 crop season.

Traits	Mean			LSD[a]			CV[b]			Heritability		
	All locations	ME1	ME5	All locations	ME1	ME5	All locations	ME1	ME5	All locations	ME1	ME5
Heading (days)	79	83	68	1.69	2.14	1.69	1.09	1.39	1.24	0.90	0.88	0.92
Grain yield (t/ha)	4.39	5.26	3.63	0.32	0.66	0.75	3.70	6.14	10.64	0.66	0.74	0.63
TKW[c] (g)	40.9	45.4	37.4	2.38	6.46	3.17	2.97	7.85	4.34	0.91	0.48	0.88
Plant height (cm)	99.7	108.3	95.4	3.0	3.2	5.5	1.5	1.5	3.1	0.93	0.93	0.84

[a] LSD – Fischer's least square difference.
[b] CV – Coefficient of variation.
[c] **TKW** – Thousand kernel weight.

Table 3
The five highest yielding entries in the 2nd CSISA HT-EM YT across 13 locations in South Asia and 2 environments in Mexico with days to heading, plant height, grain yield and thousand kernel weight during the 2010–2011 crop season.

GID[a]	Entry#	Name or pedigree	Heading (days)	Plant height (cm)	Grain yield		TKW (g)[b]
					(t/ha)	%Checks	
5994247	25	HUW234 + Lr34/Prinia*2//Kiritati	76	97.8	4.76	111	44.9
5995318	8	Weebill1/Kukuna//Tacupeto F2001/5/Baj	80	104.5	4.70	109	39.2
5995481	11	Fret2*2/4/Sonoita/Trap#1/3/Kauz*2/Trap//Kauz/5/Kachu	81	96.6	4.66	108	39.4
5994249	27	HUW234 + Lr34/Prinia*2//Kiritati	76	95.8	4.63	108	42.4
5993822	16	Fret2*2/Kukuna//Pavon/5/Fret2*2/4/Sonoita/Trap#1/3/ Kauz*2/Trap//Kauz	79	104.3	4.59	107	42.5
		Local Checks	*83*	*94.9*	*4.34*	*100*	*40.8*
		CIMMYT Check–'Baj'	*78*	*98.5*	*4.46*	*104*	*40.2*

[a] GID – Germplasm identification in CIMMYT germplasm bank.
[b] TKW – Thousand kernel weight.

CC estimates had a strong association with TKW across locations (Fig. 7, $r = 0.67$, $P < 0.001$). There were no significant correlations between CC and GY at individual locations or across locations.

4. Discussion

The wide variation in temperatures across the locations in South Asia during the crop season is aptly described by the CIMMYT-ME classifications. ME1 locations with optimal irrigation and cooler climate during crop growth and development, resulted in a 1.6 t/ha higher mean GY than ME5 locations. Similar results were reported by Sharma et al. (2012), where the ME1 environments had higher GY across several years. Variation in GY within the locations in each ME was most likely due to differences in agronomic and management practices. Sowing dates of the trial varied within each ME and may have had an impact on GY. The locations with a later sowing date were exposed to higher temperature stress early in the crop season, which may have affected crop growth and final GY. The two sowing dates in Mexico, Obregon1 and Obregon2, differed by nearly 3 t/ha in mean GY. As the agronomic practices, such as fertilization, irrigation and weed management were controlled in the two environments, it can be concluded that the difference in GY was primarily due to high temperature stress. Furthermore, the clustering of Obregon2 with the ME5 locations in the GGE analysis suggests the advantage of testing the CIMMYT germplasm under late sown conditions in Cd. Obregon. On the average, it was estimated that for every 1 °C rise in temperature there was a 7–8% loss in GY. Similar yield losses of 6–20% have been reported for South Asia and the eastern Gangetic wheat growing regions by various simulation studies (Aggarwal et al., 2010; Lobell et al., 2008).

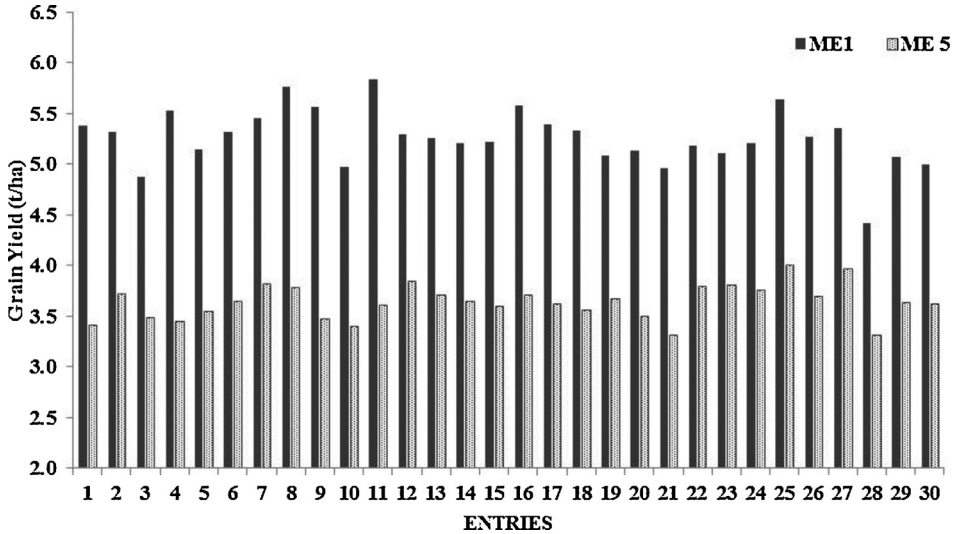

Fig. 3. Comparison of the grain yield (t/ha) in two mega-environments (ME1 and ME5) for the 30 entries in the 2nd CSISA HT-EM YT grown during 2010–2011 crop season across 13 locations in South Asia and 2 environments in Mexico.

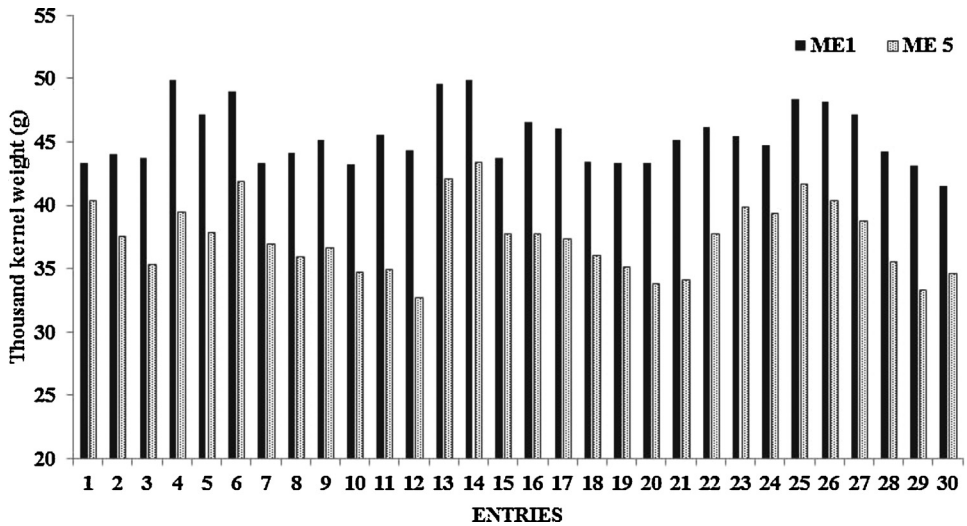

Fig. 4. Comparison of the thousand kernel weight (g) in two mega-environments (ME1 and ME5) for the 30 entries in the 2nd CSISA HT-EM YT grown during 2010–2011 crop season across 13 locations in South Asia and 2 environments in Mexico.

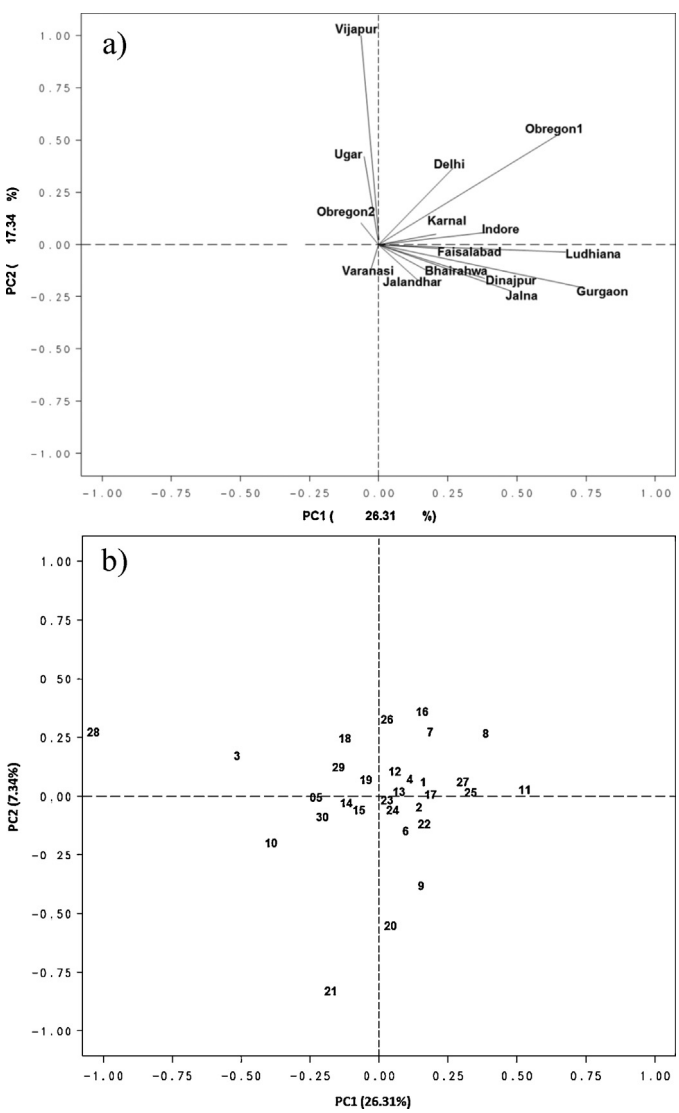

Fig. 5. GGE biplot for locations (a) and the entries (b) based on grain yield in the 2nd CSISA HT-EM YT during the 2010–2011 crop season.

For most ME5 locations, temperatures were relatively warmer during crop growth and increased above 30 °C during grain filling, which not only had an impact on GY but also PH, DH and DM. A reduction in PH was observed in the ME5 locations. Similar response of PH to increasing temperatures has been reported in other studies as well (Mohammadi et al., 2009; Zhong-hu and Rajaram, 1994). Continuous warm temperatures hastened the mean DH in ME5 locations by almost 30 days (on average) compared to ME1. Previous studies have reported similar effects of

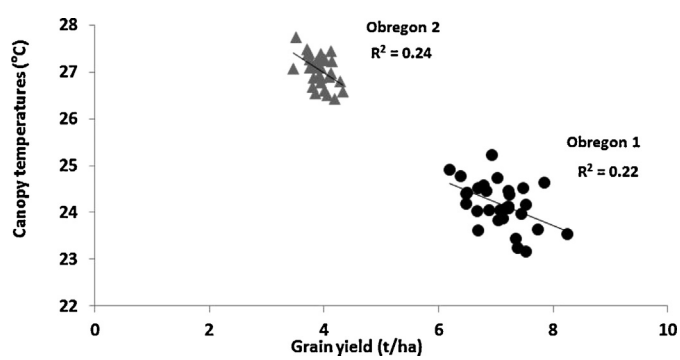

Fig. 6. Association of canopy temperature and grain yield in the 2nd CSISA HT-EM YT grown in the two environments in Ciudad Obregon, Mexico during the 2010–2011 crop season.

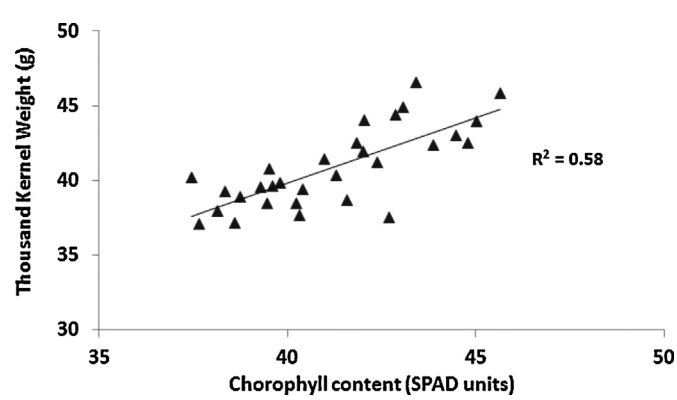

Fig. 7. Association of chlorophyll content and thousand kernel weight (g) in the 2nd CSISA HT-EM YT in Varanasi, India during the 2010–2011 crop season.

high temperature stress on DH (Mason et al., 2010; Wardlaw, 1994; Yang et al., 2002). Early heading entries generally performed well in areas suffering from terminal heat stress (ME1) as it escapes the high temperatures during grain filling stages. However, in this study the early heading entries performed well across environments (ME1 and ME5) with 5–11% higher GY than the local checks. Thus, earliness, not only favored the plants to escape terminal high temperature stress in ME1 but may also have promoted an efficient utilization of available resources in the ME5 locations and contributed to the final GY. Previous studies in India also support earliness as a key criterion in breeding for high temperature stress tolerance in South Asia (Joshi et al., 2007b; Punia et al., 2011). The GY/ha/day was estimated to understand the importance of the crop growing time with respect to GY. The shorter crop duration may be reasoned for the grain yield losses, yet the similar GY/ha/day across locations and in the ME imply otherwise. A shorter duration crop will escape the high temperatures and perform at par or superior to normally maturing wheat. When comparing the two environments in Mexico, temperatures had a significant effect on the GY/ha/day. The cooler Obregon1 had higher GY/ha/day than the late sown heat stressed Obregon2. Though GY in Obregon2 is similar to ME5 locations in South Asia, the duration and intensity of high temperature stress may have resulted in the difference in GY/ha/day. Accessing maturity data from other locations will help to further this understanding.

Continual high temperatures in ME5 also reduced TKW for all entries in these locations. Previous studies have reported similar reduction in TKW in response to high temperature stress (Hays et al., 2007; Wardlaw et al., 2002). Although TKW was reduced in ME5, it is important to note that most entries with high TKW in ME1 also maintained higher TKW in ME5. Due to its association with GY, TKW has been suggested as a selection criterion under high temperature stress (Reynolds et al., 1994; Sharma et al., 2008; Yang et al., 2002). TKW did not show any significant association with earliness, but in general high yielding, early maturing entries were able to maintain their TKW.

Cooler canopies were associated with GY performance in ME1 as well as in ME5 environments in Cd. Obregon, Mexico (Fig. 4). The association of CT in the hot irrigated condition in Cd. Obregon, Mexico was previously reported by Reynolds et al. (1994). Though previous studies in South Asia have demonstrated association of GY and CT (Kumari et al., 2012), no such associations were observed in this trial for the South Asia locations. Gutierrez et al. (2012) reported a similar result, where CT had limited associations with GY in a multi-location international trial. CT is dependent on a number of environmental factors such as soil water condition, humidity, and radiation, therefore, a lack of associations in this study may be due to the interaction of the environmental factors in the different locations.

The total CC was measured only in Varanasi, India and had significant association with mean TKW across all locations. Balouchi (2010) reported an association of high CC with heat tolerance in the Australian wheat lines. Though CC did not have a direct association with GY, it was observed that the best performing entries had relatively higher leaf CC. Physiological characterization was limited to a few locations, therefore an organized effort to characterize across all locations may provide better results.

The trial results suggest that CIMMYT entries with high yields and early maturity, selected under normal and late sown condition in Cd. Obregon, Mexico, have the potential to adapt and outperform normal maturing check varieties in ME1 as well as early maturing varieties in ME5. Simultaneous enhancement of GY potential and heat stress tolerance of early maturing wheat lines could therefore prove beneficial in South Asia in enhancing productivity under temperature stress, whilst reducing the water use by cutting the last irrigation. The early maturing, high yielding wheat entries identified in our study are under further evaluations in national trials for potential release as varieties. They are being used in the CIMMYT and national wheat improvement programs for developing superior heat tolerant wheat varieties.

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