

Combining Ability of Physiological and Yield Traits of Bread Wheat Diallel Crosses under Timely and Late Sowing Dates

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WHEAT (*Triticum aestivum* L.) is a vulnerable crop to heat stress. A set of 12 wheat genotypes were evaluated under timely and late sowing dates using physiological and yield traits during the two years of 2015/2016 and 2016/2017. Consequently, seven genotypes were used in a half-diallel mating system. The parents and their 21F₁ hybrids were evaluated under timely and late sowing dates during 2018/2019. The results indicated that both chlorophyll absorbance at anthesis and flag leaf temperature depression at milk stage were strongly associated ($r= 0.6$; $P<0.001$) with grain yield under heat stress induced by late sowing date. Therefore, using these traits is highly recommended screening tools for heat stress tolerance in wheat breeding programs. Significant differences were observed between the parental genotypes for their GCA and between their crosses for SCA for all traits under heat stress. The additive constituent of gene action was predominant. Among the seven parents, 1, 4, and 6 were the best general combiners for grain yield, 1000 grain weight, chlorophyll absorbance at anthesis, flag leaf temperature depression and canopy temperature depression at milk stage under heat stress. The best specific crosses for grain yield were 6×9, 6×11 and 1×4, for flag leaf temperature depression at milk stage were 6×11, 6×9 and 10×11 and for canopy temperature depression at milk stage were 4×6, 1×4 and 6×11 under heat stress. Taking advantage of both additive and non-additive components requires using bi-paternal and multi-parental mating approaches in wheat breeding programs targeted to develop heat-tolerant varieties.

Keywords: Wheat, Diallel crosses, Heat stress, Sowing date.

Introduction

Heat stress affects growth and productivity (Lobell & Asner, 2003 and Wahid et al., 2007) and reduces grain yield and quality in wheat (Stone & Nicolas, 1995; Dias & Lidon, 2009 and Asseng et al., 2015). Wheat (*Triticum* spp.) is susceptible to heat stress (Dias & Lidon, 2010 and Wang et al., 2016). Optimum temperature during wheat anthesis and grain filling ranges from 12-22°C (Farooq et al., 2011 and Dwivedi et al., 2017). Wheat yield declines by 3-4% for every 1°C increase above 15°C and grain number decreases by 12.5% as temperature increases by 1°C from 25/20 to 35/20°C day/night (Wardlaw & Wrigley, 1994). Other studies showed that increasing temperature more than 30°C during pre and/or post anthesis causes reduction in yield and quality of wheat (Stone & Nicolas, 1995 and Barnabas et al., 2008). The exposure of wheat plants to heat stress due to global warming or delayed sowing causes yield loss (Pandey et al., 2015). In the Mediterranean region, including Egypt, heat stress is one of the most important causes of yield loss in wheat during

pre and post-anthesis stages (Wardlaw et al., 1989). Approximately 21% of the world's food depends on the wheat (*Triticum aestivum* L.) crop (<http://www.fao.org>). Both Heat along with drought stresses affect 200 million hectares of wheat cultivated worldwide each year (Ortiz et al., 2008). This affected area might be increased in the next few decades due to global warming phenomenon.

In addition, the world population is expected to reach about 9 billion by 2050 (United Nations, 2011). The resultant population growth is expected to cause a food crisis unless efforts are made to increase the production of wheat under such circumstances. This crop is considered a staple food in many parts of the world. Therefore, wheat production has to be increased to overcome adverse effects of high temperature as well as growth of the world population.

The differences between the plant canopy, flag leaf or spike temperatures and the ambient air temperature are defined as canopy temperature depression (CTD), flag leaf temperature depression

(FLTD) or spike temperature depression (STD), respectively. These measurements have been known as an indicator of heat stress tolerance in wheat (Ayeneh et al., 2002; Balota et al., 2007 and Ali et al., 2010). In addition, they showed a strong positive association with yield and its components under heat stress during post-anthesis stages in wheat (Ali et al., 2010). Under heat stress, Ayeneh et al. (2002) reported a strong significant positive association between FLTD, STD and CTD on one side with grain yield on the other side. Blum (1988) reported that CTD varied from genotype to another according to canopy architecture. Later on, in 2002, Ayeneh et al. hypothesized that these differences in CTD were due to characteristics of the plant including a combination of both morphological and physiological structures e.g. leaf area, epicuticular wax on leaf and stem, existences of awns and the greenish of vegetative parts. In addition, they suggested that wheat organs, e.g. flag leaf and spike, shown different temperatures based on the plant architecture as well.

The most devastating effects of heat stress include speeding leaf senescence (Farooq et al., 2011 and Tovignan et al., 2016), impairment of chlorophyll biosynthesis (Tewari & Tripathy, 1998), reduction in stomatal conductance and transpiration rate (Gupta et al., 2015), increase floral abortion (Wardlaw & Wrigley, 1994), impairing pollen development (Young et al., 2004 and Kumar et al., 2013) and high rates of pollen mortality (Zhang et al., 2012).

Photosynthesis is the most sensitive physiological process to heat stress (Wahid et al., 2007) as it results in impairment of the structure and function of chloroplasts and reductions in chlorophyll content (Xu et al., 1995 and Ristic et al., 2007). Heat stress inhibits the photosynthesis process; therefore, it adversely affects plant growth and development (Mathur et al., 2014). Wheat yield can be dramatically declined due to the negative effects of high temperature on the conveyance of assimilates from green tissues to grains (Plaut et al., 2004). Therefore, the good status of chlorophylls guarantees an efficient photosynthesis process. However, heat stress causes chlorophyll loss and increases leaf senescence that adversely affects the efficiency of photosynthesis process and finally causes a dramatic loss in yield and its components. The measurements chlorophyll absorbance (CA)

using SPAD chlorophyll meter can be used to estimate the chlorophyll concentration in the leaf. A portable handheld SPAD meter has been used extensively to estimate the relative chlorophyll content in leaves (Ayeneh et al., 2002; Richardson et al., 2002 and Ali et al., 2013). Strong positive correlations were detected between CA and grain yield and its components in wheat under heat stress (Ayeneh et al., 2002 and Ristic et al., 2007).

Promising traits can be used as to screen wheat germplasm, in wheat breeding programs, to identify heat-tolerant genotypes include ability to stay green, high canopy temperature depression, high chlorophyll content, and others (Reynolds et al., 2009 and Foulkes et al., 2010). Thus, using such non-destructive measurements, i.e. CTD, FLTD, STD and CA are considered as paramount measurements in breeding programs.

Grain yield is the key component in selecting heat-tolerant genotypes in wheat breeding programs (Mesihovic et al., 2016). Yield and yield components are complex traits; hence, it is hard to increase them under heat. That is because complex traits are low heritable traits as well as they are highly affected by the environment and genotype \times environment interactions ($G \times E$) under heat stress. Therefore, using less complicated traits, e.g. CTD, FLTD, STD and CA can help identifying heat-tolerant genotypes. In addition, Heat susceptibility index (HSI) developed by Fischer & Maurer (1978) can be used efficiently to estimate yield stability across diverse environments including favorable and abiotic stress ones.

The efficacy of wheat breeding program depends on creating variability, knowing general and specific combining ability, in addition to categorizing type of gene action for yield and its attributes (Kumar et al., 2017). Selecting parental genotypes is an important step towards developing new varieties, which can be accomplished via half-diallel mating system (Griffing, 1956).

Identifying good combiners can help improving breeding programs via combining these genotypes in multiple crosses (Joshi et al., 2003). The diallel cross approach allow breaking down of linkage and enhance accumulating of favorable genes (Jensen, 1970). In self-fertilizing crops, e.g. wheat, GCA effects are more important than SCA because the improvement of these crops depends

on additive gene action, which is transferable to next generations unlike cross-fertilized crops (Joshi et al., 2003).

The objectives of the current study were: (i) Evaluate the feasibility of using flag leaf, spike and canopy temperatures depression as well as chlorophyll absorbance at anthesis and milk stages as screening tools for heat stress tolerance, (ii) Determine the association between these organs temperatures and chlorophyll absorbance and grain yield, (iii) Investigate the relationship between heat susceptibility index and organs temperatures and chlorophyll absorbance as well as grain yield, (iv) Detect genotypes with good general combining ability under heat stress, and (v) Identify superior cross combinations that may be used to develop new heat-tolerant varieties.

Materials and Methods

The current study consisted of two experiments: 1) The first experiment included evaluation of exotic germplasm and local cultivars using physiological parameters and yield traits under timely and late sowing dates and 2) The second experiment comprised a half-diallel analysis using selected genotypes based on the evaluation of the first experiment.

TABLE 1. List of genotypes.

Gen. ID	Genotype	Selection history	Origin
1	KACHU #1	CMSS97M03912T-040Y-020Y-030M-020Y-040M-4Y-2M-0Y	
2	QUAIU #1	CGSS01B00046T-099Y-099M-099M-099Y-099M-29Y-0B-12B-0Y	
3	BAJ #1	CGSS01Y00134S-099Y-099M-099M-13Y-0B	
4	FRANCOLIN #1	CGSS01B00056T-099Y-099M-099M-099Y-099M-14Y-0B	
5	KACHU/BECARD//WBLL1*2/ BRAMBLING	CMSS07B00580T-099TOPY-099M-099NJ-099NJ-10WGY-0B	CIMMYT, Mexico
6	QUAIU #1/SUP152	CMSS08Y00057S-099Y-099M-099NJ-13WGY-0B	
7	KACHU//KIRITATI/2*TRCH	CMSS08Y00152S-099Y-099M-099NJ-099NJ-40WGY-0B	
8	KIRITATI//HUW234+LR34/ PRINIA/3/BAJ #1	CMSS08Y00182S-099Y-099M-099NJ-099NJ-3WGY-0B	
9	ND643/2*WBLL1//VILLA JUAREZ F2009	CMSS08Y00233S-099Y-099M-099NJ-7WGY-0B	
10	SUP152/FRNCLN	CMSS08Y00278S-099Y-099M-099Y-5M-0WGY	
11	Sids12	BUC//7c/Ald/5/Maya74/On/1160.147/3/BB/G11/4/ Chat“S”/6/Maya/vu1//Cmh 74A.630/4* sx, SD7096-4SD- LSD-0SD	Egypt
12	Giza168	MIL/BUC/seriCM93046-8M-OY-OM-2Y-OB	

First two years experiment

Plant material and growing conditions

A set of 10 advanced breeding lines (ABL) obtained from CIMMYT's breeding program along with two Egyptian cultivars (Table 1) were grown at Assiut University Agricultural Research Station (AUARS), Assiut, Egypt for two growing seasons (2015/2016 and 2016/2017). In each growing season, the 12 genotypes were grown in two sowing dates including a timely sowing date (01 November) and a late sowing date (14 December). This late sowing date allows the exposure of genotypes to high temperature during anthesis and milk stages. The temperatures during growing seasons are shown in Table 2. Both optimum and late sowing dates were irrigated regularly as recommended to avoid the occurrence of any drought stress. Diseases, insects and weeds were controlled by applying pesticides to avoid any damage to leaves or spikes and prevent yield loss.

In each of the aforementioned sowing dates, genotypes were sown in a split-plot design with three replications. The sowing dates were assigned to the main plot whereas the genotypes were allocated in the sub-plot. Each genotype in each replication was seeded in 10.5m² plot including 10 rows (3 meters long with inter-row space of 0.35m).

TABLE 2. Summary of temperatures[†] (°C) during growing seasons.

Day	Month	Minimum			Maximum		
		2015/2016	2016/2017	2018/2019	2015/2016	2016/2017	2018/2019
15-Jan	November	13.0	13.5	12.0	30.1	31.3	31.0
16-30		11.5	12.0	11.0	26.0	27.5	26.5
15-Jan	December	10.5	8.5	10.0	26.0	22.7	23.0
16-31		8.6	6.8	8.4	23.1	21.6	22.0
15-Jan	January	4.7	6.5	4.2	18.3	21.5	20.0
16-31		7.7	4.4	4.5	24.5	19.7	24.0
15-Jan	February	7.2	5.5	6.0	23.5	32.7	32.0
16-28		7.5	8.6	8.0	23.6	27.6	28.0
15-Jan	March	11.2	12.7	11.0	27.6	29.6	30.0
16-31		12.4	11.5	11.5	30.3	28.8	31.0
15-Jan	April	12.6	14.3	12.0	28.1	34.3	35.0
16-30		14.5	15.7	13.0	34.9	37.6	33.0
15-Jan	May	18.4	19.6	18.0	34.6	38.1	39.0
16-31		22.0	19.7	22.5	39.8	40.0	42.0
Sowing date							
1-Nov	Sowing to heading	8.8	8.2	8.0	24.4	25.6	25.8
14-Dec		7.8	7.4	7.0	23.4	25.5	26.0
1-Nov	Sowing to maturity	10.8	10.7	9.97	27.0	28.7	28.8
14-Dec		11.5	11.4	10.8	28.0	30.1	30.5

[†]Source: Meteorological Center of Agricultural Research Station, Assiut University, Egypt.

Traits studied

Flowering traits: The number of days from sowing to 50% of plants showed approximately one-half of their spikes from the sheath of the flag leaf is recorded as the number of days to 50% heading (DH) for each genotype. While the number of days to 50% anthesis (DA) is calculated by subtracting the sowing date from the date when at least one anther of 50% of plants for each genotype.

Plant organs temperature depression: Five plants for each genotype were labeled at 50% anthesis. The flag leaves and spikes of these labeled plants were used to measure flag leaf and spike temperatures using a handheld infrared thermometer (Model 8866, JQA Instrument, Inc., Tokyo, Japan) at 50% anthesis and milk stages.

The temperatures of flag leaf and spike were then subtracted from the ambient air temperature to calculate the flag leaf temperature depression (FLTD) and spike temperature depression (STD). Furthermore, the canopy temperature of each plot was recorded as per Ayeneh et al. (2002). Similarly, the canopy temperature depression (CTD) was calculated as FLTD and STD as per Reynolds et al. (1994).

Chlorophyll absorbance (CA): Chlorophyll absorbance measurements were taken on the flag leaves of same aforementioned-labeled genotypes using a self-calibrating SPAD chlorophyll meter (Model 502, Spectrum Technologies, Plainfield, IL) as per Ristic et al. (2007). The measurements of CA were recorded at 50% anthesis and milk stages. The measurements of FLTD, STD,

CTD and CA on each set of five plants for each genotype in each stage were averaged to give one measurement for each replication.

Yield and its components: At harvest, a guarded squared meter from each plot was harvested to measure the yield and its components including grain yield (GYM; g/m²) and 1000-grain weight (1000-GW; g).

Heat susceptibility index (HSI)

The heat susceptibility index was calculated for individual genotypes as per Fischer and Maurer 1978 using the following equation:

$$HSI = (1 - Y_h/Y_c)/(1 - X_h/X_c)$$

where Y_h and Y_c are the grain yield/m² for each genotype under heat stress and optimum conditions, respectively, while X_h and X_c are the mean grain yield/m² over all genotypes under heat stress and optimum conditions, respectively.

Statistical analyses

Separate and combined analysis of variance overall years were accomplished using PROC GLM procedure (SAS v9.0, SAS Institute Inc., Cary, NC, USA) assuming that years as a random effect and both sowing date and genotypes as fixed effects. Pearson's correlation among all traits was conducted using PROC CORR in SAS v9.0 (SAS Institute, 2003).

Second (diallel) experiment

Plant material and growing conditions

Based on the evaluation of the first two years experiment (2015/2016 and 2016/2017), seven genotypes including heat-tolerant and heat susceptible genotypes were selected and crossed in a half-diallel scheme during growing season of 2017/2018. These seven parental genotypes were 1, 4, 5, 6, 9, 10 and 11 as indicated in Table 1. The 7 parental genotypes and their 21 non-reciprocal F1 crosses were evaluated during growing season 2018/2019 at AUARS under timely and late sowing dates as indicated in the first experiment.

Traits studied

The 7 parental genotypes and their 21 non-reciprocal F1 crosses were assessed for their tolerance to heat stress using flowering, physiological and yield traits including days to heading (DH), days to anthesis (DA), chlorophyll absorbance at anthesis stage (CA-A), flag leaf

temperature depression at milk stage (FLTD-M), canopy temperature depression at milk stage (CTD-M), grain yield per m² (GYM) and 1000 grain weight (1000GW).

Statistical analyses

The seven parental genotypes and their 21 non-reciprocal F1 diallel crosses were analyzed using Griffing's method 2, model 1 (Griffing, 1956) via AGDR-R version 4 (Rodríguez et al., 2015).

Results

First two years experiment

The differences in the minimum temperature from sowing date to heading date between the two sowing dates were 1.0°C and 1.4°C for 2016/2017 and 2017/2018, respectively. While, for the maximum temperature from sowing date to heading date, these differences between the two sowing dates were 1.0°C and 0.9°C for 2016/2017 and 2017/2018, respectively. On the other hand, from sowing to maturity, the difference in the minimum temperature between the two sowing dates was -0.7 for both two growing seasons (2016/2017 and 2017/2018), while the differences in the maximum temperature between the two sowing dates were -1.0°C and -1.4°C for 2016/2017 and 2017/2018, respectively (Table 2).

Tables 3 and 4 showed the averages of all traits for the 12 genotypes for optimum and late sowing dates in the current investigation for growing seasons 2016/2017 and 2017/2018, respectively. In addition, averages of all traits over the two growing seasons for each of optimum and late sowing dates were provided in Table 5.

In a separate analysis of variance for each growing season using the split-plot design (Table 6), genotypes showed significant differences for all traits. Similarly, sowing dates showed significant differences for all traits for both growing seasons except for CTD at anthesis stage in the second growing season (2017/2018). According to the combined analysis of variance for the two growing seasons (Table 7), genotypes showed significant differences for all traits. In addition, sowing dates exhibited significant differences for all traits except for days to anthesis. Furthermore, interactions among other sources of variation were not significant for all traits.

TABLE 3. Means of all traits for each sowing date in 2015/ 2016.

D1[†]												
Gen	DH	DA	CA-A	CA-M	FLTD-A	FLTD-M	STD-A	STD-M	CTD-A	CTD-M	GYM	1000GW
1	81.00	84.00	53.93	42.60	1.67	1.67	1.33	2.00	2.00	3.00	573.47	44.53
2	80.00	85.00	53.43	44.27	1.33	2.00	0.67	1.33	2.00	2.00	483.88	45.87
3	83.00	86.00	55.00	44.10	1.00	1.33	0.67	1.67	2.00	3.00	490.23	46.27
4	77.00	83.00	52.53	44.00	1.67	2.33	1.33	3.00	2.67	4.00	573.80	52.37
5	79.00	84.00	53.77	46.00	1.00	1.67	0.67	2.00	1.33	2.67	582.81	47.17
6	79.00	84.33	52.20	44.33	1.33	2.00	1.33	2.67	2.33	3.33	682.61	50.83
7	83.00	88.33	54.67	45.90	1.67	1.67	1.33	1.33	2.00	2.00	518.32	47.33
8	84.00	89.00	52.90	44.90	1.33	1.67	0.67	1.67	2.33	3.67	460.43	48.23
9	78.00	82.00	52.80	45.60	1.67	2.33	1.33	2.33	3.00	4.67	587.77	52.20
10	80.00	84.00	54.33	45.23	1.00	1.00	0.33	0.67	2.33	1.67	464.67	38.00
11	81.00	83.00	54.57	45.00	1.33	1.33	1.00	1.33	1.67	2.33	479.59	45.30
12	78.00	83.33	52.77	44.20	1.00	1.00	0.67	0.67	2.33	3.33	485.62	47.07
Mean	80.25	84.67	53.58	44.68	1.33	1.67	0.94	1.72	2.17	2.97	531.93	47.10
D2[‡]												
1	79.00	81.00	46.77	32.67	2.67	3.67	2.67	1.67	3.00	4.00	423.33	41.67
2	77.00	79.67	43.60	32.17	2.67	3.33	2.67	2.00	3.00	3.67	400.00	45.00
3	79.00	81.00	46.33	41.43	2.67	3.33	2.33	1.33	3.00	4.67	416.67	44.33
4	74.67	77.67	49.47	42.20	4.33	6.33	2.67	5.33	5.00	6.33	506.67	47.97
5	76.33	79.00	45.13	37.50	1.67	3.00	2.67	3.33	2.67	4.33	443.33	40.17
6	76.00	78.67	48.43	41.63	4.33	6.00	3.33	5.00	5.67	6.00	596.67	47.07
7	81.67	85.33	45.97	41.80	2.67	3.67	1.33	4.00	3.67	4.33	416.67	41.33
8	82.67	86.33	44.93	36.03	2.00	3.67	1.00	1.00	2.67	4.67	396.67	43.00
9	75.33	79.00	48.50	42.57	3.33	6.33	3.00	5.33	5.67	5.33	453.33	45.67
10	77.67	81.00	42.67	35.73	2.00	3.00	2.33	3.00	3.67	4.00	326.67	33.33
11	79.00	82.67	44.33	35.80	2.00	4.00	1.67	1.67	5.00	5.00	388.33	38.00
12	75.33	79.00	42.73	39.37	2.33	3.00	1.67	4.00	2.33	4.00	373.33	37.00
Mean	77.81	80.86	45.74	38.24	2.72	4.11	2.28	3.14	3.78	4.69	428.47	42.05
LSD _{0.05} sowing dates	0.78	1.18	2.05	1.90	0.43	1.02	0.21	0.83	1.35	1.14	45.81	1.13
LSD _{0.05} genotypes	1.42	1.29	2.15	2.11	0.74	0.76	0.75	1.11	1.04	1.13	23.05	3.03

[†] D1= The timely sowing date (01 November)

[‡] D2= The late sowing date (14 December)

DH= Days to heading, DA= Days to anthesis, CA-A= Chlorophyll content at anthesis stage, CA-M= Chlorophyll content at milk stage, FLTD-A= Flag leaf temperature depression at anthesis stage, FLTD-M= Flag leaf temperature depression at milk stage, STD-A= Spike temperature depression at anthesis stage, STD-M= Spike temperature depression at milk stage, CTD-A= Canopy temperature depression at anthesis stage, CTD-M= Canopy temperature depression at milk stage, GYM= Grain yield per m² and 1000GW= 1000 grain weight.

TABLE 4. Means of all traits for each sowing date in 2016/ 2017.

D1 [†]												
Gen	DH	DA	CA-A	CA-M	FLTD-A	FLTD-M	STD-A	STD-M	CTD-A	CTD-M	GYM	1000GW
1	80.00	82.33	53.60	42.00	1.33	2.00	1.00	1.67	2.00	2.33	545.20	43.30
2	78.67	84.00	52.37	44.07	1.33	1.67	1.00	2.00	2.33	1.33	493.73	46.00
3	81.33	85.33	52.17	44.33	1.67	1.67	1.00	2.67	2.33	2.33	453.33	43.73
4	76.00	79.67	51.27	41.67	1.33	3.00	1.33	3.00	3.67	4.33	560.43	52.47
5	78.33	81.00	51.63	43.63	1.00	1.67	1.00	2.00	2.67	1.67	550.27	45.83
6	79.00	83.00	51.90	44.00	1.67	3.00	1.00	2.67	2.67	4.00	623.33	51.53
7	82.67	88.00	52.30	44.27	1.67	2.67	1.00	1.00	1.67	3.33	500.23	45.40
8	81.00	84.33	51.23	43.20	1.67	2.00	0.67	1.33	2.67	3.00	460.23	47.53
9	76.67	80.00	51.37	42.33	1.33	3.00	1.33	2.33	3.67	3.67	523.33	51.33
10	80.33	82.67	52.27	43.53	1.67	1.33	1.00	0.67	2.00	1.33	426.67	39.13
11	78.00	81.33	51.90	44.30	1.00	1.33	1.00	1.00	2.00	3.00	456.20	42.00
12	75.00	80.33	50.70	42.17	1.33	1.33	1.33	0.67	2.00	2.67	420.10	42.33
Mean	78.92	82.67	51.89	43.29	1.42	2.06	1.06	1.75	2.47	2.75	501.09	45.88
D2 [‡]												
1	74.00	71.67	42.67	33.30	2.33	4.67	2.00	1.67	4.00	4.67	413.33	40.67
2	75.00	78.00	43.33	38.33	2.33	4.00	2.33	3.67	3.33	5.00	384.67	41.67
3	77.00	81.33	42.67	35.33	2.67	3.33	1.00	2.00	3.67	5.00	340.00	40.00
4	74.33	77.67	49.33	42.77	4.00	6.33	4.33	5.00	6.00	6.67	473.33	45.67
5	75.33	79.00	40.67	37.53	2.67	3.33	1.67	3.33	4.00	4.67	380.00	40.33
6	76.00	79.00	46.33	41.97	4.67	6.00	3.67	4.67	5.33	6.33	514.00	44.67
7	80.33	83.00	43.00	40.37	2.33	3.67	2.00	2.00	3.67	5.00	360.00	40.33
8	80.33	84.33	41.33	31.07	2.33	4.00	2.67	5.00	4.33	4.00	373.33	34.67
9	78.00	82.00	47.60	42.17	4.67	5.67	4.33	3.33	5.33	6.00	436.67	46.00
10	77.67	82.67	43.67	40.57	2.67	3.33	2.00	2.67	4.00	4.00	310.00	33.33
11	77.00	82.00	36.33	31.53	2.67	3.00	3.00	2.00	3.00	3.00	326.67	38.33
12	74.67	79.33	41.67	39.27	2.67	4.33	2.00	3.67	2.67	4.00	373.33	38.67
Mean	76.64	80.00	43.22	37.85	3.00	4.31	2.58	3.25	4.11	4.86	390.44	40.36
LSD _{0.05} sowing dates	1.35	1.15	1.27	4.26	0.72	0.95	0.67	0.90	1.88	1.04	33.56	2.23
LSD _{0.05} genotypes	1.84	1.69	2.25	2.28	0.97	0.69	0.91	1.38	1.27	1.29	24.28	2.59

[†] D1= The timely sowing date (01 November)

[‡] D2= The late sowing date (14 December)

DH= Days to heading, DA= Days to anthesis, CA-A= Chlorophyll content at anthesis stage, CA-M= Chlorophyll content at milk stage, FLTD-A= Flag leaf temperature depression at anthesis stage, FLTD-M= Flag leaf temperature depression at milk stage, STD-A= Spike temperature depression at anthesis stage, STD-M= Spike temperature depression at milk stage, CTD-A= Canopy temperature depression at anthesis stage, CTD-M= Canopy temperature depression at milk stage, GYM= Grain yield per m² and 1000GW= 1000 grain weight.

TABLE 5. Means of the traits averaged across two growing seasons for each sowing date.

D1 [†]												
Gen	DH	DA	CA-A	CA-M	FLTD-A	FLTD-M	STD-A	STD-M	CTD-A	CTD-M	GYM	1000GW
1	80.50	83.17	53.77	42.30	1.50	1.83	1.17	1.83	2.00	2.67	559.33	43.92
2	79.33	84.50	52.90	44.17	1.33	1.83	0.83	1.67	2.17	1.67	488.80	45.93
3	82.17	85.67	53.58	44.22	1.33	1.50	0.83	2.17	2.17	2.67	471.78	45.00
4	76.50	81.33	51.90	42.83	1.50	2.67	1.33	3.00	3.17	4.17	567.12	52.42
5	78.67	82.50	52.70	44.82	1.00	1.67	0.83	2.00	2.00	2.17	566.54	46.50
6	79.00	83.67	52.05	44.17	1.50	2.50	1.17	2.67	2.50	3.67	652.97	51.18
7	82.83	88.17	53.48	45.08	1.67	2.17	1.17	1.17	1.83	2.67	509.28	46.37
8	82.50	86.67	52.07	44.05	1.50	1.83	0.67	1.50	2.50	3.33	460.33	47.88
9	77.33	81.00	52.08	43.97	1.50	2.67	1.33	2.33	3.33	4.17	555.55	51.77
10	80.17	83.33	53.30	44.38	1.33	1.17	0.67	0.67	2.17	1.50	445.67	38.57
11	79.50	82.17	53.23	44.65	1.17	1.33	1.00	1.17	1.83	2.67	467.90	43.65
12	76.50	81.83	51.73	43.18	1.17	1.17	1.00	0.67	2.17	3.00	452.86	44.70
Mean	79.58	83.67	52.73	43.99	1.38	1.86	1.00	1.74	2.32	2.86	516.51	46.49
D2 [‡]												
1	76.50	76.33	44.72	32.98	2.50	4.17	2.33	1.67	3.50	4.33	418.33	41.17
2	76.00	78.83	43.47	35.25	2.50	3.67	2.50	2.83	3.17	4.33	392.33	43.33
3	78.00	81.17	44.50	38.38	2.67	3.33	1.67	1.67	3.33	4.83	378.33	42.17
4	74.50	77.67	49.40	42.48	4.17	6.33	3.50	5.17	5.50	6.50	490.00	46.82
5	75.83	79.00	42.90	37.52	2.17	3.17	2.17	3.33	3.33	4.50	411.67	40.25
6	76.00	78.83	47.38	41.80	4.50	6.00	3.50	4.83	5.50	6.17	555.33	45.87
7	81.00	84.17	44.48	41.08	2.50	3.67	1.67	3.00	3.67	4.67	388.33	40.83
8	81.50	85.33	43.13	33.55	2.17	3.83	1.83	3.00	3.50	4.33	385.00	38.83
9	76.67	80.50	48.05	42.37	4.00	6.00	3.67	4.33	5.50	5.67	445.00	45.83
10	77.67	81.83	43.17	38.15	2.33	3.17	2.17	2.83	3.83	4.00	318.33	33.33
11	78.00	82.33	40.33	33.67	2.33	3.50	2.33	1.83	4.00	4.00	357.50	38.17
12	75.00	79.17	42.20	39.32	2.50	3.67	1.83	3.83	2.50	4.00	373.33	37.83
Mean	77.22	80.43	44.48	38.05	2.86	4.21	2.43	3.19	3.94	4.78	409.46	41.20
LSD _{0.05} sowing dates	1.06	7.24	5.33	6.32	1.24	1.24	1.24	0.53	0.18	2.47	45.65	2.98
LSD _{0.05} genotypes	1.84	2.53	2.21	2.84	0.54	0.53	0.77	1.32	0.93	0.77	29.89	2.11

[†] D1= The timely sowing date (01 November)

[‡] D2= The late sowing date (14 December)

DH= Days to heading, DA= Days to anthesis, CA-A= Chlorophyll content at anthesis stage, CA-M= Chlorophyll content at milk stage, FLTD-A= Flag leaf temperature depression at anthesis stage, FLTD-M= Flag leaf temperature depression at milk stage, STD-A= Spike temperature depression at anthesis stage, STD-M= Spike temperature depression at milk stage, CTD-A= Canopy temperature depression at anthesis stage, CTD-M= Canopy temperature depression at milk stage, GYM= Grain yield per m² and 1000GW= 1000 grain weight.

TABLE 6. Mean squares of the split-plot design separated by growing season for all traits.

Source	DF	Mean squares											
		DH	DA	CA-A	CA-M	FLTD-A	FLTD-M	STD-A	STD-M	CTD-A	CTD-M	GYM	1000GW
2015/2016													
Rep	2	7.10**	7.68**	11.76*	5.37	0.68	0.60	0.93	0.39	0.26	3.79	1621.04*	9.02
Sowing date (D)	1	107.56***	260.68**	1105.28***	745.62**	34.72**	107.56**	32.00**	36.13*	46.72*	53.39*	192668.7*	459.55**
Rep × D	2	0.60	1.35	4.10	3.51	0.18	1.01	0.04	0.67	1.76	1.26	2040.06	1.24
Genotypes (G)	11	33.33**	31.77***	6.58	26.03***	1.66***	4.28***	1.19**	6.17***	3.30***	3.64***	26688.82***	92.28***
D × G	11	0.83	3.71**	11.4**	19.2***	0.87*	1.49**	0.73	3.06**	1.78*	0.84	1409.8**	9.73
Error	44	1.48	1.23	3.41	3.27	0.4	0.43	0.41	0.91	0.81	0.93	392.46	6.79
2016/2017													
Rep	2	5.01	1.63	9.07	2.38	0.17	0.35	0.43	1.13	0.54	2.39	912.42	20.42*
Sowing date (D)	1	93.39*	128**	1354.6**	533.01*	45.13**	91.13**	42.01**	40.5*	48.35	80.22*	220359.5**	548.91**
Rep × D	2	1.76	1.29	1.56	17.68	0.5	0.88	0.43	0.79	3.43	1.06	1094.79	4.84
Genotypes (G)	11	23.92***	34.09***	17.24***	24.51***	1.34	4.50***	1.98**	4.27**	3.79**	4.96***	20576.76***	88.07***
D × G	11	5.81*	18.39***	19.8***	29.92***	1.28	0.73*	1.47**	2.11	0.53	1.43	1508**	10.57*
Error	44	2.51	2.11	3.73	6.12	0.7	0.35	0.61	1.4	1.18	1.22	435.28	4.94

****Significant at the 0.05, 0.01 and 0.001 probability levels, respectively.

DH= Days to heading, DA= Days to anthesis, CA-A= Chlorophyll content at anthesis stage, CA-M= Chlorophyll content at milk stage, FLTD-A= Flag leaf temperature depression at anthesis stage, FLTD-M= Flag leaf temperature depression at milk stage, STD-A= Spike temperature depression at anthesis stage, STD-M= Spike temperature depression at milk stage, CTD-A= Canopy temperature depression at anthesis stage, CTD-M= Canopy temperature depression at milk stage, GYM= Grain yield per m² and 1000GW= 1000 grain weight.

TABLE 7. Mean squares of the split-plot design combined for the two growing seasons for all traits.

Source	DF	Mean squares											
		DH	DA	CA-A	CA-M	FLTD-A	FLTD-M	STD-A	STD-M	CTD-A	CTD-M	GYM	1000GW
Year (Y)	1	56.25***	73.67***	159.18***	28.44*	1.17	3.06**	1.56	0.17	3.67	0.03	42688.15***	75.55***
Sowing date (D)	1	200.69*	377.01	2453.55*	1269.73	79.51*	198.34*	73.67*	76.56*	95.06**	132.25	412563.56*	1006.48*
Y × D	1	0.25	11.67**	6.33	8.90	0.34	0.34	0.34	0.06	0.01	1.36	464.64	1.98
Genotypes (G)	11	53.04***	57.93**	17.75*	40.52*	2.64**	8.43***	2.45*	8.29*	5.93**	7.88***	46159.16***	174.85***
G × Y	11	4.20*	7.93***	6.07	10.02*	0.36	0.35	0.73	2.14	1.07	0.72	1106.42*	5.50
G × D	11	3.86	13.60	26.36**	38.01*	1.81**	1.72*	1.08	3.29	1.58	1.07	1939.79	10.33
G × Y × D	11	2.78	8.51***	4.11	11.11*	0.34	0.51	1.11*	1.88	0.73	1.21	978.01*	9.98
Error	92	1.96	1.65	3.54	4.96	0.54	0.41	0.50	1.13	1.06	1.08	464.03	5.75

****Significant at the 0.05, 0.01 and 0.001 probability levels, respectively.

DH= Days to heading, DA= Days to anthesis, CA-A= Chlorophyll content at anthesis stage, CA-M= Chlorophyll content at milk stage, FLTD-A= Flag leaf temperature depression at anthesis stage, FLTD-M= Flag leaf temperature depression at milk stage, STD-A= Spike temperature depression at anthesis stage, STD-M= Spike temperature depression at milk stage, CTD-A= Canopy temperature depression at anthesis stage, CTD-M= Canopy temperature depression at milk stage, GYM= Grain yield per m² and 1000GW= 1000 grain weight.

Correlation coefficients combined over the two growing seasons for each sowing date (Table 8). Under optimum sowing date, FLTD recorded during milk stage showed positive significant correlation coefficients with STD recorded during at the same stage ($r= 0.37$, $P= 0.01$), CTD recorded at anthesis stage ($r= 0.25$, $P= 0.05$), CTD recorded during milk stage ($r= 0.48$, $P= 0.001$), GYM ($r=0.43$, $P= 0.001$) and 1000GW ($r= 0.52$, $P= 0.001$). Furthermore, STD recorded during the milk stage revealed positive significant correlation ranged from moderate values ($r= 0.49$, $P= 0.001$) with GYM to moderately high ($r= 0.60$, $P= 0.001$) with 1000GW. Moreover, CTD recorded during anthesis stage was positively significantly correlated with 1000Gw ($r= 0.35$, $P= 0.01$) while CTD recorded during the milk stage showed positive significant correlation with both GYM and 1000GW with values of correlation coefficients of $r= 0.32$ ($P= 0.01$) and $r= 0.48$ ($P= 0.01$), respectively. However, CA recorded during either anthesis or milk stages was not significantly correlated with neither GYM nor 1000GW. Whereas, under late sowing date (a heat stress condition), the correlation coefficients were stronger and highly significant between both CA and organs temperature depressions and almost the rest of traits including GYM and 1000GW than under optimum conditions. Briefly, CA at anthesis stage showed moderate to moderately high correlation with CA at milk stage ($r= 0.57$; $P<0.001$), FLTD at anthesis stage ($r= 0.42$; $P<0.001$), FLTD at milk stage ($r= 0.50$; $P<0.001$), CTD at both anthesis and milk stages ($r= 0.41$; $P<0.001$), GY ($r= 0.60$; $P<0.001$) and 1000GW ($r= 0.47$; $P<0.001$). The CA at the milk stage showed significant correlations with the same traits but the strength of correlations were less comparing to CA at anthesis stage. The FLTD at milk stage exhibited stronger association with STD and CTD at both anthesis and milk stages, in addition to GY ($r= 0.63$; $P<0.001$) and 100GW ($r= 0.52$; $P<0.001$) compared to FLTD at anthesis stage. On the other hand, the strength of association between STD at both anthesis and milk stages and other traits including GY and 1000GW were moderately low. Moreover, CTD during both anthesis and milk stages was moderately associated with GY and 1000GW.

Heat susceptibility index (HSI) for the two growing seasons is shown in Fig.1. The

average temperature depression values for flag leaf, spike and canopy under optimum and heat stress recorded at both anthesis and milk stages are shown in Fig. 2. The recorded values of temperature depression for flag leaf, spike and canopy were higher at milk stage than anthesis stage. In addition, in both anthesis and milk stages, the temperature depression was the highest for canopy followed by flag leaf, while spike showed the lowest temperature depression under both optimum and heat stress. Furthermore, the values of temperature depression in the two stages for all organs were higher under heat stress than optimum.

The relationships between HSI and CA, organs temperature depression and yield traits under heat stress averaged over the two growing seasons were presented in Fig. 3. In details, the relationship between HSI and CA at anthesis stage was stronger ($r= -0.52$, $P= 0.08$) than between HSI and CA at milk stage ($r= -0.36$, $P= 0.25$); however, both of these two relationships were not significant at 5% significance level (Fig. 3 a). Regarding the relationship between HSI and FLTD at anthesis, the correlations coefficient was strongly negative and significant ($r= -0.62$, $P= 0.03$). Similar results were found between HSI and FLTD at milk stage ($r= -0.65$, $P= 0.02$) (Fig. 3 b). The relationship between HSI and STD at anthesis stage was not significant ($r= -0.43$, $P= 0.17$) while the relationship between HSI and STD at milk stage showed negative and significant correlation ($r= -0.59$, $P= 0.04$) (Fig. 3 c). The relationship between CTD at anthesis stage and HSI was not significant ($r= -0.39$, $P= 0.21$) while CTD at milk stage showed strong negative significant correlation with HSI ($r= -0.63$, $P= 0.03$) (Fig. 3 d). Both GYM and 1000GW showed negative strong correlation ($r\approx -0.60$, $P= 0.03$) with HSI (Fig. 3 e, f).

Based on the mean performance of genotypes under heat stress (Table 5), seven genotypes were selected as parents to produce 21 non-reciprocal F_1 crosses in the second experiment. In addition, according to correlation coefficients among traits (Table 8), some physiological traits (CA-A, FLTD-M and CTD-M) that showed high correlation with GYM and 1000GW, on one hand, and strong association with other physiological traits, on the other hand, were used in the second experiment.

TABLE 8. Pearson's correlation coefficients combined over two years for timely and late sowing dates among all traits.

	DH	DA	CA-A	CA-M	FLTD-A	FLTD-M	STD-A	STD-M	CTD-A	CTD-M	GYM	1000GW
DH		0.82***	0.36**	0.25*	0.07	-0.2	-0.23	-0.13	-0.23	-0.2	-0.17	-0.22
DA	0.86***		0.29*	0.39***	0.11	-0.14	-0.2	-0.11	-0.27*	-0.12	-0.12	-0.07
CA-A	-0.05	-0.14		0.41***	-0.11	-0.37**	-0.15	-0.10	-0.25*	-0.20	0.04	-0.12
CA-M	-0.06	-0.02	0.57***		0.01	-0.28*	0.01	-0.09	-0.17	0.03	0.06	0.01
FLTD-A	-0.19	-0.13	0.42***	0.43***		0.13	0.24*	0.25*	0.01	0.16	0.05	0.16
FLTD-M	-0.27*	-0.27*	0.50***	0.40***	0.62***		0.12	0.37**	0.25*	0.48***	0.43***	0.52***
STD-A	-0.28*	-0.26*	0.31**	0.23	0.37**	0.46***		0.32**	0.03	0.14	0.12	0.17
STD-M	-0.39***	-0.20	0.19	0.33**	0.38***	0.41**	0.31**		0.30*	0.17	0.49***	0.59***
CTD-A	-0.25*	-0.20	0.41***	0.32**	0.43***	0.55***	0.40***	0.40***		0.20	0.16	0.35**
CTD-M	-0.17	-0.18	0.41***	0.41***	0.43***	0.59***	0.31**	0.35**	0.44***		0.32**	0.48***
GYM	-0.19	-0.28*	0.60***	0.38***	0.53***	0.63***	0.40***	0.38***	0.43***	0.49***		0.62***
1000GW	-0.2	-0.25*	0.47***	0.32**	0.50***	0.52***	0.33**	0.18	0.31**	0.39***	0.64***	

****Significant at the 0.05, 0.01 and 0.001 probability levels, respectively.

DH= Days to heading, DA= Days to anthesis, CA-A= Chlorophyll content at anthesis stage, CA-M= Chlorophyll content at milk stage, FLTD-A= Flag leaf temperature depression at anthesis stage, FLTD-M= Flag leaf temperature depression at milk stage, STD-A= Spike temperature depression at anthesis stage, STD-M= Spike temperature depression at milk stage, CTD-A= Canopy temperature depression at anthesis stage, CTD-M= Canopy temperature depression at milk stage, GYM= Grain yield per m² and 1000GW= 1000 grain weight.

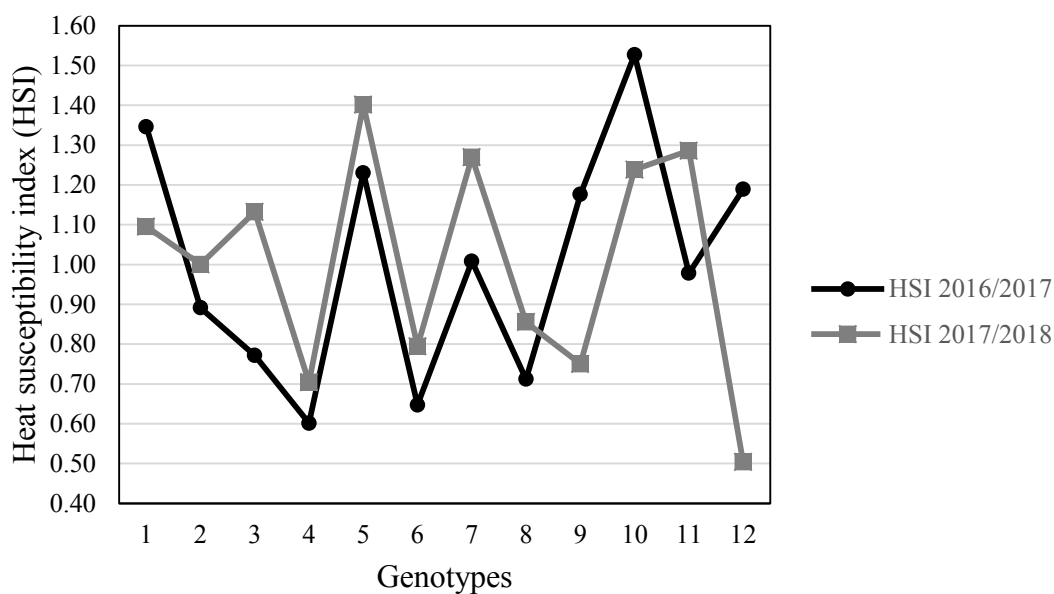


Fig. 1. HSI calculated as per Fischer and Maurer (1978) during the 2016/2017 and 2017/ 2018.

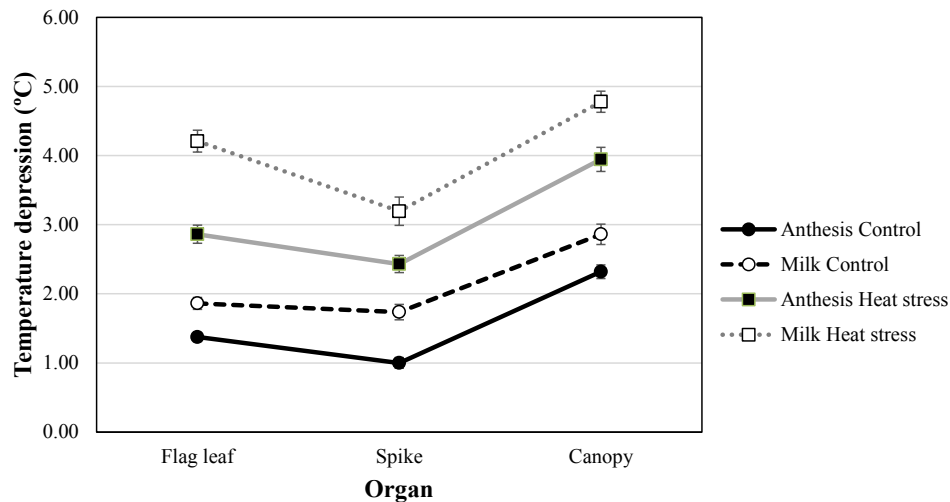


Fig. 2. Temperature depression (°C) of 12 genotypes for flag leaf, spike and canopy for optimum and heat stress over the two growing seasons measured at anthesis and milk stages.

Second (diallel) experiment

The means performance for all traits of parental genotypes and their 21 non-reciprocal F_1 crosses under optimum and heat stress conditions along with combined data are presented in Tables 9, 10 and 11, respectively. The results revealed that most F_1 hybrids performed better than the mean of their parental genotypes for physiological and yield traits.

Analyses of variance (ANOVA) of Griffing's method of parental genotypes and their non-reciprocal F_1 crosses for all traits under optimum and heat stress conditions as well as the combined analysis are presented in Table 12. Briefly, under optimum condition, DH and CA-A showed significant differences for both genotypes and GCA, while DA showed significant differences for genotypes and SCA. None of the sources of variation for FLTD-M was significant, while only GCA showed significant differences for CTD-M. All sources of variation for both GYM and 1000GW showed significant differences. On the other hand, under heat stress, all sources of variation were significant for all traits except DH showed significant differences for only genotypes and GCA. According to combined ANOVA, both FLTD-M and CTD-M showed significant differences for treatments, treatment \times genotypes, treatment \times GCA and treatment \times SCA. For GYM, all constituents of variation were significant except treatment \times GCA, while all sources of variation were significant for 1000GW except for SCA and treatment \times GCA.

General combining ability effects estimates (g) of the seven parental genotypes and the range

of the specific combining ability effects (s_{ij}) for all traits under optimum, heat stress conditions and over all conditions are presented in Table 13. In brief, under optimum condition, only significant GCA estimate for CA-A was noticed in genotype 4, which showed the smallest value of GCA (-0.99). The cross combination 9 \times 11 showed the minimum significant SCA estimate (-1.42), while 1 \times 4 showed the maximum significant SCA estimate (1.51). For FLTD-M, none of the parental genotypes showed significant differences based on GCA estimates. The cross combination 11 \times 4 showed the maximum significant SCA estimate (0.65), while 1 \times 9 exhibited the smallest SCA estimate (-0.31). For CTD-M, only one parental genotype that showed significant GCA estimate and ranked on the top highest parental genotypes with GCA estimate of 0.50, while the lowest GCA estimated was observed in parental genotype 11 (-0.24). Based on SCA estimates, none of the crosses showed significant estimates. More details about SCA estimates can be found in Supplemental Tables 1-3. For GYM, all parental genotypes showed significant estimates of GCA except parental genotype 5. The maximum significant GCA estimate was detected in parental genotype 6 (57.49) unlike parental genotype 10 (-75.83). The maximum significant SCA effects were observed in 1 \times 11, 9 \times 10 and 4 \times 5, while the opposite was noticed in 4 \times 11. For 1000GW, all parental genotypes exhibited significant GCA estimates except parental genotype 1. Parental genotype 4 showed the highest significant GCA effect (2.91) unlike parental genotype 10 (-3.91). The cross combination (9 \times 11) displayed the maximum significant SCA estimate unlike (4 \times 11).

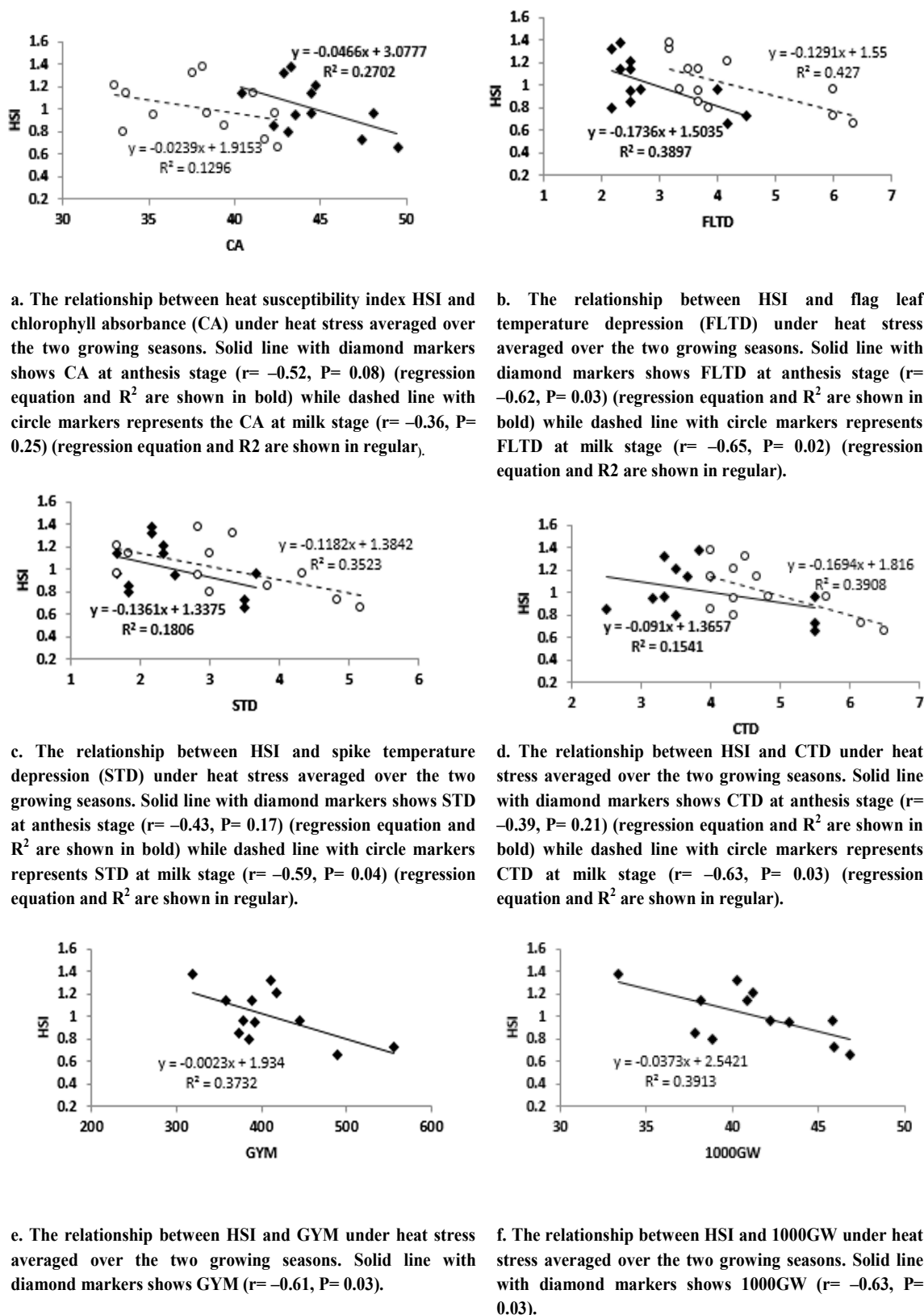


Fig. 3. The relationship between HSI and physiological and yield traits under heat stress averaged over the two growing seasons for the 12 genotypes.

TABLE 9. The mean performance of seven parents and their half-diallel crosses of wheat under timely sowing date (optimum condition).

Gen	DH	DA	CAA	FLTDM	CTDM	GYM	1000GW
1	81.00	83.67	55.67	1.33	1.67	588.67	46.50
1x4	80.00	82.33	56.00	2.33	2.33	730.23	54.17
1x5	80.00	82.67	56.00	1.67	1.67	692.83	47.00
1x6	80.00	82.33	55.00	1.67	1.67	744.87	51.00
1x9	80.00	82.33	56.00	1.33	2.33	685.30	52.00
1x10	80.00	82.33	54.00	1.67	1.67	523.37	44.30
1x11	80.00	82.00	56.00	1.33	2.00	693.53	46.03
4	80.00	84.67	52.00	1.33	2.33	611.00	56.00
4x5	80.00	82.33	55.00	1.33	1.67	701.87	52.27
4x6	79.00	81.67	55.00	1.67	1.33	723.17	52.23
4x9	79.00	82.33	54.00	2.33	2.33	633.77	53.33
4x10	80.00	82.67	54.00	1.67	2.00	533.13	44.00
4x11	80.00	82.00	53.33	1.33	1.33	465.70	46.07
5	80.00	83.67	55.00	1.33	1.67	575.67	46.00
5x6	81.00	83.33	56.00	1.33	1.67	685.63	48.27
5x9	80.00	82.33	56.00	1.67	2.33	587.83	49.00
5x10	80.33	83.00	56.00	1.33	1.67	533.43	46.20
5x11	80.33	83.00	54.67	1.67	1.67	558.83	45.17
6	80.00	83.67	56.00	1.33	1.67	683.00	52.00
6x9	79.00	81.33	54.33	1.67	2.33	705.90	52.10
6x10	80.33	82.67	55.00	1.67	1.67	553.67	48.03
6x11	79.00	82.33	55.67	1.33	1.67	641.07	46.00
9	78.33	83.67	56.00	1.33	3.00	611.33	54.00
9x10	80.00	82.67	56.00	1.67	2.33	642.23	45.73
9x11	79.67	81.67	53.67	1.67	1.67	631.07	53.27
10	81.00	84.67	55.00	1.67	1.33	467.33	40.67
10x11	80.00	82.00	53.67	1.33	1.67	499.87	43.13
11	81.33	84.33	56.00	1.33	1.33	455.67	43.23
Mean	79.98	82.77	55.04	1.55	1.86	612.86	48.49
Revised LSD _{0.05}	1.99	1.52	2.34	1.59	1.44	13.43	1.41

DH= Days to heading, DA= Days to anthesis, CA-A= Chlorophyll content at anthesis stage, FLTD-M= Flag leaf temperature depression at milk stage, CTD-M= Canopy temperature depression at milk stage, GYM= Grain yield per m² and 1000GW= 1000 grain weight.

TABLE 10. The mean performance of seven parents and their half-diallel crosses of wheat under late sowing date (heat stress).

Gen	DH	DA	CA-A	FLTD-M	CTD-M	GYM	1000GW
1	79.00	80.67	46.00	5.00	5.33	496.67	45.33
1x4	76.00	77.67	46.00	5.33	5.67	573.43	46.57
1x5	78.00	79.67	45.00	4.33	4.67	533.93	42.80
1x6	77.00	78.33	46.00	4.67	4.67	545.80	45.60
1x9	78.00	79.00	45.00	4.33	5.00	476.03	45.97
1x10	77.00	78.33	45.00	3.67	4.33	451.90	39.50
1x11	78.00	79.33	46.00	4.67	4.33	475.90	36.00
4	74.00	76.33	47.00	5.33	4.33	483.67	47.33
4x5	76.00	77.33	46.00	4.67	4.33	521.67	43.50
4x6	75.00	77.00	51.00	5.00	6.00	534.37	45.40
4x9	76.00	77.33	52.00	3.67	4.33	437.73	46.13
4x10	77.00	78.33	48.00	3.33	3.67	474.43	39.53
4x11	76.00	77.33	48.00	3.33	3.33	410.50	37.40
5	77.00	79.33	44.00	4.33	4.33	471.00	41.00
5x6	76.00	77.33	47.67	4.33	4.67	489.87	43.43
5x9	77.33	79.00	50.33	3.33	3.67	480.33	43.47
5x10	77.67	78.67	47.33	3.33	3.67	446.40	37.10
5x11	76.67	78.33	46.33	3.67	4.33	462.37	36.50
6	75.00	76.67	49.00	5.00	5.00	456.00	43.00
6x9	75.00	76.00	47.00	5.33	5.67	548.83	46.00
6x10	76.00	77.00	47.67	4.00	4.33	434.20	38.10
6x11	77.00	78.67	51.00	5.33	5.33	520.17	40.00
9	76.33	78.67	47.00	5.00	5.67	405.00	46.00
9x10	77.33	79.00	45.67	3.00	3.33	363.40	36.60
9x11	78.00	79.00	47.67	3.33	3.33	376.90	37.00
10	77.33	80.00	43.67	3.33	4.67	336.67	33.33
10x11	79.33	80.33	44.33	3.00	3.67	372.70	35.47
11	79.67	82.33	43.67	4.00	4.00	367.67	34.00
Mean	76.88	78.46	46.90	4.20	4.49	462.41	41.15
Revised LSD _{0.05}	1.50	1.57	1.85	0.97	1.11	16.69	1.15

DH= Days to heading, DA= Days to anthesis, CA-A= Chlorophyll content at anthesis stage, FLTD-M= Flag leaf temperature depression at milk stage, CTD-M= Canopy temperature depression at milk stage, GYM= Grain yield per m² and 1000GW= 1000 grain weight.

TABLE 11. The mean performance of seven parents and their half-diallel crosses of wheat combined over two treatments (optimum and heat stress conditions).

Gen	DH	DA	CA-A	FLTD-M	CTD-M	GYM	1000GW
1	80.00	82.17	50.83	3.17	3.50	542.67	45.92
1x4	78.00	80.00	51.00	3.83	4.00	651.83	50.37
1x5	79.00	81.17	50.50	3.00	3.17	613.38	44.90
1x6	78.50	80.33	50.50	3.17	3.17	645.33	48.30
1x9	79.00	80.67	50.50	2.83	3.67	580.67	48.98
1x10	78.50	80.33	49.50	2.67	3.00	487.63	41.90
1x11	79.00	80.67	51.00	3.00	3.17	584.72	41.02
4	77.00	80.50	49.50	3.33	3.33	547.33	51.67
4x5	78.00	79.83	50.50	3.00	3.00	611.77	47.88
4x6	77.00	79.33	53.00	3.33	3.67	628.77	48.82
4x9	77.50	79.83	53.00	3.00	3.33	535.75	49.73
4x10	78.50	80.50	51.00	2.50	2.83	503.78	41.77
4x11	78.00	79.67	50.67	2.33	2.33	438.10	41.73
5	78.50	81.50	49.50	2.83	3.00	523.33	43.50
5x6	78.50	80.33	51.83	2.83	3.17	587.75	45.85
5x9	78.67	80.67	53.17	2.50	3.00	534.08	46.23
5x10	79.00	80.83	51.67	2.33	2.67	489.92	41.65
5x11	78.50	80.67	50.50	2.67	3.00	510.60	40.83
6	77.50	80.17	52.50	3.17	3.33	569.50	47.50
6x9	77.00	78.67	50.67	3.50	4.00	627.37	49.05
6x10	78.17	79.83	51.33	2.83	3.00	493.93	43.07
6x11	78.00	80.50	53.33	3.33	3.50	580.62	43.00
9	77.33	81.17	51.50	3.17	4.33	508.17	50.00
9x10	78.67	80.83	50.83	2.33	2.83	502.82	41.17
9x11	78.83	80.33	50.67	2.50	2.50	503.98	45.13
10	79.17	82.33	49.33	2.50	3.00	402.00	37.00
10x11	79.67	81.17	49.00	2.17	2.67	436.28	39.30
11	80.50	83.33	49.83	2.67	2.67	411.67	38.62
Mean	78.43	80.62	50.97	2.87	3.17	537.63	44.82
Revised LSD _{0.05}	1.43	1.45	1.90	1.14	1.08	15.07	1.28

DH= Days to heading, DA= Days to anthesis, CA-A= Chlorophyll content at anthesis stage, FLTD-M= Flag leaf temperature depression at milk stage, CTD-M= Canopy temperature depression at milk stage, GYM= Grain yield per m² and 1000GW= 1000 grain weight.

TABLE 12. Griffing's method 2 analysis of variance of the seven-parent half-diallel crosses.

		MS						
		DH	DA	CA-A	FLTD-M	CTD-M	GYM	1000GW
Source	DF	Timely sowing date (optimum condition)						
Rep	2	3.48	0.15	0.11	0.23	0.75	528.96	0.54
Gen	27	1.33*	2.35***	3.42**	0.23	0.50	22305.70***	49.74***
GCA	6	3.07**	0.94	6.81***	0.18	1.62***	64315.81***	183.33***
SCA	21	0.83	2.75***	2.45	0.24	0.19	10302.81***	11.57***
Error	54	0.76	0.72	1.49	0.33	0.32	88.40	0.97
		Late sowing date (heat stress)						
Rep	2	6.05	3.96	0.87	0.51	1.08	253.42	0.04
Gen	27	5.39***	5.98***	14.76***	1.86***	1.74***	11658.85***	57.48***
GCA	6	19.72***	19.71***	30.71***	5.20***	3.56***	37771.74***	237.52***
SCA	21	1.29	2.06*	10.20***	0.91**	1.22**	4198.03***	6.04***
Error	54	0.91	0.99	1.50	0.38	0.44	136.50	0.65
		Combined						
Treat	1	402.38***	780.02***	2776.72***	296.01***	290.72***	950603.28***	2265.27***
Rep (Treat)	4	4.76	2.06	0.49	0.37	0.92	391.1869	0.29
Gen	27	4.51*	5.26	8.53	0.98	1.30	28496.514***	96.05***
GCA	6	15.96	10.95	14.55	2.82	3.26	92957.619***	400.03***
SCA	21	1.24	3.63**	6.81	0.46	0.74	10079.055*	9.20
Treat × Gen	27	2.21***	3.07***	9.65***	1.10***	0.94***	5468.0399***	11.17***
Treat × GCA	6	6.83***	9.70***	22.97**	2.56*	1.92*	9129.9293	20.82
Treat × SCA	21	0.89	1.18	5.84***	0.69*	0.66*	4421.7858***	8.41***
Residual	108	0.84	0.86	1.49	0.36	0.38	112.45049	0.81

*, **, *** Significant at 0.05, 0.01 and 0.001 probability levels, respectively.

DH= Days to heading, DA= Days to anthesis, CA-A= Chlorophyll content at anthesis stage, FLTD-M= Flag leaf temperature depression at milk stage, CTD-M= Canopy temperature depression at milk stage, GYM= Grain yield per m² and 1000GW= 1000 grain weight.

Under heat stress condition, for CA-A, all parental genotypes exhibited significant GCA estimates expect for parental genotype 1. The maximum significant GCA estimate was observed in parental genotype 6 (1.46) unlike parental genotype 1. Cross combination 4×9 showed the highest SCA estimate while the opposite was noticed in 6×9. For FLTD-M, only three parental genotypes displayed significant estimates of GCA. Parental genotype 6 showed the highest significant GCA estimate, while parental genotype 10 showed the minimum value. The maximum significant SCA effects were detected in cross combination 6×11, 6×9 and 10×11 unlike 4×11. For CTD-M, only four parental genotypes showed significant GCA estimates. Parental genotype 6 showed the maximum significant GCA estimate

(0.53) unlike parental genotype 11 (-0.40). The maximum significant SCA estimates were observed in 4×6, 1×4 and 6×11, but the minimum significant SCA was detected in 9×10 and 9×11. Regarding GYM, all parental genotypes showed significant GCA estimates. Parental genotype 1 ranked on the top with GCA estimate of 39.00, while parental genotype 10 ranked on the bottom with a value of -37.99. The maximum significant SCA estimates were shown in cross combinations 6×9, 6×11 and 4×1 unlike 4×11. For 1000GW, all parental genotypes displayed significant GCA estimates except parental genotype 5. Parental genotype 4 came on the top with GCA estimate of 2.76 unlike parental genotype 11. The cross combination 10×11 possessed the highest significant SCA effect.

TABLE 13. General combining ability estimates (g_i) and the range of the specific combining ability (s_{ij}) for the seven parental genotypes.

g_i	DH	DA	CA-A	FLTD-M	CTD-M	GYM	1000GW	
Timely sowing date (optimum condition)								
1	0.24	-0.10	0.45	0.03	0.02	38.29***	-0.05	
4	-0.20	0.05	-0.99*	0.11	0.09	11.89***	2.91***	
5	0.21	0.20	0.38	-0.08	-0.10	0.99	-0.89**	
6	-0.16	-0.13	0.30	-0.04	-0.13	57.49***	1.52**	
9	-0.61**	-0.24	0.19	0.07	0.50*	22.88***	2.84***	
10	0.32	0.28	-0.18	0.03	-0.13	-75.83***	-3.91***	
11	0.21	-0.06	-0.14	-0.12	-0.24	-55.72***	-2.42***	
SE(g_i)	0.16	0.15	0.21	0.10	0.10	1.68	0.18	
S_{ij}	Min.	-1.02*	-1.06*	-1.42*	-0.31	-0.48	-103.33***	-3.49***
	CC†	6×11	6×9	9×11	1×9	4×6	4×11	4×10
	Max.	0.98*	0.49	1.51*	0.65*	0.37	98.10***	4.36***
	CC	5×6	5×6	1×4	1×4	1×4	1×11	9×11
Late sowing date (heat stress condition)								
1	0.77**	0.66**	-1.14**	0.38*	0.38*	39.00***	1.99***	
4	-1.23***	-1.12***	1.08**	0.26	0.01	24.46***	2.67***	
5	0.07	0.14	-0.51	-0.14	-0.21	19.70***	-0.04	
6	-1.01**	-1.12***	1.46***	0.56**	0.53**	31.77***	1.71***	
9	-0.08	-0.12	0.71*	-0.07	0.08	-22.90***	2.00***	
10	0.44*	0.44*	-1.10**	-0.74***	-0.40*	-53.66***	-4.02***	
11	1.03***	1.11***	-0.51	-0.25	-0.40*	-38.38***	-4.31***	
SE(g_i)	0.17	0.18	0.22	0.11	0.12	2.08	0.14	
S_{ij}	Min.	-1.31*	-1.38	-2.07	-0.88*	-0.84*	-37.99***	-2.83***
	CC†	5×11	5×11	6×9	4×11	9×10 9×11	4×11	1×11
	Max.	0.98	0.77	3.30***	0.82*	0.97*	77.55***	2.65***
	CC	10×11	4×6	4×9	6×11	4×6	6×9	10×11
Combined								
1	0.51***	0.28*	-0.34*	0.20**	0.20*	38.65***	0.97***	
4	-0.71***	-0.53***	0.04	0.19*	0.05	18.18***	2.79***	
5	0.14	0.17	-0.07	-0.11	-0.15*	10.34***	-0.47**	
6	-0.58***	-0.62***	0.88***	0.26**	0.20*	44.63***	1.62***	
9	-0.34**	-0.18	0.45**	0.00	0.29**	-0.01	2.42***	
10	0.38**	0.36**	-0.64**	-0.35***	-0.26**	-64.74***	-3.97***	
11	0.62***	0.52***	-0.33*	-0.19*	-0.32**	-47.05***	-3.37***	
SE(g_i)	0.08	0.08	0.11	0.05	0.05	0.94	0.08	
S_{ij}	Min.	-0.81*	-1.15**	-1.63**	-0.54*	-0.64**	-70.67	-2.51***
	CC†	1×10	6×9	6×9	4×11	9×11	4×11	4×11
	Max.	0.52	0.17	1.81***	0.57*	0.58*	57.37***	1.81***
	CC	5×6	5×6	5×9 6×10	1×4	1×4	1×4	10×11

*, **, *** Significant at 0.05, 0.01 and 0.001 probability levels, respectively.

DH= Days to heading, DA= Days to anthesis, CA-A= Chlorophyll content at anthesis stage, FLTD-M= Flag leaf temperature depression at milk stage, CTD-M= Canopy temperature depression at milk stage, GYM= Grain yield per m² and 1000GW= 1000 grain weight.

For GCA and SCA estimates across both optimum and heat stress conditions, all parental genotypes showed significant estimates except two parental genotypes for CA-A, where parental genotype 6 ranked on the top with GCA estimate of 0.88 unlike parental genotype 10. The cross combinations 5×9 and 6×10 were on the top based on their SCA estimates unlike 6×9. For FLTD-M, all parental genotypes displayed significant GCA estimates except parental genotype 5. Parental genotype 6 showed the maximum significant GCA estimate (0.26) unlike parental genotype 10 (-0.35). The maximum significant SCA estimated was noticed in cross combination 1×4 unlike 4×10, which showed the minimum significant SCA estimate. For CTD-M, parental genotype was the only non-significant parental genotype based on GCA estimates. The maximum significant GCA estimate was detected in parental genotype 9 (0.29) unlike parental genotype 11 (-0.32). The maximum significant SCA estimate was observed in cross combination 1×4 unlike 9×11. For yield traits, all parental genotypes showed significant estimates of GCA except parental genotype 9 for GYM. The maximum significant GCA was noticed in parental genotype 6 (44.63) unlike parental genotype 10 (-64.74). The maximum significant SCA estimate was shown in cross combination 1×4 unlike 4×11. Finally for 1000GW, all parental genotypes exhibited significant GCA estimates with maximum value found in parental genotype 4 (2.97) and minimum value in parental genotype 10 (-3.97). The maximum significant SCA estimate was found in cross combination 10×11 unlike 4×11.

Discussion

First two years experiment

The temperature depression values were higher under heat stress than optimum condition for all organs; in addition, the canopy temperature depression was the highest under all conditions compared to flag leaf and spike. In this regard, Ayeneh et al. (2002) emphasized the same pattern as the results of the current study. Moreover, the temperature of depression measured during the milk stage was higher than anthesis. This was due to the cooling effect of leaf rolling during this stage because of higher temperature either under optimum or heat stress; however, the depression under heat stress was higher as the degree of leaf rolling was higher as response of high temperature. Similarly, my results were similar to

those obtained by Ayeneh et al. (2002). This was because the temperature inside the rolled leaf was very much cooler than the ambient air temperature compared to unrolled leaves. Moreover, the canopies temperature depression showed the highest depression as they have more area under knees to transmit heat over to the ambient air through convection and reflectance (Blum, 1988).

In a similar study accomplished by Ayeneh et al. (2002), they found that STD was lower than FLTD and CTD. In addition, they reported that under heat stress conditions induced by late sowing date, FLTD and CTD were close to each other. In this context, the results of the current study were consistent with Ayeneh et al. (2002). Furthermore, they reported that FLTD, STD and CTD were significantly correlated with grain yield under heat stress. These findings were in consistency with the results of the current investigation. Under heat stress, both FLTD and CTD showed higher association with grain yield at milk stage comparing to anthesis. This due to the exposure to a higher temperature during milk stage compared to anthesis stage. These results matched the findings of Ayeneh et al. (2002).

The CA at anthesis stage showed higher association with GYM compared to milk stage. This can be due to the impairment of chlorophyll and leaf senescence, which led to an increase in the amount of chlorophyll loss at the milk stage. High temperature can damage photosynthesis (Sharkey, 2005), which reduce the CA measured by SPAD meter. Sharkey (2005) reported similar results. Significant correlations were found between GYM, on one hand, and CTD and CA, similar results found by Dwivedi et al. (2017). They indicated that under heat stress conditions induced by late sowing date, yield and its components were used as determinants of heat-stress tolerance (Dwivedi et al., 2017). In addition, late sowing date as well as delayed harvesting negatively affected wheat cultivation due to exposure to heat stress during both anthesis and grain filling stages (Hays et al., 2007). The exposure to heat stress (37/17°C) starting from anthesis up to harvesting reduced wheat grain yield due to the reduction in starch accumulation time, comparing to favorable growing conditions (24/17°C) (Hurkman et al., 2003). Dwivedi et al. (2017) reported that this reduction in starch synthesis accelerated pollen mortality and finally led to a massive loss in grain yield.

Second (diallel) experiment

The current results showed that the most F1 hybrids showed higher values for CA-A, FLTD-M, CTD-M, GYM and 1000GW than the average of their parental genotypes. In this context, the current results were consistent with the findings of Yildirim et al. (2013) who reported that chlorophyll content measured with SPAD meter and CTD were significantly associated with grain yield and could be used as indirect selection tool in early segregating generations under heat stress condition induced by late sowing date.

As indicated in the ANOVA table for combining ability, under optimum condition, GCA was the only significant constituent for CA-A and CTD-M, showing the importance of additive gene action for both traits. For GYM and 1000GW displayed significant variation for both GCA and SCA, revealing the importance of both additive and non-additive constituents of gene action. Nevertheless, the additive constituent was largest for both GYM and 1000GW as they showed greater values of mean squares for GCA than SCA. Under heat stress condition, both GCA and SCA showed significant variance for all traits except SCA for DH. However, the additive gene action was more important than non-additive gene action. Wheat represents self-fertilized crops where additive gene action is more important than non-additive gene action; therefore, GCA effects contribute to improvement wheat (Joshi et al., 2003). The additive and additive \times additive gene actions are transferable to later generations, which facilitate the tasks of plant breeders. Kumar et al. (2017) reported similar results under heat stress conditions using CTD, chlorophyll content and grain yield and found that additive gene action was also more important for these traits than non-additive.

These results suggest using good general combiners' parental genotypes in multiple mating to accumulate the majority of favorable genes of traits of interest. This allow incorporating additive gene action in the development of targeted improved varieties. Joshi et al. (2003) supported these results when they analyzed yield and its components in spring wheat. Jensen (1970) explained that the diallel procedure is an advantageous approach that allows accumulating favorable genes into a single gene pool through multiple crosses. In this regard, the current study revealed that parental genotypes 1, 4 and 6 were

the best combiners for GYM, 1000GW, CA-A, FLTD-M and CTD-M under heat stress. Therefore, I suggest using multiple crosses of these parental genotypes in order to accumulate favorable genes of these traits to develop heat stress tolerant breeding materials. The best specific crosses for GYM were 9 \times 6, 11 \times 6 and 4 \times 1 under heat stress.

Conclusion

The magnitude of the correlation coefficient between CA at anthesis stage under heat stress with GY and 1000GW make it a feasible nondestructive tool to assess heat stress tolerance. Furthermore, FLTD at milk stage is an important nondestructive tool associated with GY and 1000GW under heat stress induced by late sowing date. Therefore, using both CA at anthesis stage and FLTD at milk stage are paramount to verify and confirm heat stress tolerant genotypes. The association between FLTD and HSI was strong and significant with values of -0.6 and -0.7 at anthesis and milk stages, respectively. Similarly, both STD and CTD at milk stage in addition to GY and 1000GW exhibited strong significant correlation ($r = -0.6$) with HSI. Therefore, using these nondestructive measurements of heat stress tolerance is paramount in wheat breeding programs.

Furthermore, the current study elucidates that both additive and non-additive constituents of gene action were tangled in controlling the genetic of studied traits; however, additive constituent was the largest. In order to exploit both constituents of gene action, it is important include both bi-parental and multiple parental crosses in wheat breeding program. This will lead to tangible improvement of grain yield in wheat. In addition, a local cultivar Sids12 was a good specific combiner with certain exotic germplasm. This implies the importance of creating genetic diversity via using adapted exotic germplasm in Egyptian wheat breeding programs.

References

- Ali, M.B., Ibrahim, A.M., Hays, D.B., Ristic, Z. and Fu, J. (2010) Wild tetraploid wheat (*Triticum turgidum* L.) response to heat stress. *Journal of Crop Improvement*, **24**, 228-243.
- Ali, M.B., Ibrahim, A.M., Malla, S., Rudd, J. and Hays, D.B. (2013) Family-based QTL mapping of

- heat stress tolerance in primitive tetraploid wheat (*Triticum turgidum* L.). *Euphytica*, **192**, 189-203.
- Asseng, S., Ewert, F., Martre, P., Rötter, R.P., Lobell, D.B., Cammarano, D., Kimball, B.A., Ottman, M.J., Wall, G.W., White, J.W. and Reynolds, M.P. (2015) Rising temperatures reduce global wheat production. *Nature Climate Change*, **5**, 143-147.
- Ayeneh, A., Van Ginkel, M., Reynolds, M.P., and Ammar, K. (2002) Comparison of the leaf, spike, peduncle and canopy temperature depression in wheat under heat stress. *Field Crops Research*, **79**, 173-184.
- Balota, M., Payne, W.A., Evett, S.R. and Lazar, M.D. (2007) Canopy temperature depression sampling to assess grain yield and genotypic differentiation in winter wheat. *Crop Science*, **47**, 1518-1529.
- Barnabas, B., Jager, K. and Feher, A. (2008) The effect of drought and heat stress on reproductive processes in cereals. *Plant, Cell & Environment*, **31**, 11-38.
- Blum, A. (1988) Plant breeding for stress environments. CRC Press, Boca Raton, FL, P.72.
- Dias, A.S. and Lidon, F.C. (2009) Evaluation of grain filling rate and duration in bread and durum wheat, under heat stress after anthesis. *Journal of Agronomy and Crop Science*, **195**, 137-147.
- Dias, A.S. and Lidon, F.C. (2010) Bread and durum wheat tolerance under heat stress: a synoptical overview. *Emirates Journal of Food and Agriculture*, **22**, 412-436.
- Dwivedi, S.K., Basu, S., Kumar, S., Kumar, G., Prakash, V., Kumar, S., Mishra, J.S., Bhatt, B.P., Malviya, N., Singh, G.P. and Arora, A. (2017) Heat stress-induced impairment of starch mobilization regulates pollen viability and grain yield in wheat: Study in Eastern Indo-Gangetic Plains. *Field Crops Research*, **206**, 106-114.
- Farooq, M., Bramley, H., Palta, J. A. and Siddique, K. H. (2011) Heat stress in wheat during reproductive and grain-filling phases. *Critical Reviews in Plant Sciences*, **30**, 491-507.
- Fischer, R. A. and Maurer, R. (1978) Drought resistance in spring wheat cultivars. I. Grain yield responses. *Australian Journal of Agricultural Research*, **29**, 897-912.
- Foulkes, M.J., Slafer, G.A., Davies, W.J., Berry, P.M., Sylvester-Bradley, R., Martre, P., Calderini, D.F., Griffiths, S. and Reynolds, M.P. (2010) Raising yield potential of wheat. III. Optimizing partitioning to grain while maintaining lodging resistance. *Journal of Experimental Botany*, **62**, 469-486.
- Griffing, B.R.U.C.E. (1956) Concept of general and specific combining ability in relation to diallel crossing systems. *Australian Journal of Biological Sciences*, **9**, 463-493.
- Gupta, N.K., Khan, A., Maheshwari, A., Narayan, S., Chhapola, O.P., Arora, A. and Singh, G. (2015) Effect of post-anthesis high-temperature stress on growth, physiology and antioxidative defense mechanisms in contrasting wheat genotypes. *Indian Journal of Plant Physiology*, **20**, 103-110.
- Hays, D., Mason, E., Hwa, D.J., Menz, M. and Reynolds, M. (2007) Expression quantitative trait loci mapping heat tolerance during reproductive development in wheat (*T. aestivum*). In: "*Wheat Production in Stressed Environments*", Buck, H.T., Nisi, J.E., Salomon, N. (Eds.), pp. 373-382. Springer, Amsterdam.
- Jensen, N.F. (1970) A Diallel Selective Mating System for Cereal Breeding 1. *Crop Science*, **10**, 629-635.
- Joshi, S.K., Sharma, S.N., Singhania, D.L. and Sain, R.S. (2003) Genetic analysis of yield and its component traits in spring wheat. *Acta Agronomica Hungarica*, **51**, 139-147.
- Hurkman, W.J., McCue, K.F., Altenbach, S.B., Korn, A., Tanaka, C.K., Kothari, K.M., Johnson, E.L., Bechtel, D.B., Wilson, J.D., Anderson, O.D. and DuPont, F.M. (2003) Effect of temperature on expression of genes encoding enzymes for starch biosynthesis in developing wheat endosperm. *Plant Science*, **164**, 873-881.
- Kumar, R.R., Sharma, S.K., Goswami, S., Singh, G.P., Singh, R., Singh, K., Pathak, H. and Rai, R.D. (2013) Characterization of differentially expressed stress-associated proteins in starch granule development under heat stress in wheat (*Triticum aestivum* L.). *Indian Journal of Biochemistry and Biophysics*, **50**, 126-138.
- Kumar, S., Singh, S.K., Gupta, S.K., Vishwanath, Y.P., Kumar, S., Kumar, J., Bind, H.N. and Singh, L. (2017) Combining ability in relation to wheat

- (*Triticum aestivum* L.) breeding programme under heat stress environment. *Int. J. Curr. Microbiol. App. Sci.* **6**, 3065-3073.
- Lobell, D.B. and Asner, G.P. (2003) Climate and management contributions to recent trends in US agricultural yields. *Science*, **299**, 1032-1032.
- Mathur, S., Agrawal, D. and Jajoo, A. (2014) Photosynthesis: response to high temperature stress. *Journal of Photochemistry and Photobiology B: Biology*, **137**, 116-126.
- Mesihovic, A., Iannacone, R., Firon, N. and Fragkostefanakis, S. (2016) Heat stress regimes for the investigation of pollen thermos tolerance in crop plants. *Plant Reproduction*, **29**, 93-105.
- Ortiz, R., Sayre, K.D., Govaerts, B., Gupta, R., Subbarao, G.V., Ban, T., Hodson, D., Dixon, J.M., Ortiz-Monasterio, J.I. and Reynolds, M., (2008) Climate change: can wheat beat the heat? *Agriculture, Ecosystems & Environment*, **126**, 46-58.
- Pandey, G.C., Mamrutha, H.M., Tiwari, R., Sareen, S., Bhatia, S., Siwach, P., Tiwari, V. and Sharma, I. (2015) Physiological traits associated with heat tolerance in bread wheat (*Triticum aestivum* L.). *Physiology and Molecular Biology of Plants*, **21**, 93-99.
- Plaut, Z., Butow, B.J., Blumenthal, C.S. and Wrigley, C.W. (2004) Transport of dry matter into developing wheat kernels and its contribution to grain yield under post-anthesis water deficit and elevated temperature. *Field Crops Research*, **86**, 185-198.
- Reynolds, M.P., Balota, M., Delgado, M.I.B., Amani, I. and Fischer, R.A. (1994) Physiological and morphological traits associated with spring wheat yield under hot, irrigated conditions. *Functional Plant Biology*, **21**, 717-730.
- Reynolds, M., Manes, Y., Izanloo, A. and Langridge, P. (2009) Phenotyping approaches for physiological breeding and gene discovery in wheat. *Annals of Applied Biology*, **155**, 309-320.
- Richardson, A.D., Duigan, S.P. and Berlyn, G.P. (2002) An evaluation of noninvasive methods to estimate foliar chlorophyll content. *New Phytologist*, **153**, 185-194.
- Ristic, Z., Bukovnik, U. and Prasad, P.V.V. (2007) Correlation between heat stability of thylakoid membranes and loss of chlorophyll in winter wheat under heat stress. *Crop Science*, **47**, 2067-2073.
- Rodríguez, F., Alvarado, G., Pacheco, Á., Crossa, J. and Burgueño, J. (2015) AGD-R (Analysis of genetic designs with R for Windows) version 4.0. *International Maize and Wheat Improvement Center* (CIMMYT).
- SAS Institute (2003) User manual for SAS for window version 9. Cary, NC: SAS Institute.
- Sharkey, T.D. (2005) Effect of moderate heat stress on photosynthesis: The importance of thylakoid reactions, rubisco deactivation, reactive oxygen species and thermos tolerance provided by isoprene. *Plant, Cell & Environment*, **28**, 269-277.
- Stone, P.J. and Nicolas, M.E. (1995) Comparison of sudden heat stress with gradual exposure to high temperature during grain filling in two wheat varieties differing in heat tolerance. I. Grain growth. *Functional Plant Biology*, **22**, 935-944.
- Tewari, A.K. and Tripathy, B.C. (1998) Temperature-stress-induced impairment of chlorophyll biosynthetic reactions in cucumber and wheat. *Plant Physiology*, **117**, 851-858.
- Tovignan, T.K., Fonceka, D., Ndoeye, I., Cisse, N. and Luquet, D. (2016) The sowing date and post-flowering water status affect the sugar and grain production of photoperiodic, sweet sorghum through the regulation of sink size and leaf area dynamics. *Field Crops Research*, **192**, 67-77.
- United Nations (2011) World Population Prospects: The 2010 Revision: Highlights and Advance Tables, UN Department of Economic and Social Affairs: Population Division, New York, U.S.
- Wahid, A., Gelani, S., Ashraf, M. and Foolad, M.R. (2007) Heat tolerance in plants: an overview. *Environmental and Experimental Botany*, **61**, 199-223.
- Wang, X., Xin, C., Cai, J., Zhou, Q., Dai, T., Cao, W. and Jiang, D. (2016) Heat priming induces trans-generational tolerance to high temperature stress in wheat. *Frontiers in Plant Science*, **7**, 501.
- Wardlaw, I.F. and Wrigley, C.W. (1994) Heat tolerance in temperate cereals—an overview. *Australian*
- Egypt. J. Agron.* **41**, No .2 (2019)

- Journal of Plant Physiology*, **21**, 695-703.
- Wardlaw, I.F., Dawson, I.A. and Munibi, P. (1989) The tolerance of wheat to high temperatures during reproductive growth. 2. Grain development. *Australian Journal of Agricultural Research*, **40**, 15-24.
- Xu, Q., Paulsen, A. Q., Guikema, J. A. and Paulsen, G.M. (1995) Functional and ultrastructural injury to photosynthesis in wheat by high temperature during maturation. *Environmental and Experimental Botany*, **35**, 43-54.
- Yıldırım, M., Koç, M., Akıncı, C. and Barutçular, C. (2013) Variations in morphological and physiological traits of bread wheat diallel crosses under timely and late sowing conditions. *Field Crops Research*, **140**, 9-17.
- Young, L.W., Wilen, R.W. and Bonham-Smith, P.C. (2004) High-temperature stress of *Brassica napus* during flowering reduces micro-and mega gametophyte fertility, induces fruit abortion, and disrupts seed production. *Journal of Experimental Botany*, **55**, 485-495.
- Zhang, H., Xua, C., He, Y., Zong, J., Yang, X., Si, H., Sun, Z., Hud, J., Liang, W. and Zhang, D. (2012) Mutation in CSA creates a new photoperiod-sensitive genic male sterile line applicable for hybrid rice seed production. *Proceedings of the National Academy of Sciences*, **110**, 76-81.

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القدرة على الانتلاف للصفات الفسيولوجية والمحصولية للهجن الدائرية في قمح الخبز تحت مواعيد الزراعة المناسبة والمتأخرة

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تم تقييم 12 تركيب وراثي لدراسة تأثير الحرارة على الصفات الفسيولوجية والمحصولية في قمح الخبز بالزراعة في ميعادين مختلفين ميعاد الزراعة المناسب والمتأخر لمدة عامين. بناءً على هذا التقييم، تم انتخاب 7 تراكيب وراثية تم استخدامها لتكوين هجن نصف دائرية بنظام diallel crosses. تم تقييم الإباء وهجنها الـ 21 تحت ميعادي الزراعة المناسب والمتأخر خلال موسم 2019/2018. أوضحت النتائج أن كلا من امتصاص الكلوروفيل عند مرحلة نثر حبوب اللقاح و انخفاض درجة حرارة ورقة العلم في مرحلة النضج اللبني مرتبط بشدة ($r=0.6$)، ($P < 0.001$) مع محصول الحبوب تحت الإجهاد الحراري الناتج عن ميعاد الزراعة المتأخر. لذلك، فإن استخدام امتصاص الكلوروفيل في مرحلة نثر حبوب اللقاح وكذلك انخفاض درجة حرارة ورقة العلم في مرحلة النضج اللبني يوصى به بشدة كأدلة انتخابية لتحمل الإجهاد الحراري في برامج تربية القمح. تم ملاحظة وجود اختلافات معنوية بين الآباء في قدرتهم العامة على الانتلاف وبين هجنهم في القدرة الخاصة على الانتلاف لجميع الصفات تحت الإجهاد الحراري. المكون المضيف من الفعل الوراثي كان هو السائد. 1، 4، 6 أفضل الآباء في قدرتهم العامة على الانتلاف لصفات محصول الحبوب ووزن 1000 حبة وامتصاص الكلوروفيل خلال مرحلة نثر حبوب اللقاح وانخفاض درجة حرارة ورقة العلم والكساء الخضري في مرحلة النضج اللبني تحت الإجهاد الحراري. أفضل الهجن كانت 6×9، 6×11، 1×4، 1×6، 6×11، 6×9، 10×11 لانخفاض درجة حرارة ورقة العلم في مرحلة النضج اللبني، 4×6، 1×4، 6×11 لانخفاض درجة حرارة الكساء الخضري في مرحلة النضج اللبني. الاستفادة من كل من التأثير المضيف وغير المضيف يتطلب استخدام التهجين الثنائي والمتعدد بين الآباء في برامج تربية القمح التي تهدف إلى استنباط أصناف متحملة للحرارة.