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Identifying Physiological Traits Associated with High Temperature Tolerance in Sunflower (*Helianthus annuus* L.) Genotypes

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

The objective of the study is to identify the physiological traits associated with seed yield in sunflower. An experiment was conducted at ICAR-Indian Institute of Oilseeds Research, Narkhoda Farm, Rajendranagar, Telangana during *rabi* (Jan-May) 2019 and 2020 to find out the response of Sunflower genotypes to high temperature (HT) stress. Here, 47 genotypes were screened in the first year and 14 genotypes were identified which are evaluated in the second year under timely (control, S1) and delayed (HT stress, S2) sowings. These traits in the two years are correlated with seed yields (SY) which were differed under S1 and S2. The per se performance indicated that the expression of most traits was reduced under S2 except canopy temperature in 2019. The genotype

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AKSF 6-3B with the highest SY were characterized by chlorophyll content, maximum quantum efficiency, relative water content, pollen viability, leaf area index, photosynthetic rate and transpiration at vegetative stage under high temperature. The diverse genotypes identified with promising traits can be used in breeding programs to develop new varieties.

Keywords: Correlation; high temperature; seed yield; sunflower; traits; quantum efficiency; crop productivity; photo-insensitive crop; flowering stages.

1. INTRODUCTION

The climate change drastically affects the agricultural resources (land and water) through increased evapo-transpiration and increased land-degradation, more emission of greenhouse gases, ammonia immobilization, de-nitrification, increasing crop-water requirements, and unavailability of plant-nutrients. The frequency of extreme weather events like heat and cold waves, drought, floods, tropical cyclones and tornadoes, dust and thunder storms, etc., is increasing with negative consequences to the crop productivity.

Climate change threatens worldwide crop productivity with new solutions urgently needed to adapt crops to these environmental changes. The domesticated sunflower, *Helianthus annuus* L., is a global oil crop that has promise for adapting to changing environments because it can maintain stable yields across a wide range of environmental conditions, and has been proposed as a potential model crop for adaptation to a changing climate.

Climate change effects on crop growth [1] development, yield (Lakho et al., 2017), and crop management globally. Even a small fluctuation in temperature can cause more difficulties for crop production. Growth period of many crops was shortened with increasing temperature [2]. HT reduces the yield by accelerating phenological phases and by decreasing time of dry matter production [3]. Hence, climate smart agriculture is a crucial factor to minimize the severe effects of climate change on crop productivity.

Sunflower is photo-insensitive crop, grown both in *kharif* and *rabi* predominantly as a rainfed crop. World Sunflower area accounts 27.37 mha, production of 56.07 mt and productivity of 2049 kg ha^{-1} [4]. Major countries cultivating sunflower are Russia (8.41 mha), Ukraine (5.95 mha), USA (2.66 mha), Africa (2.21 mha), Argentina (1.88 mha), and Romania (1.28 mha) [4]. The area under this crop in India is 0.26 m ha, with a production of 0.22 mt and productivity of 826 kg ha^{-1}. In India, its cultivation is concentrated mainly in states, Karnataka, Maharashtra, Odisha, Andhra Pradesh and Haryana [4]. 25–30°C is the optimal temperature for germination and growth, while temperatures exceeding 30°C pose stress on the plant. Temperature stress affects plant developmental and physiological processes. Here, the traits involved in HT stress (S2) of different sunflower genotypes and their association with seed yield $plant^{-1}$ (SY) were identified. The objectives of this study were to: (i) identify the best-performing inbreds under control (S1) and HT (S2), (ii) characterize the association of traits with SY

2. MATERIALS AND METHODS

The experiments were conducted during the late *Rabi* (Jan-May) season of 2019 and 2020 at ICAR-IIOR Research Farm, Narkhoda, Hyderabad, India (17°1501600 N, 78°1803000 E; 542 m above sea level).

2.1 Plant Material

A set of 47 sunflower (*Helianthus annuus* L.) genotypes including 42 inbred lines and 5 hybrid checks were provided by ICAR-IIOR for the experimental study.

2.2 Crop Management and Temperature treatment

The 2019 experiment was carried out using a split-plot design with two temperature treatments using staggered sowings (S1- Timely sowing and S2- Delayed sowing). Each genotype was sown in 0.6×3.6 m plots with a spacing of 60 cm (between rows) x 15 cm (between plants); there were three replicates for each treatment. The response of various physiological traits SPAD chlorophyll readings, membrane thermostability, leaf surface temperature and SY and Heat Susceptibility Index (HSI) to HT were studied and 14 genotypes were screened for futher study in next year. In depth studies were carried out in late *rabi*, 2020 with the selected sunflower genotypes. The experiment was laid out in split plot design with two temperature treatments i.e., two sowings (timely sowing S1 and delayed sowing S2).

2.3 Physiological Traits

In first season the physiological traits, namely chlorophyll meter readings (SPAD), canopy temperature (CT), and membrane stability index (MSI), were recorded at vegetative and flowering stages using SPAD-502 Plus (Konica Minolta, Inc.), IR thermal gun (AGRI-THERM-6210L; Everest Inter-science Inc.) and Electric Conductivity meter. The c anopy temperature measurements were made on sunny days between 10:00 and 13:00 h. The second season evaluation data on the physiological traits, namely relative water content (RWC), photosynthetic rate (PN), stomatal conductance (gS), transpiration rate (E), internal CO_2 concentration (Ci), pollen viability, leaf area index (LAI), leaf angle (LA), leaf chlorophyll content (Chl) and maximum quantum yield (Fv/Fm). SY was recorded during both the years.

2.4 Statistical Analysis

The data were summarized using descriptive statistics and analyzed using correlation analysis and CA. Analysis of variance (ANOVA) was conducted for each trait under S1 and S2 conditions as described by Panse and Sukhatme [5]. Phenotypic correlations were determined following Johnson et al. [6].

3. RESULTS

3.1 Temperature Difference during Crop Growth Period

During first year study, the mean maximum (Tmax) and mean minimum temperature (Tmin) from sowing to flowering for S1 were 34.9ºC and17.8ºC while for S2 was 37.9ºC and 20.2ºC, from flowering to harvest were 39.4ºC and 21.9ºC and 41.1ºC and 25.0ºC respectively. The difference in Tmax recorded in two sowings was 3.0ºC at sowing to flowering and 1.7ºC at flowering to harvest. During second year study, the Tmax and Tmin from sowing to flowering for S1 was 32.2ºC and 16.4ºC while for S2 was 35.3ºC and 20.2ºC. The Tmax and Tmin from flowering to harvest for S1 was 36.1ºC and 20.8ºC while for S2 was 38.3ºC and 23.8ºC. The difference in Tmax recorded in two sowings was 3.1ºC at sowing to flowering and 2.2ºC at flowering to harvest.

3.2 Mean Performance of Sunflower Genotypes under Normal Temperature and HT Conditions during Late Rabi, 2019

The sunflower genotypes showed variation among most of the traits under S1 as well as S2 conditions (Tables 1). ANOVA indicated that there were significant differences among temperature treatments (A), genotypes (B) and their interaction (A×B). During 2019, the physiological parameters like SPAD value and MSI has reduced under HT.

3.2.1 SPAD values

Significant variation was observed among the genotypes within the sowing dates for SPAD values during both the vegetative and flowering stages. At vegetative stage, the SPAD values varied significantly from 32.30 to 48.73 with mean 39.92 under S1 and from 21.76 to 46.10 with an average 33.78 under S2. The maximum SPAD values were noticed in hybrid check DRSH 1 during S1 (48.73) and S2 (46.10), while inbreds CMS 144B (46.73) under S1 and ARM 248B (40.07) under S2 recorded maximum SPAD value. Inbreds CMS 108B (2%), -275B (2%), FMS 400B (2%), ARM 248B (3%) has recorded lowest percent reduction in SPAD reading compared to checks. At flowering SPAD values varied from 30.13 to 45.87 under S1 (37.82) and from 19.63 to 42.03 under S2 (31.24). The maximum SPAD values were noticed in hybrid checks KBSH 44 (45.87) under S1 and DRSH 1 (42.03) under S2, while inbred CMS 144B recorded maximum SPAD values under S1 (45.10) and S2 (37.27). Inbreds FMS 400B (0%), CMS 108B (2%) and -275B (3%) has recorded lowest percent reduction in SPAD readings compared to checks.

3.2.2 Membrane stability index (MSI)

The MSI varied significantly from 25.7 to 45.8 under S1 (36.2) and from 9 to 31.2 under S2 (22.1). The maximum MSI values were noticed in inbreds CMS 2023B (45.8%) and NDL 5B (31.2%) under S1 and S2 respectively. The percent reduction in MSI in delayed sowing ranged from 12 to 74 in inbreds and from 15 to 21 in hybrid checks. During flowering, the MSI values varied significantly from 59.5 to 78.6 under S1 (68.6) and from 44.3 to 64.1 under S2 (57.4). The maximum MSI values were noticed in inbreds CMS 135B (78.6%) and CMS Pet 2-7-1B (64.1%) under S1 and S2. The percent reduction in MSI in delayed sowing ranged from 7 to 28 in inbreds and from 8 to 15 in hybrid checks. Inbred line AKSF 6-3B has recorded lowest percent reduction in MSI compared to checks during vegetative (12%) and flowering (7%) stages.

3.2.3 Canopy temperature

During vegetative stage, CT ranged from 22.9ºC to 30.4ºC under S1 (26.4ºC) and from 26.8ºC to 34.6ºC under S2 (30.7ºC). The highest CT was recorded in inbreds CMS 275B (30.4ºC) and HA 292B (34.6ºC) under S1 and S2 respectively. Inbreds AKSF 6-3B (7%), CMS lines -144B (9%), -234B (10%) and -275B (10%) has recorded lowest percent change compared to checks. At flowering, CT varied from 27.0ºC to 32.9ºC under S1 (30.4ºC) and from 30.8ºC to 35.9ºC under S2 (33.6ºC). The inbred CMS lines -853B and -2023B recorded maximum CT under S1 and S2. CMS lines -144B (2%), -108B (5%), -275B (5%) has recorded lowest percent change compared to checks.

3.2.4 Seed yield (g/plant)

There is significant difference for SY between the two sowing dates, in response of genotypic differences within a sowing and between the sowings. Among the genotypes tested, maximum SY was recorded in checks RSFH 130 (32.2), CSFH 12205 (24.3), KBSH 44 (21), DRSH 1 (20.1) followed by inbreds NDL 3B (12.4), CMS 519B (10.5) in control (S1). Under S1, the SY ranged from 1.5 to 32.2 whereas in S2 it ranged from 0.1 to 16.5. Maximum SY was recorded among checks KBSH 44 (16.5), CSFH 12205 (10.8), RSFH 130 (9.8), DRSH 1 (9.5) followed by inbreds CMS 853B (8.3), -127B (7.3) and AKSF 6-3B (7.1) under HT (S2). Subjecting the plants to a HT resulted in reduction in SY from a mean of 7.5 (S1) to 3.9 (S2) which is about 13 to 97% reduction in inbreds and 16 to 70% reduction in hybrid checks over control. Inbreds AKSF 6-3B (1%), CMS lines -59B (8%), -127B (10%), -302B (11%), -135B (12%), -107B (13%) has shown lowest reduction percent compared to checks.

3.2.5 Heat susceptibility index

The HSI values for the inbreds ranged between -0.28 (CMS 144B) to 2.04 (HA 248B) and for checks ranged between 0.34 (CO 2) to 1.46 (RSFH 130). CMS lines-144B (-0.28), -42B (-0.29), -59B (0.14), -127B (0.20), -135B (0.23), -107B (0.27) and AKSF 6-3B (0.03), recorded lower HSI. Higher values were noted in HA 248B (2.04), CMS 607B (1.81), -103B (1.76), -850B (1.60) and NDL 3B (1.52). The genotypes with lower HSI values are considered as heat tolerant. The performance of the inbreds and checks were assessed based on the field tolerance in the first year and 10 inbreds (6 tolerant and 4 susceptible inbreds) were selected for the second year study. AKSF 6-3B, CMS lines -42B, -107B, -127B, -135B, -144B were selected as tolerant genotypes and CMS lines -17B, -70B, -125B, ARM 243B as susceptible genotypes. CO 2, CSFH 12205, DRSH 1 and KBSH 44 were taken as checks respectively.

3.3 Mean Performance of Sunflower Genotypes under Normal Temperature and HT Conditions during Late Rabi, 2020

3.3.1 Relative water content (RWC)

During vegetative stage the RWC ranged from 57.9 to 67.3% under S1 (62.7%) and from 49.2 to 59.4% under S2 (54.4%). Check DRSH 1 under S1 (67.3%) and S2 (59.4%) has highest RWC (Table 2). At flowering, RWC varied from 63.8 to 68.0% under S1 (63.8%) and from 51.1 to 61.0% under S2 (55.6%). Checks DRSH 1, KBSH 44 noted maximum RWC under both S1 and S2. Inbred AKSF 6-3B at vegetative (4%) and flowering (2%) has recorded least percent reduction for the trait RWC compared to checks.

3.4. Photosynthetic Parameters

3.4.1 Photosynthetic Rate (P_N) µmol (CO_2) $m^{-2} s^{-1}$

Significant negative effect due to HT was observed among the genotypes for P_N during both vegetative and reproductive stages. At vegetative stage P_N varied from 16.74 to 29.88 with a mean of 23.6 in S1 and from 12.6 to 26.36 with a mean of 19.9 in S2. In S1 check CSFH 12205 (29.88), followed by inbred AKSF 6-3B (27.99) and in S2 condition inbred AKSF 6-3B (26.36), followed by check CSFH 12205 (25.78), recorded highest P_N values. Inbred AKSF 6-3B (6%) has recorded least percent reduction compared to checks. At flowering P_N varied from 17.6 to 34.4 with a mean of 25.6 in S1 and from 13.3 to 32.8 with a mean of 22.4 in S2. Inbred AKSF 6-3B, followed by checks CSFH 12205, DRSH 1 has recorded maximum P_N. Inbred AKSF 6-3B has recorded least percent reduction in P_N at vegetative (6%) and flowering (0%) compared to checks.

Table 1. SPAD values, Membrane stability index (MSI), canopy temperature (CT) and seed yield (SY) of sunflower during vegetative and flowering stages, *late rabi* 2019

	SPAD value		MSI		CT		SY
	Vegetative stage	**Flowering**	**Vegetative stage**	**Flowering**	**Vegetative stage**	**Flowering**	
Mean	36.85	34.53	29.15	63	28.55	32	5.7
Temperature							
CD (P<0.05)	1.92	1.25	1.7	3.3	0	0	0.5
CV (%)	10.2	7.1	11.6	10.1	1	2	16.2
Genotypes							
CD (P<0.05)	4.36	3.19	5	6	1	1	1.3
CV (%)	10.2	8.1	15.2	8.3	4	2	20.2
Interaction	NS	4.59	7.1	NS	2	1	1.9

NS-nonsignificant at p<0.05

Table 2. Physiological parameters and seed yield of sunflower genotypes in vegetative (veg) and flowering (flow) stages during *late rabi*, 2020

	RWC		P_N µmol (CO_2) m^{-2} s^{-}		g_S mol (H_2O) m^{-2} s^{-1}		E mmol (H_2O) m^{-2} s^{-1}		C_i ppm		PV
	Vegetative	**Flowering**	**Vegetative**	**Flowering**	**Vegetative**	**Flowering**	**Vegetative**	**Flowering**	**Vegetative**	**Flowering**	
Mean	58.5	59.7	21.6	24	95.5	104	1.8	2.6	518	567.5	80.1
Mainplot Temperature treatments											
CD (P<0.05)	1.3	1	3.3	2.9	18	5	0.2	0.2	66	105	1.5
CV (%)	2.4	1.8	16.2	12.7	20	5	13.7	8.8	14	20	2.1
Subplot Genotypes											
CD (P<0.05)	NS	NS	3.9	2.1	NS	20	0.3	0.6	107	77	4
CV (%)	7.4	7.5	15.7	7.4	23	17	15.9	8.8	18	12	4.3
Interaction	NS	NS	NS	NS	NS	29	NS	NS	NS	NS	5.7

	LAI		LA		TC		Fv/Fm		SY
	Vegetative	**Flowering**	**Vegetative**	**Flowering**	**Vegetative**	**Flowering**	**Vegetative**	**Flowering**	
Mean	0.9	2.44	41.5	36	3.355	4.445	0.727	0.7515	16.55
Mainplot Temperature treatments									
CD (P<0.05)	0.08	NS	7	2	0.3	0.36	0.04	NS	1.7
CV (%)	8.9	13.4	17	5	3.97	8.53	5.8	17.1	11.2
Subplot Genotypes									
CD (P<0.05)	0.12	0.25	7	7	0.38	0.47	0.07	NS	1.4
CV (%)	11.9	8.8	13	16	9.8	9.22	8.3	8.5	23.2
Interaction	0.18	NS	NS	NS	NS	NS	NS	NS	NS

RWC relative water content, P_N photosynthetic rate, g_S stomatal conductance, E transpiration, C_i internal CO_2 concentration, LAI leaf area index, LA leaf angle, TC total chlorophyll, Fv/Fm maximum quantum efficiency, SY seed yield

3.4.2 Stomatal conductance (g_s) mol H_2O m^{-2} s^{-1}

There is significant difference for g_s were observed between the two sowing dates during both vegetative and flowering stages. During vegetative stage, g_s varied from 90 to 145 under S1 (110) and from 60 to 109 under S2 (81). At flowering, g_s varied from 94 to 150 (119) in S1 and from 64 to 113 (89) in S2 condition. During both stages, CMS 135B and AKSF 6-3B recorded maximum gs under S1 and S2 respectively. Inbred AKSF 6-3B has recorded least percent reduction in g_s at vegetative (3%) and flowering (6%) compared to checks.

3.4.3 Transpiration (E)

Genotypes differed significantly for E with the sowing dates during both vegetative and flowering stage. During vegetative stage, E value varied from 1.1 to 2.9 (2) in S1 and from 0.9 to 2.1(1.6) in S2. Inbreds CMS 42B (2.9), -135B (2.4), followed by check KBSH 44 (2.3) in S1 while checks CO 2 (2.1), KBSH 44 (2) has highest E values in S2. At HT a reduction in E values was observed among all the genotypes. At flowering, E ranged from 2.1 to 3.8 (3) in S1 and from 1.2 to 3.1(2.2) in S2. Inbreds CMS 135B (3.8), -70B (3.6) in S1 while check DRSH 1 (2.6), KBSH 44 (2.6), and inbred ARM 243B (2.6) in S2 has highest E. Inbred AKSF 6-3B has recorded least percent reduction in E at vegetative (5%) and flowering (10%) stages compared to checks.

3.4.4 Internal CO_2 concentration (C_i) ppm

C_i at vegetative stage varied from 447 to 711 (571) in S1 and from 364 to 624 (465) in S2. In S1, inbred CMS 125B (711), followed by check DRSH 1 (705) and in S2, check DRSH 1 (624), followed by inbred ARM 243B (537) has highest C_i. Inbreds AKSF 6-3B (11%), ARM 243B (16%) and CMS 107B (17%) has recorded percent reduction on par with checks. At flowering, C_i varied from 490 to 793 (627) in S1 and from 379 to 631 (503) in S2. In S1 inbreds CMS 125B (793), followed by CMS 127B (757), check DRSH 1 (721), and in S2, check DRSH 1 (631), followed by inbred CMS 127B (589), has recorded maximum C_i. Inbred AKSF 6-3B (10%) has recorded percent reduction on par with checks.

Li et al. [7] observed HT treatment resulted in a significant increase in stomatal conductance and transpiration rate in rice. Khetrapal et al. [8] reported that stomatal conductance of chickpea crop decreased under elevated temperature significantly at all growth stages. Balla et al. [9] observed increased evaporation occurred in spite of the strong reductions in stomatal conductance, unrelated to the phenophase.

3.4.5 Pollen viability (PV)

PV ranged from 76 to 91.9 (85.4) in S1 and from 58 to 88.7 (74.8) in S2. PV was reduced by 3 to 7% among checks and by 1 to 29% among inbreds at HT over control. Among the genotypes maximum reduction in PV was observed in inbred CMS lines -125B (29%), -135B (23%), -42B (21%) and minimum reduction was observed in AKSF 6-3B (1%). Kaur and Behl (2010) reported HT of above 30°C during floret development may cause complete sterility in wheat depending on genotypes.

3.4.6 Leaf area index (LAI)

During vegetative and flowering stages significant differences for LAI were observed among the genotypes, with the two sowing dates and the interaction effect. During vegetative stage LAI ranged from 0.72 to 1.44 (1.02) in S1 and from 0.46 to 1.14 (0.78) in S2. Maximum LAI was observed in check KBSH 44 (1.44), followed by inbreds ARM 243B (1.42), AKSF 6-3B (1.21) in S1 and in check KBSH 44 (1.14), followed by inbreds AKSF 6-3B (0.95), CMS 42B (0.93) in S2. The percent reduction in LAI due to delayed sowing ranged from 12 to 68 in inbreds and from 9 to 21 in checks. Inbreds CMS 127B (12%), -107B (13%), -42B (14%), -144B (17%), -70B (20%) has recorded percent reduction on par with checks. At flowering, LAI ranged from 1.01 to 4.04 (2.57) in S1 and from 0.69 to 3.86 (2.31) in S2. Inbred AKSF 6-3B (3%) has recorded least percent reduction compared to checks.

3.4.7 Leaf angle (LA)

At vegetative stage, LA ranged from 39 to 58° (45°) in S1 and from 29 to 50° (38°) in S2. Maximum LA was recorded in inbreds CMS 42B followed by check CO 2 (48°) in S1 and S2. Minimum LA was noted in inbreds AKSF 6-3B (39°), CMS 107B (39°) and CMS 127B (39°) in S1 and in inbreds CMS 125B (29°), -17B (32°) and -127B (32°) in S2. The percent reduction in LA due to delayed sowing varied from 3 to 8 among checks and from 5 to 36 among the inbreds. At flowering stage, LA ranged from 33 to

52° in S1 (39°) and from 23 to 46° in S2 (33°). Maximum LA was recorded in inbred CMS 42B followed by check DRSH 1 in both S1 and S2. Minimum LA was recorded in inbreds AKSF 6-3B (33°), CMS 125B (33°), -17B (36°) and ARM 243B (36°) in S1 and in inbreds CMS 125B (23°), -17B (28°) and in AKSF 6-3B (30°) in S2. The percent reduction in leaf angle due to delayed sowing varied from 7 to 13 among checks and from 8 to 30 among the inbreds.

3.4.8 Total chlorophyll (TC) mg g^{-1} FW

In vegetative stage, the TC varied from 2.20 to 4.30 (3.60) in S1 and from 1.46 to 3.98 (3.11) in S2. Among the genotypes maximum TC was recorded in checks DRSH 1, CSFH 12205, KBSH 44, CO 2 in S1 and S2 conditions respectively. The percent reduction in TC due to delayed sowing (HT) ranged from 4 to 34 in inbreds and from 6 to 10 in checks. At flowering stage TC varied from 3.55 to 6.04 (4.88) in S1 and from 2.36 to 5.36 (4.01) in S2. Maximum TC was noted in checks DRSH 1, KBSH 44, CO 2, CSFH 12205 among both the sowings. The percent reduction in TC due to delayed sowing (HT) ranged from 9 to 34 in inbreds and from 8 to 14 in checks. Inbred AKSF 6-3B has recorded percent reduction on par with checks during both vegetative (4%) and flowering stages (9%). Mohammed and Tarpley [10] reported a decline in Chl pigment as a result of lipid peroxidation of chloroplast and thylakoid membranes in sorghum due to heat stress (40/30°C, day/night).

3.4.9 Maximum quantum efficiency (Fv/Fm)

During vegetative stage, significant differences for Fv/Fm were observed with the two sowing dates among the genotypes. In S1, inbreds AKSF 6-3B (0.816), CMS 107B (0.814), followed by checks CO 2 (0.807), KBSH 44 (0.807) and in S2, check CO 2 (0.786), inbred AKSF 6-3B (0.772), checks DRSH 1 (0.732), KBSH 44 (0.720) has maximum Fv/Fm. The percent reduction in Fv/Fm due to HT ranged from 5 to 26 in inbreds and from 3 to 13 in checks. Inbreds AKSF 6-3B (5%) and ARM 243B (13%) recorded on par reduction percent for the trait Fv/Fm during vegetative stage compared to checks. At flowering, maximum Fv/Fm noted in inbred AKSF 6-3B (0.837) followed by check CO 2 (0.830), inbred CMS 107B (0.821) in S1 and in inbred AKSF 6-3B (0.776), followed by checks CO 2 (0.752), DRSH 1 (0.738) in S2. The percent reduction in Fv/Fm due to HT ranged from 7 to 21 in inbreds and from 9 to 10 in checks. Inbred AKSF 6-3B (7%) recorded least reduction percent for the trait Fv/Fm during flowering stage compared to checks.

3.4.10 Seed yield (SY) g/pl

Genotypic difference was significant for SY with the sowing dates. Subjecting the plants to a HT resulted in reduction in SY from a mean of 18.5 (S1) to 14.6 (S2) which is about 3 to 10% reduction among checks and 3 to 47% reduction among the inbreds over control. Inbred line AKSF 6-3B (3%) has recorded least percent reduction among the inbreds and on par with checks. Inbred CMS lines -17B and -107B showed on par SY with checks CO-2 and CSFH-12205. Among the genotypes tested, maximum SY was recorded in checks KBSH 44 (25.3), DRSH 1 (25.1), followed by CMS 17B (21.6) and AKSF 6-3B (20.8) in S1 and in checks DRSH 1 (23.7), KBSH 44 (23.5), followed by AKSF 6-3B (20.5) in S2.

3.4.11 Association of traits with SY

The traits associated with SY can be used to aid the selection of superior genotypes. Under first year, the correlation analysis revealed that the traits SPAD value at both the stages, were positively correlated with SY under S1. The traits SPAD value and MSI at both vegetative and flowering stages were positively correlated with SY while CT at both vegetative and flowering stages were negatively correlated with SY under S2.

Under second year, the traits like PV were positively correlated with SY under S1. The traits like TChl, Fv/Fm, RWC, LAI at vegetative and flowering stages, PN, transpiration at vegetative stage, PV were positively correlated with SY under S2. CT was negatively correlated with SY, indicating that higher CTs limit the yield of genotypes.

4. DISCUSSION

Chlorophyll synthesis is sensitive to HS and is a good indicator of HS injury [11]. Lower SPAD meter value indicates the decreased P_N and the inability of a plant to produce higher yield.

Cell membrane stability varies with the age of plant tissue, growth stage, growing season, plant species, and intensity of heat stress [12]. HS inactivates the enzymes and denatures the membrane protein, resulting in membrane permeability and integrity changes causing reduction in ion flux, electrolyte leakage, production of toxic compounds, changes in RWC, and disruption of homeostasis thus reducing cell viability [13]. HT leads to swelling of grana stacks and an aberrant stacking, accompanied by ion-leakage from leaf cells and changes in energy allocation to the photosystems [14]. The maintenance of cellular membrane function under HS is essential for a sustained photosynthetic performance [15].

CT is the more accurate estimate of the consequences of HS on the crop than air temperature [16]. Small lobed leaves and conifers tend to reach lower temperatures whereas, large leaves tend to reach higher temperatures [17]. An increase in average air temperature results in higher mean canopy temperature during anthesis.

The leaf RWC is the result of the equilibrium between water absorption and evapo transpiration [18]. At HT, water absorption through the roots is promoted. The movement of water within the plant is attributed to changes in membrane fluidity and permeability, changes in water viscosity or a combination of both [19]. HS affects plant root conductance despite of enough water supply and this becomes more fatal when HS is combined with drought [20].

In chloroplasts, carbon metabolism of the stroma and photochemical reactions in thylakoid lamellae are the primary sites of injury at HT [21]. HT reduce the activation state of ribulose-1,5-bisphophate carboxylase/ oxygenase (rubisco) [22], which has often been ascribed to thermolability and the loss of activity in rubisco activity [23] or by changing the affinity of RubisCO for CO_2 [24]. By increasing chlorophyllase activity and decreasing the amount of photosynthetic pigments, HS ultimately reduces the plant photosynthetic and respiratory activity [25]. HT disrupts the metabolic processes in the guard cells thus stomatal response is often complicated as temperature affects photosynthesis, VPD, transpiration, and plant water status, which all feedback on stomatal behaviour [26]. Higher VPD increases the leaf atmosphere diffusion gradient, driving greater water loss [27] and C_i [28] which effect the stomatal closure to maintain plant water status [29]. Evaporative demand as determined by the vapour pressure deficit would increase by about 5 to 6% per degree warming [30]. HS-induced damage to chloroplasts leads to the inactivation of heat-sensitive proteins such as Rubisco activase (RCA) and the down-regulation of important chloroplast components, thereby leading to decreased photosynthetic efficiency, redox imbalance and possible cell death [7].

HT alters carbohydrate accumulation thus decreasing the availability of energy resources and osmotic power of carbohydrates, leading to a failure in pollen development [31]. These results are supported in sorghum in which the decrease of PV under HS was mainly correlated with a decrease of sucrose and starch in late stages of pollen development, due to decreased expression of several sugar metabolism genes [32]. HS during pre-anthesis (sporogenesis) decreases PV and fewer pollen grains, in grain sorghum [33], at heading stage significantly reduced anther dehiscence and pollen fertility rate in rice (Ahmed et al., 2010) and at floret development alters pollen morphology and results in an abnormal exine wall, degeneration of tapetum cells, and membrane damage in grain sorghum [34], wheat [35] leading to pollen sterility. HS adversely affects pollen cell and microspore resulting into male sterility (Anjum et al., 2008) which reduces the yield due to impairment of pollen development [36].

Reduction in photosynthesis at HT was reflected in reduced LAI. Warmer conditions both accelerate rate of organ initiation and shorten duration of organ growth thereby leading to reduced growth of plant organs [37]. Temperature modifies leaf orientation by affecting pulvinal region tissues resulting in active heliotropic movements [38]. Downward leaf inclination was a general response of the species and is considered to be a susceptible reaction to HS [39]. HT induce differential petiole-driven upward growth of leaves by allocating active resources to the petiole and leaf veins to keep them in a static position [40]. Plants adjust their canopy according to irradiance while petioles were stiffer at HT [41].

Under HS, a decrease in chlorophyll biosynthesis due to inhibition of photosynthetic electron transport chain [42] and the inhibition of enzymes. HT alters the anatomical structure in leaves, and result in reduced photosynthetic and respiratory activities [43]. Therefore, the amount of Chl content strongly depends on the species physiological responses and their ability to tolerate stress. HS results in plant leaf pigment loss and significantly damages photosynthetic activities [44]. The decrease in chlorophyll content was due to the inhibition of chlorophyll biosynthesis or chlorophyll degradation [45]. The effect of HT on the pigments and other photosynthetic apparatus is due to the production of toxic oxygen species (oxidative damage) and reduction in antioxidative defense [46]. The loss of chlorophyll is typical of leaf senescence and is used as an indicator [47].

The approximate optimal Fv/Fm value for many of the crop species is in the range of 0.79 to 0.84, with lowered values indicating plant stress [48]. A decrease in the Fv/Fm values indicated a reduction in PSII efficiency, mainly by photoinhibition [49] under HS. Enzyme degradation at HT impede the function of PSII, decrease electron transport rates, inhibit Rubisco activity and decrease chlorophyll content [35]. Use of chlorophyll fluorescence measurements have been shown to be useful in quantifying the impact of drought and heat stress on plants [50].

The decrease in SY with late plantings is attributable to higher air temperatures at seed development period, and thus pollination and fertilization were obstructed resulting in hastened maturity, poor seed setting, lesser accumulation/translocation of metabolites. Major yield losses were mainly attributed to limited nutrient translocation rather than a reduction in photosynthetic production under HT and poor quality oil compared to timely sowings. HT affect the SY by affecting phenological development processes as reduction in SN and increase in small grains. Loss of productivity in HS is chiefly related to decreased assimilatory capacity [51] which is due to reduced photosynthesis by altered membrane stability [52] and enhanced maintenance respiration costs [53], reduction in radiation use efficiency.

Heat indices used for screening heat tolerant genotypes provides a measure of yield loss under HT conditions in comparison to normal as done in case of drought stress by Mitra [54]. Heat susceptibility index (HSI) was calculated to determine the most desirable heat tolerant genotypes.

5. CONCLUSION

The traits associated with SY under S1 and S2 differed among the sunflower genotypes studied. The inbreds and hybrids with different genetic backgrounds resulted in trait variation. Variation in the S2 condition of specific traits measured among genotypes aids the selection of these traits. These trait-specific genotypes could be used in sunflower breeding programs to develop location-specific varieties. The values of most of the traits were reduced under S2.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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