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FULL-LENGTH RESEARCH ARTICLE

Genotypic Variation in Physiological Traits Under High Temperature Stress in Maize

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Abstract Maize (*Zea mays* L.) is a major cereal crop in India and worldwide whose production and productivity are greatly affected by high temperature stress. Twenty-one maize genotypes were staggered sown and evaluated for the variations in different physiological traits under high temperature stress. Observations were recorded for net photosynthetic rate, transpiration rate, stomatal conductance, leaf temperature, canopy temperature, maximum quantum yield PSII photochemistry (F_v/F_m), SPAD, ASI, stover and grain yield. Meteorological data of cropping season for first and second date of sowings showed maximum and mean day time temperature of 37.6, 37.2 and 41.4, 37.5 °C, respectively, during reproductive stage. These temperatures were optimal for photosynthesis, fertilization and grain filling in early sown crop, while for the late sown crop, it was optimal for photosynthesis but above threshold and detrimental for fertilization and grain filling. Combined analysis of ANOVA showed that all the parameters were found significant with respect to genotypes (*G*), date of sowings (*T*) and their interaction (*G* * *T*) except leaf temperature. The high temperature stress increased the plant stover weight due to increased photosynthesis coupled with maximum quantum yield PSII photochemistry which may improve the total plant growth. Results revealed that high temperature promoted the growth of vegetative plant parts but affected yield-related parameters. Higher temperatures during vegetative growth improved net photosynthetic rate resulting in higher total stover yield (28 %) at maturity. It impacted pollen viability and source to sink supply of photosynthates leading to reduced grain yield (13 %) in all genotypes.

Abbreviations
Pn: Net photosynthetic rate; LT: Leaf temperature; CT: Canopy temperature; Tr: Transpiration rate; F_v/F_m: Maximum quantum yield PSII photochemistry; gs: Stomatal conductance; SPAD: Soil–plant analysis development; ASI: Anthesis and silking interval;

Introduction

Maize (*Zea mays* L.) is the world's most extensively grown cereal and is the principal staple food in many developing countries [34]. Maize is grown throughout the year in India and is the third most important cereal crop after rice and wheat. However, it is predominantly as a kharif crop. It accounts for about 9 % of total food grain production in the country. India is highly vulnerable to climate change, and its economy is highly dependent on climate sensitive sectors like agriculture. Temperature increases above 2.5 °C will generally have overall negative effects on world agriculture. Heat stress due to high ambient temperatures is a serious threat to crop production worldwide [10]. The global air temperature is predicted to rise by 0.2 °C per decade, which will lead to temperatures 1.8–4.0 °C higher than the current level by 2100 [15].

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Maize is highly productive under optimal environmental and crop management conditions. However, maize plants are also very susceptible to drought and heat and each year on an average of 15–20 % of the potential world maize production is lost due to these stresses [24].

Maize production in India has grown at a compound annual growth rate (CAGR) of 5.5 % over the last 10 years from 14 m t in 2004–2005 to 23 m t in 2013–2014. During 2009–2010, there was a decline in production primarily due to drought that affected production of kharif crops in the country. The area under maize cultivation in the period has increased at a CAGR of 2.5 % from 7.5 m ha^{-1} in 2004–2005 to 9.4 m ha^{-1} in 2013–2014; the remaining increase in production is due to increase in yield. Productivity of maize has increased at a CAGR of 2.9 % from 1.9 t ha^{-1} in 2004–2005 to 2.5 t ha^{-1} in 2013–2014 [14]. Maize production and productivity are prone to rapid and constant changes due to global warming-related environmental changes [39].

Development of stress-tolerant plant varieties will play an important role in alleviating the negative impacts of abiotic stresses on agricultural production [37]. Maize has capability of utilizing solar energy more efficiently and can tolerate relatively high temperature up to a crucial factor [4]. Leaf photosynthesis of maize has a very high optimum temperature of 33–38 °C [8]. Furthermore, higher temperature at flowering and grain formation stages is the most alarming factor that determines the crop growth and ultimate yields [38]. Net photosynthetic rate of maize was inhibited at leaf temperature above 38 °C [8, 25]. However, the photosynthetic rate of some maize cultivars was not reduced until 40 °C [25]. Therefore, maize photosynthesis appeared to be heat resistant up to a certain range.

In temperate zones, high temperatures affect crop production adversely, particularly impairing fertilization due to disruption of pollen viability [28]. However, the decrease in grain yield has been ascribed to a variety of mechanisms including the reduction in grain filling and increase in flower and embryo abortion [5]. It is observed that at high temperature such as 35 °C, kernel mass in vitro failed to increase even if its soluble sugar concentration is high enough [18]. Reduction in starch concentration in the endosperm of maize has been observed with elevation of sucrose concentrations and decrease in fructose as well as glucose concentration in the pedicel by high temperature [11]. This assumption stated that abortion of kernel growth by high temperature is mainly due to altering the invertase activity which fails to unload sucrose in the pedicel that leads to prevention of starch synthesis in the endosperm. Hence, improving heat tolerance in maize has become one of the top priorities for maize breeding programs. Identification of maize germplasm with higher heat tolerance is essential and prerequisite for the purpose.

Materials and Methods

The research work was conducted at ICAR-Central Research Institute for Dryland Agriculture (ICAR-CRIDA), Santoshnagar, Hyderabad, India, during 2013 summer season. Seed material was received from diverse sources including ICAR-National Bureau of Plant Genetic Resources, New Delhi, ICAR-Directorate of Maize Research, New Delhi, and CIMMYT, Mexico.

The experimental material of 21 genotypes of maize used in the present study, namely HKI 161, HKI 3-4-8-6-ER, Z 40-183, HKI 324-17 AN, Z 162-12, RJR 068, PSRJ 13099, NSJ 155, RJR 270, NSJ 189, SNJ 2011-15, Harsha, NSJ 176, Varun, PSRJ 13086, RJR 163, NSJ 221, Z 59-11, Z 59-9, PSRJ 13038 and PSR 13247, was inbred lines received from sources indicated above. The experiment was laid out in a randomized complete block design with three replications having net plot size of 18 × 10 m^2. Staggered sowing was done during the off season in the end of January and February, 2013, with 30-day interval. This was planned so that the reproductive stage of plants sown on second date of sowing was exposed to high temperatures during the month of April and May. The field was immediately irrigated after sowing.

Recommended dose of NPK (300–150–125 kg ha^{-1}) was applied. Full dose of P, K and 1/8 of total N was applied at sowing, while remaining 1/5 N at four-leave stage, 1/3 N at grand growth stage and 1/3 N was applied just before flowering. All the recommended cultural practices were kept constant for all the genotypes for uniform growth.

Standard evaluation system for maize was followed for data collection. Data regarding plant net photosynthetic rate, transpiration rate, stomatal conductance and leaf temperature were recorded by using LI-COR (LI-6400) portable photosynthesis system using a light intensity of 1500 mol m^{-2} s^{-1} PAR and a constant 390 bar partial pressure of CO_2 in the sample chamber, Maximum Quantum yield PSII photochemistry (F_v/F_m) by Fluorpen (FluorPen FP 100), Canopy temperature with Canopy meter (Fluke IR Thermometer) and SPAD by SPAD 502 plus (Konica Minoltkoptics Inc).

Data were recorded in triplicates for individual genotypes. The analysis of variance (ANOVA) was done with one- and two-factor [genotype and treatment (different date of sowing)] factorial analysis program of MSTAT program, and the critical difference (CD) values of genotypes × treatment were calculated at $P < 0.05$ and $P < 0.01$ significant level.

Meteorological data were also recorded during cropping season. During the reproductive stage, early sown crop faced maximum and mean day time temperature of 37.6

and 37.2 °C, whereas the late sown crop faced 41.4 and 37.5 °C, respectively. Mean data of temperature of each month showed that late sown crop faced severe heat shocks during its grain filling period, which is above threshold value of maize crop at flowering and grain filling stage (Fig. 1).

Results and Discussion

Most of the tissue injuries caused by high temperature stress in crop plants grown under field conditions are mostly irreversible [5, 6]. Temperature affects the plant system at all levels, ranging from molecular and cellular effects to whole plant growth [6]. Arvin and Donnthy [3] have reported measurement of electrical conductivity to screen potato genotypes against abiotic stress tolerance.

The analysis of variance showed significant differences among diverse genotypes for all the parameters studied under high temperature (Table 1). The optimum temperature for growth and yield of maize is about 30–35 °C. Even short periods (3–4 days) of very high temperature (38–42 °C) significantly decrease grain yield. Maize-growing areas in India experience 35–40 °C of temperature during reproductive and grain filling stage, resulting in reduction in yield. In the present study, maize genotypes were screened by sowing on different dates, wherein plants faced high temperature stress at their grain development stage under natural growing conditions.

The combined statistical analysis of the 21 genotypes evaluated during summer, 2013, showed that the parameters such as net photosynthetic rate (Pn), transpiration rate (Tr), maximum quantum yield PSII photochemistry (F_v/F_m), canopy temperature (CT), stomatal conductance (gs),

SPAD, anthesis and silking interval (ASI), stover and grain yield were found highly significant at genotypes (G), different dates of sowing (T) and interaction (G * T) except leaf temperature (LT).

The mean data and combined ANOVA of Pn is highly significant for genotypes, different dates of sowing and their interaction. In the combined analysis, Pn ranged from 46.27 to 71.98 with a mean value of 59.94. All the genotypes showed induced Pn in II date of sowing (T_2) compared to I date of sowing (T_1). The percentage increase in Pn ranged from 0.24 to 183 %. Over all mean data revealed that highest Pn was recorded by HKI-161 (71.98), followed by HKI-324-17AN (71.30) and Z-40-183 (68.07). This increase in Pn was due to the average leaf and canopy temperature 35–36 and 38–40 °C recorded in reproductive phase of two different dates of sowing, respectively (Figs. 2, 3).

Crafts and Salvucci [8] and Massad et al. [25] have reported that optimum temperatures for photosynthesis (light harvesting) and carbon-fixing enzymes are approximately 30–38 °C for corn. Net photosynthetic rate in corn was inhibited at leaf temperatures exceeding 38 °C though a rise in growth temperature increases this optimum value for photosynthesis [8, 41].

Maximum quantum yield of the PSII photochemistry (F_v/F_m) was used to determine genotypic differences in high temperature stress effects and plant response to the stress. In all the genotypes except Z 162-12, RJR 270, SNJ 2011–2015, Harsha, NSJ 176, NSJ 221 and Z 59-9, F_v/F_m increased in II date of sowing (T_2) and was superior to I date of sowing (T_1). Based on the ANOVA results (Table 2), the genotypes Z-40-183 (0.58), NSJ-189 (0.57), Z 162-12 (0.53) recorded the maximum F_v/F_m with the mean values of 0.46 and mean difference between
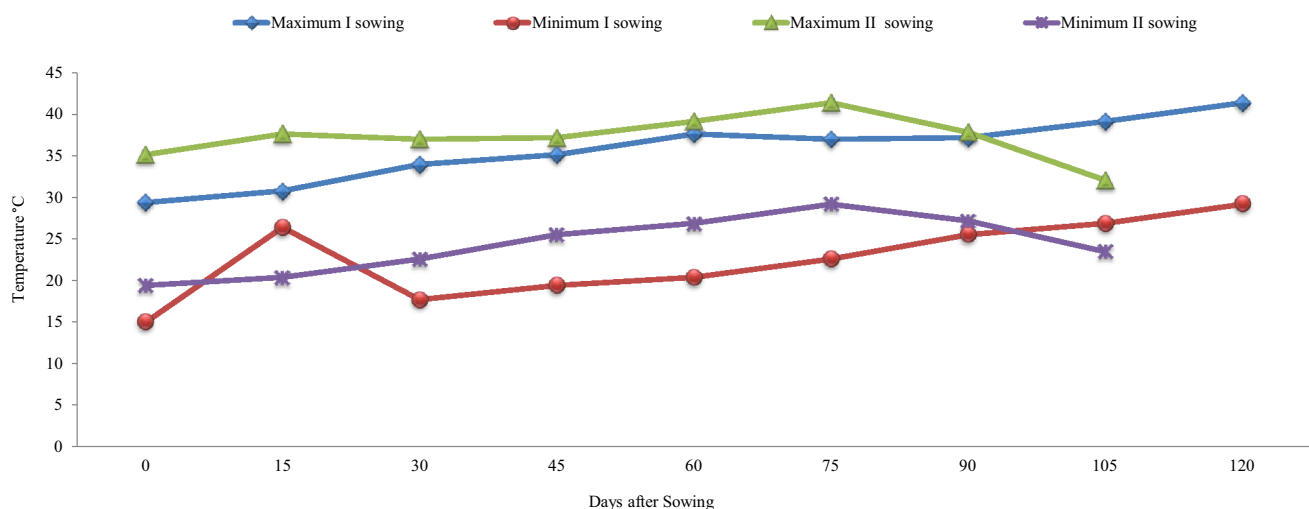
Fig. 1 Minimum and maximum temperatures recorded during the cropping season for the maize genotypes sown on two different dates

Table 1 Analysis of variance for different parameters in maize genotypes exposed to high temperature stress by sowing on two different dates

Source	df	Net photosynthetic rate (μmol CO_2 m^{-2} s^{-1})	Stomatal conductance (mol H_2O m^{-2} s^{-1})	Transpiration rate (m mol H_2O m^{-2} s^{-1})	Leaf temperature (°C)	Maximum quantum yield PSII photochemistry	Canopy temperature (°C)	Soil–plant analysis development	Anthesis silking interval (days)	Stover (g plant^{-1})	Yield (g plant^{-1})
Replications	2	2.69	0.00	0.01	0.21	0.0025	0.49	2.38	0.19	142.10	9.35
Treatments	41	666.91**	0.06**	31.90**	3.36 NS	0.0220**	17.66**	121.27**	14.40**	2987.28**	1773.89**
Genotypes	20	367.38**	0.05**	16.43**	3.84 NS	0.0350**	11.78**	110.28**	23.28**	4850.46**	3010.74**
DOS	1	13,697.92**	0.93**	742.72**	55.95**	0.0492**	380.15**	1102.42**	7.62**	13,270.49**	721.44**
Genotypes × DOS	20	314.88**	0.02**	11.84**	0.26 NS	0.00774**	5.42**	83.21**	5.86**	609.95**	589.67**
Error	82	4.40	0.00	0.13**	5.49	0.0006	0.43	1.19	0.17	37.78	7.19
Total	125	221.67	0.021	10.55	4.71	0.00772	6.08	40.60	4.84	1006.89	586.70

NS non significant

** Significant at 1 % level; * significant at 5 % level

genotypes was 1.70. However, under moderate heat stress (<40 °C), no inhibition of PSII was observed, even though there was substantial reduction in carbon assimilation [9, 22]. PSII appears to be influenced by temperatures above 45 °C [9] but is not severely affected by moderately high temperatures (<40 °C) [2].

An increase in air temperature reduces the relative humidity, which increases the evaporative demand and transpiration rate. Where water supply is restricted, closure of stomata led to fall in transpiration rate, resulting in an increase in leaf temperature. Where water supply is not limiting, transpirational cooling is an effective form of heat avoidance.

In our experimental environments, where high temperatures are not necessarily combined with water deficit, genotypes showing high stomatal conductance were shown to be more tolerant to high temperature stress. In fact, stomatal conductance measurements along with direct measurements of reduced canopy temperatures are among the most valuable parameters for selecting cultivars for warm environments.

The analysis of variance (ANOVA) carried out on stomatal conductance, transpiration rate and leaf temperature assessed under I and II date of sowing (under high temperature stress) and combined analysis ($P < 0.01$) were significant. The mean data reflected that significant increase was observed in gs (85.97 %) and Tr (84.39 %) with increased canopy temperature (9.85 %). The mean data revealed that gs and Tr were maximum in RJR 068 (0.51, 11.49) followed by HKI 161 (0.48, 10.74), respectively. The highest percentage increase in gs and Tr was observed in genotypes PSRJ 13038 (247, 206 %) followed by NSJ 189 (224, 188 %). Defects in transpiration were observed to increase the susceptibility of well-watered plants to heat stress by impairing evaporative cooling [26].

The LT was reduced drastically with increased gs and Tr in the genotypes RJR 163 (6.7 %) with temperature decrease of 2.37 °C and NSJ 221 (6.5 %) with reduced temperature of 2.31 °C, respectively. Our results are correlating with the previous reports where transpiration cooling often reduces leaf temperatures to 5 °C below ambient [32, 33], while temperatures can be reduced by 15 °C in extreme cases. Under II date of sowing, the LT was increased for all the genotypes, and with maximum increase, it was recorded in genotypes HKI-3-4-8-6-ER (20.65 %), Varun (16.36 %) and RJR 270 (16.04 %). However, genotypes NSJ 221 (4.38 %) PSRJ 13086 (4.37 %) showed the least increase in LT. Our results indicated that increased gs and Tr might lead to reduced LT.

SPAD is also considered as one of the important characters in maize to screen for heat tolerance. It is a rapid, low-cost technique to detect heat tolerance of light-
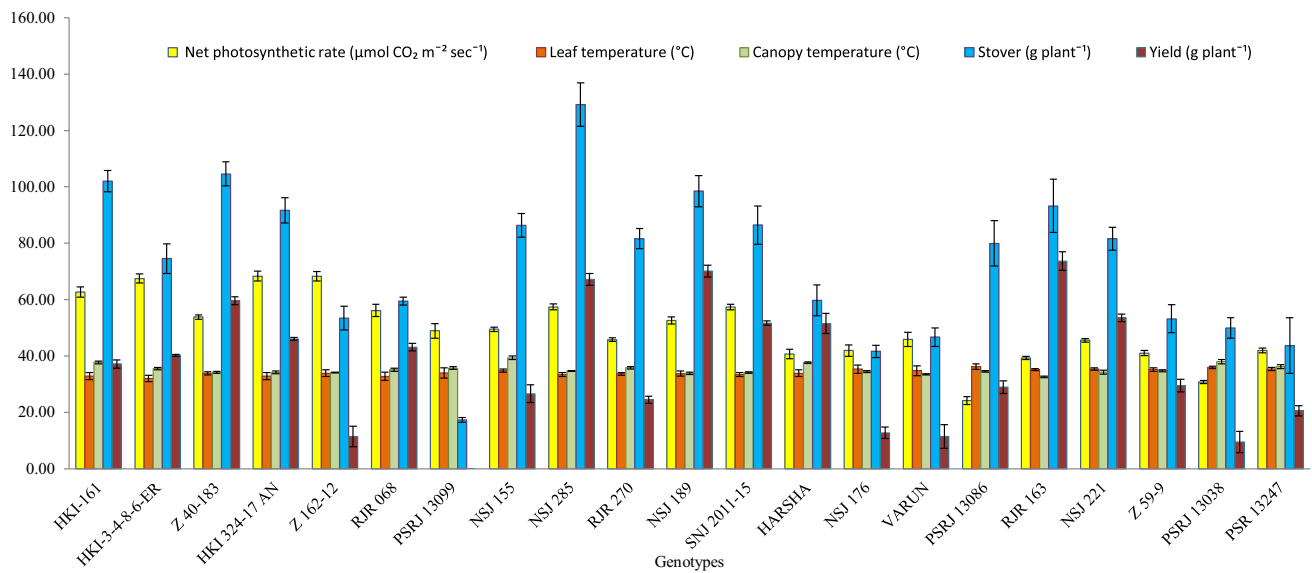
Fig. 2 Effect of high temperature on physiological and yield parameters at reproductive stage in maize genotypes sown on first date of sowing
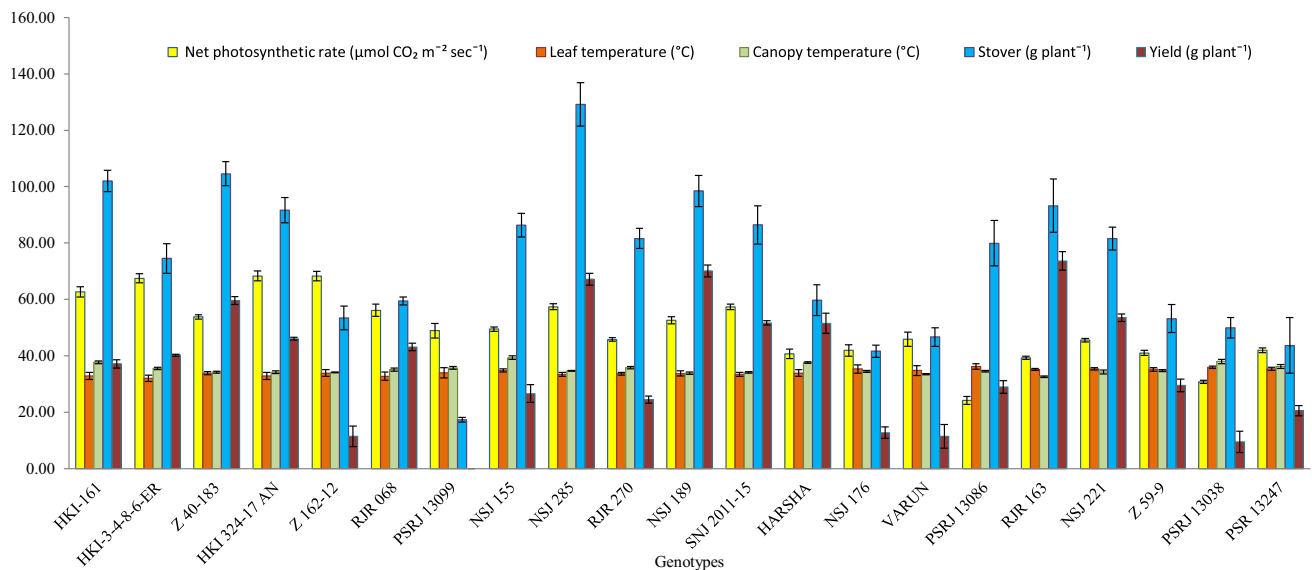
Fig. 3 Effect of high temperature on physiological and yield parameters at reproductive stage in maize genotypes sown on second date of sowing

harvesting apparatus. Different genotypes had great variation for SPAD ranging from 32.9 5 (NSJ 155) to 48.28 (NSJ 189) followed by NSJ 221 (45.63) and SNJ 2011–2015 (45.35) with mean difference of 1.46. Highly significant difference was observed between I and II date of sowing with the mean values of 42.75 and 36.84, respectively. The reduction percentage of SPAD is very high with increased canopy temperature, and maximum reduction was recorded by HKI 161 (41.16 %). Interestingly, few genotypes had showed increased SPAD values with low canopy temperature difference in between I and II date of

sowing. Elevated temperatures can impair light-harvesting apparatus and inactivate critical carbon-fixing enzymes, thereby reducing assimilation rates and ultimate yield potential [31].

The analysis of variance concludes that the 50 % tasseling was ranging from 40 to 64 days with 22-day interval in I date of sowing, while it was 36–55 days with 19-day interval in II date of sowing. It revealed that the earliness in reproductive stage was hastened because of high temperature stress during crop growing period. Duration of 50 % anthesis and silking were also significantly reduced under

Table 2 Means, ranges, standard deviation and coefficient of variability (CV%) for characters evaluated in maize genotypes sown on two different dates

Character	First date of sowing					Second date of sowing					Combined analysis				
	Mean	SE (±)	Min	Max	CV (%)	Mean	SE (±)	Min	Max	CV (%)	Mean	SE (±)	Min	Max	CV (%)
Pn (μmol CO_2 m^{-2} s^{-1})	59.94	1.70	46.27	71.98	4.22	70.36	1.74	54.67	84.60	3.03	59.94	1.71	46.27	71.98	3.99
gs (mol H_2O m^{-2} s^{-1})	0.20	0.01	0.16	0.51	8.41	0.37	0.02	0.19	0.71	8.58	0.29	0.02	0.16	0.51	9.19
Tr (m mol H_2O m^{-2} s^{-1})	5.75	0.21	5.43	11.49	4.55	10.61	0.36	5.80	15.53	4.14	8.18	0.29	5.43	11.49	4.75
LT (°C)	34.23	0.46	32.01	35.39	1.66	37.95	0.08	36.52	40.49	0.27	36.09	1.91	34.82	37.64	9.01
F_v/F_m	0.44	0.02	0.34	0.58	5.62	0.48	0.02	0.31	0.60	5.89	0.47	0.02	0.34	0.58	5.87
CT (°C)	35.26	0.51	34.73	40.22	1.78	38.73	0.56	35.13	42.73	1.76	36.99	0.54	34.73	40.22	1.78
SPAD	42.75	0.99	32.95	48.28	2.84	36.84	0.78	31.27	44.27	2.58	39.80	0.89	32.95	48.28	2.91
ASI (days)	2.03	0.34	0.00	8.00	20.75	2.52	0.34	0.00	8.00	16.52	2.27	0.34	0.00	8.00	17.49
Stover (g plant^{-1})	73.09	6.24	29.32	144.03	10.46	93.62	3.52	41.30	183.47	4.60	83.35	5.02	29.32	144.03	7.52
Yield (g plant^{-1})	36.63	2.61	0.00	70.42	8.74	31.85	1.58	0.00	81.20	6.06	34.24	2.19	0.00	70.42	7.90

the influence of high temperature. In I date of sowing, duration of anthesis and silking was 20 days, whereas in II date of sowing durations were 14 days, respectively (data not shown).

The results of the experiment indicated that combined analysis of ASI was significant between genotypes, different date of sowing (T) and interaction of genotype and treatments. The maize genotypes PSRJ 13099 produced the highest ASI (8.0) followed by genotypes Z 162-12 (6.0) and RJR 270 (5.0). Lowest ASI of 0 days was observed in RJR 068 followed by NSJ 221, NSJ 176 with 1 day.

Maize reproductive stage is more sensitive to high temperature than vegetative stage, and tassel blast is the most noticeable phenotype with reduced pollen shedding, viability and pollination efficiency, which affects kernel size, weight and development resulting in a reduction in seed number [5, 41]. Post-anthesis stage is a very critical in maize for thermal environment, and a temperature of above 30 °C during this period dramatically reduced subsequent kernel growth rate (potential) and final kernel size [19].

Maize stover is composed of the stalk, leaves, tassels, cobs, shanks, silks and husks [29]. Seventy percent of total corn stover biomass includes stalks, leaves, and the remaining 30 % being husks, shanks, silks and cobs [12]. The stover data presented in (Fig. 3) showed increased stover due to increased Pn with F_v/F_m which may improve the overall plant growth. The II sowing date experienced marginal high temperatures which were optimal for net photosynthetic rate and may be lethal to the source to sink supply of photosynthates and consequently produced high total stover at maturity with reduced yield (Table 2).

High temperature treatment promoted the growth of vegetative plant parts but reduced ear expansion, particularly suppression of cob extensibility by impairing

hemicellulose and cellulose synthesis through reduction in photosynthate supply [36]. Therefore, plant biomass production was enhanced and grain yield reduced by the high temperature treatment due to effects on sink activity rather than source activity.

The impact of high temperature stress on leaf area expansion and dynamics are relatively less understood and needs attention. Heat stress resulted in significant increases in leaf numbers, particularly when reproductive development was arrested without any decrease in leaf photosynthetic rates [30]. The importance of the leaf development and duration of crop growth is reflected in the amount of solar radiation that can be intercepted and used to accumulate crop biomass [35]. The following table shows the optimum, maximum and lethal temperature for a range of processes in maize [21].

The optimal, maximum and lethal temperature for a range of important physiological processes in maize (see Larcher [21] for a comparison of lethal temperatures across a range of ecosystems)

	Optimal (°C)	Maximum (°C)	(°C)
Maize			
Germination	30	>40	–
Seedling growth	25	>40	52
Net photosynthetic rate	30–40	>40	–
Fertilization (pollen viability)	28	<35	35
Grain filling (kernel mass)	20–35	>40	–

Grain yield of the crop is the expression of combined effects of various yield components. High temperature may affect the pollen viability and fertilization which result in

large yield reduction in maize [17, 23, 32]. Among different genotypes Z 40-183 produced the highest grain yield (70.42 g plant^{-1}), followed by NSJ 189 (70.32 g plant^{-1}), RJR 163 (70.27 g plant^{-1}) and NSJ 221 (60.07 g plant^{-1}) significant for interaction. This difference in grain yield among different genotypes might be due to their genetic variation and difference in adaptation to high temperature, which reduced the yield drastically due to its detrimental effects on metabolism and duration of phenological phases [1, 16]. Sucrose loading from source tissues into the phloem channel is specifically inhibited in Mg-deficient maize plants [26].

Brief exposure of plants to high temperature during seed filling can accelerate senescence, diminish seed set and seed weight and reduce yield [9]. Temperatures above 30 °C increasingly impaired cell division and amyloplast replication in maize kernels and thus reduced grain sink strength and yield [7].

The high temperature stress decreased antioxidant enzymes activity leading to accumulation of H_2O_2 and consequently increased lipid peroxidation [20] and ethylene production. This resulted in reduction in growth and consequently grain weight which associated with a decrease in starch accumulation (carbohydrate content) and the disruption of normal protein synthesis (protein content) under high temperature stress. The decrease in starch synthesis under high temperature might be due to the reduced conversion of sucrose to starch or to the alteration in catalytic activity of a number of enzymes in the pathway of starch synthesis [40].

Previous research results have found temperatures above 35 °C were lethal to maize pollen viability and germination [13]. Several authors have reported adverse effects of high temperature on source sink relationship in grain filling in maize [27, 36].

The results obtained from the present study reiterate previous reports while presenting a new insight into the physiology of temperature acclimation on the part of the plant by undertaking a holistic approach and examining the influence of the perturbed environment on the source and sink organs in combination. High temperature improved stover of the vegetative organs marginally, but it had a negative effect on cob growth. Such effects were more pronounced in maize showing reproductive stage to be more susceptible. The difference in stress resistance could not be attributed to a variation in source activity, because high temperature did not depress leaf photosynthesis in either of the genotypes used in the experiment.

In maize, leaf photosynthesis is affected at temperature above 38 °C, [8] and in present study, the leaf temperature did not exceed this limit. It is possible that genotypes possessed a large-sized cob, and hence, it might have a higher temperature limit for growth than grain. These results further revealed that temperature optimum for growth of source and sink organs are not identical in maize and the grain filling stage is more sensitive to high temperature than the vegetative stage [27].

The key result from this study was the significantly lower grain yield and associated SPAD values in the II date of sowing (T_2) compared to the I date of sowing (Table 1). The maize crop sown in February experienced extremely high air temperatures over several days at the time of anthesis and silking and grain filling stages, whereas the maize sown in January did not face such high temperatures. The results indicated significant contribution of high temperature to reduced grain numbers and grain yields of maize planted in the II date of sowing (T_2).

To conclude, we can say that a complete understanding of thermotolerance mechanisms remains indefinable and needs further appropriate research strategy. Successful improvement of crop tolerance to high temperature by altering sensing, signaling, or regulatory pathways will depend on identifying targets for modification that do not disrupt other vital processes importantly yield. Superior yield performance under high temperature stress conditions is an important and reliable index of heat tolerance. The maize genotypes namely NSJ 221, NSJ 189 and Z 40-183 performed better in terms of grain yield and hence were promising under high temperature stress growing conditions. Earlier experiments on high temperature stress effects were limited to laboratory conditions and short-term studies only. It is essentially required to be extension of field level experiments and physiological, biochemical and molecular approaches coupled with agronomic management practices for elucidation of authentic high temperature stress responses and their cumulative effects on crop productivity under different agro-climatic conditions. It is crucial to understand the mechanisms responsible for yield loss at high temperature stress to stabilize the maize yields under stressed environments.

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