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Genetic Potential of Tropically Adapted Exotic Maize (*Zea mays* L.) Heat-Tolerant Donor Lines in Sub-Tropical Breeding Programs

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Abstract: Breeding for heat stress tolerance became a priority in sub-Saharan Africa (SSA), as projections are showing an increase in frequency, duration, and severity. In this study, 14 heat stress tolerant-donor lines (HSTDLs) sourced from CIMMYT-India (males) were crossed with 15 locally adapted elite lines (females) developed within the CIMMYT-Zimbabwe maize-breeding program using the North Carolina Design II mating scheme. The resultant 175 single crosses were evaluated alongside five commercial hybrids and adjacent to the trial of parental lines used in the crosses across two locations representing heat stress and optimal environments in Zimbabwe. The design II analysis showed significant ($p < 0.01$) general combining ability (GCA) effects for exotic heat donor lines and specific combining ability (SCA) effects on grain yield under heat stress, optimal conditions, and across locations; demonstrating additive and non-additive genetic inheritance of grain yield. High Baker's ratios observed in this study indicate predominance of additive over non-additive gene effects. Three exotic HSTDLs, namely CAL14138, CAL152, and CAL1440, exhibited significant ($p < 0.001$) and positive GCA effects under heat stress conditions. The results imply that these exotic lines could serve as valuable genetic resources for introgression of heat tolerant alleles into local maize populations for accelerated yield genetic gains. Single crosses, DJ265-15 × VL1018816 and DJ267-9 × CAL1440, exhibited positive and significant ($p < 0.01$) and ($p < 0.05$) SCA effects for grain yield under heat stress conditions, respectively. These crosses can be used for further breeding and can contribute to grain yield performance under heat stress conditions. The exotic HSTDLs, CAL14138, CAL152, and VL109126 showed superior *per se* performance under heat, optimal conditions, and across environments. Overall data demonstrate the potential of exotic HSTDLs for improving the adaptation of maize to heat stress in sub-tropical breeding programs.

Keywords: combining ability; exotic germplasm; gene action; heat stress; grain yield

1. Introduction

Over 650 million people in sub-Saharan Africa (SSA) depend on maize (*Zea mays* L.) for their livelihoods and for daily calorie intake [1]. However, despite the importance of maize in SSA, heat stress, which can occur at any growth stage, became an important abiotic stress constraining yield, especially during the flowering and early grain-filling

stages. The stress induces anatomical, biochemical, morpho-physiological, and molecular changes in crops, resulting in significant grain yield losses [2]. During the pollination and grain filling stages, a temperature of 35 °C on maize caused a daily grain yield reduction of 101 kg ha^{-1} [3]. Moreover, maize grain yield losses of up to 42% and 70% due to heat stress were reported by Khodarahmpour et al. and Badu-Apraka et al. [4,5], respectively. Climate projections show that heat stress frequency, duration, and severity is increasing and that a temperature rise of 0.3 °C is expected to reach approximately 1 °C above the present value by the year 2025 [6,7], and this will cause a decline in global maize grain yield potential by 45% [8]. Hence, acceleration of breeding for heat stress tolerance became a priority objective in maize breeding to ensure food security under these predicted climatic scenarios [9].

Breeding for heat stress tolerance in tropical maize is in its infancy stage, as most programs focus on developing maize cultivars that are tolerant to drought stress, poor soil fertility, diseases, and pests [4,10–12]. In Zimbabwe, no heat-tolerant maize cultivars are commercialized, despite most of the maize production taking place in heat stress-prone areas. It is, therefore, imperative to develop and release maize cultivars that are tolerant to heat stress. On the other hand, literature pertaining to gene action controlling important traits in maize under heat stress is limited [13–15], and this warrants considerable attention. In order to start an appropriate heat stress tolerance breeding program, it is essential to have knowledge on genetic diversity for heat tolerance, gene action, and inheritance of the traits of interest [16]. Additionally, information on general combining ability (GCA) and specific combining ability (SCA) of the breeding population is a fundamental prerequisite for effective selection, genetic improvement, and adoption of the appropriate breeding strategy [17–19].

As part of its maize genetic improvement for stress adaptation agenda, the International Maize and Wheat Improvement Centre (CIMMYT)-Zimbabwe sourced heat-tolerant donors from CIMMYT-India. These lines are the products of targeted breeding for heat stress tolerance under the project 'Heat tolerant maize for Asia (HTMA)' funded by the United States Agency for International Development (USAID), wherein multi-parent populations were improved using genomic selection approach. The lines were extracted from the improved cycle (C3) of the populations using doubled haploid (DH) technology and test cross progenies evaluated across locations under natural heat stress conditions in South Asia, resulting in the identification of lines with high GCA for heat stress tolerance [1]. However, the genetic value of these heat-tolerant lines in SSA is not known. Therefore, to determine the breeding value of these lines for their utility in crop improvement, selection of parents based on their combining ability is important [20]. General and specific combining ability are, respectively, associated with additive gene action and non-additive gene action modulated by dominance and epistatic gene effects [19,20].

Combining ability for heat tolerance in maize was studied by several researchers, and both additive and non-additive gene action were reported on the expression of grain yield, anthesis-silking interval, leaf firing, tassel blasting, and anthesis dates [15,21,22]. Studies conducted by Jodage et al. and Chapman et al. [15,21] showed that additive genetic effects play a major role in conditioning grain yield under heat stress conditions in tropical maize. However, some researchers reported contrasting genetic effects for grain yield under heat stress conditions [14]. Hence, there is a need to conduct further research to have conclusive results. Therefore, the objectives of this study were to: (i) identify Indian HSTDLs that can positively and significantly contribute to grain yield performance in combination with CIMMYT-Zimbabwe elite lines under heat stress and optimal conditions, (ii) identify single crosses with significant positive SCA that can be used in further breeding for heat stress in SSA, and (iii) determine the gene action that controls the inheritance of grain yield under heat stress. We hypothesize that exotic HSTDLs can significantly contribute to adaptation of maize under heat stress conditions in SSA.

2. Materials and Methods

2.1. Germplasm

A total of 14 HSTDLs sourced from CIMMYT-India were crossed with 15 elite lines developed within the CIMMYT-Zimbabwe program, using the North Carolina Design II mating scheme [23], yielding a total of 175 crosses which had sufficient seed for four sites replicated two times. The exotic donor lines were selected for reduced anthesis-silking interval, good combining ability for yield under heat stress, and desirable agronomic traits (including; standability, husk cover, and disease tolerance) [15], making them ideal donor lines for heat stress tolerance breeding in the sub-tropical maize breeding programs. The exotic lines were used as males, while the elite CIMMYT-Zimbabwe lines were used as females. The crossing nursery was established at CIMMYT-Muzarabani station (altitude = 343 m above sea level (masl), GIS = −16°39′ S, 31°01′ E, soil type = red clay soils, average minimum winter temperature = 14 °C, and average maximum winter temperature = 28 °C) during the 2019 winter season and yielded 175 single crosses with sufficient seed to use in trials. The crosses were evaluated together with five commercial hybrids (CZH15429, SC633, SC608, SC727, and SC719) at two locations during the 2020 winter season, under two management regimes (i.e., managed heat stress and well-watered conditions) in the lowveld area of Zimbabwe (Table 1). The male and female parental lines, together with six check inbred lines, constituted the line trial (Table 2), which was planted side by side with the hybrid trials at all the locations.

Table 1. Description of experimental sites used in the evaluation of the single-cross hybrids and the parents.

Location	Management	Altitude (masl)	Latitude	Longitude	Soil Type
Chisumbanje	Managed heat stress and optimal	423	−20°47′97.10″ S	32°14′05.0″ E	Black clays
Save Valley	Managed heat stress and optimal	450	−20°51′94.9″ S	33°15′93.3″ E	Ferralsols

masl = Meters above sea level.

Table 2. Description of the local lines and the exotic heat tolerant donor lines inter-mated in design II scheme at the CIMMYT-Muzarabani station during the 2018 winter season.

Entry	Line Name	Heterotic Group	Grain Color	Germplasm Source
Local Lines				
FL1	DJ194-3	B	White	CIMMYT-Zimbabwe
FL2	DJ267-5	A	White	CIMMYT-Zimbabwe
FL3	DJ267-6	A	White	CIMMYT-Zimbabwe
FL4	DJ267-7	A	White	CIMMYT-Zimbabwe
FL5	DJ267-8	A	White	CIMMYT-Zimbabwe
FL6	DJ194-10	A	White	CIMMYT-Zimbabwe
FL7	DJ194-2	B	White	CIMMYT-Zimbabwe
FL8	DJ267-9	A	White	CIMMYT-Zimbabwe
FL9	DJ265-6	B	White	CIMMYT-Zimbabwe
FL10	DJ265-8	A	White	CIMMYT-Zimbabwe
FL11	DJ265-10	A	White	CIMMYT-Zimbabwe
FL12	DJ265-15	A	White	CIMMYT-Zimbabwe
FL13	DJ265-13	B	White	CIMMYT-Zimbabwe
FL14	DJ265-14	B	White	CIMMYT-Zimbabwe
FL15	DJ265-15	B	White	CIMMYT-Zimbabwe
Exotic lines				
ML1	CAL14113	B	Yellow	CIMMYT-India
ML2	CAL1412	A	Yellow	CIMMYT-India

Table 2. *Cont.*

Entry	Line Name	Heterotic Group	Grain Color	Germplasm Source
ML3	CAL14135	B	Yellow	CIMMYT-India
ML4	CAL14138	A	Yellow	CIMMYT-India
ML5	CAL1440	A	Yellow	CIMMYT-India
ML6	CAL1469	A	Yellow	CIMMYT-India
ML7	CAL152	A	Yellow	CIMMYT-India
ML8	VL1010762	A	Yellow	CIMMYT-India
ML9	VL1018816	B	Yellow	CIMMYT-India
ML10	VL109126	A	Yellow	CIMMYT-India
ML11	VL143518	B	Yellow	CIMMYT-India
ML12	ZL111056	A	Yellow	CIMMYT-India
ML13	ZL1312	B	Yellow	CIMMYT-India
ML14	ZL132077	A	Yellow	CIMMYT-India

FL—Female line, ML—male line.

2.2. Experimental Design and Trial Management

The hybrid trial (175 single crosses + 5 commercial check hybrids) was laid out in the field using an alpha (0.1) lattice design and replicated two times with 36 incomplete blocks nested in each replicate with a block size of five. On the other hand, the line trial, which consisted of 35 lines (14 exotic + 15 local elite + 6 checks), was also laid out in the field using alpha (0.1) lattice design and replicated twice, with 5 incomplete blocks nested within each replicate, with a block size of five. Each entry was planted in a single-row plot measuring 4 m in length, with an in-row spacing of 0.25 m and inter-row spacing of 0.75 m. Two seeds were planted per each planting station and thinned to one plant/station two weeks after germination to give a plant population of approximately 53,000 plants ha^{-1}.

Heat stress was induced by adjusting planting dates so that the flowering period coincided with the hottest period (October–November), and this was achieved by establishing the trials in the last week of July 2020. Trials under optimal management were planted earlier in May and were supplied with irrigation water whenever the need arose. All trials received basal fertilizer (compound D: 7% N, 14% P, and 7% K), which was applied at a rate of 300 kg ha^{-1}. Top dressing was split and applied at a rate of 150 kg ha^{-1} AN (ammonium nitrate) per application at four and eight weeks after crop emergence. Karate (*Lambdacyhalomethrin*) was applied at a rate of 100 mL per hectare before sowing to control ants and termites. Emamectin benzoate and acetamiprid were applied to the crop at a rate of 250 mL ha^{-1} to control fall armyworm *(Spodoptera frugiperda)* and maize stalk borer *(Busseola fusca)*. Hand weeding was the predominant form of weed control at both sites; however, selective application of paraquat at the rate of 1.5 lha^{-1} was conducted at both sites between 10 and 11 weeks.

2.3. Data Collection

In all the trials, data for flowering dates (days to 50% anthesis and 50% silking), plant height (PH; cm), ear height (EH; cm), and yield (GY; kg) were recorded (Table 3). Some derived traits such as anthesis-silking interval (ASI) and grain yield (12.5% moisture adjustment) were calculated. Weather data (i.e., maximum and minimum temperature (°C) and relative humidity (%)) were measured using the Davis automatic weather station (Table 4). The weather readings were measured using sensors attached to the station through wireless connection.

Table 3. Description of traits recorded in the study.

Trait	Trait Measurement
Grain yield (GY)	Shelled grain weight (kg) per plot adjusted to 12.5% grain moisture.
Plant height (PH)	Distance (cm) of two average plants measured from the ground up to the flag leaf collar.
Ear height (EH)	Distance (cm) of two average plants measured from the ground up to the ear height.
Silking date (SD)	Number of days after planting when 50% of the plants in each plot produce silks
Anthesis date (AD)	Number of days after planting when 50% of the plants in each plot shed pollen.
Anthesis-silking interval (ASI)	Difference between the silking date and anthesis date ASI = SD − AD.

Table 4. Temperatures and relative humidity measured during 2020 winter season.

	Chisumbanje Experiment Station							Save Valley Experiment Station						
Temp (°C)	May	June	July	Aug	Sept	Oct	Nov	May	June	July	Aug	Sept	Oct	Nov
Max	27.0	23.8	23.7	28.2	30.0	31.2	34.1	29.7	26.4	26.3	30.4	32.1	34.6	36.3
Min	13.9	12.2	10.9	13.0	15.4	16.5	20.1	15.8	13.9	12.5	15.0	17.1	19.3	21.7
R.H (%)	59.0	65.9	60.3	53.4	55.2	55.7	57.4	52.1	59.7	54.1	50.5	51.5	52.7	56.2

M = May, Ju = June, J = July, A = August, S = September, O = October, N = November, Max = maximum temperature, Min = minimum temperature, Temp = temperature, and RH = relative humidity.

2.4. Data Analysis

Analysis of variance (ANOVA) for the grain yield within and across environments was performed using restricted maximum likelihood (REML) analysis using the linear mixed models in the Genstat Discovery Software V20.0 [24]. In the analysis, entries were regarded as fixed factors, whilst sites, replications, and incomplete blocks were considered random factors. The Wald statistic ($p < 0.05$) was used to test the significance of various ANOVA components. Bartlett's chi-square test was used to test the homogeneity of residual variances between the environments before combined analysis was performed. The test revealed the heterogeneity of residual variance for grain yield. Therefore, square root transformation was carried out to improve normality of the residuals [25].

The ANOVA for a single site was computed according to the linear model by Barreto et al. [26] as follows:

$$Y_{ijk} = \mu + r_i B_k + E_j + \varepsilon_{ijk} \tag{1}$$

where Y_{ijk} is the response variable, μ is the grand mean, $r_i \cdot B_K$ is the effect of the *k*th block nested in the *i*th replication, k represents blocks, and i stands for replications.

A combined ANOVA was also carried out according to the linear model by Barreto et al. [26] as follows:

$$Y_{ijkl} = \mu + r_j B_k + L_i + El + EL_{il} + \varepsilon_{ijkl} \tag{2}$$

where Y_{ijkl} is the response variable, μ is the grand mean, $r_j \cdot B_K$ is the effect of the *k*th block nested in the *j*th replication, k represents blocks, j represents replications, L_i is the effect of *i*th location, i represents locations, E_l is the effect of the *l*th entry and l represents entries, EL_{il} is the interaction effect of the lth entry and the *i*th location, and ε_{ijkl} is the experimental error.

Best linear unbiased predictions (BLUPs) of the parents and hybrids were computed using the Multi-Environment Trials Analysis in R (META-R) V2.1 R package software [27] and mean separation was conducted using Fisher's unprotected least significant differences (LSD) procedure at a 0.05 probability level. The relative importance of general (GCA) and specific (SCA) combining ability effects were calculated as a proportion of the cross effect sum of squares using the North Carolina Design II analysis model in the Analysis of Genetic Designs in R (AGD-R) V3.0 R software [28].

The relative importance of additive and non-additive gene action in the expression of the grain yield under heat stress, optimal conditions, and across environments, was estimated using Baker's ratio [29], which was calculated from the GCA and SCA variance components following Falconer [30],

$$\text{Baker's ratio} = (\sigma^2 GCA_f + \sigma^2 GCA_m)/(\sigma^2 GCA_f + \sigma^2 GCA_m + \sigma^2 SCA) \tag{3}$$

where $\sigma^2 GCA_f$ is the GCA female variance, $\sigma^2 GCA_m$ is the GCA male variance, and $\sigma^2 SCA$ is the SCA variance. If the Baker's ratio is >0.5, it implies that GCA is more important than SCA in the inheritance of the character, and a ratio < 0.5 implies that SCA is more important than GCA in the inheritance of the character [29].

From the factorial mating design, narrow sense heritability (h^2) was determined based on female additive variance following Dabholkar [31],

$$h^2_f = 4\sigma^2 GCA_f/(\sigma^2 e/r + 4\sigma^2 SCA + \sigma^2 GCA_f) \tag{4}$$

where h^2_f is the female narrow sense heritability based on GCA and SCA variances; $\sigma^2 GCA_f$, is variance for general combining ability of female parents; $\sigma^2 SCA$ is the variance of specific combining ability; $\sigma^2 e$ is the error variance; and r is number of replications.

Heritability was computed based on the female additive variance because from a balanced factorial design, the magnitude of SCA and GCA are equal, and if not, then there should be a maternal effect. Therefore, female additive variance was preferred to males because it accounts for any maternal effects in the cross [31]. Broad-sense heritability (H^2) was calculated following Dabholkar [31] as follows:

$$H^2 = 4\sigma^2 GCA_f + 4\sigma^2 SCA/(\sigma^2 e/r + 4\sigma^2 SCA + \sigma^2 GCA_f). \tag{5}$$

3. Results

3.1. Performance of the Hybrids and the Parents under Heat Stress and Non-Stress Conditions

Combined analysis of variance (ANOVA) showed significant ($p < 0.05$) effects for grain yield under managed heat stress, optimal conditions, and across environments (Table 5). The general combining ability–female (GCAf) and specific combining ability (SCA) mean squares also showed significant ($p < 0.001$) effects for grain yield under managed heat stress, optimal conditions, and across environments (Table 5). Similarly, the general combining ability–male (GCAm) mean squares showed significant ($p < 0.01$) effects for grain yield under managed heat stress, optimal conditions, and across environments. The genotype by environment interaction (GEI) mean squares for GCA_f, GCA_m, and SCA were significant ($p < 0.001$) for grain yield across environments. Additive gene action showed to be more important than dominance gene action under both heat stress and optimal conditions (Table 5).

The male variance was generally higher than the female variance across all the test environments. Similarly, genotypic variances were larger than male-by-female variances for grain yield across environments. Additive variances were larger than dominance variances under managed heat stress, optimal conditions, and across environments. Both the additive and dominance variances were larger than the environmental variance. Variation due to the environment was higher than genotypic variation under all the environments used (Table 5).

The broad-sense heritability (H^2) for grain yield was higher than narrow sense heritability (h^2) across all the environments. Broad-sense heritability estimates for grain yield were greater than 80% across environments. Baker's ratio estimates for grain yield were 0.68, 0.5, and 0.62 under heat stress, optimal conditions, and across environments, respectively.

Table 5. Analysis of variance for grain yield performance of the North Carolina Design II crosses evaluated during the 2020 winter season in Zimbabwe.

	Managed Heat Stress		**Optimal Management**		**Across**	
	DF	**MS**	**DF**	**MS**	**DF**	**MS**
Site	1	48.02 ***	1	501.71 ***	3	437.49 ***
Rep (site)	2	50.68 ***	2	7.98 **	4	29.35 ***
Block (rep × site)	140	0.67 ns	140	2.47 **	280	1.78 ***
Female	14	2.44 ***	14	9.41 ***	14	7.82 ***
Male	13	1.97 **	13	8.47 ***	13	7.72 ***
Female × male	182	0.78 ns	182	3.61 *	182	2.85 ***
Female × site	14	0.83 ns	14	7.49 ***	42	3.7 ***
Male × site	13	2.10 ***	13	6.82 ***	39	6.12 ***
Female × male × site	182	0.84 ns	182	2.6 **	728	1.93 ***
Male variance		0.596		0.744		0.667
Female variance		0.008		0.054		0.007
Male × female variance		0.287		0.808		0.405
Genotype variance		0.871		1.581		1.061
Additive variance (AV)		3.486		6.325		4.244
Dominance variance (DV)		1.149		3.234		1.620
Environmental variance (EV)		0.473		1.704		0.631
Baker's ratio		0.68		0.50		0.62
Narrow sense heritability (h^2_f)		0.023		0.052		0.01
Broad-sense heritability (H^2)		0.85		0.83		0.85

*, **, and *** are significant at the 0.05, 0.01, and 0.001 probability levels, respectively, ns = non-significant, DF = degrees of freedom, MS = mean squares, and Rep = replication.

3.2. Exotic Donor Lines That Confer Heat Tolerance Attributes in Combination with the Locally Adapted Parental Lines

The best exotic HSTDLs with positive GCA effects for grain yield and high *per se* performance (PSP) values for grain yield under managed heat stress were identified as: CAL14138 (GCA = 1.89 t ha^{-1}, PSP = 1.84 t ha^{-1}), CAL152 (GCA = 1.02 t ha^{-1}, PSP = 1.71 t ha^{-1}), and CAL1440 (GCA = 0.83 t ha^{-1}, PSP = 1.23 t ha^{-1}) (Table 6). Under optimal conditions, the exotic HSTDLs: CAL14138 (GCA = 1.84 t ha^{-1}, PSP = 1.6 t ha^{-1}), CAL152 (GCA = 0.95 t ha^{-1}, PSP = 2.09 t ha^{-1}), and CAL1440 (GCA = 0.99 t ha^{-1}, PSP = 1.76 t ha^{-1}) had the highest GCA effects for grain yield coupled with high PSP for grain yield. Across environments, the exotic HSTDLs: CAL14138 (GCA = 1.92 t ha^{-1}, PSP = 1.72 t ha^{-1}), CAL1440 (GCA = 0.94 t ha^{-1}; PSP = 1.41 t ha^{-1}), and CAL152 (GCA = 1.02 t ha^{-1}; PSP = 1.92 t ha^{-1}) had the highest positive GCA effects as well as PSP for grain yield. It is interesting to note that the exotic HSTDLs CAL14138, CAL152, and CAL1440, all showed significant and positive GCA effects for grain yield under managed heat stress, optimal conditions, and across environments, which was in every case, coupled with superior *per se* performance grain yield (Table 6).

Table 6. Estimates of the general combining ability of heat-tolerant donor lines and their *per se* grain yield performance in North Carolina Design II crosses and line trials conducted in Zimbabwe during the 2020 winter season.

Line	Exotic Donors	Managed Heat			Optimal Management			Across Environments		
		PSP	GCA	Rank_GCA	PSP	GCA	Rank_GCA	PSP	GCA	Rank_GCA
A. Exotic HSTDLs (males)										
ML1	CAL14113	0.43	−0.374 ^{ns}	8	0.60	−0.597 ^{ns}	12	0.51	−0.500 *	10
ML2	CAL1412	0.88	−0.761 **	14	1.28	−0.585 ^{ns}	10	1.08	−0.709 *	13
ML3	CAL14135	0.58	−0.385 ^{ns}	10	0.58	−0.981 *	14	0.58	−0.723 **	14
ML4	CAL14138	1.84	1.889 ***	1	1.60	1.840 ***	1	1.72	1.918 ***	1
ML5	CAL1440	1.23	0.826 ***	3	1.76	0.990 **	2	1.41	0.942 ***	3
ML6	CAL1469	0.52	−0.235 ^{ns}	6	0.53	0.450 ^{ns}	4	0.53	0.134 ^{ns}	5
ML7	CAL152	1.71	1.017 ***	2	2.09	0.952 *	3	1.92	1.022 ***	2
ML8	VL1010762	0.33	−0.376 ^{ns}	9	0.55	−0.650 ^{ns}	13	0.44	−0.531 *	11
ML9	VL1018816	0.94	−0.186 ^{ns}	5	0.91	−0.069 ^{ns}	6	0.93	−0.124 ^{ns}	6
ML10	VL109126	1.57	0.275 ^{ns}	4	2.22	0.016 ^{ns}	5	1.89	0.147 ^{ns}	4
ML11	VL143518	1.33	−0.541 *	13	1.27	−0.415 ^{ns}	9	1.30	−0.491 ^{ns}	9
ML12	ZL111056	0.39	−0.247 ^{ns}	7	0.58	−0.107 ^{ns}	7	0.47	−0.176 ^{ns}	7
ML13	ZL1312	0.71	−0.428 ^{ns}	11	0.98	−0.251 ^{ns}	8	0.87	−0.357 ^{ns}	8
ML14	ZL132077	1.08	−0.474 *	12	0.62	−0.593 ^{ns}	11	0.85	−0.553 *	12
B. CIMMYT-Zimbabwe elite lines (females)										
FL1	DJ194-3	0.68	−0.014	12	1.14	−0.068	11	0.90	−0.014	12
FL2	DJ267-5	0.31	0.044	2	1.04	−0.042	10	0.64	0.005	6
FL3	DJ267-6	1.77	−0.001	8	2.43	−0.124	14	2.08	−0.019	13
FL4	DJ267-7	0.71	0.012	5	0.72	0.02	4	0.71	0.007	5
FL5	DJ267-8	1.34	−0.045	14	1.23	0.013	6	1.27	−0.011	10
FL6	DJ194-10	0.88	−0.008	11	0.90	−0.039	8	0.88	−0.008	9
FL7	DJ194-2	0.79	0.023	4	0.59	0.007	7	0.68	0.008	4
FL8	DJ267-9	1.76	0.066	1	2.27	0.251	1	2.02	0.058	1
FL9	DJ265-6	1.20	−0.022	13	1.04	0.014	5	1.09	−0.004	8
FL10	DJ265-8	1.67	0.025	3	1.74	−0.04	9	1.72	0.001	7
FL11	DJ265-10	1.81	−0.003	9	1.94	0.226	2	1.89	0.035	2
FL12	DJ265-12	0.60	−0.003	10	1.03	−0.083	12	0.81	−0.014	11
FL13	DJ265-13	0.67	0.003	7	0.33	−0.152	15	0.48	−0.023	14
FL14	DJ265-14	1.95	0.010 ^{ns}	6	2.22	0.131	3	2.08	0.023	3
FL15	DJ265-15	0.65	−0.087 ^{ns}	15	0.73	−0.115	13	0.69	−0.044	15
Grand mean		1.05			1.23			1.14		
LSD (0.05)		0.74			0.77			0.77		
Heritability		0.27			0.57			0.77		

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ^{ns} = non-significant, PSP = per se performance; GCA = general combining ability; and GYD = grain yield.

3.3. Exotic HSTDLs That Can Positively Contribute to Grain Yield Performance in Single-Cross Hybrid Combinations with Local Elite Lines under Managed Heat Stress and Optimal Conditions

Table 7 and Table S1 shows the estimates of SCA for grain yield performance of the exotic HSTDLs and CIMMYT-Zimbabwe elite line crosses under managed heat stress, optimal conditions, and across environments. The crosses with positive and significant SCA effects for grain yield under managed heat stress were identified as DJ265-15 × VL1018816 (SCA = 1.05 t ha^{-1}, Mean grain yield performance of the cross (MGYP$_{cross}$) = 5.36 t ha^{-1}) and DJ267-9 × CAL1440 (SCA = 0.73 t ha^{-1}; MGYP$_{cross}$ = 5.65 t ha^{-1}). Under optimal conditions, the best specific combiners were: DJ26-13 × CAL1469 (SCA = 1.49 t ha^{-1}; MGYP$_{cross}$ = 7.61 t ha^{-1}), DJ265-10 × VL109126 (SCA = 1.42 t ha^{-1}; MGYP$_{cross}$ = 7.56 t ha^{-1}), DJ267-8 × CAL1440 (SCA = 1.35 t ha^{-1}, MGYP$_{cross}$ = 8.08 t ha^{-1}), and DJ265-10 × CAL14138 (SCA = 1.33 t ha^{-1}, MGYP$_{cross}$ = 8.49 t ha^{-1}). Genotypes DJ265-10 × CAL14138 (SCA = 0.89 t ha^{-1}, MGYP$_{cross}$ = 8.49 t ha^{-1}) and DJ265-10 × VL109126 (SCA = 0.88 t ha^{-1}, MGYP$_{cross}$ = 7.56 t ha^{-1}) were the best specific combiners across environments.

Table 7. Best specific combiners for grain yield performance among the exotic HSTDLs and CIMMYT-Zimbabwe crosses evaluated under heat stress and optimal conditions during the 2020 winter season in Zimbabwe.

Hybrid	Managed Heat		Optimal Management		Across Environments	
	MGYP (tha^{-1})/Rank	SCA Effect	MGYP (tha^{-1})/Rank	SCA Effect	MGYP (tha^{-1})/Rank	SCA Effect
DJ265-15 × VL1018816	5.36 (12)	1.05 **	5.56 (77)	0.03	5.46 (35)	0.526
DJ267-9 × CAL1440	5.65 (7)	0.73 *	7.28(9)	0.7	6.62 (5)	0.739
DJ265-15 × CAL14138	6.45 (1)	0.697	6.19 (40)	−0.21	6.40 (10)	0.199
DJ265-14 ×ZL1312	4.23 (58)	0.673	6.48 (27)	0.93	5.64 (29)	0.857
DJ194-3 × CAL1412	4.21 (64)	0.624	5.33 (95)	0.3	4.76 (81)	0.492
DJ267-7×VL1010762	3.10 (146)	0.603	5.52 (83)	−0.23	4.42 (114)	0.174
DJ267-7×VL143518	4.37 (50)	0.6	5.65 (69)	0.39	5.04 (60)	0.516
DJ265-15 × CAL14113	4.40 (44)	0.541	6.23 (39)	1	5.42 (37)	0.825
DJ265-8 × VL1010762	4.46 (40)	0.54	5.96 (50)	0.63	5.27 (45)	0.624
DJ267-5 × CAL1440	5.40 (10)	0.533	5.40 (90)	−0.43	5.40 (39)	−0.003
Heritability	80%		66%		80%	
Grand Mean	3.95		5.43		4.7	
LSD	0.83		1.47		0.96	
CV	21.76		24.35		23.96	

*, ** are significant at the 0.05 and 0.01 probability levels, respectively, LSD = least significant differences, CV = coefficient of variation, SCA = specific combining ability, and MGYP = mean grain yield.

3.4. Per se Performance of Exotic HSTDLs and the CIMMYT-Zimbabwe Elite Lines under Stress and Non-Stress Conditions

The *per se* performance of the CIMMYT-Zimbabwe and exotic HSTDLs with respect to grain yield, days to 50% anthesis (AD), and anthesis-silking interval (ASI) are presented in Table 8. The three best performing exotic HSTDLs in terms of grain yield under managed heat stress were identified as CAL14138 (1.84 t ha^{-1}), CAL152 (1.71 t ha^{-1}), and VL109126 (1.5 t ha^{-1}). Under optimal conditions, the best three yielders among the exotic HSTDLs were VL109126 (2.22 t ha^{-1}), CAL152 (2.09 t ha^{-1}), and CAL1440 (1.76 t ha^{-1}). Across environments, the best exotic HSTDLs yielders were CAL152 (1.92 t ha^{-1}), VL109126 (1.89 t ha^{-1}), and CAL14138 (1.72 t ha^{-1}). Interestingly, the exotic lines CAL152 and VL109126 showed superior performance under both stress and optimal conditions. The number of days to 50% anthesis ranged from 69 to 78, 72 to 80, and 71 to 79 under managed heat stress, optimal, and across environments, respectively. On the other hand, ASI ranged from −0.5 to 3.25, −0.75 to 4.25, and −0.87 to 3.73 under managed heat stress, optimal, and across environments, respectively. In addition, the number of days to 50% anthesis and ASI were shortened under managed heat stress conditions. The broad-sense heritability estimates of 27%, 57%, and 77% were observed for grain yield under managed heat stress, optimal, and across environments, respectively. The number of days to 50% anthesis was highly heritable under both managed heat stress and optimal conditions (Table 8).

Table 8. Agronomic performance of the CIMMYT-Zimbabwe elite lines and the exotic HSTDLs evaluated under heat stress and optimal conditions during the 2020 winter season in Zimbabwe.

		Managed Heat Stress			Optimum Management			Across Environments		
Exotic	Lines	GY (t ha^{-1})	AD (Days)	ASI (Days)	GY (t ha^{-1})	AD (Days)	ASI (Days)	GY (t ha^{-1})	AD (Days)	ASI (Days)
A. Exotic HSTDLs										
ML4	CAL14138	1.84	73	0.50	1.60	74	1	1.72	74	0.37
ML7	CAL152	1.71	73	−0.50	2.09	75	0.75	1.92	74	−0.25
ML10	VL109126	1.57	69	0.52	2.22	72	1.5	1.89	71	0.62
ML11	VL143518	1.33	77	0.75	1.27	80	4.25	1.30	78	0.87
ML5	CAL1440	1.23	75	0	1.76	77	0.5	1.41	76	1.50
ML14	ZL132077	1.08	79	−0.74	0.62	78	0.25	0.85	79	−0.87
ML9	VL1018816	0.94	79	−0.01	0.91	80	0	0.93	79	−0.13
ML2	CAL1412	0.88	71	1.26	1.28	74	0.5	1.08	72	1.50
ML13	ZL1312	0.71	73	−0.01	0.98	73	0.75	0.87	73	0.75
ML3	CAL14135	0.58	75	0.75	0.58	79	−0.75	0.58	77	0.62
ML6	CAL1469	0.52	74	0	0.53	75	1.5	0.53	74	−0.12
ML1	CAL14113	0.43	77	−0.25	0.60	79	1	0.51	78	0
ML12	ZL111056	0.39	74	1.50	0.58	75	−0.75	0.47	75	1.50
ML8	VL1010762	0.33	77	−0.01	0.55	77	2.75	0.44	77	0.25
B. CIMMYT-Zimbabwe elite lines										
FL14	DJ265-14	1.945	74	−1.26	2.22	77	−0.25	2.08	75	−0.88
FL11	DJ265-10	1.81	76	1.76	1.94	79	−1	1.89	77	1.37
FL3	DJ267-6	1.77	76	3.23	2.43	77	1	2.08	76	3.73
FL8	DJ267-9	1.76	74	1.75	2.27	76	−0.25	2.02	75	1.88
FL10	DJ265-8	1.67	78	0	1.74	79	3	1.72	78	0.38
FL5	DJ267-8	1.34	77	0.50	1.23	79	1.5	1.27	78	0.37
FL9	DJ265-6	1.20	78	0.33	1.04	81	1.75	1.09	79	0.28
FL6	DJ194-10	0.88	78	0.75	0.90	79	−0.5	0.88	79	0.62
FL7	DJ194-2	0.79	73	1.00	0.59	76	0.75	0.68	75	0.12
FL4	DJ267-7	0.71	77	0.50	0.72	78	0.25	0.71	78	0.50
FL1	DJ194-3	0.68	75	1.24	1.14	76	1	0.90	75	1.12
FL13	DJ265-13	0.67	77	−1.25	0.33	78	0.75	0.48	77	−0.76
FL15	DJ265-15	0.649	75	1.75	0.73	76	−0.25	0.69	75	1.25
FL12	DJ265-12	0.60	76	1.25	1.03	75	1.75	0.81	76	1.37
FL2	DJ267-5	0.31	77	−0.01	1.04	78	0.75	0.64	77	0.88
G.variance		0.06 ***	4.67 ***	0.42 **	0.18 ***	4.55 ***	0.23 ns	0.19 ***	5.26 ***	0.55 ***
G × E variance		0.29 ***	0.56 ns	0.17 ns	0.19 ***	2.26 **	0.57 ns	0.16 ***	0.75 **	0.15 ns
Heritability		0.27	0.80	0.47	0.57	0.67	0.18	0.77	0.88	0.63
Grand mean		1.05	75.44	0.45	1.23	77.16	0.75	1.14	76.31	0.6
LSD (0.05)		0.74	3.72	2.41	0.77	4.11	3.39	0.77	3.92	2.99
CV (%)		35.65	2.52	274.36	31.79	2.72	230.67	34.27	2.62	255.33

, and * are significant at the 0.01, and 0.001 probability levels, respectively, ns = non-significant, GY = grain yield, AD = anthesis date, ASI = anthesis-silking interval, CV = coefficient of variation, LSD = least significant difference, G.variance = genotypic variance, and GxE variance = genotype by environment variance.

4. Discussion

Availability of sufficient genetic variability is a key component for effective selection in any breeding program. In the absence of sufficient genetic diversity, exotic germplasm can be sourced and introduced to the program to introgress the required genes [32,33]. Generally, breeders conduct combining ability studies before using exotic germplasm in their breeding programs to identify good parents for the development of hybrids and

superior parents to use in breeding cycles [16,34]. The selection of good parents for hybrid development is based on the performance of the parents in hybrid combination [20], while selection of superior parents for use in the breeding cycle is based on the *per ser* performance of parents [35].

In the current study, a set of heat-tolerant exotic donor lines from CIMMYT-India and elite lines from CIMMYT-Zimbabwe were evaluated for their combining ability effects and *per se* performance under managed heat stress and optimal conditions. The results of this study reveal significant GCA and SCA effects under managed heat stress, optimal, and across locations. This reflects the presence of wide genetic variability for heat stress tolerance among the inbred lines and their single-cross hybrids, providing an opportunity for selection. These findings suggest that both additive and non-additive genetic effects are important for the inheritance of grain yield. Therefore, hybridization and recurrent selection might be helpful for genetic enhancement of heat tolerance and superior performance under heat stress conditions [20]. The findings concur with several authors [17,19,22,36–38] who reported significant GCA and SCA for grain yield under heat-stressed and optimal conditions.

The significant GCA_f and GCA_m effects observed for grain yield under managed heat stress and optimal conditions imply that both parents contributed to the inheritance of grain yield in the hybrids under these conditions. The significant $GCA_m \times E$, $GCA_f \times E$, and $SCA \times E$ effects on grain yield performance observed under optimal conditions, show that the optimal sites were different from each other, an indication that the combining ability of the parental lines was not consistent under optimal conditions and the environment had an effect on grain yield. This suggests the need for selecting different parental lines for hybrids to be used in specific environments. Additionally, these results suggest that both additive and non-additive genetic effects interacted with the environment in the expression of grain yield, thus justifying a multi-location improvement strategy in the development of lines with tolerance to heat stress.

The non-significant $GCA_m \times E$, $GCA_f \times E$, and $SCA \times E$ effects observed on grain yield performance under managed heat stress conditions reflect that the heat stress sites were comparable, and the inbred lines performed consistently across heat stress conditions; hence, the environment had no effect on the grain yield. These observations were inconsistent with the previous study by Osuman et al. [19], who reported significant interactions for grain yield under heat stress conditions. The findings also contradict with those of Derera et al. [39], who reported significant GCA_m, GCA_f, and SCA by environment interactions for grain yield under stress environments. The absence of significant $SCA \times E$ interaction for grain yield under heat stress environments suggested that grain yield would be stable in specific hybrid combinations under heat stress conditions. These results are consistent with those found by Ifie et al. and Oyekunle et al. [40,41], who reported lack of significant $SCA \times E$ interaction variances for grain yield under stress environments.

The prevalence of additive gene effects over dominance revealed by this study suggests that additive gene action was more important in the inheritance of grain yield under heat stress, optimal conditions, and across locations for the germplasm tested. These results are in line with the findings of Begna and Fasahat [20,34], who reported that when GCA effects prevail over SCA effects, early generation testing of crosses can be effectively conducted, and promising hybrids can be identified and selected based on the GCA effects of the crosses. However, using the GCA effects of the parents alone to predict hybrid performance will not always be sufficient because of the significant SCA [39]. This also implies that heat-tolerant inbred lines with high GCA effects could be extracted from improved cycles of selection of derived populations for hybrid development [42]. Additionally, this observation has the implication that strategies for population improvement that make use of additive gene action, such as S1 family selection, full-sib family, and half-sib family procedures, can be conducted to advance the development of superior hybrids for heat stress-prone environments. The high estimates of Baker's ratio (>0.5) observed on grain yield under all the test environments confirm the importance of additive genetic effects in the inheritance

of grain yield, which implies that the genes controlling grain yield can easily be fixed in advanced generations. The presence of additive gene effects indicates a high chance for predicting the performance of progenies based on the phenotypic scores of the parents [43].

Predominance of additive gene action over the non-additive gene action was revealed by several authors under stress conditions in maize [19,38,39,44–46]. Because additive genetic variance is heritable and genotype is controlled, it affects the parent's breeding value [32]. Hence, the substantial additive variance over dominant variance observed in this study pointed out that the parents used were of high breeding value, allowing for rapid genetic improvement in the production of desired high yielding heat-tolerant genotypes.

The differences in heritability values for grain yield observed under stress, optimal conditions, and across environments were in line with the reports of several researchers [11,22,47]. The higher value of broad-sense heritability for yield, under heat stress, optimal conditions, and across environments suggests that environmental effects had a small role in the variation observed [48]. This result points to less of a need for using many locations and replications in this type of trial. This also reflects the genetic potential of the parents to largely pass on the grain yield trait to subsequent generations. The low narrow sense heritability observed suggests high environmental effects [48]. This also implies that grain yield is controlled by non-additive gene action. These results concur with those reported by Nasser et al. [38].

The GCA effects of an inbred line provide important information for the improvement of a target trait in a population [40]. Significant positive GCA effects for grain yield exhibited by heat donor lines CAL14138, CAL152, and CAL1440 in this study under heat stress, non-stress, and across environments reflect the high potential of these lines to transfer desirable traits to their offspring [38]. Therefore, these lines could be utilized in maize improvement programs as sources of favorable alleles for the genetic enhancement of grain yield under heat stress [22]. Additionally, this result implies that the favorable alleles for grain yield could be easily introgressed into local material and hence improve heat stress tolerance in local material. These results are in agreement with those reported by Nasser et al. [38].

High GCA indicates the inherent genetic value of a parent due to the presence of additive genetic effects. Therefore, the heat-tolerant donors that exhibited positive significant GCA could produce superior segregates in the F2 and later generations, as they could serve as vital sources of beneficial alleles [49]. Furthermore, the presence of high GCA effects for grain yield suggest that continued advancement could be made in selecting for increased grain yield under heat stress.

The significant positive SCA effects for grain yield that were observed under managed heat stress, optimal conditions, and across environments showed a significant deviation from what was expected based on the performance of the parents. The results of this study are in line with those of Jodage et al. and Akula et al. [7,13], who identified specific combiners for grain yield under heat stress conditions. The positive significant SCA observed on crosses, DJ265-15 × VL1018816, and DJ267-9 × CAL1440 implies that the crosses had desirable grain yield alleles for heat stress [34]. The genotypes with high and positive significant SCA estimates from the current study could be used in pedigree starts or doubled haploid in further breeding for heat tolerance in maize in SSA [46].

Information on *per se* performance of the inbred lines is vital for establishing a yield improvement program in plant breeding. Breeders are interested in developing hybrids from vigorous inbred lines that have good *per se* performance and in cross combinations [50]. This study identified the exotic HSTDLs CAL14138, CAL152, and VL109126 as the best donor lines, as they showed significant GCA and superior *per se* performance under heat stress. The *per se* performance of CAL1440, which was among the best combiners, was not pleasing, as it was slightly above the trial mean as compared to other donors that showed high yield potential. This means that the lines CAL14138 and CAL152 can be effectively used in introgression crosses with local lines, while CAL1440 needs further improvement to enhance its tolerance to heat stress. The exotic HSTDL CAL1440 with

average *per se* performance may require crossing with other donor lines, such as CAL14138 and CAL152, which showed good *per ser* performance and positive significant GCA under managed heat stress conditions. The lines with superior *per ser* performance are potential breeding lines that can be used in gene pyramiding schemes with other exotic donor lines. Gene pyramiding through crossing heat-tolerant exotic-by-exotic or exotic-by-local lines can enhance heat tolerance in local material. Additionally, heat-tolerant donor lines can be exposed to gamma irradiation for induction to enhance heat tolerance in sub-tropical breeding material. Good performance exhibited by the exotic HSTDLs, CAL152, and VL109126 across all the test locations shows their wide adaptation; hence the lines can be used in the breeding program to produce high yielding and adaptable heat-tolerant inbred lines. Parents with high GCA effect have greater adaptability and are less affected by the environment [20]. The exotic HSTDL VL1010762, ZL111056, and CAL14113, which exhibited poor *per se* performance under heat stress, can also be used as heat donors in the introgression of heat tolerance into local material.

Results of this study show that the number of days to 50% anthesis and ASI of the inbred lines shortened under managed heat stress conditions. The shortened flowering period could be due to rapid accumulation of heat units [51], leading to the fast initiation of growth phases [52–54]. The shortened ASI observed in this study contradicts with the findings of Osuman et al., Nyombayire et al., and Rezende et al. [19,22,55], who reported an increase in ASI in maize under heat stress conditions. The increase in ASI in maize under heat stress conditions might be due to pollen shedding way before silk emergence [38]. Additionally, Zinn et al. [51] reported that susceptible genotypes allocate less assimilates to the developing ears during stress, and this delays silk appearance. Researchers affirmed the role of heat stress in the lengthening of ASI and considered it an indicator of poor tolerance to drought and heat stress [56], but the materials used in this study differ in this trait.

5. Conclusions and Recommendations

This study demonstrated the potential of exotic HSTDLs from India in improving the adaptation of maize to heat stress in sub-tropical breeding programs. The information generated can help to optimize the breeding strategy and is useful for laying a foundation for heat tolerance breeding programs in SSA. The exotic HSTDLs; CAL14138, CAL152, and CAL1440, that exhibited significant positive GCA effects under heat stress, could be used as important genetic resources for the introgression of heat-tolerant favorable alleles into local maize populations. Single crosses, DJ265-15 × VL1018816, and DJ267-10 × CAL1440 that show high positive and significant SCA effects for grain yield under heat stress conditions can be used for further breeding and contribute to grain yield performance under heat stress conditions. However, backcrossing is recommended to recover the desirable traits of the local female lines.

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