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Predicting zinc-enhanced maize hybrid performance under stress conditions

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Abstract
The low yield potential of most biofortified maize is a barrier to its full adoption and reduces its potential to curb various macro- and micronutrient deficiencies highly prevalent in low-income regions of the world, such as sub-Saharan Africa (SSA). By crossing biofortified inbred lines with different nutritional attributes such as zinc (Zn), provitamin A and protein quality, breeders are attempting to develop agronomically superior and stable multi-nutrient maize of different genetic backgrounds. A key question, however, is the relationship between the biofortified inbred lines per se and hybrid performance under stress and non-stress conditions. In this study, inbred line per se and testcross performance were evaluated for grain yield and secondary traits of Zn-enhanced normal, provitamin A and quality protein maize (QPM) hybrids and estimated heterosis under combined heat and drought (HMDS) and well-watered (WW) conditions. Responses of all secondary traits, except for the number of days to mid-anthesis, significantly differed for HMDS and WW conditions. The contribution of heterosis to grain yield was highly significant under both management levels, although higher mid and high-parent heterosis was observed under WW than HMDS conditions. However, the findings suggest that inbred line performance was the best determinant of hybrid performance under HMDS. Strong correlations were observed between grain yield and secondary traits for both parents and hybrids, and between secondary traits of inbred lines and hybrids under both management levels, indicating that hybrid performance can be predicted based on intrinsic inbred line performance. Phenotypic correlation between grain yield of inbred lines and hybrids was higher under HMDS than WW conditions. This study demonstrated that under HMDS conditions, performance of Zn-enhanced hybrids could be predicted based on the performance of their corresponding inbred lines. However, the parental inbred lines should be systematically selected for desirable secondary traits correlated with HMDS tolerance during inbred line development.

KEYWORDS
combined heat and drought stress, hybrids, inbred lines, zinc biofortification

JEL CLASSIFICATION
Plant Science, Agriculture, Plant Biotechnology

1 | INTRODUCTION

Breeding for high yielding and stable biofortified maize varieties across environments remains a top priority for plant breeders globally, as they strive to curb various macro- and micronutrient deficiencies, prevalent in both medium and low-income regions of the world (Bouis & Saltzman, 2017; Gupta et al., 2020). Maize, rice and wheat provides about 70% of total dietary calories in SSA, Latin America and South-East Asia (Palacios-Rojas et al., 2020). This over-reliance on cereal-based diets exposes a large fraction of this population to various micronutrient deficiencies such as for Zn and vitamin A (Gibson & Anderson, 2009; Prasanna et al., 2020), as well as lack of essential dietary amino acids such as lysine and tryptophan. Breeding efforts of the International Maize and Wheat Improvement Centre (CIMMYT) for nutritionally enhanced maize cultivars dates back to the 1960s, when QPM was developed to close the protein inadequacy gap in vulnerable societies across the world (Nuss & Tanumihardjo, 2011; Vivek et al., 2008). Currently, breeders are taking further steps to develop maize cultivars enhanced with micronutrients such as vitamin A and Zn (Menkir, 2008; Prasanna et al., 2020) since maize has been selected by HarvestPlus as a model crop for micronutrient enhancement (Pfeiffer & McClafferty, 2007). Demographic statistics from the World Health Organization (WHO) show that both vitamin A and Zn deficiency are among the top leading risk factor causes of Disability Adjusted Life Years (DALYs) in low-income countries (Gibson & Anderson, 2009).

Among other intervention strategies such as food fortification, dietary diversification and pharmaceutical supplementation, breeding for Zn-enhanced maize cultivars using normal or other biofortified germplasm is an attractive, cost-effective and sustainable strategy to alleviate the impact of both macro-and micronutrient deficiency in SSA (Hindu et al., 2018; Shahzad et al., 2014). High levels of Zn and carotenoid content in maize genotypes have been reported (Menkir, 2008; Prasanna et al., 2020; Shahzad et al., 2014), but scientists have found a negative correlation between nutrient concentration and grain yield potential in most biofortified maize (Bänziger & Long, 2000). One of the strategies to increase yield of biofortified maize is to exploit heterosis under stress and non-stress conditions. Heterosis is described as the increase in vigour and resistance to biotic and abiotic stresses of the F_1 hybrids compared to their parental inbred lines (Ali et al., 2019). Heterosis was important in raising grain yield (GY) potential of hybrid maize eight decades ago when the first hybrid cultivars were commercialized (Araus et al., 2010). In addition, several studies reported the use of heterosis in helping maize to better adapt to different stress conditions (Ali et al., 2019). For instance, Betrán et al. (2003) reported an increase of grain yield for hybrids compared to their parental inbred lines under drought conditions. In another study by Zaidi et al. (2007), heterosis was more important under normal moisture conditions, whereas mid-parent yield predicted high grain yield for hybrids under excessive moisture conditions. Similarly, heterosis has been reported for both nitrogen and water-use efficiency (Araus et al., 2010; Li et al., 2014).

Genetic variation for tolerance to combined heat and drought conditions in Zn-enhanced maize inbred lines is of paramount importance and enables breeders to select tolerant inbred lines with favourable alleles to use in different cross combinations (Makumbi et al., 2011). However, the best yielding Zn-enhanced inbred lines may not necessarily result in high yielding hybrids. Therefore, it is important to know the extent to which the inbred line per se performance for GY and secondary traits can be used to predict hybrid performance under stress and non-stress conditions. Very few studies have been reported so far on inbred line and hybrid performance using Zn-enhanced, provitamin A and QPM germplasm. The objectives of this study were to (i) evaluate line per se and testcross performance for GY and secondary traits of Zn-enhanced F_1 hybrids, (ii) to assess the correlation between GY and secondary traits of Zn-enhanced parental lines and their hybrids and (iii) examine whether heterosis causes better hybrid performance, regardless of adverse effects of combined heat and drought conditions.

The hypothesis was that inbred line performance is a good predictor of Zn-enhanced maize hybrid performance under combined heat and drought stress conditions.

2 | MATERIALS AND METHODS

2.1 | Plant materials

Eleven introduced and advanced Zn-enhanced inbred lines were crossed with seven testers from normal, provitamin A and QPM genetic backgrounds in an 11×7 line by tester design to form 77 Zn-enhanced hybrids. These tropically adapted Zn donors (Table 1) were introduced to Zimbabwe from CIMMYT-Mexico and the International Institute of Tropical Agriculture (IITA). Testers used in this study were adapted to the tropical lowlands, and mid-altitude and subtropical environments of SSA, and have been extensively evaluated and selected for resistance to foliar diseases and tolerance to various abiotic stresses, including low nitrogen and combined heat and drought stress (HMDS) conditions. These testers have been widely used in different breeding programs at CIMMYT to evaluate new exotic and locally developed experimental germplasm. Therefore, the developed 77 F_1 testcross hybrids were of three distinct nutritional profiles namely Zn plus normal (Zn+NML), Zn plus provitamin A (Zn+PROA), and Zn plus quality protein maize (Zn+QPM). The F_1 seed was generated during the 2017/18 winter season at Muzarabani in Zimbabwe and again in the 2018/19 summer season at CIMMYT's Harare Experimental Station. The parental inbred lines were selected from a number of lines that were previously analysed for nutritional composition. These lines were selected on the basis of high nutrient composition, considerable mineral bioavailability, HMDS tolerance and sufficient seed quantities. The 77 Zn-enhanced single cross hybrids were evaluated together with seven commercial checks from the normal, provitamin A and QPM nutritional groups, under well-watered or winter irrigated (WW) and HMDS conditions. The inbred lines comprised of 11 Zn donors, seven testers, and six checks (Table 1).

2.2 | Experimental sites

The inbred line and hybrid trials were planted adjacent to each other in the 2018/19 and 2019/20 winter seasons at off-season experimental sites managed by CIMMYT in Zimbabwe. This was done to subject them to similar environmental conditions, but in separate trials to avoid plant height interactions. Both HMDS and WW trials were planted at the CIMMYT maize experimental stations in Chiredzi and Chisumbanje (Table 2). Chiredzi is characterized by deep red and well drained clay loam

TABLE 1 Description of the inbred lines used to generate Zn-enhanced F_1 testcross hybrids.

Inbred line code	Genotype name	Nutritional profile	Heterotic groups[a]	Adaptation[b]
Lines				
D2	CLWQHZN14	Zinc donor	A	ST
D3	CLWQHZN19	Zinc donor	A	ST
D5	CLWQHZN49	Zinc donor	B	ST
D6	CLWQHZN53	Zinc donor	B	ST
D7	CLWQHZN69	Zinc donor	A	ST
D8	OBATANPA6	Zinc donor	B	LT
D9	ITZN344	Zinc donor	A	MA
D10	ITZN324	Zinc donor	A	MA
D11	ITZN313	Zinc donor	B	ST
D12	ITZN294	Zinc donor	B	MA
D13	ITZN277	Zinc donor	A	LT
Testers				
PROA1	HPYDL18190	Provitamin A	B	MA
PROA3	CLHP0213	Provitamin A	A	MA
QPM4	TL115798	QPM	A	MA
QPM6	CML144	QPM	B	MA
NML1	CZL16154	Normal	A	MA
NML3	CZL16160	Normal	AB	MA
NML5	CML546	Normal	B	MA

[a]Heterotic group classification: Group A = Tuxpeno, B73 types; Group B = Eto, Ecuador, and Mo17 types.
[b]MA, mid-altitude; LT, lowland tropical; ST, subtropical.

TABLE 2 Description of testing environments used for this study.

Location	Location code	Latitude	Longitude	Altitude (masl)	Management
Chiredzi	CHDRS	21°02′ S	31°57′ E	433	Heat and drought
Chiredzi	CHDRS	21°02′ S	31°57′ E	433	Well-watered
Chisumbanje	CHSRS	20°47′ S	32°13′ E	480	Heat and drought
Chisumbanje	CHSRS	20°47′ S	32°13′ E	480	Well-watered

Abbreviation: masl, meter above sea level.

soils, whereas Chisumbanje has black alluvial soils. These HMDS sites are located in the lowveld of Zimbabwe and experience relatively higher temperatures (32–43°C) than other regions during the rain-free winter season, making it possible to grow irrigated maize in winter.

2.3 | Trial layout

The inbred line trial comprising of 24 entries was laid out in a 6×4 alpha (0.1) lattice experimental design with two replications at all sites. The hybrid trial comprising of 84 entries was planted using a 6×14 alpha (0.1) lattice design, replicated twice. The plots were single rows of 4 m long, with 17 planting stations, 0.75 m inter-row and 0.25 m within row spacing. All the entries were over sown and thinned to one plant per planting station at the V_2 growth stage to give a final plant density of 53,000 ha^{-1}. The final net plot length was 3.5 m at harvesting since the last two plants were discarded at both sides of the plot to eliminate border effects. Inbred line and hybrid border rows were planted at the end of the line and hybrids trials, respectively.

2.4 | Well-watered conditions

Trials evaluated under WW conditions were grown in winter with full irrigation from planting to physiological maturity. Trials at both sites across years received a basal application of 400 kg ha^{-1} compound D fertilizer (7% N: 14% P_2O_5: 7% K2O). This translates to a basal fertilizer application providing 28 kg N ha^{-1}, 56 kg P ha^{-1} and 28 kg K ha^{-1} at planting. The basal fertilizer was broadcasted and incorporated into the soil by a disc plough mounted on a tractor. Ammonium Nitrate (AN) was used for top dressing with two split applications at a rate of 69 kg N ha^{-1} per split. The first N application was done at 4 weeks after crop emergence and the second split was applied at 6 weeks after crop emergence or V10 stage.

Glyphosate and atrazine (Atrazine WP) were applied as pre- and post-emergence herbicides, respectively. In addition to atrazine, Bentazone was applied as post-emergence herbicide for controlling nutsedge weeds (*Cyperus rotundus* and *Cyperus esculentus*) that emerged under well-watered conditions. Hand weeding was also done where necessary. Integrated insect pest management was done during all crop developmental stages.

2.5 | Combined heat and drought stress

These trials were planted around mid-August during the 2 years of evaluation and flowered during the hottest period in the lowveld. In addition, rainfall incidences were negligible during this period, coupled with relatively low humidity of >50%. Planting during this period of the year exposed trials to combined effects of drought and elevated temperature conditions (Figure 1). All trials were planted and managed in a similar manner to WW trials except for different water supply. At Chisumbanje, the water supply was through furrow irrigation, whereas at Chiredzi, sprinkler irrigation was applied. Trials were initially grown under WW conditions to about 45 days from planting, and thereafter exposed to HMDS conditions. Thus irrigation was withdrawn 2 weeks before flowering around mid-October when mean daily temperature was above 35°C in both years. This means that combined effects of HMDS coincided with the most sensitive reproductive phase, which ultimately has the greatest impact on grain yield. Irrigation was resumed after 21 days but applied once a week only to allow grain filling to occur.

2.6 | Data collection

Plant height (PH) was recorded using a laser distance meter by measuring all the plants in the plot and recording the average (Hämmerle & Höfle, 2016). Plant height measurements were taken after completion of 50% male flowering, as the distance from the ground surface to the node bearing the flag leaf (Zaidi et al., 2007). Number of days from planting to male anthesis or tasselling (AD) was recorded daily when 50% of the plants had tassels shedding pollen. Likewise, the female (silking) anthesis (SD) was recorded when 50% of the plants had protruding silks. Anthesis silking interval (ASI) was determined as the difference between days to silking and anthesis. Leaf

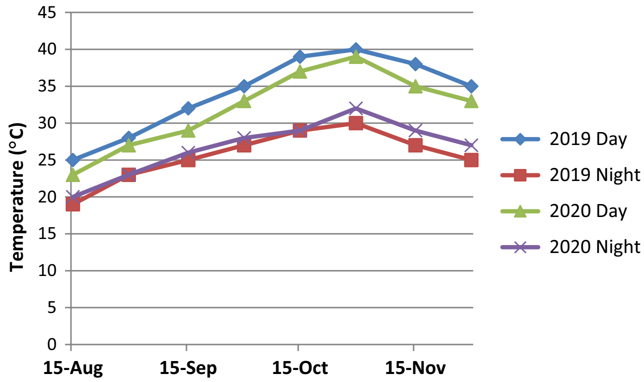

FIGURE 1 Day and night temperatures recorded at Chiredzi and Chisumbanje during the growing period.

senescence (SEN) was recorded as the average of three recordings taken at 2, 4 and 6 weeks after mid-silking using a scale of 1 to 10 and final score expressed as a proportion of number of plants showing senescence in the plot. Number of ears was recorded per plot and number of ears per plant (EPP) was calculated as the proportion of the total number of ears harvested divided by the total number of plants at harvest. Trials were left to dry in the field, but in some cases, ears were dried artificially to a constant moisture content as described by MacRobert et al. (2014). Dried ears were shelled either by hand or by an Almaco sheller and GY was recorded and adjusted to 12.5% moisture content. GY was only measured for the net plot area as the two border plants close to the alley were discarded.

2.7 | Statistical analysis

Analysis of variance (ANOVA) was done using the PROC MIXED procedure (SAS, 2002). This procedure uses the Restricted Maximum Likelihood (REML) method in the mixed model. In the model, the genotypes (inbred lines or hybrids), environments and their interactions were considered as fixed, and years, replication and incomplete blocks as random factors. Combined analysis for all the sites and over seasons was done using Spatial Multi-Environmental Trial Analysis with R (META-R) (Rodríguez et al., 2016), which indicated that year and year × entry effects were insignificant for all the traits. Data for both years was pooled after further testing the homogeneity of error variance using Hartley's F_{max}-test (Zaidi et al., 2007). Mean separation was done using Fisher's protected Least Significant Difference (LSD) test at 5% significance level, by comparing pairwise differences between factor level means. The following statistical model (1) was used for computing analysis of variance for the measured traits.

$$Y_{ijkl} = \mu + E_k + B(E)_{l\,(k)} + G_{ij} + GE_{ijk} + \varepsilon_{ijkl} \quad (1)$$

where Y_{ijkl} is the response variable observed on an inbred line or hybrid, μ = population mean; E_k = the effect of the kth environment; $B(E)_{l(k)}$ = effect of block lth block within kth environment, G_{ij} = effect of the ith or jth genotype (inbred line or hybrid), $G_{ij} \times E_k$ = interaction effect of the ith or jth genotype with kth environment; ε_{ijk} = residual error.

Broad sense heritability (H^2) of the observed traits was estimated using META-R statistical software as shown in Equation (2). H^2 indicated the ratio of genotypic variance (VG) to the total phenotypic variance (VP) (Rukundo et al., 2017). Variance components explained for phenotypic traits included the genotypic variance, genotype × environment (G × E) interaction t and residual variance. The formula for estimating H^2 used was:

$$H^2 = \frac{\sigma^2 G}{\sigma^2 G + \sigma^2 G \times E + \sigma^2 \varepsilon} \quad (2)$$

where $\sigma^2 G$ is the genotypic variance, $\sigma^2 G \times E$ is the variance due to $G \times E$ interaction effect, and $\sigma^2 \varepsilon$ is the error or residual variance.

High-parent (HPH) and mid-parent heterosis (MPH) were determined as the percentage superiority in terms of agronomic performance of F_1 testcross hybrids over the best or the mid-parent respectively (Makumbi et al., 2011). MPH referred to the superiority of an F_1 testcross hybrid compared to the average performance of its two parents (Ali et al., 2019). HPH or heterobeltiosis represented the superiority of F_1 hybrid performance over the better or high-parent value (Ali et al., 2019). Hence, mid-parent heterosis was calculated as:

$$\mathrm{MPH} = \left[\left(F_1 - \mathrm{MP}\right) / \mathrm{MP}\right] \times 100. \quad (3)$$

where F_1 = Mean trait performance of the F_1 hybrid and mid-parent value (MP) was the average performance of the two parental inbred line parents [MP = (P1 + P2)/2].

High-parent heterosis was calculated as:

$$\mathrm{HPH} = \left[\left(F_1 - \mathrm{HP}\right) / \mathrm{HP}\right] \times 100 \quad (4)$$

where HP was the performance of the better performing inbred parent.

The multi-trait selection index (Cerón-Rojas & Crossa, 2018) was used to select the best and worst performing Zn donor lines and hybrids. Traits were ranked according to importance using a score of 1 to 5, where GY had the maximum weight (+5). Correlations and regressions between secondary traits and final grain yield for both parental inbred lines and hybrids, and between mid-parents and hybrids were computed using linear regression in Genstat, 18th version (VSN, 2017). Amongst the hybrids, the best and worst five entries were selected using a multi-trait selection index based on phenotypic scores.

3 | RESULTS

3.1 | Combined heat and drought effects on agronomic performance of hybrids and their parental inbred lines

The combined ANOVA across management levels and years showed that mean squares for genotype, management, genotype by year and management by year were highly significant ($p \leq 0.01$) for all traits (data not shown). All the traits except for number of days to 50% anthesis were significantly affected by the adverse effects of combined heat and drought stress (Table 3). In susceptible hybrids and parents, HMDS significantly reduced grain yield, increased the ASI, and accelerated senescence. In addition, severe barrenness and drastic reduction of plant height was observed under HMDS for both hybrids and their parents. Based on the mean GY, the effects of HMDS were more pronounced on the hybrids than their parents, despite that hybrids showed significantly higher phenotypic performance than their parental lines under both management levels due to heterotic effect. GY for inbred lines under HMDS was 72.2% of the GY observed under WW, as compared to 35.4% for hybrids (Table 3). Despite the large reduction of GY of hybrids under HMDS, GY of inbred lines was only 56.5% and 27% of GY of hybrids under HMDS and WW conditions, respectively. Hence, hybrids were consistently much higher yielding than inbred lines across all management conditions. The impact of HMDS on both parents and hybrids was not significant for AD, but increased the ASI by 150% and 200%, respectively, compared to the performance observed under WW conditions. Similarly, EPP was reduced by almost half of that observed under WW conditions (Table 3). Inbred lines were relatively shorter than hybrids under all management conditions. However, the mean PH for the inbred lines under WW conditions (180.3 cm) was comparable to the mean PH of hybrids under HMDS conditions (178.4 cm), indicating significant reduction of PH of hybrids under HMDS.

Trait means for the selected best and worst performing hybrids and inbred lines are shown in Table 4. For the hybrids under HMDS conditions, significant differences ($p \leq 0.05$) were observed between the best and worst groups for all the measured traits. However, these hybrids were not significantly different for AD, ASI, and

TABLE 3 Differences between parental lines and their F_1 hybrids under combined heat and drought stress and well-watered conditions.

	Combined heat and drought stress (HMDS)						Well-watered (WW)					
	GY	AD	ASI	PH	EPP	SEN	GY	AD	ASI	PH	EPP	SEN
Parents												
Mean	1.3	71.0	1.8	149.6	0.6	0.8	1.8	69.6	1.2	180.3	0.9	0.5
Maximum	2.0	76.2	4.3	171.2	1.1	0.9	3.3	72.6	1.7	200.3	1.0	0.6
Minimum	0.6	64.4	−0.3	135.1	0.4	0.4	1.2	64.7	0.2	165.3	0.6	0.4
LSD (0.05)	0.6	3.6	0.9	13.9	0.2	0.1	0.6	1.2	0.3	12.3	0.1	0.1
CV (%)	36.5	1.3	55.2	6.6	28.2	11.6	21.6	1.1	28.8	5.1	23.5	12.1
H^2	0.42	0.52	0.55	0.49	0.58	0.46	0.61	0.56	0.67	0.63	0.69	0.59
Av HMDS/WW (%)	72.2	102.0	150.0	82.9	66.7	160.0						
Hybrids												
Mean	2.3	69.8	2.4	178.4	0.6	0.7	6.5	70.1	1.2	212.6	1.0	0.5
Maximum	3.8	76.0	3.1	190.3	0.8	0.7	7.9	74	2.1	222.9	1.0	0.5
Minimum	0.9	64.3	1.9	165.8	0.5	0.5	3.6	65.8	0.5	198.2	0.9	0.5
LSD	0.9	2.6	1.0	12.4	0.2	0.0	1.0	2.3	1.1	14.4	0.1	0.1
CV (%)	39.7	2.5	44.3	6.2	22.3	14.1	15.9	2.0	0.6	5.6	15.2	15.8
H^2	0.62	0.66	0.3	0.65	0.54	0.47	0.68	0.81	0.75	0.49	0.3	0.24
Av HMDS/WW (%)	35.4	99.6	200.0	83.9	60.0	140.0						

Abbreviations: AD, number of days to mid-anthesis; ASI, anthesis-silking-interval; CV, coefficient of variation; EPP, number of ears per plant; GY, Grain yield ($t\,ha^{-1}$); H^2, broad sense heritability; LSD (0.05), least significant difference ($p \leq 0.05$); PH, plant height (cm); SEN, senescence.

TABLE 4 Means of grain yield and secondary traits of best and worst performing hybrids and parental lines under combined heat and drought stress and well-watered conditions.

Traits	Moisture	Hybrids Best	Hybrids Worst	Hybrids t-value	Hybrids LSD (0.05)	Parents Best	Parents Worst	Parents t-value	Parents LDS (0.05)
Grain yield ($t\,ha^{-1}$)	HMDS	3.0	1.6	12.46**	0.9	1.7	0.7	9.14**	0.6
	WW	7.5	5.4	12.34**	1.0	2.3	1.5	3.01*	0.6
Mid-anthesis (days)	HMDS	69.5	70.5	−2.61*	2.6	70.2	72.2	-1.51^{ns}	3.6
	WW	69.6	69.8	-1.18^{ns}	2.3	69.6	70.4	-0.77^{ns}	1.2
Anthesis silking interval (days)	HMDS	2.4	3.9	−4.29**	1.0	1.8	3.9	−6.04**	0.9
	WW	1.1	1.2	-0.9^{ns}	1.1	1.0	1.3	-1.02^{ns}	0.3
Plant height (cm)	HMDS	181.3	173.9	4.36**	12.4	161.9	146.3	3.36*	13.9
	WW	214.2	210.9	2.38*	14.4	182.5	176.6	1.14^{ns}	0.3
Ears per plant	HMDS	0.7	0.6	4.80**	0.2	0.8	0.5	2.87*	0.2
	WW	1.0	0.9	6.81**	0.1	0.9	0.9	0.58^{ns}	0.1
Senescence (%)	HMDS	0.5	0.6	−5.92**	0.0	0.5	0.6	-1.46^{ns}	0.1
	WW	0.5	0.5	-2.14^{ns}	0.1	0.5	0.5	-0.44^{ns}	0.1

Note: Best and worst hybrids, 20 each, were selected based on their performance under combined heat and drought (HMDS) and well-watered (WW) conditions using multi-trait selection index. Student's *t*-test was used to test the significance between the means of the best and worst groups of experimental genotypes.

*$p \leq 0.05$; **$p \leq 0.01$. LSD $_{(0.05)}$ is the least significant differences ($p \leq 0.05$).

TABLE 5 Heterosis (%) in the selected best and worst hybrids over mid and high-parents under combined heat and drought stress and well-watered conditions.

Traits	Performance	Heat and drought MP	Heat and drought HP	Well-watered MP	Well-watered HP
Grain yield ($t\,ha^{-1}$)	Best	141.2**	217.2*	380.5*	432.7**
	Worst	92.6^{ns}	186.2^{ns}	260.5*	311.2*
Mid-anthesis (days)	Best	−1.9*	−4.1**	-0.5^{ns}	-2.1^{ns}
	Worst	−1.1**	−3.2**	0.9^{ns}	-0.9^{ns}
Anthesis silking interval (days)	Best	9.28*	−20.8**	14.2*	−20.4**
	Worst	32.2**	−15.7**	42.7*	−14.0**
Plant height (cm)	Best	22.5**	21.0**	20.1**	18.3**
	Worst	18.1^{ns}	18.4^{ns}	17.7**	17.8*
Ears per plant	Best	16.2**	1.6**	24.0**	20.4**
	Worst	-2.3^{ns}	-5.5^{ns}	20.5*	13.5*
Senescence (%)	Best	5.6^{ns}	−5.5**	0.3*	−8.9**
	Worst	12.1^{ns}	0.4^{ns}	9.0*	−1.6**

Abbreviation: ns, not significant.

*$p \leq 0.05$; **$p \leq 0.01$.

SEN under WW conditions. For parental inbred lines, the differences between the best and worst groups for all traits except for GY were not significant ($p \leq 0.05$) under WW conditions. In contrast, these line groups significantly differed ($p \leq 0.05$) for GY, EPP, PH and ASI performance.

3.2 | Heterosis over mid and high-parent

Heterosis was more pronounced under WW conditions than under HMDS (Table 5). Grain yield and plant height showed the highest heterosis across all the management conditions. The best and worst groups showed positive and significant mid-parent and high-parent heterosis for GY in almost all growing conditions except for worst hybrids under HMDS. Hence, the worst hybrids performed similar to the mid-parents and best parents under HMDS. Although small differences were observed for AD between inbred lines and hybrids across management levels, negative and significant heterosis was observed among the best and worst hybrids under HMDS. This implies that Zn-enhanced hybrids had a lower number of days to mid-anthesis than their parents. Negative and significant HPH was observed for ASI for both best and worst hybrids across all managements. However, small but positive heterosis was observed over mid-parents, indicating that Zn-enhanced hybrids had shorter ASI than their worst inbred parents. For EPP, MPH was more important than HPH across both management levels. Positive heterosis for EPP was observed for the best hybrids under WW and HMDS. However, the worst hybrids showed negative but non-significant heterosis for EPP under HMDS conditions. This means that the extent of barrenness due to combined heat and drought effects on susceptible hybrids was comparable to that of susceptible inbred lines. Despite the small magnitude of heterosis for senescence, HPH was more important than MPH under all management conditions.

3.3 | Phenotypic correlation between hybrid and mid-parent grain yield and secondary traits

Phenotypic correlations between GY and secondary traits indicated a strong effect of the combined heat and drought stress on hybrids and inbred parental lines (Table 6). EPP showed strong positive and significant correlation with GY for hybrids ($r=0.73^{**}$) as well as GY for mid-parents ($r=0.61^{**}$) under HMDS conditions. Under WW conditions, EPP remained a good determinant of GY for hybrids ($r=0.77^{**}$), but for mid-parents, the magnitude of the correlation was weak and non-significant (Table 6). Plant height was strongly and positively correlated with GY under both management conditions, for both hybrids and mid-parents, but correlation was stronger under HMDS than WW conditions. Negative correlation was more apparent between AD and GY for hybrids under HMDS compared to WW conditions. A similar trend was also observed for the mid-parents, although under WW conditions, the sign of the correlation coefficient was positive (Table 6). The correlation of ASI with GY was negative for both hybrids and mid-parents under HMDS and WW conditions. However, highly negative and significant correlations between ASI and GY were observed under HMDS for hybrids ($r=-0.48^{**}$) and mid-parents ($r=-0.32^{**}$). Under WW conditions, these traits were weakly and negatively correlated on hybrids ($r=-0.23^{ns}$) as well as mid-parents ($r=-0.11^{ns}$). SEN was negatively correlated with GY for hybrids and mid-parents under stress and non-stress conditions. A similar relationship observed between ASI and GY was evident for SEN and GY, where stronger and negative correlations were observed under HMDS than under WW conditions.

3.4 | Phenotypic correlation between secondary traits of parents and hybrids and their relationship with hybrid yield

Across management levels, all the secondary traits of hybrids and mid-parents except for SEN under WW conditions were positively and significantly correlated (Table 7). Among the secondary traits, PH and EPP correlated the highest under both HMDS and WW conditions. Apparently, the correlation coefficients between traits of parental lines and hybrids were comparably higher under HMDS than WW conditions. Correlation between line secondary traits and the GY of hybrids was positive and significant, except for flowering traits (Table 7). Under HMDS, both AD and ASI of mid-parents were positively correlated with AD and ASI of hybrids, but these traits were negatively correlated

TABLE 6 Phenotypic correlation (r) between grain yield and secondary traits of Zn-enhanced hybrids and their mid-parents under combined heat and drought and well-watered conditions.

	Hybrids		Mid-parents	
Traits	**HMDS**	**WW**	**HMDS**	**WW**
Mid-anthesis (days)	−0.48*	-0.03^{ns}	-0.10^{ns}	0.01^{ns}
Anthesis silking interval (days)	−0.48**	-0.23^{ns}	−0.32**	-0.11^{ns}
Plant height (cm)	0.55**	0.48**	0.67**	0.06^{ns}
Ears per plant	0.73**	0.77**	0.61**	0.19^{ns}
Senescence (%)	−0.56**	−0.36**	−0.57**	-0.29^{ns}

Abbreviations: HMDS, heat and drought stress; ns, not significant; WW, well-watered.
*$p \le 0.05$; **$p \le 0.01$.

TABLE 7 Phenotypic correlation between secondary traits of parental inbred lines and hybrids and between line traits and grain yield of hybrids under heat and drought stress and well-watered conditions.

Line traits	Hybrid traits		Hybrid yield	
	HMDS	WW	HMDS	WW
Grain yield ($t\,ha^{-1}$)	–[a]	–[a]	0.62**	0.35**
Mid-anthesis (days)	0.29*	0.44**	−0.31**	0.25^{ns}
Anthesis silking interval (days)	0.48**	0.18*	−0.51**	−0.44^{ns}
Plant height (cm)	0.52**	0.33**	0.47**	0.56**
Ears per plant	0.41**	0.56**	0.55**	0.36**
Senescence (%)	0.30**	0.13^{ns}	0.33*	0.12^{ns}

Abbreviation: ns, not significant.

[a]Not measured.

*$p \le 0.05$; **$p \le 0.01$.

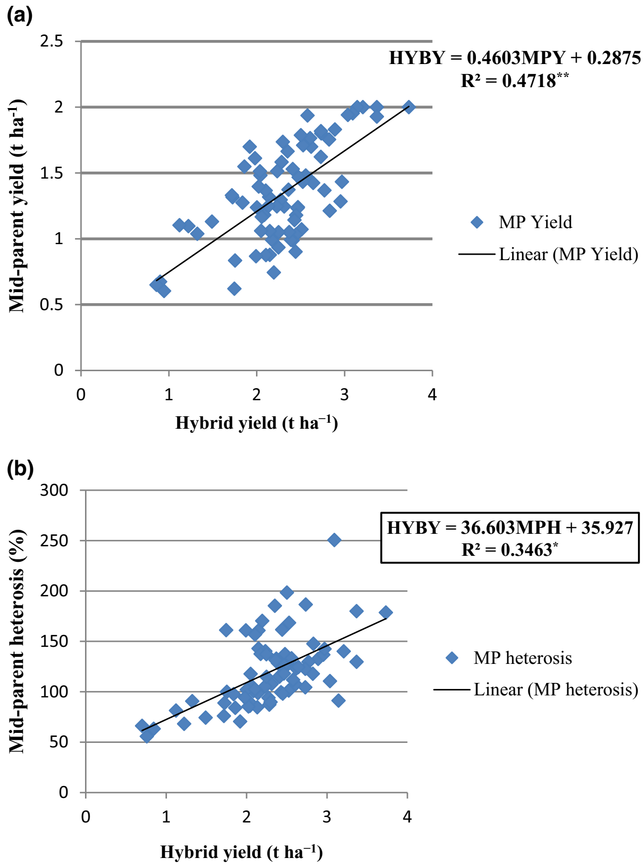

FIGURE 2 Relationship between the GY of Zn-enhanced hybrids with (a) GY of the mid-parents and (b) heterosis over mid-parent under combined heat and drought stress conditions. *$p \le 0.05$, **$p \le 0.01$; HYBY, hybrid yield; MPH, mid-parent heterosis; MPY, mid-parent yield.

($r = -0.31$**) for mid-parents and hybrid yield. However, positive and non-significant correlation between AD and hybrid yield was observed under WW conditions. However, ASI of mid-parents remained a good determinant of hybrid yield under WW conditions. In addition, significant and positive correlations between PH and EPP of inbred lines and GY of hybrids were observed, and the relationship was strong under both management conditions. Delayed SEN of mid-parents was important to determine high GY potential of hybrids under HMDS and WW conditions, although a fairly strong relationship ($r = 0.33$*) was observed under HMDS conditions. All these relationships between the secondary traits of parental inbred lines and hybrids eventually yielded positive and significant correlation between the GY of parental inbred lines and their corresponding hybrids under HMDS stress as well as under WW conditions.

3.5 | Relationship between mid-parent yield, mid-parent heterosis and hybrid yield

Linear regression was used to assess the relationship between GY performance of mid-parents and final GY of the Zn-enhanced hybrids. The relationship between hybrid GY and heterosis over mid-parent was also determined. This was useful to determine the contribution of the inherent inbred line performance as well as mid-parent heterosis to the final GY of the hybrids grown under HMDS and WW conditions. As shown in Figure 2, the contribution of mid-parent yield was more important ($R^2 = 0.47$**) in explaining the GY of hybrids compared to mid-parent heterosis ($R^2 = 0.35$*) under HMDS conditions. However, the opposite trend was observed under WW conditions (Figure 3), where mid-parent heterosis was more important ($R^2 = 0.52$**) in contributing to the GY of Zn-enhanced hybrids than mid-parent yield.

Based on GY performance and stability under both management conditions, the seven best and seven worst Zn-enhanced hybrids were selected (Figure 4). The best hybrids identified were stable and high yielding under HMDS and WW conditions and these were entry 7 (NML5/D2), 13 (NML3/D3), 28 (NML5/D6), 35 (NML5/D7), 58 (PROA3/D11), 73 (QPM4/D13), and 74 (QPM6/D13). The

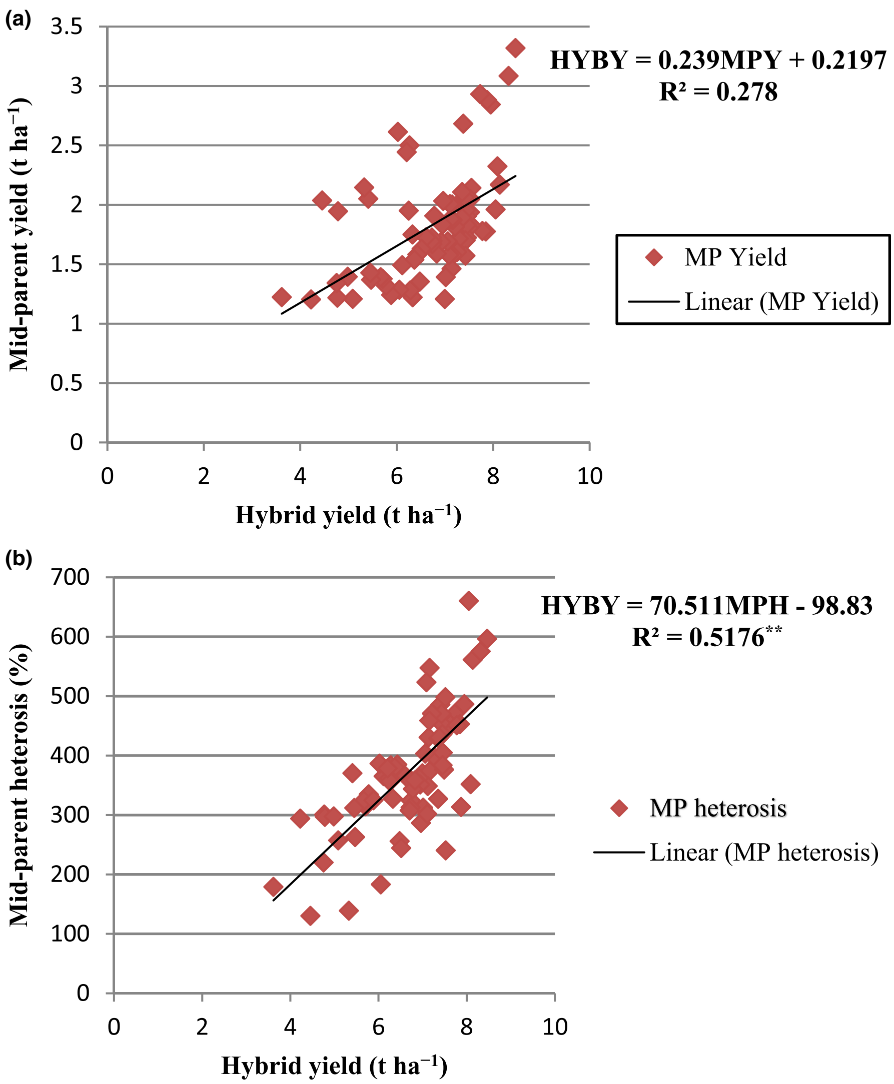

FIGURE 3 Relationship between the grain yield of Zn-enhanced hybrids with (a) GY of mid-parents and (b) heterosis over mid-parents under well-watered conditions. *$p \leq 0.05$, **$p \leq 0.01$; HYBY, hybrid yield; MPH, mid-parent heterosis; ns, not significant; MPY, mid-parent yield.

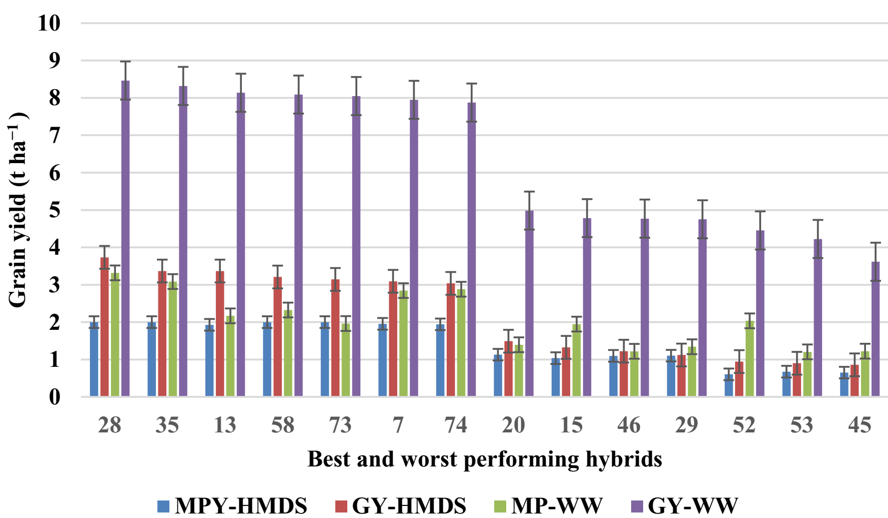

FIGURE 4 Hybrid and mid-parent yield of seven selected best and worst performing hybrids under combined heat and drought stress (HMDS) and well-watered (WW) conditions. HYBY, hybrid yield; MPY, mid-parent yield.

worst hybrids identified were entry 15 (PROA1/D5), 20 (NML5/D5), 29 (PROA1/D7), 45 (QPM4/D9), 46 (QPM6/D9), 52 (QPM4/D10), and 53 (QPM6/D10). Among the best performing hybrids in terms of GY, the differences between the mid-parent yields across management conditions were not large, whereas the difference between

GY of hybrids under HMDS and WW conditions differed significantly (Figure 4). However, the mid-parent yield observed under WW was greater than mid-parent yield for HMDS and a similar trend was observed for hybrids.

4 | DISCUSSION

All the traits were significantly affected by the adverse effects of HMDS except for AD. Little and non-significant impact of HMDS on the male flowering could be explained by the time when stress was applied. Irrigation was withheld 2 weeks before male flowering, but the tassel primordia were already initiated and elongating, and therefore, the number of days to mid-anthesis was not affected in any way. However, prolonged high temperatures during pollination could have reduced the final GY as a result of significant injury to pollen production and viability (Meseka et al., 2018). Exposure to most abiotic stress factors has been reported by several authors to increase the number of days to silking in maize genotypes rather than the AD (Alam et al., 2017; Magorokosho et al., 2003; Zaidi et al., 2007). Hence, in susceptible hybrids and parents, the ASI was increased due to delayed silking.

Under HMDS conditions, significant differences between the best and worst performing hybrids and mid-parents in terms of secondary traits, highlight the importance of using secondary traits for indirect selection for HMDS tolerance. Thus prior identification of secondary traits linked to HMDS tolerance is of paramount importance. Among the traits, ASI differed significantly between the best and worst performing hybrids and mid-parents grown under HMDS, while no significant differences were observed under WW conditions. Several studies on abiotic stress tolerance reported the usefulness of ASI as good indicator for stress tolerance (Bolaños & Edmeades, 1996; Ribaut et al., 1996; Santos et al., 2020). The highest yielding hybrids were taller than the poorest yielders under both HMDS and WW conditions, and this implies that selection of taller plants could improve GY. However, the best strategy would be to select for taller plants under HMDS conditions, since indirect selection for GY using PH under WW conditions will increase lodging (Nasser et al., 2020). For inbred lines, genotypic variation for PH between the best and worst performing hybrids was only significant under HMDS conditions, suggesting the possibility of identifying inbred lines with acceptable PH, suitable for hybrid-seed production systems (Nelimor et al., 2020; Su et al., 2019).

In the present study, hybrids were consistently higher yielding than inbred lines under HMDS and WW conditions. This indicates the importance of heterosis in increasing GY potential of maize genotypes when grown under stress and non-stress environments (Ali et al., 2019; Araus et al., 2010). Either mid-parent or high-parent heterosis was significant for all traits except for SEN in the best performing hybrids grown under HMDS conditions. This shows the relative superiority of hybrids over the inbred line per se in terms of trait performance. In hybrid state, favourable and dominant alleles for HMDS tolerance might have been complemented or overexpressed as previously reported (Kaeppler, 2012; Wolko et al., 2019). Perhaps the stress was too intense to show remarkable differences in the rate of SEN between the tolerant and susceptible genotypes. Contrary to our findings, some previous studies reported high GY for hybrids that would have delayed their senescence, and such trait is commonly known as the stay-green trait (Araus et al., 2012). Compared to other traits, GY and PH exhibited the highest magnitude of heterosis across crop management levels. These results are in agreement with findings of Gissa et al. (2007), where all the hybrids showed positive mid-parent and high-parent heterosis for PH and GY under optimum conditions. The negative mid- and high-parent heterosis values observed for AD indicated that the hybrids flowered earlier than their corresponding inbred parents under HMDS stress (Akaogu et al., 2020). In addition, negative values for high-parent heterosis for ASI observed in the present study show a slight improvement in hybrids in terms of shortening the ASI compared to the high-parent.

The sign and magnitude of the correlation coefficients were significantly affected by the type of trial management. Higher and significant correlations were observed under HMDS than WW conditions. Similar observations were also reported by Zaidi et al. (2007), where S_5 maize inbred lines were compared to their corresponding hybrids under excessive moisture stress. This could be explained by less genotypic variation for traits observed under WW conditions (Betrán et al., 2003; Zhao et al., 2019). Strong and negative correlations were observed between GY and AD, ASI and SEN for both hybrids and parents under HMDS than WW conditions. This suggests that HMDS tolerant genotypes expressed stress-adaptive mechanisms, resulting in earlier flowering, shorter ASI and more expression of the stay green trait than the susceptible ones. These results corroborate several previous studies on maize under various stress conditions (Akaogu et al., 2020; Meseka et al., 2018). Similarly, GY for both hybrids and inbred lines were positively and significantly correlated with PH as well as EPP, which concurs with previous studies (Nasser et al., 2020; Tandzi & Mutengwa, 2020). Generally, under stress conditions efficient utilization of the available resources is critical, enabling tolerant genotypes to complete their reproductive cycle (Liu et al., 2018). The significant contribution of secondary traits to GY under

HMDS elucidate the genetic complexity of GY, and therefore such traits could be used along with GY to develop multiple trait base selection indices for improved HMDS tolerance in Zn-enhanced germplasm.

The relationship between the secondary traits of parents and hybrids was also investigated. Interestingly, the correlation of several secondary traits of parents and their hybrids, ranged from weak to moderate, but all the correlation coefficients were significant under both management conditions except for SEN under WW conditions. In addition to that, the correlation between the inbred line traits and hybrid GY was moderate to fairly strong and relationships were significant for all traits under HMDS conditions. Several previous studies have also reported weak to strong correlation between line and hybrid traits, including final GY under various stress conditions (Prado et al., 2013; Wang et al., 1999; Zaidi et al., 2007). Liu et al. (2018) also observed significant correlations between traits of parental lines and their hybrid progenies under low and optimal phosphorus conditions. Findings of this study indicate the preponderance of additive gene action in affecting the hybrid trait performance. Additive effects are useful to plant breeders as they contribute a considerable and predictable portion of the genetic effect to the phenotype (Nzuve et al., 2014; Prado et al., 2013). Therefore, the present study suggests that trait scores measured in inbred lines could be used to predict hybrid performance. However, the results of this study are contrary to findings of Gama and Hallauer (1977), who reported very weak correlation between inbred line and hybrid yield and recommended that evaluation of hybrid GY performance is the most effective method to determine the potential usefulness of inbred lines. This could be explained by differences in population size, environmental conditions or other confounded factors. Zaidi et al. (2007) postulated that strong correlation between inbred lines and hybrid performance depends on the level of generation advancement of the inbred lines. They suggested the use of advanced generation fixed inbred lines for studies on heterosis since these inbred line would have gone through extensive selections based on stress-adaptive traits.

Analysis of the individual contribution of inbred line performance (mid-parents) and mid-parent heterosis revealed that under HMDS stress, mid-parent yield was more important than mid-parent heterosis in determining the GY performance of hybrids. However, the opposite occurred under WW conditions, where mid-parent heterosis was strongly linked to the GY of hybrids. These results indicate the importance of selecting high yielding inbred lines as parents for developing hybrids that can be grown under HMDS. Betrán et al. (2003) also found a significant positive correlation between mid-parent and hybrid grain yield under different nitrogen regimes. Similarly, studies on breeding for disease resistance in maize revealed that the correlation between intrinsic inbred line performance and general combining ability effects in hybrids was significant (Beyene et al., 2017; Nyaga et al., 2020). Selecting for resistance to maize streak virus and grey leaf spot during inbred line development has significantly contributed to the successful development of hybrids with considerable resistance in SSA (Nkurunziza et al., 2019). The presence of stress-adaptive secondary traits such as shorter ASI, high EPP, reduced AD and delayed SEN in genotypes under HMDS reflects their capacity to tolerate the harsh growing environment (Meseka et al., 2018; Zaidi et al., 2007). Such traits are highly heritable, and ideally, strong expression of these secondary traits is essential in the corresponding hybrid progenies. Although heterosis was more important than mid-parent yield under WW, it also contributed significantly towards hybrid GY performance under HMDS.

Selections based on the GY performance of hybrids under both conditions showed that under HMDS conditions, GY performance of hybrids was strongly associated with the yield of mid-parents. Although the mid-parent yield under WW was slightly above the mid-parent yield observed under HMDS, GY of hybrids between these management conditions was significantly different. This indicates that heterosis contributed more towards GY of hybrids under WW than mid-parent yield. These findings support earlier observations that mid-parent yield was more important under HMDS, while the opposite is true for WW conditions. The overall goal of this study was to develop high yielding and nutritious maize genotypes. The presence of Zn-enhanced genotypes from the normal, provitamin A and quality protein maize nutritional profiles, among the best performing hybrids is quite encouraging. Current breeding efforts focus on improving the yield potential and stability of biofortified cultivars and this facilitates quick adoption by farmers (Bänziger & Long, 2000; Palacios-Rojas et al., 2020). The present study demonstrated that, apart from heterosis, per se performance of advanced generation inbred lines is also important in developing hybrids with HMDS tolerance. Stress-adaptive secondary traits such as PH, ASI, AD and EPP could be used in selection indices for breeding for biofortified maize with HMDS tolerance.

5 | CONCLUSIONS

The results of this study supported the hypothesis that under combined heat and drought stress conditions, performance of Zn-enhanced hybrids could be predicted from the performance of their corresponding inbred lines.

This adds novel information in the quest of developing biofortified maize hybrids for abiotic stress conditions as experienced by farmers in the region. Heat and drought stress significantly reduced GY, increased the ASI, accelerated senescence and caused barrenness on some Zn-enhanced genotypes. Mid and high-parent heterosis was highly significant for GY and most secondary traits under HMDS conditions. In addition to heterosis, mid-parent yield contributed significantly to GY performance of hybrids under HMDS, while heterosis dominated under WW conditions. The results demonstrated that advanced inbred line performance can be used to predict Zn-enhanced maize hybrid performance under HMDS stress. However, this assumption is based on rigorous selection that inbred lines would have gone through for stress-adaptive secondary traits during development. Therefore, HMDS tolerance would be a result of fixation of favourable alleles during generation advancement. Further studies should be done to determine whether the performance of inbred biofortified parents would also be good predictors of hybrid performance under other types of abiotic stress conditions, such as low soil nitrogen, a condition frequently experienced by small-scale farmers.

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CONFLICT OF INTEREST STATEMENT

The authors have stated explicitly that there are no conflicts of interest in connection with this article.

DATA AVAILABILITY STATEMENT

Data is available from the authors.

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