

Article

The Influence of Parental Heat-Stress Priming on Drought-Tolerant Maize Progenies' Field Performance

Uchekukwu Paschal Chukwudi ^{1,2,*} , Funso Raphael Kutu ³  and Sydney Mavengahama ¹

¹ Food Security and Safety Niche Area, School of Agricultural Sciences, Faculty of Natural and Agricultural Sciences, North-West University, Mmabatho 2745, South Africa; sydney.mavengahama@nwu.ac.za

² Department of Crop Science, Faculty of Agriculture, University of Nigeria, Nsukka 410002, Nigeria

³ School of Agricultural Sciences, University of Mpumalanga, Mbombela 1200, South Africa; funso.kutu@ump.ac.za

* Correspondence: uchekukwu.chukwudi@unn.edu.ng

Abstract: Maize (*Zea mays* L.) is a staple crop and an industrial crop. Improving its thermotolerance will be a crucial step in ensuring food security. The objective of this research was to assess the influence of the parental growth environment on their progenies in a non-heat stress environment. The progenies evaluated in this field study were obtained from a 2 × 3 × 3 factorial in a completely randomised greenhouse experiment. Two contrasting growth environments, three maize varieties, and three soil amendments were used in the greenhouse study. A randomised complete block design experiment with three replications was used to grow the progenies. The progenies were examined for nineteen morphological attributes. In this study, 69.51% of the yield variation was explained by the first and second principal component axes. Among the studied attributes, grain weight and cob weight explained more variations in the progenies than the other attributes. The interaction of the parental heat-stress and soil amendment conditions elicited different responses from the drought-tolerant maize progenies. Based on the differences in their yield attributes, the progenies were grouped as poor yielders (Cluster IV), good yielders (Cluster I) and high yielders (Clusters II and III). The parental growth environment influenced the progenies' field performance in a non-heat-stress environment. Further evaluation of the progenies under a heat-stress environment and molecular analyses are required to establish that a transgenerational effect has occurred.

Keywords: heat stress; maternal effect; stress memory; thermotolerance; transgenerational effect; *Zea mays* L.



Citation: Chukwudi, U.P.; Kutu, F.R.; Mavengahama, S. The Influence of Parental Heat-Stress Priming on Drought-Tolerant Maize Progenies' Field Performance. *Agriculture* **2021**, *11*, 1229. <https://doi.org/10.3390/agriculture11121229>

Academic Editor: Ming Chen

Received: 19 October 2021

Accepted: 26 November 2021

Published: 7 December 2021

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

In the field, plants are exposed to a wide range of stressors at various stages of development. Plants, as sedentary organisms, respond to stress by modifying their physiological and genomic architecture [1]. These adjustments frequently result in decreased resource utilisation efficiency, which can result in yield losses ranging from minor to severe losses, or, in the worst-case scenario, plant death [2–4].

Plants use phenotypic alteration as a stress-resistance mechanism. Depending on the type of stress, the severity of the stress, and the developmental phase of the plant during which the stress was encountered, the plant's developmental process can be altered in anticipation of future occurrences of the stress [5–8]. Stress memory refers to the ability to remember stressful events. Stress memory can last anywhere from hours to months, and it can be passed down to a stressed plant's progeny in the hopes that the progeny will be exposed to stress in the future [6,7]. The parental effect, interorganismal effect, or transgenerational effect refers to the inheritance and expression of stress memory in plants that have not been exposed to the stress (primed) [9,10]. Stress memory inheritance

is classified as epigenetic inheritance, which refers to the transmission of phenotypic variations that do not result from a change in DNA sequence [11].

The stress memories of rice (*Oryza sativa* L.) and wheat (*Triticum aestivum* L.) plants exposed to heat or water stress were passed down to the second filial generations who were not exposed to the stress [5,12,13]. Rice grown in an N-deficient environment also passed on the stress memory to its second generation [14,15]. In these studies, progenies from primed ancestors outperformed control ancestors in a stressful environment. However, there were no significant differences between the progenies in a stress-free environment [5,12,14,15]. Therefore, parental priming can help reduce crop yield losses due to stress by improving plant stress tolerance.

The mechanisms of stress memory formation, retention, and transfer are not well understood, as the formed memory can be adaptive or maladaptive to the primed plant and its progeny [6,8,12,16]. However, transgenerational plasticity can boost thermotolerance in heat-sensitive crops such as maize (*Zea mays* L.). Maize is a staple crop and an industrial crop in developing and developed economies, respectively, so improving its thermotolerance will be a strategic step toward ensuring food security. The need for heat-tolerant maize varieties is becoming more pressing, as the most recent Intergovernmental Panel on Climate Change report [17] predicted increased severity and frequency of heat waves (high confidence).

Heat stress has an impact on maize's physiological development and genetic expression. Under heat stress conditions, heat-sensitive maize varieties produced lower photosynthetic activity, lower ear growth rate, and lower soluble sugar and starch contents than heat-tolerant types [18]. Heat stress slows crop growth and may cause a shift in phenological development, resulting in a yield loss in maize [19]. Heat stress caused various reactions in maize plants in different regions [20]. This finding highlights the importance of including heat stress tolerance in maize cultivar development [20]. It has been demonstrated that the response of maize plants to a single stressor differs from the synergistic effect of multiple stressors [3,4]. However, more research is needed to determine how these stressors affect maize progeny. We tested the hypothesis that, in a control environment, the parental growth environment of drought-tolerant maize progenies has no effect on their phenotypes. This knowledge will be used to guide seed production systems for heat-stressed environments. The objective of this research was to assess the influence of the parental growth environment on their progenies in a non-heat stress environment.

2. Materials and Methods

2.1. Description of the Study Site

In the 2019/2020 and 2020/2021 summer planting seasons, field evaluations were conducted at the North-West University Experimental Farm (−25.7902166, 25.6187922 3.5 mi) Mafikeng campus, North West Province, South Africa. The experimental soil used for the greenhouse study and field evaluation was composed of 82% sand, 4% silt, and 14% clay (loamy sand), had a pH (KCl) of 4.98, 11 mg P kg^{−1} (Bray1), 290 mg K kg^{−1}, 390 mg Ca kg^{−1}, 163 mg Mg kg^{−1}, 5 mg Na kg^{−1}, 376 mg kg^{−1} total N, and 0.37% organic C [21]. The South African Weather Services provided weather data for the experimental site during the two planting seasons (Figure 1).

2.2. Experimental Design, Treatments and Cultural Practices

2.2.1. Parental Evaluation

The treatments evaluated in this field study were developed from a 2 × 3 × 3 factorial in a completely randomised greenhouse experiment [3,21]. The greenhouse experiment is described briefly. The greenhouse study included two contrasting growth environments (heat stress [HS] environment and non-heat stress [NHS] environment), three medium-maturing drought-tolerant maize varieties (WE3128, WE5323, and ZM1523), and three soil amendments (poultry manure application [PM], mineral fertiliser application [MF], and combination of poultry manure/mineral fertiliser (50:50) application [MPM]). The weekly

temperature range for the NHS was from 15 to 33.9 °C and from 16.2 to 32.5 °C for the first and second planting seasons, respectively. In the HS, the weekly temperature ranges for the first and second planting seasons were from 16.38 to 40.88 °C and from 19.83 to 44 °C. Recommended greenhouse maize production protocols were followed. The cobs were harvested and shelled when they reached physiological maturity. The seeds were packaged and stored as per the eighteen treatment interactions.

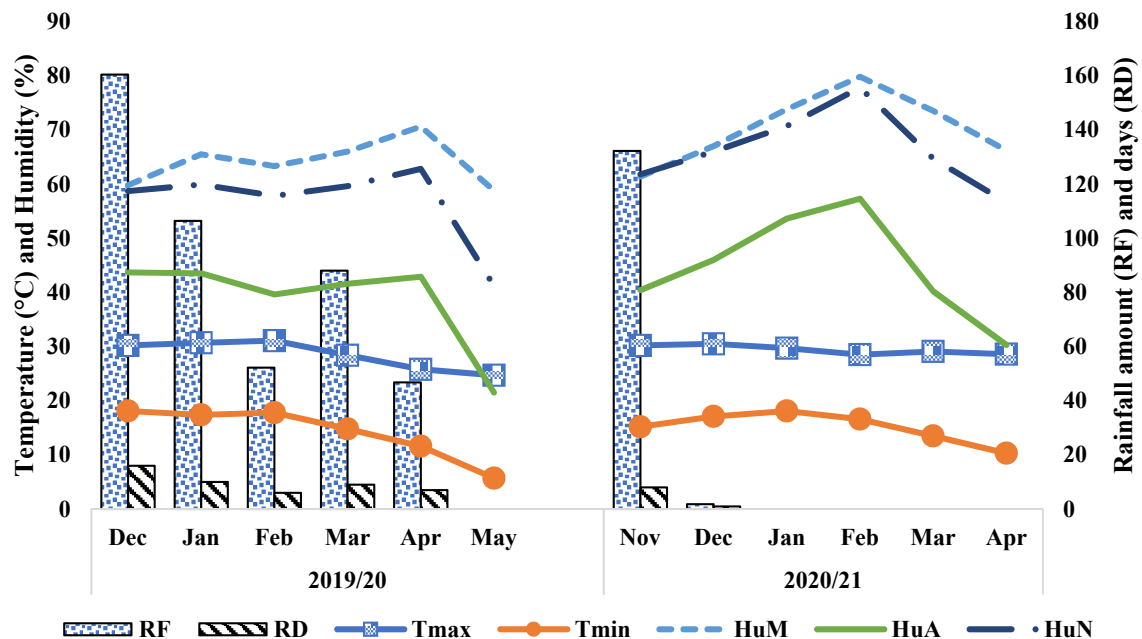


Figure 1. Weather data for 2019/20 and 2020/21 summer planting seasons at the North-West University Experimental Farm (−25.7902166, 25.6187922 3.5 mi) Mafikeng campus. RF, rainfall amount (mm); RD, rainfall days; Tmax, maximum temperature (°C); Tmin, minimum temperature (°C); HuM, humidity morning (%); HuA, humidity afternoon (%); and HuN, humidity night (%).

2.2.2. Progeny Field Evaluation

The seeds were evaluated in the field using a randomised complete block design with three replications to assess the impact of the different parental growth conditions on their progenies. The average minimum and maximum temperatures during the field evaluation for 2019/20 planting season were 13.89 °C and 29.78 °C, respectively, while for 2020/21 planting season, the average minimum and maximum temperatures were 17.27 °C and 31.81 °C, respectively.

The land was mechanically ploughed and harrowed, and plots (235 cm by 100 cm) were manually marked. Both 100 cm and 50 cm pathways were maintained between and within blocks, respectively. Three replications (blocks) were created, each with eighteen plots for each treatment interaction. On each plot, three maize seeds were planted per hole at 75 cm by 30 cm inter- and intra-row spacing, according to treatment interactions. Four weeks after planting (WAP), the seedlings were thinned to one plant per hole. A total of sixteen plants were established per plot, resulting in 68,085 plant population per hectare. Mineral fertiliser was applied at a rate of 350 kg N ha⁻¹. At planting, inorganic NPK grade 13:7:10 (30) + 0.5% Zn + 5% S + 3% Ca supplied 60% of the N requirement, while the remaining 40% was top-dressed with lime ammonium nitrate (28% N) at seven weeks after planting. The plots were manually kept weed free, and irrigation was provided by a sprinkler.

2.3. Data Collection

The emergence percentage (EP) was calculated by counting the number of seedlings that emerged in each plot at two WAP over the number of planted seeds. Growth and yield data were collected from the inner four plants in each plot, while phenological data

was collected from all the plants in a plot. Plant height (PH) was measured from the soil surface to the tip of the last leaf using a 5 m steel measuring tape. Leaf length and width were measured with a measuring tape from the base of the leaf on the maize stalk to the tip and at the widest part of the leaf. The leaf area (LA) was calculated by multiplying the product of leaf length and width by a constant of 0.75 [22]. The number of leaves (NoL) per plant was counted and the leaf chlorophyll content (LCC) was determined using a portable chlorophyll content metre (CCM-200 plus, Opti-Sciences, Hudson, NY, USA). The stem diameter (SD) was measured using a digital Vernier calliper (153-006-11, ACCUD, Vienna, Austria). The growth traits were measured at 4, 7, and 10 WAP.

Plants were monitored at the start of the reproductive phase to determine the number of days until tassel appearance (DT₅₀) and silk appearance (DS₅₀) in half of the plants in a plot. The tassel silk interval (TSI) was calculated by subtracting the DT₅₀ from the DS₅₀.

The plants were harvested with sharp secateurs when they reached physiological maturity. The number of cobs per plant (CN) and columns per cob (CC) were counted. The cobs were shade-dried to a moisture content of 12%, while the shoots were oven-dried to a constant weight at 65 °C to determine the stover dry weight in grams (SDWt). A measuring tape and a digital Vernier calliper were used to determine the length of the cob (CL) and width of the cob (CW). Individual cob was weighed to determine the gram weight of the cob (CWt). For the grain weight determination, each cob was shelled, and the grains weighed. The obtained CWt and GWt were used in calculating the shelling percentage (SP) as:

$$\text{Shelling percentage (\%)} = \frac{\text{Grain weight (g)}}{\text{Cob weight (g)}} \times 100.$$

Numigral seed counter (CHOPIN Technologies, Villeneuve-la-Garenne, France) was used to count the grains to obtain the grain number (GN). Thereafter, the 100-seed weight (SWt) was obtained by weighing 100 seeds from each treatment interaction.

2.4. Data Analysis

For the purposes of analysis, the data from the two field evaluations were combined. Analysis of variance (ANOVA) was performed on the data, following the procedure for randomized complete block design using GenStat Software (VSN Int. Ltd., Hemel Hempstead, UK). Protected Fisher's least significant difference test was used as a post hoc test for mean separation at $p \leq 0.05$. Bar charts were plotted using a Microsoft Excel spreadsheet (Microsoft Office 365, Microsoft, Redmond, WA, USA) to show the trend of measured attributes. A principal component biplot was created using GenStat Software (VSN Int. Ltd., Hemel Hempstead, UK) based on the yield attributes of the treatment interactions.

3. Results

3.1. Analysis of Variance

The SD, DT₅₀, CW, and CC were all significantly affected by the growth environment, while LA, PH, SD, DT₅₀, CW, and SWt were all significantly influenced by the maize variety (Table 1). The effects of soil amendment on EP, LA, PH, DT₅₀, DS₅₀, CN, GN, and SWt were significant. The interaction of growth environment and maize variety significantly influenced LA, LCC, PH, SD, DT₅₀, DS₅₀, CL, CC, CW, SP, CWt, GWt, and SWt, whereas growth environment × soil amendment interaction significantly influenced EP, LA, NoL, PH, DS₅₀, DT₅₀, CN, CL, CW, CC, CWt, GN, GWt, and SWt. The interaction of the maize variety with the soil amendment had a significant impact on EP, LA, NoL, LCC PH, DS₅₀, DT₅₀, CN, CN, CW, CC, CWt, GN, GWt, SWt, and SDWt. The second-order interaction had a significant effect on the EP, LA, NoL, LCC PH, DS₅₀, DT₅₀, CN, CL, CW, CC, CWt, GN, GWt, SWt, and SDWt. Table 1 shows the growth characteristics measured at 10 WAP.

Table 1. First-order, second-order, and third-order interactions of parental heat-stress, varietal differences, and soil amendment on the growth and yield attributes of maize.

Traits	ENV	MVA	SAM	ENV. MVA	ENV. SAM	MVA. SAM	ENV. MVA. SAM
Emergence percentage	n.s	n.s	*	n.s	*	*	*
Leaf area at 10 WAP	n.s	*	*	*	*	*	*
Leaf chlorophyll content at 10 WAP	n.s	n.s	n.s	*	n.s	*	*
Number of leaves at 10 WAP	n.s	n.s	n.s	n.s	*	*	*
Plant height at 10 WAP	n.s	*	*	*	*	*	*
Stem diameter at 10 WAP	*	**	n.s	*	*	*	*
Days until 50% silking	n.s	n.s	*	*	*	*	*
Days until 50% tasselling	*	*	*	**	*	*	*
Tassel silk interval	n.s	n.s	n.s	n.s	n.s	n.s	n.s
Stover dry weight	n.s	n.s	n.s	n.s	n.s	*	*
Number of cobs	n.s	n.s	*	n.s	*	*	*
Length of cobs	n.s	n.s	n.s	*	**	n.s	*
Width of cobs	*	*	n.s	*	*	*	*
Cob Column	*	n.s	n.s	*	*	*	*
Weight of cobs	n.s	n.s	n.s	*	**	*	*
Number of grains	n.s	n.s	*	n.s	**	*	*
Weight of grains	n.s	n.s	n.s	*	**	*	*
Shelling Percentage	n.s	n.s	n.s	*	n.s	*	*
100-Seed Weight	n.s	*	*	*	*	*	*

n.s, non-significant difference; * = significant difference at probability level of 0.001, ** = significant difference at probability level of 0.05, ENV, parental heat stress conditions; MVA, maize variety; and SAM, parental soil amendment.

3.2. Effect of Parental Heat Stress on the Progenies' Growth and Yield Attributes

Despite being statistically similar, NHS provided higher quantitative EP and LA at 10 WAP, NoL at 4, 7, and 10 WAP, PH at 10 WAP, and SD at 4 WAP than HS (Table 2). HS was higher than NHS in LA at 4 and 7 WAP, LCC at 4, 7 and 10 WAP, PH at 4 and 7 WAP, and SD at 7 and 10 WAP.

Table 2. Main effects of parental heat stress environments on the progenies' growth attributes.

Environment	WAP	HS	NHS	F-LSD (0.05)
Emergence percentage (%)		81.2	82.6	n.s.
Leaf area (cm ²)	4	285.0	284.0	n.s.
	7	662.5	654.5	n.s.
	10	699.6	714.6	n.s.
Leaf chlorophyll content (CCI)	4	38.7	37.4	n.s.
	7	43.1	38.5	4.3
	10	53.3	51.3	n.s.
Number of leaves	4	9.1	9.2	n.s.
	7	15.3	15.5	n.s.
	10	17.9	18.1	n.s.
Plant height (cm)	4	39.8	39.5	n.s.
	7	139.9	136.4	n.s.
	10	250.5	257.6	n.s.
Stem diameter (mm)	4	15.5	16.2	n.s.
	7	33.5	31.9	n.s.
	10	32.1	30.2	1.7

WAP, weeks after planting; HS, heat stress environment; NHS, non-heat stress environment; and n.s., non-significant difference.

Although HS took a longer number of days to reach DT₅₀ and DS₅₀, its TSI was lower than NHS (Figure 2). SDWt, CL, CW, CC, CWt, GN, GWt, SP, and SWt were all higher in the NHS.

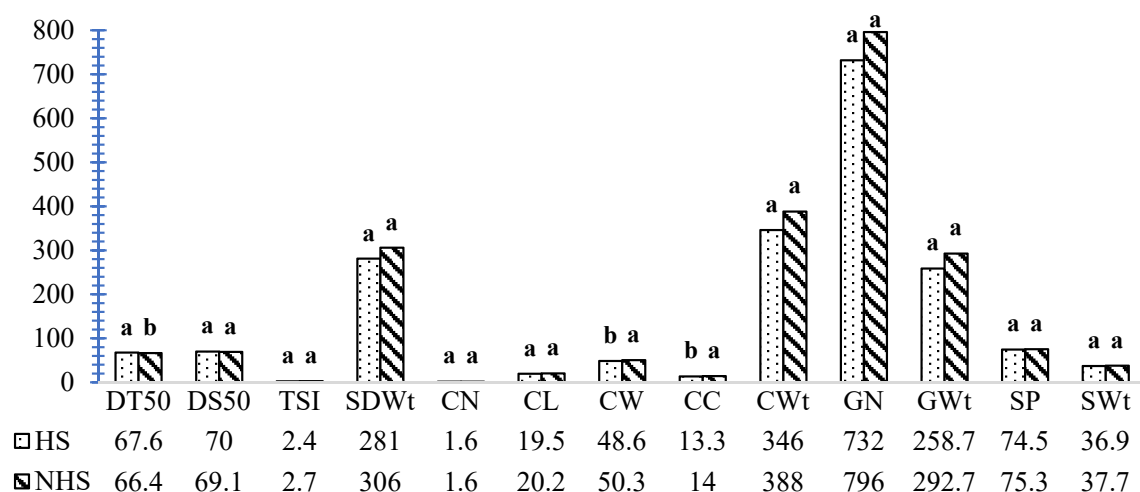


Figure 2. Main effects of parental growth environments on the progenies' morphological attributes. Bars with the same alphabet are not significantly different at $p < 0.05$; HS, heat stress environment; NHS, non-heat stress environment; DT50, number of days until 50% tasselling; DS50, number of days until 50% silking; TSI, tassel silk interval; SDWt, stover dry weight (g plant^{-1}); CN, number of cobs plant^{-1} ; CL, length of cob (cm); CC, number of column cob $^{-1}$; CW, width of cob (mm); CWt, weight of cob (g plant^{-1}); GN, number of grains plant^{-1} ; GWt, weight of grain (g plant^{-1}); SWt, 100-seed weight (g plant^{-1}); and SP, shelling percentage (%).

3.3. Varietal Influence on the Progenies' Growth and Yield Attributes

Variety WE5323 produced the largest LA, which was significantly higher than ZM1523 and WE3128 at 7 and 10 WAP (Table 3). At 4 and 7 WAP, its LCC was higher than ZM1523 and WE3128. It also produced the tallest PH at 4 WAP as well as the widest SD at 7 and 10 WAP. ZM1523 had the greatest LCC at 10 WAP, the highest NoL at 4 and 7 WAP, the tallest PH at 7 WAP, and the widest SD at 4 WAP. WE3128 produced the highest NoL and PH at 10 WAP, and the highest EP. Its LCC at 7 WAP, SD at 4 and 10 WAP were significantly lower than WE5323 and ZM1523.

Table 3. Main effects of maize variety on their progenies' growth attributes.

Maize Variety	WAP	WE3	WE5	ZM1	F-LSD (0.05)
Emergence percentage (%)		83.0	81.9	80.9	n.s.
Leaf area (cm^2)	4	268.2	300.6	284.7	29.6
	7	647.1	699.3	629.1	46.8
	10	696.6	744.9	679.8	38.5
Leaf chlorophyll content (CCI)	4	37.0	38.8	38.4	n.s.
	7	35.7	43.7	43.1	5.3
	10	50.8	51.4	54.7	n.s.
Number of leaves	4	8.9	9.1	9.4	n.s.
	7	15.3	15.5	15.6	n.s.
	10	18.0	17.9	17.9	n.s.
Plant height (cm)	4	38.3	41.4	39.3	n.s.
	7	131.6	137.0	145.9	13.5
	10	262.4	252.6	247.2	11.7
Stem diameter (mm)	4	14.8	16.4	16.4	1.4
	7	31.4	35.2	31.5	2.5
	10	28.9	33.2	31.4	2.1

WAP, weeks after planting; WE3, WE3128; WE5, WE5323; ZM1, ZM1523; and n.s., non-significant difference.

WE3128 required the most days to achieve DT₅₀ and DS₅₀ (Figure 3). It had higher CL, CW, CWt, GWt, and SWt than WE5323 and ZM1523. WE5323 produced the highest CC and GN, whereas ZM1523 had the highest TSI, SDWt, CN, and SP.

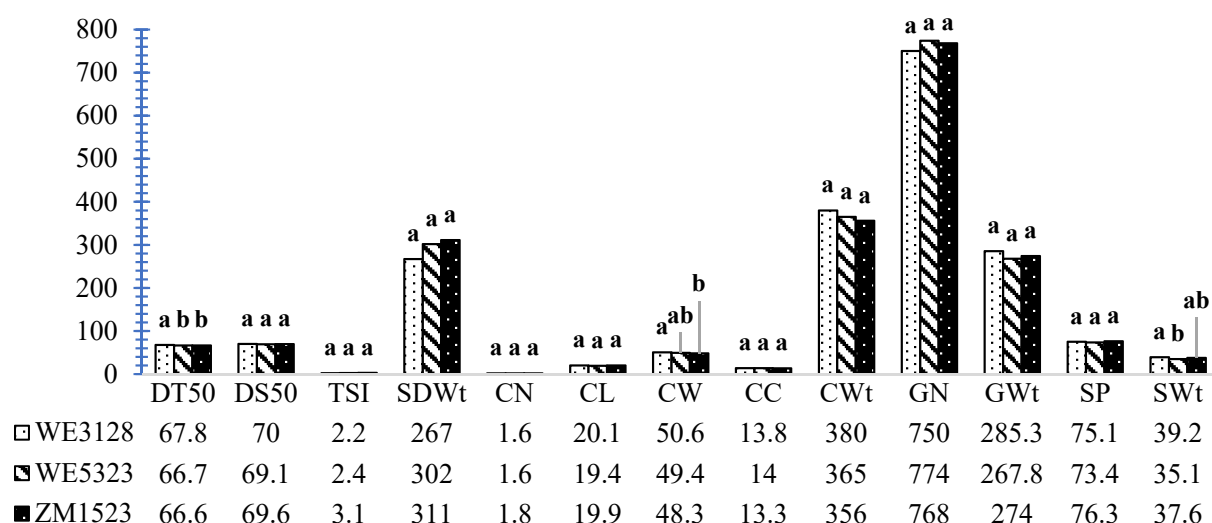


Figure 3. Main effects of maize variety on their progenies' phenological and yield attributes. Bars with the same alphabet are not significantly different at $p < 0.05$; DT50, number of days until 50% tasselling; DS50, number of days until 50% silking; TSI, tassel silk interval; SDWt, stover dry weight (g plant^{-1}); CN, number of cobs plant^{-1} ; CL, length of cob (cm); CC, number of column cob $^{-1}$; CW, width of cob (mm); CWt, weight of cob (g plant^{-1}); GN, number of grains plant^{-1} ; GWt, weight of grain (g plant^{-1}); SWt, 100-seed weight (g plant^{-1}); and SP, shelling percentage (%).

3.4. Effect of Parental Soil Amendment on the Progenies' Growth and Yield Attributes

The MF amendment produced the highest LCC at 7 WAP, while the PM amendment gave the highest LCC at 4 WAP, the largest NoL at 4 WAP, and the widest SD at 4 and 10 WAP (Table 4). The MPM amendment had the greatest EP, LA, NoL, PH, and LCC at 10 WAP and the widest SD at 7 WAP. It was significantly higher than MF and PM in LA at 7 and 10 WAP, and PH at 10 WAP.

Table 4. Main effects of parental soil amendment on the progenies' growth attributes.

Soil Amendment	WAP	MF	MPM	PM	F-LSD (0.05)
Emergence percentage (%)		82.3	88.5	75.0	9.5
Leaf area (cm^2)	4	268.2	300.6	284.7	29.6
	7	647.1	699.3	629.1	46.8
	10	696.6	744.9	679.8	38.5
Leaf chlorophyll content (CCI)	4	36.4	37.2	40.5	n.s.
	7	42.5	41.5	38.6	n.s.
	10	51.3	52.9	52.6	n.s.
Number of leaves	4	8.7	9.2	9.6	0.5
	7	15.3	15.7	15.3	n.s.
	10	17.9	18.3	17.7	n.s.
Plant height (cm)	4	38.5	40.3	40.2	n.s.
	7	137.0	141.3	136.1	n.s.
	10	248.9	263.0	250.3	11.7
Stem diameter (mm)	4	14.7	16.0	16.9	1.4
	7	32.0	33.6	32.4	n.s.
	10	30.0	31.4	32.1	n.s.

WAP, weeks after planting; PM, poultry manure; MF, mineral fertilizers; MPM, complementary (50:50) application of poultry manure/mineral fertilizer; and n.s., non-significant difference.

The longest number of days to complete DT₅₀ and DS₅₀ was observed in PM amendment (Figure 4). The PM amendment was also significantly higher than the MF in CN. The MF amendment produced the longest TSI, widest CW, highest SDWt, and SWt. It was significantly lower in GN compared with MPM and PM amendments. The MPM amendment produced the highest CL, CC, CWt, CN, GWt, and SP.

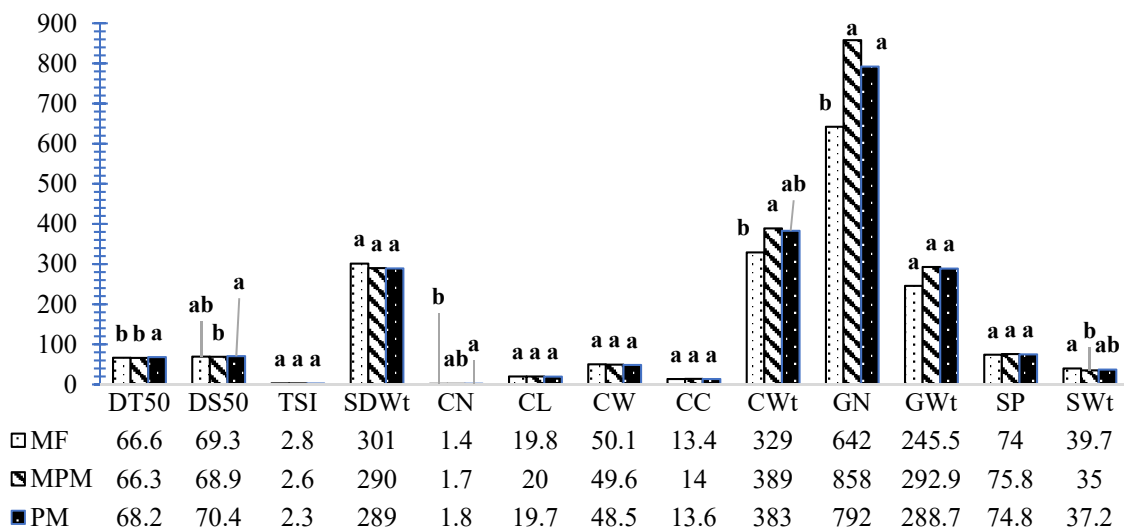


Figure 4. Main effects of parental soil amendment on the progenies' phenological and yield attributes. Bars with the same alphabet are not significantly different at $p < 0.05$; PM, poultry manure; MF, mineral fertilizers; MPM, complementary (50:50) application of poultry manure/mineral fertilizer; DT50, number of days until 50% tasselling; DS50, number of days until 50% silking; TSI, tassell silk interval; SDWt, stover dry weight (g plant^{-1}); CN, number of cobs plant^{-1} ; CL, length of cob (cm); CC, number of column cob $^{-1}$; CW, width of cob (mm); CWt, weight of cob (g plant^{-1}); GN, number of grains plant^{-1} ; GWt, weight of grain (g plant^{-1}); SWt, 100-seed weight (g plant^{-1}); and SP, shelling percentage (%).

3.5. Interaction of Parental Heat Stress, Maize Variety and Soil Amendment on the Progenies' Growth and Yield Attributes

EP ranged from 54.2% in HS-WE3-PM-P₁ to 97.9% in HS-ZM1-MPM-P₁ (Table 5). At 4 and 7 WAP, the LA ranged from 229.1 cm^2 to 354.8 cm^2 , and from 566.7 cm^2 to 743 cm^2 , respectively. The LA ranged from 597.9 cm^2 in HS-ZM1-PM-P₁ to 743 cm^2 in HS-WE3-MPM-P₁. The range of LCC was 30.6 to 48.1 CCI at 4 WAP, 29.5 to 57.7 CCI at 7 WAP and 41.1 to 62.6 CCI at 10 WAP. NoL spread from 7.8 to 10.8 at 4 WAP, 13.4 to 16.2 at 7 WAP and from 16 to 19.7 at 10 WAP.

Among the treatment interactions at 4 WAP, the shortest and tallest plants were produced by HS-WE3-PM-P₁ and HS-WE5-MPM-P₁, respectively (Table 6). PH ranged from 102.2 cm to 158.8 cm at 7 WAP, while at 10 WAP, it ranged from 223.7 cm to 279.3 cm. SD ranged from 11.2 mm to 20.3 mm at 4 WAP, from 27.4 mm to 38 mm at 7 WAP, and from 25.3 mm to 36.7 mm at 10 WAP.

NHS-ZM1-MPM-P₁ produced the fewest number of days to attain DT₅₀ and DS₅₀, whereas the longest number of days to reach DT₅₀ and DS₅₀ came from NHS-WE3-PM-P₁ and HS-ZM1-PM-P₁. The TSI ranged from 1.3 d to 3.7 d. SDWt ranged from 182 g plant^{-1} in HS-WE3-PM-P₁ to 424 g plant^{-1} in NHS-WE5-PM-P₁.

NHS-ZM1-PM-P₁ had the highest CN, GN and SP, while HS-ZM1-MF-P₁ gave the highest SWt (Table 7). NHS-WE3-PM-P₁ had the highest CL, CW, CC, GWt and CWt. The following ranges were obtained for the yield attributes: 1.2 to 2.4 for CN, 17.7 to 22.4 cm for CL, 44.3 to 54 mm for CW, 12.2 to 15.2 for CC, 248 to 590 g plant^{-1} for CWt, 502 to 1113 for GN, 185.2 to 423.2 g plant^{-1} for GWt, 68.9 to 79.8% for SP and 28.6 to 44.3 g plant^{-1} for SWt.

The first and second principal component axes explained 69.51% (PC1 = 46.45%, PC2 = 23.06%) of the yield attributes variations in the treatment interactions. The treatment interactions were divided into three groups and an outlier using the principal component biplot (Figure 5). Group I consist of the following: H1, H2, H8, N2, N5, N6, and N7. The outlier N9 represented Group II, while H5 and N3 comprised Group III. Group IV contained the remaining treatment interactions, which included H3, H4, H6, H7, H9, N1, N4, and N8.

Table 5. Parental heat-stress, varietal difference, and soil amendment effects on maize progenies' emergence and leaf attributes.

Treatment Interactions	EP (%)	Leaf Area (cm ²)			Leaf Chlorophyll Content (CCI)			Number of Leaves		
		4 WAP	7 WAP	10 WAP	4 WAP	7 WAP	10 WAP	4 WAP	7 WAP	10 WAP
HS-WE3-MF-P ₁	91.7	256.3	590.6	664.3	34.4	42.0	51.7	9.0	15.8	19.7
HS-WE3-MPM-P ₁	93.8	275.7	743.0	765.8	35.5	39.3	53.7	9.8	15.8	17.7
HS-WE3-PM-P ₁	54.2	229.1	579.9	609.7	42.0	35.5	52.0	7.8	13.4	16.0
HS-WE5-MF-P ₁	87.5	317.3	733.8	747.2	33.2	44.2	46.4	9.0	15.6	17.3
HS-WE5-MPM-P ₁	79.2	352.3	729.8	819.0	45.9	48.4	62.6	10.0	16.2	19.0
HS-WE5-PM-P ₁	83.3	321.0	707.7	728.6	38.0	38.8	53.9	9.2	15.2	16.7
HS-ZM1-MF-P ₁	83.3	271.8	724.5	755.3	41.9	57.7	62.0	8.6	14.8	17.0
HS-ZM1-MPM-P ₁	97.9	264.8	566.7	609.0	38.3	43.2	45.6	9.0	15.4	19.0
HS-ZM1-PM-P ₁	60.4	276.7	586.1	597.9	39.3	39.1	51.4	9.2	15.8	18.3
NHS-WE3-MF-P ₁	89.6	236.2	640.1	731.1	30.6	29.5	41.1	8.2	15.4	18.3
NHS-WE3-MPM-P ₁	93.8	257.1	628.8	654.0	31.5	30.4	53.8	8.2	15.6	18.0
NHS-WE3-PM-P ₁	75.0	354.8	700.0	755.0	48.1	37.5	52.6	10.6	15.6	18.3
NHS-WE5-MF-P ₁	72.9	235.0	688.0	714.6	38.3	44.5	47.3	8.2	14.6	17.3
NHS-WE5-MPM-P ₁	79.2	256.5	677.2	751.4	33.8	41.6	51.1	8.6	15.0	18.3
NHS-WE5-PM-P ₁	89.6	321.5	659.2	708.5	43.4	44.6	46.8	9.8	16.2	19.0
NHS-ZM1-MF-P ₁	68.7	303.9	640.0	706.4	40.0	36.9	59.5	9.0	15.6	17.7
NHS-ZM1-MPM-P ₁	87.5	296.3	572.5	659.5	38.4	45.8	50.8	9.6	16.0	17.7
NHS-ZM1-PM-P ₁	87.5	294.7	684.6	750.6	32.1	35.9	58.7	10.8	15.8	18.0
F-LSD (0.05)	23.18	72.52	114.61	94.32	12.13	12.86	13.12	1.13	1.32	1.69
CV (%)	17.0	1.4	3.3	3.5	25.3	7.6	8.8	9.8	6.8	2.7

EP, seedling emergence percentage; WAP, weeks after planting; HS, heat stress environment; NHS, non-heat stress environment; WE3, WE3128; WE5, WE5323; ZM1, ZM1523; PM, poultry manure; MF, mineral fertilizer; MPM, complementary (50:50) application of poultry manure/mineral fertilizer; and P₁, first progeny.

Table 6. Parental heat-stress, varietal differences, and soil amendment effects on maize progenies' growth and phenological attributes.

Treatment Interactions	Plant Height (cm)			Stem Diameter (mm)			DS ₅₀	DT ₅₀	TSI	SDWt (g Plant ⁻¹)
	4 WAP	7 WAP	10 WAP	4 WAP	7 WAP	10 WAP				
HS-WE3-MF-P ₁	40.2	151.8	279.3	16.2	31.4	28.8	70.3	68.0	2.3	314
HS-WE3-MPM-P ₁	40.4	158.8	276.7	15.8	34.7	32.6	69.0	66.7	2.3	273
HS-WE3-PM-P ₁	28.0	109.8	223.7	11.2	27.5	27.1	68.7	67.3	1.3	182
HS-WE5-MF-P ₁	43.4	134.8	240.0	16.1	38.0	31.3	68.7	65.7	3.0	254
HS-WE5-MPM-P ₁	48.8	139.8	254.7	17.9	37.7	36.7	69.3	67.3	2.0	282
HS-WE5-PM-P ₁	40.4	153.2	248.0	17.4	36.3	36.3	71.0	68.7	2.3	274
HS-ZM1-MF-P ₁	39.2	135.2	230.0	14.4	31.7	30.1	70.3	67.3	3.0	319
HS-ZM1-MPM-P ₁	36.6	147.0	271.3	15.4	32.7	33.5	71.0	68.0	3.0	333
HS-ZM1-PM-P ₁	41.5	128.6	231.0	15.5	31.0	32.4	72.0	69.7	2.3	300
NHS-WE3-MF-P ₁	37.0	122.6	260.0	12.6	27.4	25.3	69.3	67.3	2.0	313
NHS-WE3-MPM-P ₁	36.6	102.2	267.7	12.6	32.1	25.3	69.3	68.0	1.3	265
NHS-WE3-PM-P ₁	47.4	144.4	267.3	20.3	35.1	34.2	73.3	69.7	3.7	256
NHS-WE5-MF-P ₁	33.0	128.6	233.7	13.1	32.5	30.7	68.7	66.0	2.7	284
NHS-WE5-MPM-P ₁	38.4	141.4	268.7	15.4	31.9	31.4	68.0	65.0	3.0	297
NHS-WE5-PM-P ₁	44.4	124.0	270.3	18.4	34.5	32.8	68.7	67.3	1.3	424
NHS-ZM1-MF-P ₁	38.2	149.0	250.3	15.7	31.3	33.5	68.7	65.0	3.7	325
NHS-ZM1-MPM-P ₁	40.8	158.8	239.0	18.7	32.1	29.0	66.7	63.0	3.7	287
NHS-ZM1-PM-P ₁	39.6	156.6	261.7	18.8	30.1	29.6	69.0	66.3	2.7	299
F-LSD (0.05)	8.11	33.09	28.62	3.40	5.75	5.09	2.95	2.57	n.s.	164
CV (%)	16.2	19.0	3.2	17.0	14.0	7.0	2.6	2.3	67.7	33.7

WAP, weeks after planting; HS, heat stress environment; NHS, non-heat stress environment; WE3, WE3128; WE5, WE5323; ZM1, ZM1523; PM, poultry manure; MF, mineral fertilizer; MPM, complementary (50:50) application of poultry manure/mineral fertilizer; n.s., non-significant difference; P₁, first progeny DT₅₀, number of days until 50% tasselling; DS₅₀, number of days until 50% silking; and TSI, tassel silk interval.

Table 7. Parental heat-stress, varietal differences, and soil amendment effects on maize progenies' yield attributes.

SN	Treatment Interactions	CN	CL	CW	CC	CWt	GN	GWt	SP	SWt
		(cm)	(mm)	(g plant ⁻¹)	(g Plant ⁻¹)	(%)	(g Plant ⁻¹)			
H1	HS-WE3-MF-P ₁	1.8	18.8	48.5	13.6	365	793	273.6	73.5	34.9
H2	HS-WE3-MPM-P ₁	1.8	20.8	49.4	13.8	394	847	304.2	77.3	36.7
H3	HS-WE3-PM-P ₁	1.2	17.7	49.0	12.4	248	511	185.2	76.2	38.8
H4	HS-WE5-MF-P ₁	1.2	19.6	49.5	13.2	270	508	190.3	70.4	37.7
H5	HS-WE5-MPM-P ₁	2.0	20.8	53.3	14.4	579	1067	415.1	71.6	39.3
H6	HS-WE5-PM-P ₁	1.8	17.9	45.7	13.4	307	773	239.7	77.1	31.7
H7	HS-ZM1-MF-P ₁	1.4	19.9	49.5	12.4	336	619	255.3	76.1	44.3
H8	HS-ZM1-MPM-P ₁	1.6	21.0	48.1	14.6	350	967	270.2	77.2	28.6
H9	HS-ZM1-PM-P ₁	2.0	18.5	44.3	12.2	269	502	195.0	71.3	39.5
N1	NHS-WE3-MF-P ₁	1.4	20.1	51.9	13.0	330	593	252.3	76.7	43.6
N2	NHS-WE3-MPM-P ₁	1.4	20.9	50.7	14.6	352	740	273.2	77.6	38.9
N3	NHS-WE3-PM-P ₁	1.8	22.4	54.0	15.2	590	1013	423.2	68.9	41.9
N4	NHS-WE5-MF-P ₁	1.2	20.0	49.9	14.0	291	568	207.8	71.2	37.6
N5	NHS-WE5-MPM-P ₁	1.8	17.9	48.1	14.2	371	888	275.9	74.3	31.2
N6	NHS-WE5-PM-P ₁	1.6	20.3	49.5	14.8	371	839	278.2	75.5	33.2
N7	NHS-ZM1-MF-P ₁	1.6	20.4	51.5	14.4	385	770	293.7	76.2	39.8
N8	NHS-ZM1-MPM-P ₁	1.6	18.3	48.0	12.6	285	638	219.1	77.0	35.4
N9	NHS-ZM1-PM-P ₁	2.4	21.4	48.7	13.4	514	1113	410.6	79.8	38.0
	F-LSD _(0.05)	0.7	2.6	4.8	2.0	142	363.8	119.5	7.2	7.3
	CV (%)	33.9	10.3	7.7	11.6	30.7	37.7	34.4	7.7	15.4

HS, heat stress environment; NHS, non-heat stress environment; WE3, WE3128; WE5, WE5323; ZM1, ZM1523; PM, poultry manure; MF, mineral fertilizer; MPM, complementary (50:50) application of poultry manure/mineral fertilizer; P₁, first progeny; CN, number of cobs plant⁻¹; CL, length of cob (cm); CC, number of column cob⁻¹; CW, width of cob (mm); CWt, weight of cob (g plant⁻¹); GN, number of grains plant⁻¹; GWt, weight of grains (g plant⁻¹); SWt, 100-seed weight (g plant⁻¹); and SP, shelling percentage (%).

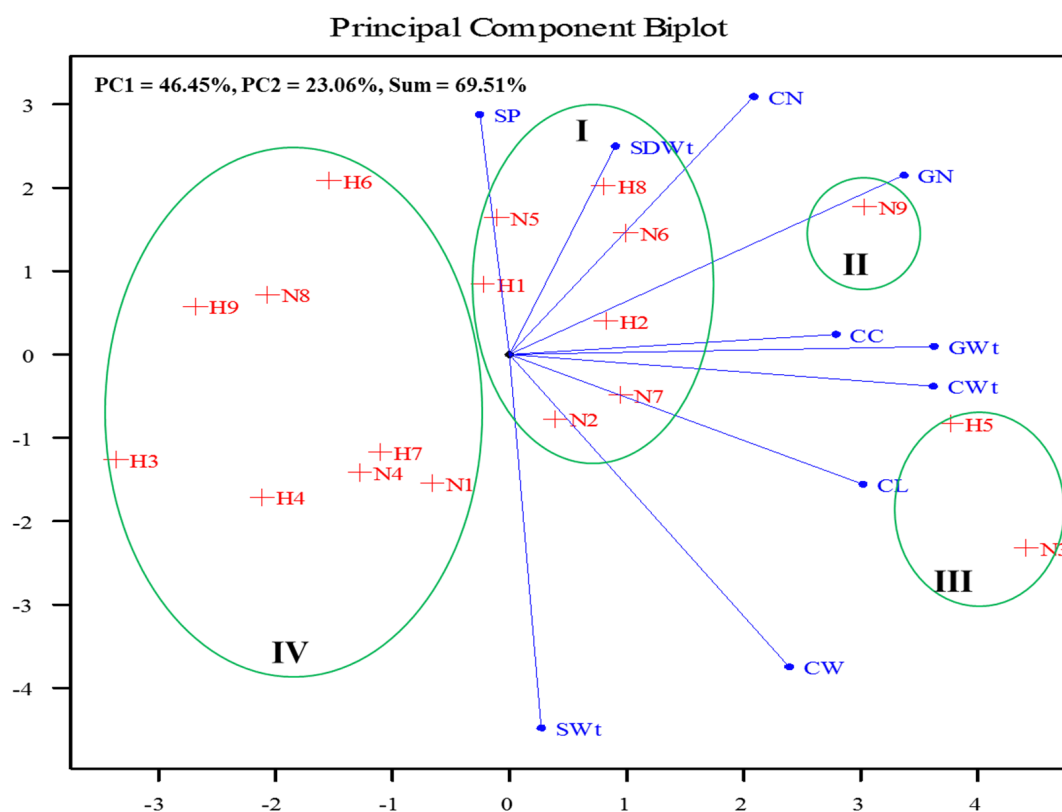


Figure 5. Principal component biplot for the progenies of the treatment interactions. +H1 to +H9 and +N1 to +N9, treatment interactions' progenies; SDWt, stover dry weight (g plant⁻¹); CN, number of cobs plant⁻¹; CL, length of cobs (cm); CC, number of column cob⁻¹; CW, width of cobs (mm); CWt, weight of cobs (g plant⁻¹); GN, number of grains plant⁻¹; GWt, weight of grains (g plant⁻¹); SWt, 100-seed weight (g plant⁻¹); and SP, shelling percentage (%).

Group I had the highest SDWt group average (Table 8). It performed better than the population mean in CN, CL, CW, CC, CWt, GN, GWt, and SP. It did, however, provide the least SWt. The CN, GN, and SP of the outlier N9 were the highest. In SDWt, CL, CWt, GWt, and SWt, it performed better than the population mean, whereas in CW and CC, it performed below the population mean. Among all the groups, Group III had the best CL, CW, CC, CWt, GWt, and SWt. Its CN and GN were higher than the population mean, but it had the lowest SDWt and SP. Group IV performed above-population mean in SWt and below-population means in SDWt and SP. It produced the least group means in CN, CL, CW, CC, CWt, GN and GWt.

Table 8. Principal component biplot cluster average.

Attributes	I	II	III	IV	Population Mean
Stover dry weight (g plant ⁻¹)	318.7	299.0	269.0	276.6	293.4
Number of cobs	1.7	2.4	1.9	1.5	1.6
Length of cob (cm)	20.0	21.4	21.6	19.0	19.8
Width of cob (mm)	49.4	48.7	53.6	48.5	49.4
Cob Column	14.3	13.4	14.8	12.9	13.7
Weight of cob (g plant ⁻¹)	369.7	514.0	584.5	292.0	367.1
Number of grains	834.9	1113.0	1040.0	589.0	763.8
Weight of grains (g plant ⁻¹)	281.3	410.6	419.2	218.1	275.7
Shelling Percentage (%)	75.9	79.8	70.3	74.5	74.9
100-Seed Weight (g plant ⁻¹)	34.8	38.0	40.6	38.6	37.3

The grain weight and cob weight were the most discriminatory and representative yield attributes, followed by CC, CL, and GN, whereas SP and SWt were the least discriminatory and representative attributes. This categorization was based on each attribute's vector length and angle to the biplot origin (Figure 5).

4. Discussion

4.1. Effect of Parental Heat Stress on the Progenies' Growth and Yield Attributes

Heat waves are expected to become more severe and frequent, posing a risk to global food security [17]. Heat stress has a negative effect on maize plants [3,21]. As plants are exposed to constant temperature fluctuations in the field, improving their thermotolerance is critical for their survival [7]. Plants exposed to sublethal heat stress (heat priming) during an early growth phase improved their thermotolerance [1,5–7,12,23]. Wang, et al. [23] reported that the progeny of heat-primed wheat plants produced higher grain yield, better leaf photosynthesis, higher antioxidant enzyme activity, and less cell membrane damage when exposed to high temperatures than unprimed (control) wheat plants. Heat priming in the first generation induced transgenerational thermotolerance, according to the study [23]. Kushawaha et al. [13] observed that heat priming improved the grain yield of a heat-sensitive rice variety (Pusa Basmati I) under heat-stress conditions. Due to the retention of the initial stress memory, heat primed plants outperform unprimed plants under heat stress conditions. The duration of the stress, the severity of the stress, and the developmental stage in which the plant encountered the stress can all influence the progeny's ability to remember the stress [5–8]. Stress memory transfer occurs as a result of epigenetic inheritance, which involves heritable patterns of phenotypic variation that are unrelated to DNA sequence variation [11].

According to Sultan, et al. [24], depending on the progeny's growth environment, stress memory can have an adaptive or maladaptive effect on progeny development. Plants' development and yield are hampered by the expression of maladaptive stress memory [6,24]. The progenies of drought-primed wheat outperformed their control counterparts under drought conditions, but there was no significant difference when the two progenies were grown under control conditions [8]. A similar observation was made for *Arabidopsis thaliana*, with no significant difference in progenies that differ in ancestral

temperature exposure under control conditions, but the descendants of the heat-primed ancestor outperformed the descendants of the unprimed ancestor in heat stress environments [1,9].

The non-significant differences in the heat primed and control progenies under control environments observed in the aforementioned studies [1,9] corresponded to the non-significant differences in this study between the HS and NHS progenies under control environments. The lower EP in the HS progenies corroborated Kaushal, et al. [25] findings that heat stress slows seedling emergence. The HS progenies' higher LA, LCC, and PH could be early adaptive traits, as the plants experienced the highest maximum and minimum field temperatures during the first ten WAP (Figure 1). Wang, et al. [8] found that primed wheat progenies had higher photosynthetic activity, antioxidant capacity, and osmolyte accumulation than control progenies under stress.

When the temperature in the field dropped, the NHS progenies produced more LA, NoL, and PH, which likely resulted in more SDWt, CL, CW, CC, CWt, GN, GWt, SP, and SWt. According to Crisp, et al. [6], the events that occur during the stress recovery period determine whether the acquired stress memory is adaptive or maladaptive. A proper recovery and memory reset will result in resources being allocated to growth and/or reproduction, whereas an impaired recovery may result in resources being allocated to the acclimation process [6]. This could explain the HS progenies' longer vegetative phase as measured by DT₅₀ and DS₅₀, as well as their lower yield attributes when compared to the NHS progenies in this study. Plant genotypes play a role in the creation and retention of stress memory, in addition to abiotic and biotic stress effects [16,26].

4.2. Varietal Influence on the Progenies' Growth and Yield Attributes

Environmental stresses affect maize plants in different ways. Therefore, high yield consistency in both favourable and unfavourable conditions is a desirable attribute in maize. According to Edreira and Otegui [27], the identification of stress-tolerant maize varieties is a critical step toward reducing maize yield losses.

The significant differences in the maize population's growth and yield attributes observed in this study are indicators of their diversity. Balla, et al. [5] found significant differences between wheat cultivars, not only in yielding abilities under control conditions, but also in heat sensitivity. When stress occurs on a regular basis, genotypic adaptation to stress is beneficial [28]. Heat stress is an environmental challenge that plants in natural populations face [10], and it is expected to become more severe and common in the future [17]. Therefore, improving thermotolerance in maize is of strategic importance to global food security.

In comparison to WE5323 and ZM1523, the most depressive heat stress effect was seen in variety WE3128 during parental heat stress priming. According to Crisp, et al. [6], maternally stressed plants may allocate more resources to their seeds in order to increase the survivability of their progenies, in preparation for the stress experienced by the mother plant. The higher values recorded in important attributes such as EP, CWt, and GWt in WE3128 may be an indication of adaptive stress memory, even though there were no significant differences in most of the yield attributes measured in the maize varieties' progenies. The formation and transfer of stress-memories is genotype-dependent [14,26].

4.3. Effect of Parental Soil Amendment on the Progenies' Growth and Yield Attributes

Biotic and abiotic stress conditions, such as nutrient deficiency, can cause epigenetic effects. Plants are subjected to nutrient stress when nutrients are in short supply or are available in forms that are inaccessible to the plants. Under such a stressful environment, plants change their physiology to adapt to the new environment. These phenotypic changes have been shown to influence progenies even in second generations that were not exposed to the stress [9,14,15,29].

Kou, et al. [15] observed that N deficiency in rice (*Oryza sativa* L.) caused DNA methylation in stressed plants, which was passed down to the progeny. Despite the fact

that the N stress was only applied to the parents, the stress memory was expressed in the second generations [15].

In this study, progenies of the MF amendment had the lowest levels of CN, GN, CWt, and GWt, all of which were also low in their parents. Similarly, the highest CL, SP, GN, CWt, and GWt obtained from the MPM amendment progenies were consistent with the observations from their parents. A uniform mineral fertiliser was applied during the progeny evaluations. Hence, similar patterns in yield attributes may be linked to the parental growth environment.

Fan, et al. [14] investigated the effect of N deficiency in rice and found reduced growth and yield in stressed parents and their progenies, even when the progenies were grown in N-sufficient conditions. They hypothesised that the progenies inherited their stressed parents' stress memory, which hampered their growth and development in stress-free environments.

4.4. Interaction of Parental Heat Stress, Maize Variety and Soil Amendment on the Progenies' Growth and Yield Attributes

Plants often respond physiologically and genomically to abiotic stresses such as heat waves, droughts, and nutrient deficiency [6]. These stress responses can be reversed or passed down to the progenies of stressed plants after stress recovery. However, the exact mechanisms underlying stress memory formation, transfer, and reversal are not clearly understood [6,8,16]. Studies have shown that plants respond differently to single stress encounters and repeated occurrences of the same stress [5,28,30]. Similarly, a plant's response to a single source of stress differs from its response to multiple stress factors [31,32]. Sun, et al. [32] proposed that plant evolution included both resistance to a single type of stress and the ability to counter multiple types of environmental stresses at the same time.

Balla, et al. [5] used morphological and grain yield-related attributes to identify seven distinct groups in the wheat population exposed to single and repeated heat stress. Since grain yield determines the economic value of maize varieties, the treatment interactions' progenies were clustered in this study based on yield-related attributes. The findings in this study that GWt and CWt were the most informative attributes agreed with previous reports on maize studies [3,33,34].

The combination of heat stress and soil amendment elicited a wide range of phenotypic responses in the progenies. The progenies were not grouped based on a single factor when they were clustered. Instead, the population's variation may have been influenced by a possible interactive effect of the factors. Herman and Sultan [10] observed that stress memory may not be expressed uniformly among close relatives. This lack of alignment in the treatment interactions' progenies was consistent with previous studies [1,8,9] that found no significant differences between the progenies of primed and control plants in a stress-free environment. Clusters II and III contained the best performing treatment interaction for each maize variety among the four identified clusters in the biplot. WE3128 and ZM1523 (NHS-WE3-PM [N3] and NHS-ZM1-PM [N9]) produced their highest yields from PM amendments in the NHS environment, whereas WE5323 produced its highest yield from the MPM amendment in the HS environment (HS-WE5-MPM [H5]).

Phenotypic variation within and between populations can be provided by transgenerational plasticity, allowing for further adaptive evolution [35]. As a result, persistent transgenerational effects in controlled environments can serve as a crop diversity reservoir that plant breeders can tap into if a new environmental condition arises [29]. Increased expression of transposable elements results in more mutations in plants when they are stressed by the environment [26].

5. Conclusions

The parental growth environment influenced the progenies' field performance in a non-heat stress environment. Further evaluation of the progenies under a heat stress environment and molecular analyses are required to establish that a transgenerational effect has occurred.

Author Contributions: Conceptualization, U.P.C., F.R.K. and S.M.; methodology, U.P.C., F.R.K. and S.M.; formal analysis, U.P.C.; investigation, U.P.C.; data curation, U.P.C.; writing—original draft preparation, U.P.C.; writing—review and editing, U.P.C., F.R.K. and S.M.; and supervision, F.R.K. and S.M. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are available on request from the corresponding author.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Yadav, N.S.; Titov, V.; Ayemere, I.; Byeon, B.; Ilnytsky, Y.; Kovalchuk, I. Multigenerational exposure to heat stress induces phenotypic resilience, and genetic and epigenetic variations in *Arabidopsis thaliana* offspring. *bioRxiv* **2020**. [[CrossRef](#)]
2. Colicchio, J.M.; Herman, J. Empirical patterns of environmental variation favor adaptive transgenerational plasticity. *Ecol. Evol.* **2020**, *10*, 1648–1665. [[CrossRef](#)] [[PubMed](#)]
3. Chukwudi, U.P.; Kutu, F.R.; Mavengahama, S. Heat stress effect on the grain yield of three drought-tolerant maize varieties under varying growth conditions. *Plants* **2021**, *10*, 1532. [[CrossRef](#)]
4. Chukwudi, U.P.; Kutu, F.R.; Mavengahama, S. Maize response to combined heat and water stresses under varying growth conditions. *Agron. J.* **2021**, 1–18. [[CrossRef](#)]
5. Balla, K.; Karsai, I.; Kiss, T.; Horváth, Á.; Berki, Z.; Cseh, A.; Bónis, P.; Árendás, T.; Veisz, O. Single versus repeated heat stress in wheat: What are the consequences in different developmental phases? *PLoS ONE* **2021**, *16*, e0252070. [[CrossRef](#)] [[PubMed](#)]
6. Crisp, P.A.; Ganguly, D.; Eichten, S.R.; Borevitz, J.O.; Pogson, B.J. Reconsidering plant memory: Intersections between stress recovery, RNA turnover, and epigenetics. *Sci. Adv.* **2016**, *2*, e1501340. [[CrossRef](#)] [[PubMed](#)]
7. Oyoshi, K.; Katano, K.; Yunose, M.; Suzuki, N. Memory of 5-min heat stress in *Arabidopsis thaliana*. *Plant Signal. Behav.* **2020**, *15*, 1778919. [[CrossRef](#)] [[PubMed](#)]
8. Wang, X.; Zhang, X.; Chen, J.; Wang, X.; Cai, J.; Zhou, Q.; Dai, T.; Cao, W.; Jiang, D. Parental drought-priming enhances tolerance to post-anthesis drought in offspring of wheat. *Front. Plant Sci.* **2018**, *9*, 261. [[CrossRef](#)] [[PubMed](#)]
9. Whittle, C.; Otto, S.; Johnston, M.O.; Krochko, J. Adaptive epigenetic memory of ancestral temperature regime in *Arabidopsis thaliana*. *Botany* **2009**, *87*, 650–657. [[CrossRef](#)]
10. Herman, J.; Sultan, S. Adaptive Transgenerational Plasticity in Plants: Case studies, mechanisms, and implications for natural populations. *Front. Plant Sci.* **2011**, *2*, 1–10. [[CrossRef](#)]
11. Eichten, S.R.; Schmitz, R.J.; Springer, N.M. Epigenetics: Beyond chromatin modifications and complex genetic regulation. *Plant Physiol.* **2014**, *165*, 933–947. [[CrossRef](#)]
12. Kushawaha, A.K.; Khan, A.; Sopory, S.K.; Sanan-Mishra, N. Priming by high temperature stress induces microRNA regulated heat shock modules indicating their involvement in thermopriming response in rice. *Life* **2021**, *11*, 291. [[CrossRef](#)] [[PubMed](#)]
13. Kushawaha, A.K.; Khan, A.; Sopory, S.K.; Sanan-Mishra, N. Light regulated Osa-miR169e is implicated during priming under high temperature stress in rice. *Am. J. Plant Sci.* **2019**, *10*, 1662–1674. [[CrossRef](#)]
14. Fan, X.; Liu, L.; Qian, K.; Chen, J.; Zhang, Y.; Xie, P.; Xu, M.; Hu, Z.; Yan, W.; Wu, Y.; et al. Plant DNA methylation is sensitive to parent seed N content and influences the growth of rice. *BMC Plant Biol.* **2021**, *21*, 211. [[CrossRef](#)] [[PubMed](#)]
15. Kou, H.P.; Li, Y.; Song, X.X.; Ou, X.F.; Xing, S.C.; Ma, J.; Von Wettstein, D.; Liu, B. Heritable alteration in DNA methylation induced by nitrogen-deficiency stress accompanies enhanced tolerance by progenies to the stress in rice (*Oryza sativa* L.). *J. Plant Physiol.* **2011**, *168*, 1685–1693. [[CrossRef](#)]
16. Bilichak, A.; Kovalchuk, I. Transgenerational response to stress in plants and its application for breeding. *J. Exp. Bot.* **2016**, *67*, 2081–2092. [[CrossRef](#)]
17. IPCC. Summary for Policymakers. In *Climate Change 2021: The Physical Science Basis*; Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change; Cambridge University Press: Cambridge, UK, 2021; p. 41.
18. Niu, S.; Du, X.; Wei, D.; Liu, S.; Tang, Q.; Bian, D.; Zhang, Y.; Cui, Y.; Gao, Z. Heat stress after pollination reduces kernel number in maize by insufficient assimilates. *Front. Genet.* **2021**, *12*, 728166. [[CrossRef](#)] [[PubMed](#)]
19. Fatima, Z.; Ahmed, M.; Hussain, M.; Abbas, G.; Ul-Allah, S.; Ahmad, S.; Ahmed, N.; Ali, M.A.; Sarwar, G.; Haque, E.u.; et al. The fingerprints of climate warming on cereal crops phenology and adaptation options. *Sci. Rep.* **2020**, *10*, 18013. [[CrossRef](#)] [[PubMed](#)]
20. Seetharam, K.; Kuchanur, P.H.; Koirala, K.B.; Tripathi, M.P.; Patil, A.; Sudarsanam, V.; Das, R.R.; Chaurasia, R.; Pandey, K.; Vemuri, H.; et al. Genomic regions associated with heat stress tolerance in tropical maize (*Zea mays* L.). *Sci. Rep.* **2021**, *11*, 13730. [[CrossRef](#)] [[PubMed](#)]

21. Chukwudi, U.P.; Kutu, F.R.; Mavengahama, S. Influence of heat stress, variations in soil type, and soil amendment on the growth of three drought-tolerant maize varieties. *Agronomy* **2021**, *11*, 1485. [[CrossRef](#)]
22. Mokhtarpour, H.; Teh, C.B.; Saleh, G.; Selamat, A.B.; Asadi, M.E.; Kamkar, B. Non-destructive estimation of maize leaf area, fresh weight, and dry weight using leaf length and leaf width. *Commun. Biometry Crop Sci.* **2010**, *5*, 19–26.
23. Wang, X.; Xin, C.; Cai, J.; Zhou, Q.; Dai, T.; Cao, W.; Jiang, D. Heat priming induces trans-generational tolerance to high temperature stress in wheat. *Front. Plant Sci.* **2016**, *7*, 501. [[CrossRef](#)] [[PubMed](#)]
24. Sultan, S.E.; Barton, K.; Wilczek, A.M. Contrasting patterns of transgenerational plasticity in ecologically distinct congeners. *Ecology* **2009**, *90*, 1831–1839. [[CrossRef](#)] [[PubMed](#)]
25. Kaushal, N.; Bhandari, K.; Siddique, K.H.M.; Nayyar, H. Food crops face rising temperatures: An overview of responses, adaptive mechanisms, and approaches to improve heat tolerance. *Cogent Food Agric.* **2016**, *2*, 1134380. [[CrossRef](#)]
26. Migicovsky, Z.; Yao, Y.; Kovalchuk, I. Transgenerational phenotypic and epigenetic changes in response to heat stress in *Arabidopsis thaliana*. *Plant Signal. Behav.* **2014**, *9*, e27971. [[CrossRef](#)] [[PubMed](#)]
27. Edreira, J.I.R.; Otegui, M.E. Heat stress in temperate and tropical maize hybrids: Differences in crop growth, biomass partitioning and reserves use. *Field Crop. Res.* **2012**, *130*, 87–98. [[CrossRef](#)]
28. Hilker, M.; Schmülling, T. Stress priming, memory, and signalling in plants. *Plant Cell Environ.* **2019**, *42*, 753–761. [[CrossRef](#)]
29. Herman, J.J.; Sultan, S.E.; Horgan-Kobelski, T.; Riggs, C. Adaptive transgenerational plasticity in an annual plant: Grandparental and parental drought stress enhance performance of seedlings in dry soil. *Integr. Comp. Biol.* **2012**, *52*, 77–88. [[CrossRef](#)] [[PubMed](#)]
30. Ding, Y.; Virilouvet, L.; Liu, N.; Riethoven, J.-J.; Fromm, M.; Avramova, Z. Dehydration stress memory genes of *Zea mays*; comparison with *Arabidopsis thaliana*. *BMC Plant Biol.* **2014**, *14*, 141. [[CrossRef](#)]
31. Johnsen, Ø.; Dæhlen, O.G.; Østreng, G.; Skråppa, T. Daylength and temperature during seed production interactively affect adaptive performance of *Picea abies* progenies. *New Phytol.* **2005**, *168*, 589–596. [[CrossRef](#)]
32. Sun, C.; Ali, K.; Yan, K.; Fiaz, S.; Dormatey, R.; Bi, Z.; Bai, J. Exploration of epigenetics for improvement of drought and other stress resistance in crops: A review. *Plants* **2021**, *10*, 1226. [[CrossRef](#)] [[PubMed](#)]
33. Inyang, P.; Ene, C.O.; Emmanuel, A.; Chukwudi, U.P.; Ikeogu, U.N. Environmental impact and genetic expressions of new drought-tolerant maize genotypes in derived savannah agro-ecology. *Not. Sci. Biol.* **2021**, *13*, 10691. [[CrossRef](#)]
34. Uba, C.U.; Agbo, C.U.; Chukwudi, U.P.; Efusie, A.A.; Muojijama, S.O. Field evaluation of yield and yield component traits of breeding lines of maize over two seasons in derived Savannah agro-ecology. *Not. Sci. Biol.* **2018**, *10*, 567–574. [[CrossRef](#)]
35. Fox, R.J.; Donelson, J.M.; Schunter, C.; Ravasi, T.; Gaitán-Espitia, J.D. Beyond buying time: The role of plasticity in phenotypic adaptation to rapid environmental change. *Philos. Trans. R. Soc. B Biol. Sci.* **2019**, *374*, 20180174. [[CrossRef](#)] [[PubMed](#)]