Article

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Abstract

Monitoring genetic gain is critical for evaluating breeding program performance. This study assessed genetic trends in the Zambia national maize breeding program using historical data (2001–2017) from 2,225 hybrids tested across years and locations. Best linear unbiased estimates (BLUEs) were calculated, and genetic trends were determined by regressing entry means on first-year testing data. Mean heritability was moderate for grain yield, plant height, and ear height, and high for anthesis and silking dates, indicating strong reliability for flowering traits. Significant positive genetic gains were observed for most traits except days to silking. Grain yield increased at 0.021 t ha^{-1} per year (0.85% annually), reflecting progress but remaining below levels required to meet future production demands. Plant and ear height increased by more than 1.3 cm annually, suggesting directional selection for taller plant architecture. Grain texture declined by 1.28% per year, indicating a shift toward flint-type kernels. Anthesis date and ears per plant showed minimal genetic variation. Regression models explained more than 15% of the total variation in plant height, ear height, ear number, and grain texture, confirming consistent genetic progress. Although measurable gains were achieved, accelerating yield improvement will require rapid-cycle breeding, enhanced trait heritability, modern breeding tools, and strategic reallocation of resources to sustain long-term impact.

Keywords: maize; genetic gain; grain yield; complementary agronomic traits; Zambia

1. Introduction

Zambia is situated within the savanna ecological zone. It is characterized by three major agroecological regions (I, II, and III), each with distinct rainfall patterns, altitudes, growing seasons, temperatures, and soil productivity, which significantly impact maize production [1,2]. Maize plays a dual role in Zambia's agricultural economy, serving as both a staple for household nutrition and a key tradable commodity in domestic and regional markets. It is the principal staple crop and strategic commodity that underpins the livelihoods of millions of smallholders and commercial farmers. Despite historic breeding programs that have developed improved maize varieties suited to diverse conditions, smallholder farmers, who contribute approximately 85% of total maize output [3,4], continue to face systemic constraints. Climate change, erratic rainfall, limited access to inputs, and inadequate extension services threaten productivity and food security. Addressing these challenges requires integrated interventions that combine technological innovation, policy support, and farmer capacity-building. This includes a directed effort by the Zambia Agriculture Research Institute (ZARI) maize breeding program to align its breeding strategies with the integrated interventions. ZARI plays a pivotal role in this process by directing its breeding strategies toward the development of climate-resilient cultivars. These resource-efficient varieties complement broader interventions to ensure sustainable maize production and national food security.

The ZARI maize breeding program was established in 1962 with technical support from the United Kingdom, Yugoslavia, and Sweden. The program has played a pivotal role in developing resilient, high-yielding varieties adapted to diverse agroecological zones [5]. Initial efforts focused on maintaining and improving the parent inbred lines of the widely used hybrid SR52, as well as on developing local composites and hybrids adapted to Zambian conditions. In the 1970s and 1980s, the maize breeding program expanded, leading to the development of local composite and hybrid varieties. However, many of these varieties struggled to match SR52's performance under smallholder conditions [6]. Collaboration with Yugoslavian breeder Dr D. Ristanovic introduced valuable European germplasm, resulting in the production of hybrids such as MM752 and MM603/604. Supported by Swedish and American funding, these initiatives increased the adoption of improved maize varieties to about 60% by the early 1980s [7]. According to [8], institutional and seed-system reforms transformed Zambia’s maize industry. Until the mid-1980s, public sector institutions dominated maize breeding, production, and distribution. However, from the late 1980s through the 1990s, the private sector increasingly assumed a leading role in maize breeding and seed supply, becoming a key driver of the industry’s growth.

Since then, more than 60 maize varieties have been released by ZARI, emphasizing drought tolerance, pest resistance, and yield stability [9–11]. These breeding efforts in Zambia have led to the introduction of numerous improved maize varieties, broadening the production base and enhancing smallholder participation in the maize value chain. Smallholder farmers, who constitute about 80% of the Zambian agricultural sector, play a central role in the adoption, selection, and marketing of improved varieties, contributing significantly to both household and national food security [3,9].

Despite this progress, maize production remains constrained by climate change, characterized by erratic rainfall and an increase in extreme weather events that threaten yields in rain-fed systems [2,12]. Additional challenges include limited access to high-quality seeds, fertilizers, and extension services, compounded by poverty and inadequate infrastructure [10,13]. Socio-economic inequalities and knowledge gaps further hinder the adoption of sustainable farming practices [13]. Promoting conservation agriculture and strengthening partnerships among farmers, research institutions, and extension services are crucial for enhancing productivity, resilience, and food security amid changing climatic conditions [11,14,15]. There is therefore an immediate need for targeted interventions, based on an understanding of breeding efforts, local contexts and practices, to close the identified performance gaps [16].

In response to current challenges, policymakers and stakeholders must prioritize investments in agricultural research and development, focusing on strengthening infrastructure along the maize value chain from production to marketing [15]. This has also been extended to the maize breeding program, through collaborative partnerships among farmers, extension services, and research institutions, which are essential for sharing innovations. The Consultative Group on International Agricultural Research (CGIAR)-led Excellence in Breeding (EiB) platform [17] has modernized the program by refining breeding objectives, identifying market segments, and optimizing breeding schemes through advanced techniques such as double-haploid and single-seed descent, as well as through expanded multi-environment testing. This has also been extended to collaborative germplasm exchange among ZARI, the International Maize and Wheat Improvement Centre (CIMMYT), and the International Institute of Tropical Agriculture (IITA), thereby enhancing the adaptability of local lines and hybrid varieties to both biotic and abiotic stresses. Since 2011, over 30 stress-tolerant and nutritionally enhanced maize varieties have been released and adopted by farmers.

Despite the effort, ZARI's maize breeding program has not established a baseline for genetic gain, thereby limiting the data-driven development of climate-smart, stable, and market-oriented maize varieties. In contrast, several regional maize breeding programs have emphasized establishing genetic gain baselines as essential for continuous improvement. [18] reported annual genetic gains of 61, 25, 6, and 2 kg ha^{-1} yr^{-1} under optimal, random drought stress, heat stress, and managed drought stress conditions, respectively, for released varieties by the Zimbabwe's Department of Research and Specialized Services (DR&SS) in developing high-yielding hybrids. Similarly, [19] observed positive grain yield gains across management conditions (28–35 kg ha^{-1} yr^{-1}), in high-yield potential environments (17–61 kg ha^{-1} yr^{-1}), and in low-yield potential environments (0–16 kg ha^{-1} yr^{-1}) for the final two (intermediate and advanced variety trials) stages of evaluation of the DR&SS breeding pipeline. Equally, [20] reported gains of 88 kg ha^{-1} yr^{-1} and 26 kg ha^{-1} yr^{-1} for the Kenya highland maize breeding program for the preliminary and advanced yield trials, respectively. Likewise, [21] also documented notable genetic gains for grain yield in Uganda's national performance trials (81 kg ha^{-1} yr^{-1}), era trials (106 kg ha^{-1} yr^{-1} for CIMMYT entries), and for NARO and private sector entries (59 kg ha^{-1} yr^{-1} and 79 kg ha^{-1} yr^{-1}, respectively). In Mozambique, [22] found no significant trends in genetic gain for grain yield in the Agricultural Research Institute of Mozambique (IIAM) maize breeding program. Thus, measuring genetic gains across regional maize breeding programs ensures that each program remains data-driven, efficient, and responsive to changing production and market needs.

Refs. [19,23] emphasize that although assessing current selection gains is valuable for individual breeding programs, a broader evaluation of genetic gains across maize breeding programs in sub-Saharan Africa is also essential. Such quantification helps determine whether current yield trends are adequate to meet future food demands and assess the region's capacity to contribute effectively to climate adaptation strategies. The primary objective of this study was to estimate genetic gain trends in Zambia's ZARI maize breeding pipeline using historical data from 2001 and 2017. Thus, refine breeding strategies to maximize genetic gain per unit time, cost, and resource investment.

2. Materials and Methods

2.1. Maize Germplasm

The study used data from germplasm developed through the ZARI maize breeding program, including three-way crosses, single crosses, and commercial check hybrids. Selected inbred lines are crossed to produce F_1 hybrid seed. Individual plants were then selected from the F_2 generation and advanced to F_6 using the pedigree method. The inbred lines are crossed with an inbred line and single-cross testers from a complementary heterotic group to produce single-cross and three-way hybrids. Single-cross and three-way hybrid combinations were also generated from CIMMYT x ZARI and IITA x ZARI inbred lines. Additional single-cross hybrids were developed using combinations of pedigree-derived inbred lines and double-haploid-derived inbred lines Appendix B, Figure A1. These single-cross hybrids served as parents for generating three-way hybrids. *The ZARI maize breeding program employs a stage-gate advancement protocol [42], providing a structured, sequential framework that guides germplasm advancement through three trial stages: preliminary, intermediate, and advanced yield trials. At each stage, advancement is based on accumulated performance data and the candidate's fit with the target product profile Appendix, Table A.1.* This study utilized data from 2,225 hybrid maize varieties in preliminary and advanced yield trials conducted from 2001 to 2017. Over the years, various local and commercial check varieties were included in the trials, with common checks maintained to ensure data connectivity and facilitate the estimation of genetic gain. A total of 72 experiments (comprising year × trial × location combinations) were used, with the number of experiments per year varying from 1 to 21 (Table 1).

Table 1. Summary of the number of ZARI maize experiments used in the analysis and the number of hybrid variety entries per year.

Year	No. of Experiments	No. of hybrid varieties
2001	7	547
2003	6	1325
2005	2	31
2006	5	25
2007	4	62
2010	1	11
2011	1	11
2015	21	8
2016	13	61
2017	12	154

2.2. Description of Locations and Trials

The trials were conducted across five locations in Zambia: Golden Valley (Chisamba), Kabwe, Misamfu, Mount. Makulu (Chilanga), and Msekera (Chipata), under varying management conditions (Table 2 and Figure 1). The locations served as the target environments for the varieties developed by the breeding program, offering opportunities to identify the best candidate varieties under relevant stress conditions. The number of entries per experiment varied widely, ranging from fewer than five to 1,303, and experiments varied by year (Figure 2). Commercial hybrids and open-pollinated varieties (OPVs) from private seed companies and CIMMYT were used as checks. Although some commercial checks varied across trials over the years, most were consistently included across experiments, enabling connectivity to estimate genetic gain. All experiments were conducted using an alpha-lattice design with 2 or 3 replications. The experiments were established in 1- to 4-row plots, with row lengths of 3 or 5 m, spaced 75 cm apart and 25 cm within rows, resulting in a final plant density of approximately 53,333 plants ha^{-1}. Agronomic practices at each site followed locally recommended management *guidelines.*

Table 2. *Agro-ecological details of ZARI maize trials sites (2001-2017).*

Site	**Latitude (°S)**	**Longitude (°E)**	**Altitude (m)**	**Mean Annual Temp (°C)**	**Mean Annual Rainfall (mm)**	**Management Condition**	**Key Environmental Features**
Golden Valley	14.98	28.07	1150	20–26	800–900	Low N	Semi-arid; sandy loam soils; nutrient-stress site
						Optimum	Medium-altitude site; favourable growing conditions
Kabwe	14.44	28.45	1,200	20–25	850–950	Low N	Central plateau; low-N site; sandy clay loam soils
Misamfu	10.17	31.2	1400	18–23	1,200–1,300	Optimum	High rainfall, ferrallisol soils; favourable conditions
						Low pH	Acidic soils; high rainfall zone
Mt Makulu	15.55	28.25	1,210	19–26	800–1,000	Optimum	Medium-altitude, well-drained loamy soils
Msekera	13.63	32.6	1030	20–28	950–1,100	Optimum	Eastern plateau; well-structured ferrosols
						Low pH	Low-pH soils; moderately high temperatures

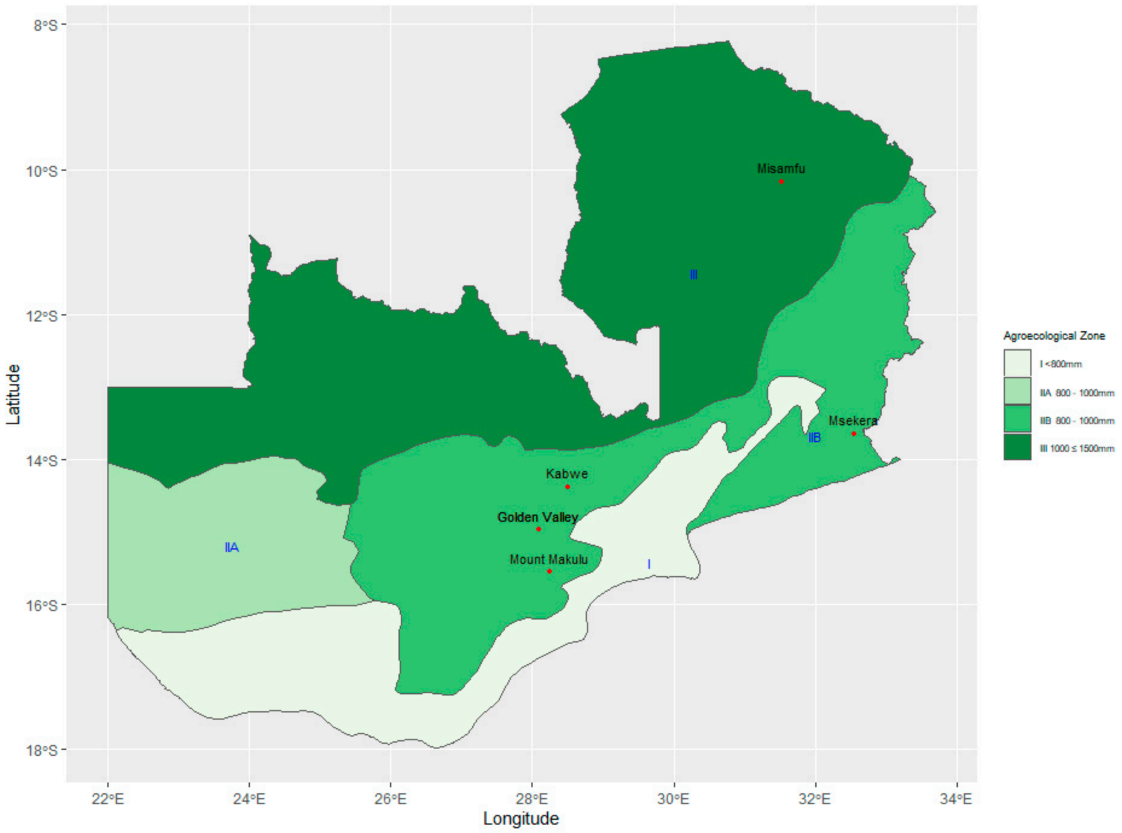

Figure 1. *Agroecological zones of Zambia and key phenotyping sites employed by the ZARI Maize program.*

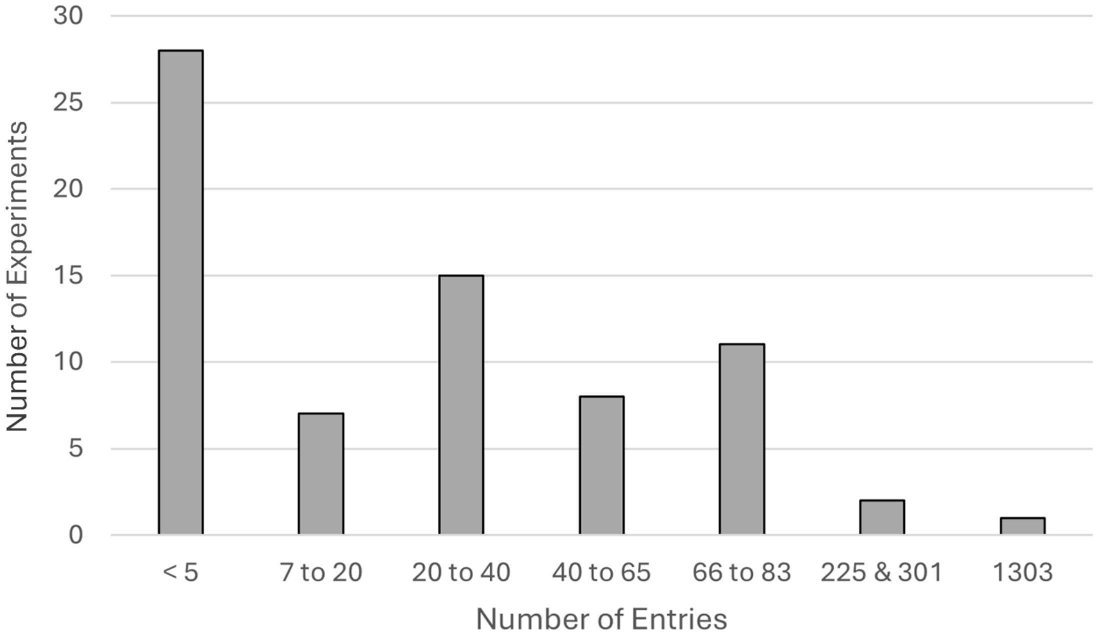

Figure 2. Number of ZARI Maize field experiments (year/location combinations) within a range of entries.

2.3. Measurement of the Agronomic Traits

For grey leaf spot (GLS, *Cercospora zeae-maydis)* and Turcicum leaf blight (ET, *Exserohilum turcicum*, formerly *Helminthosporium turcicum*), disease severity was visually assessed on a plot basis using a 1–5 scale, where 1 indicated no visible symptoms, and 5 indicated nearly all leaf tissue was destroyed. Specifically, 2 denoted lesions on lower leaves with minimal infection above the ear leaf; 3, disease present on most leaves with some lower leaves dead; and 4, extensive lesions on upper leaves completely dead. Ear rot (ER, *Fusarium verticillioides*) severity was scored visually from 1 (no infection) to 5 (severe infection). The anthesis–silking interval (ASI) was calculated as the difference in days between the silking date (SD) and the anthesis date (AD), both of which were recorded when 50% of the plants in a plot had reached the respective flowering stage. Before harvest, plant and ear heights were measured as an average of five representative plants per plot. At harvest, the number of plants (NP) per plot was determined by counting plants within the net plot area, excluding border and end plants. Similarly, the total number of ears was calculated as the number of ears per plot (EPP). The percentages of root- and stalk-lodged plants (RL, SL) were computed relative to the total stand count. Grain texture (TEX) was visually scored following CIMMYT maize descriptors and classified on a 1-5 scale, where 1 represented flint kernels with round grains and 5 indicated dent kernels with a floury endosperm. Ear aspect (EA) was visually scored to assess overall ear quality, including ear shape, kernel arrangement, uniformity, and grain fill. Lower scores (1-3) indicated well-filled, uniform, and desirable ears, whereas higher scores (4-5) reflected poor ear development, tip-fill deficiencies, or irregular kernel set. Two border plants at each end of the plot were excluded from yield estimation, and the remaining plants were hand-harvested. Core weight (CW) was determined as the dry weight of the cob after complete removal of grain. A sample of 5-10 ears harvested at physiological maturity was dried to approximately 12–15% moisture content, shelled completely, and cleaned of residual husk and debris. The resulting bare cobs were weighed using a digital balance (0.1 g precision), and the mean core weight per plot was calculated from multiple representative ears. Fresh Seed Weight (SW) of grain was determined for each plot by measuring the weight of all ears harvested from the net plot area after drying and shelling. Grain yield (GY) and moisture content were recorded, with yield adjusted to 12.5% moisture and expressed in t ha^{-1}. Thousand-seed weight (TSW) was determined by counting and weighing a subsample of 1,000 kernels per plot using a digital seed counter and precision balance. When fewer than 1,000 kernels were available, the sample was adjusted to a standard weight based on the average weight of a randomly selected subsample of the same size. Not all traits were recorded in every trial; more comprehensive trait evaluation was conducted in the advanced trial than in the preliminary trial.

2.4. Statistical Analysis

In this analysis, an experiment was defined as year x location x trial combination. For each of the 72 experiments, analyses of variance were performed using the following model (Equation 1):

$$y_{ij} = \mu + g_i + r_j + e_{ij} \qquad (1)$$

where y_{ij} is the mean phenotypic value of the trait within an experiment, g_i is the random effect of the *i*th genotype with $g_i \sim N(0, \sigma^2_{g_i})$, r_j is the random effect of the *j*th replication with $r_j \sim N(0, \sigma^2_{r_j})$, and e_{ij} is the residual error with $e_{ij} \sim N(0, \sigma^2_{e_{il}})$. Mean heritability was calculated within each experiment as (Equation 2):

$$EMH = \frac{\sigma_g^2}{\sigma_g^2 + \langle \frac{\sigma_e^2}{r} \rangle} \qquad (2)$$

where, σ_g^2 , σ_e^2 are the genetic and error variances, and r is the number of replications.

The standardized residual for each plot within each experiment was calculated as eij/σe, where eij is the error residual for the plot with the ith genotype in the jth replication and σ_e is the error

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standard deviation. Plots where the absolute value of e_{ij}/σ_e was greater than 1.75 were removed from analyses. For every trait, data from experiments with EMH < 0.20 were excluded from further analysis. Data from all experiments were combined, and a mixed model analysis was conducted to obtain the Best Linear Unbiased Estimates (BLUE) of each entry using the model (Equation 3):

$$y_{ijkl} = \mu + g_i + c_j + t_k + r(t)_{kl} + gt_{ik} + \varepsilon_{ijkl} \quad (3)$$

where y_{ijklm} is the phenotypic value for the i^{th} genotype from the jth control group *j*, in the kth experiment *k*, the lth replication. μ is the overall mean; g_i is the fixed effect of the i^{th} genotype, c_j is the fixed effect of the j^{th} control, where *j*=1 for the control population consisting of the checks and *j*=2 for the lines group; t_k is a random effect for the k^{th} experiment with $t_k \sim N(0, \sigma^2_{t_k})$; $r(t)_{kl}$ is a random effect for the l^{th} replication nested in the k^{th} experiment with $r(t)_{kl} \sim N(0, \sigma^2_{r(t)})$; gt_{ik} is the random effect of the interaction of the i^{th} genotype and k^{th} experiment with $gt_{ik} \sim N(0, \sigma^2_{gt_{ik}})$; and $\varepsilon_{ijkl.}$ is the residual error with $\varepsilon_{ijkl} \sim N(0, \sigma^2_e)$.

We analyzed the gain in GY from selecting GY in low-yield experiments and from selecting GY in high-yield experiments. Experiments with a mean GY > than the median were placed in the GY-High set, and those with average GY < the median were placed in the GY-Low set. The genotypic (r_g) correlation for the hybrid's GY across yield levels was calculated. r_g was calculated as

$$r_g = \frac{r_p}{\sqrt{EMH_H EMH_L}} \quad (4)$$

where rp is the phenotypic correlation of GY in high and low experiments, and EMHh and EMHl are the heritability of yield in high and low yield experiments, respectively. The relative efficiency of improving yield in GY-Low sites by selecting for yield in GY-High experiments was calculated as

$$RE = r_g \frac{\sqrt{EMH_h}}{\sqrt{EMH_l}} \quad (5)$$

Genetic trends within the ZARI breeding pipeline were estimated by regressing the Best Linear Unbiased Estimates (BLUEs) of only the ZARI hybrid varieties against the first year of testing (FYT). The FYT was defined as the first year in which a hybrid appeared in the 2001-2017 dataset. The regression slope provides an estimate of genetic gain per year of testing, in units of the trait. This slope was also expressed as a percentage of the grand mean of all hybrid varieties as estimated from equation 3. Genetic trends were estimated across all experiments. The number of entries of hybrid varieties at each FYT level ranged from 0 to 1323 (Figure 3).

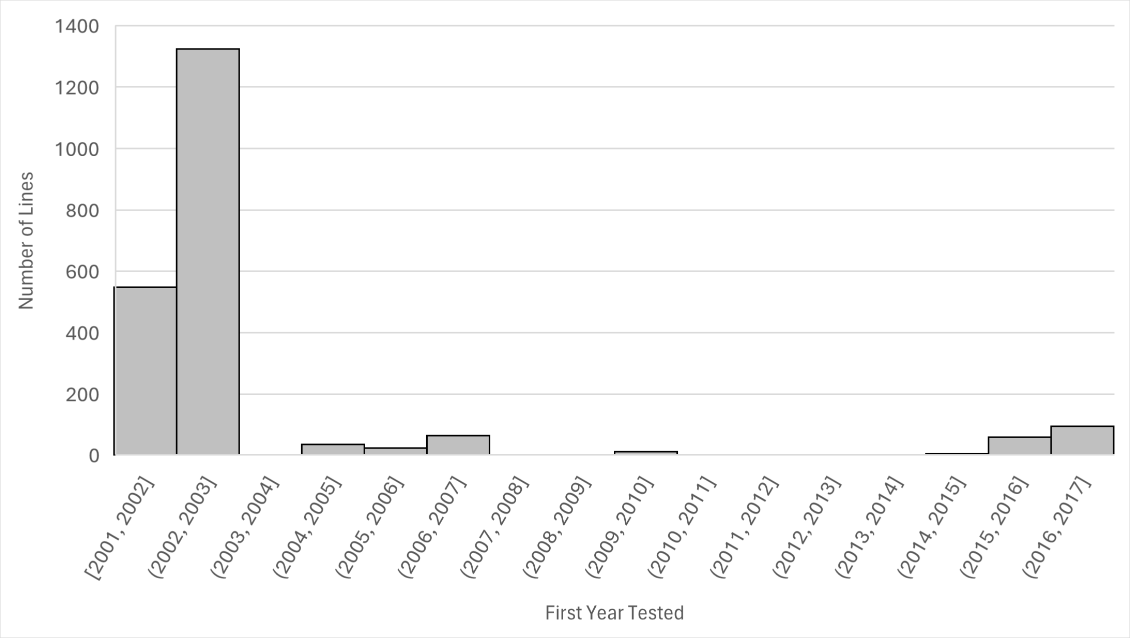

Figure 3. Number of ZARI Maize lines in each range of the first year tested.

3. Results

The dataset used in the study comprised 72 experiments (i.e., year × trial × location combinations) and 2,225 unique hybrid varieties. The number of entries included per experiment varied widely (Figure 2). The 2003 preliminary trial at the Golden Valley included 1,303 entries, representing over 300 hybrid varieties from multiple families. In contrast, only eight hybrid varieties were tested in 2015 (Table 1). There were many trials with very few entries, including 38 experiments (52.8% of all experiments with < 5 entries (Figure 2). The number of hybrid varieties at each level of First Year Tested (FYT) ranged from 0 to 1323 (Figure 3); a value of 0 indicates that no new entries were included in the experiment. The number of experiments conducted per year also varied significantly, ranging from one to 21 (Table 1). The number of experiments in which trait data were collected ranged from 6 (ER) to 68 (FW) (Table 3). Several agronomic traits (GY, FW, PH, EH, SD, AD, ASI, NE, TEX) were extensively evaluated, with data from 45 to 68 experiments each. The range of trait averages across experiments was wide, primarily because some experiments had extremely low averages. For example, the average GY across experiments ranged from 0.18 to 8.03 t ha^{-1}; the maximum average was 44.15 times the minimum. The ranges underscore the extent of phenotypic variation across environments in Zambia. Additional traits such as RL, GLS, and EA also had broad experimental representation. In contrast, ER, SL, FW, SH, ET, and NE were assessed less frequently, reflecting their specialized nature or limited expression under field conditions.

Table 3. Summary of the number of experiments per trait and trait means, minimum per experiment.

	Units	Number of Experiments	Average Trait Values of Experiments			
			Average	Minimum	Maximum	Max. / Min.
GY-All*	t ha^{-1}	64	2.25	0.18	8.03	44.15
GY-High	t ha^{-1}	32	3.27	2.08	8.03	3.96
GY-Low	t ha^{-1}	32	1.20	0.18	2.06	11.44
FW*	t ha^{-1}	68	3.15	0.24	8.34	35.51
PH*	cm	56	203.8	72.3	282.4	3.90
EH*	cm	56	100.0	27.3	161.8	5.92
SD*	days	65	66.8	57.1	83.1	1.45
AD*	days	65	64.6	55.7	81.5	1.46
ASI*	days	62	2.18	-1.04	2.35	2.35
NE*	count	68	0.91	0.3	3.66	11.81
TEX*	1-5	45	2.18	1.23	3.54	2.87

SW	t ha^{-1}	27	0.91	0.15	2.56	16.73
RL	%	33	2.28	0.04	8.90	216.43
SL	%	18	0.38	0.00	3.27	
CW	g	17	0.26	0.05	1.53	30.21
GLS	1-5	30	1.29	1.00	3.53	3.53
SH		17	61.4	0.6	86.0	143.58
ER	1.5	6	1.05	0.02	2.17	107.96
ET	1-5	19	1.86	1.24	2.47	2.00
EA	1.5	40	2.68	1.63	3.83	2.35

*Traits that were analyzed for genetic gain. GY=grain yield, FW=fresh weight of grain, PH=plant height, EH=ear height, SD=days to silking, AD=days to anthesis, NE=number of ears, TEX=grain texture.

3.1. Heritability

The evaluation of experiment-level mean heritability (EMH) revealed substantial variation in data quality across traits. Heritability was moderate to low for most traits (Table 4). The yield-related traits of GY and FW exhibited moderate average EMH values (0.37–0.38). More than 35% of these experiments had EMH < 0.20 and were excluded from the genetic gain analysis. More than 25% of the experiments had EMH of 0, indicating that genetic variation was not significant. The median GY was 2.06 t ha^{-1} (Table 3). An analysis was done using data from the 32 experiments with means above the median (GY-High) and the 32 experiments below the median (GY-Low). EMH was greater in GY-High than in GY-Low experiments, even though 31.3% of the GY-High experiments had an EMH of zero. There was a moderate correlation of mean GY with EMH in the GY-High set (Table 4). An analysis of EMH (assume five experiments, three reps each) produced an EMH of 0.331 for GY-High experiments, but just 0.168 for GY-Low experiments.

The number of ears per plant (NE) showed the lowest average EMH among all traits, with 48.5% of experiments excluded from the genetic gain analysis and 39.5% with an EMH of zero. Flowering traits, SD and AD, had the highest average EMH values, whereas ASI had moderate to low EMH. Plant height (PH) and ear height (EH) had intermediate EMH values. For any given trait, at least 19% of experiments had an EMH < 0.20 and were thus excluded from the genetic gain analysis. All traits showed EMH values of 0 in more than 15% of their experiments. It is possible that the large number of experiments (28) with fewer than 5 entries led to trials in which no genetic differences were detected. The low-trait means (Table 3) may also have reduced EMH, as the correlation between trait mean and EMH in experiments was greater than 0.20 for GY, GY-High, FW, and NE (Table 4). It is common to obtain low EMH when traits are not well expressed.

Table 4. Summary of entry-mean heritability (EMH) within experiments of ZARI maize traits. An experiment (Exp) was a year/trial/location combination. Values are shown only for traits with sufficient experiments to estimate genetic gain.

Trait	Total # Exp.	# Exp. used in GG	Average EMH	% Exp. with EMH		Correlation of Exp. Mean with EMH
				< 0.20	= 0	
GY-All	64	45	0.371	38.7%	25.8%	0.30
GY-High	32	22	0.414	34.4%	31.3%	0.44
GY-Low	32	23	0.325	40.6%	18.8%	-0.18
FW	69	44	0.380	36.2%	29.0%	0.21
PH	57	43	0.469	24.6%	17.5%	0.09
EH	57	41	0.420	28.1%	21.1%	-0.19
SD	63	48	0.517	23.8%	15.9%	-0.14
AD	63	51	0.512	19.0%	19.0%	0.03
ASI	62	28	0.331	53.2%	29.0%	0.15
NE	69	43	0.293	48.5%	39.4%	0.23
TEX	46	34	0.495	26.1%	19.6%	-0.12

GY=grain yield, FW=fresh weight of grain, PH=plant height, EH=ear height, SD=days to silking, AD=days to anthesis, NE=number of ears, TEX=grain texture.

3.2. Genetic Gains

The slope obtained by regressing the BLUE of each hybrid on its FYT value is an estimate of genetic gain. The slopes were significantly different from zero for all traits except SD and GY in the low-yield experiments, indicating significant temporal changes in these traits (Table 5). The regression modelled >15% of the total variation among the BLUEs for TEX, PH, and EH, but <3.5% for all the other traits. Grain yield is always a primary trait for grain crop breeders. Using data from all experiments with EMH > 0.20, GY and FW showed consistent improvement, with GY and FW increasing by 0.83% (0.021 t ha^{-1}) and 1.85% (0.058 t ha^{-1}) of their respective means per year (Table 5, Figures 4 and 5). Genetic gain in the GY-High experiments was 0.041 t ha^{-1} per year and 1.14% of the mean, while genetic gain in the GY-Low experiments was not significant (Table 5).

We estimated the effect of selecting maize hybrids for high grain yield in GY-High experiments on grain yield at GY-Low sites. The phenotypic correlation for grain yield at low- and high-yielding sites was 0.146, whereas the corresponding genetic correlation was 0.617. The relative efficiency of improving grain yield in GY-Low sites by selecting for grain yield in GY-High sites, versus directly selecting for yield in GY-Low sites, was 0.866.

Prolificacy, assessed using NE, showed a significant trend, but the regression accounted for only 1.4% of the variation, and the slope was -0.01 ears per plant per year (Table 5, Figure 6). Plant height (PH) and ear height (EH) exhibited moderate but significant genetic gains, indicating gradual increases in height and plant vigour (Table 5, Figures 7 and 8). In contrast, grain texture (TEX) showed a significant negative trend (-1.28%), suggesting a shift toward flint kernel types over time (Table 5, Figure 9). Flowering traits displayed minimal directional change; anthesis date (AD) increased slightly (0.87 days per year), ASI decreased slightly (-0.38 days per year), while silking date (SD) showed no significant trend (Table 5). AD and SD were among the more heritable traits, so there has likely been little selection pressure on them, as indicated by their low genetic gain per year, expressed as a percentage of the mean.

Table 5. Summary of genetic gains for traits in the ZARI maize breeding program from 2001 to 2017. Slope indicates the predicted change in the trait per year of testing in the first year and is an estimate of genetic gain.

Trait	No. of Entries	No. of Experiments	Mean	Intercept	Slope	Prob	r^2	Slope as % Mean
GY-All	757	45	2.5	-41.9	0.021	<0.0001	0.0335	0.83%
GY-High	686	22	3.6	-82.17	0.041	<0.0001	0.0359	1.14%
GY-Low	483	23	1.2	11.73	-0.006	0.2505	0.0027	-0.49%
FW	2061	44	3.1	-107.2	0.058	<0.0001	0.0313	1.85%
PH	294	43	210.8	-210.8	1.461	<0.0001	0.1526	0.69%
EH	294	41	99.6	-2664	1.324	<0.0001	0.2392	1.33%
SD	685	48	62.2	31.4	-0.014	0.5276	0.0006	-0.02%
AD	684	51	65.4	-174.4	0.087	<0.0001	0.0234	0.13%
ASI	653	28	2.2	79.3	-0.038	0.0003	0.0202	-1.73%
TEX	265	34	3.5	89.7	-0.045	<0.0001	0.1684	-1.28%
NE	2067	43	0.9	19.60	-0.010	<0.0001	0.0138	-0.05%

GY=grain yield, FW=fresh weight of grain, PH=plant height, EH=ear height, SD=days to silking, AD=days to anthesis, NE=number of ears, TEX=grain texture.

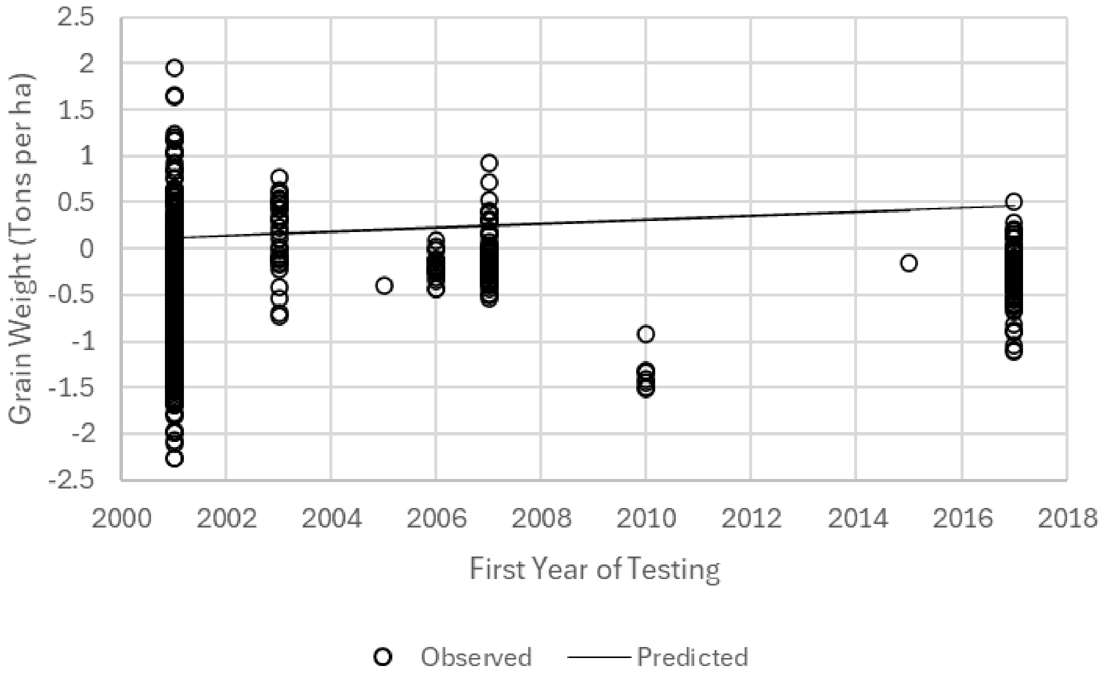

Figure 4. Regression of grain yield (GY) BLUEs of ZARI maize lines onto their first year of testing value.

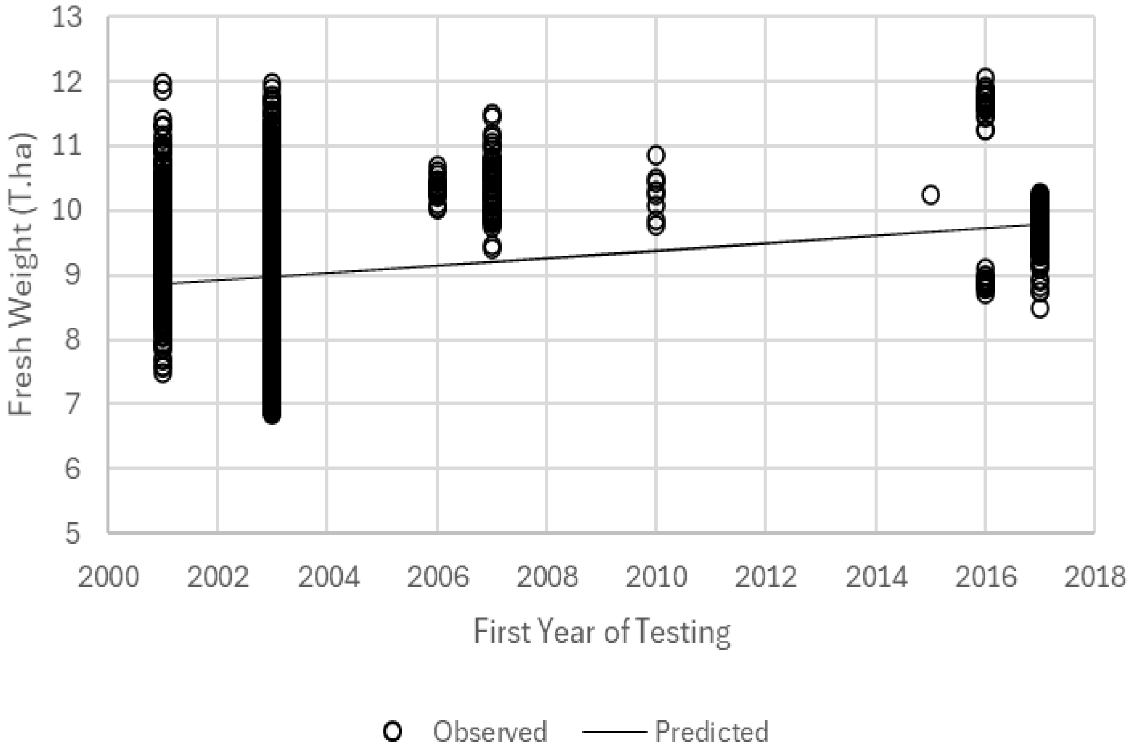

Figure 5. Regression of fresh yield weight (FW) BLUEs of ZARI maize lines onto their first year of testing value.

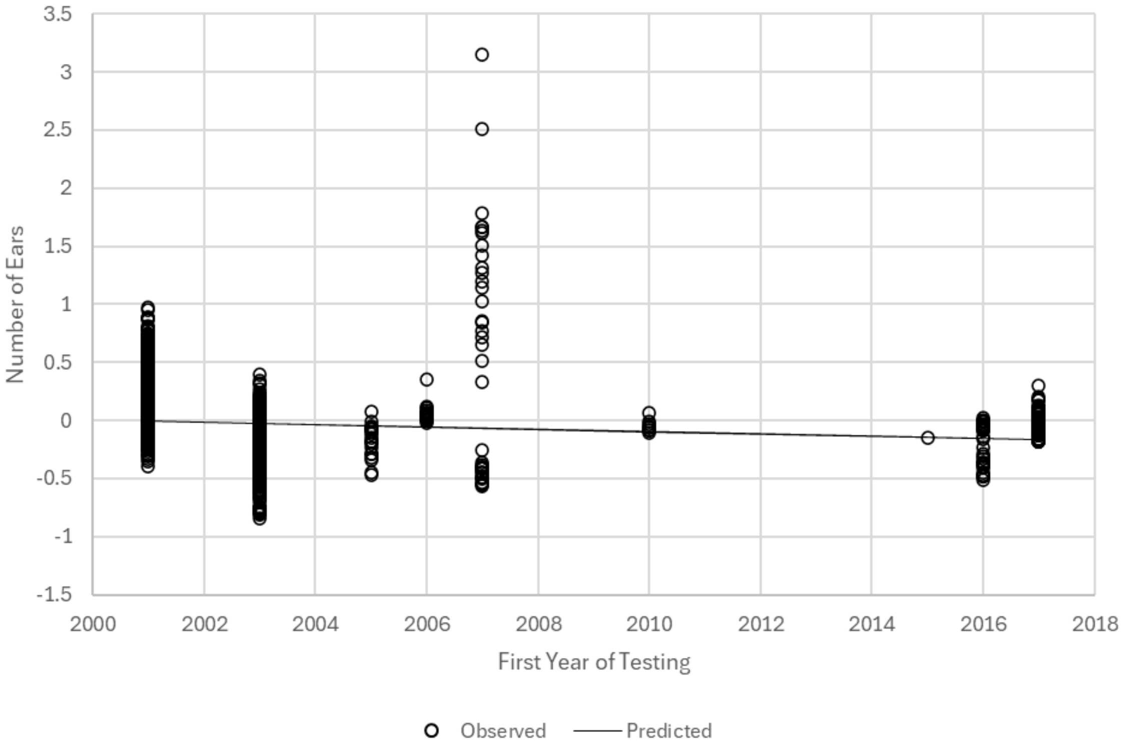

Figure 6. Regression of the number of ears (NE) BLUEs of ZARI maize lines onto their first year of testing value.

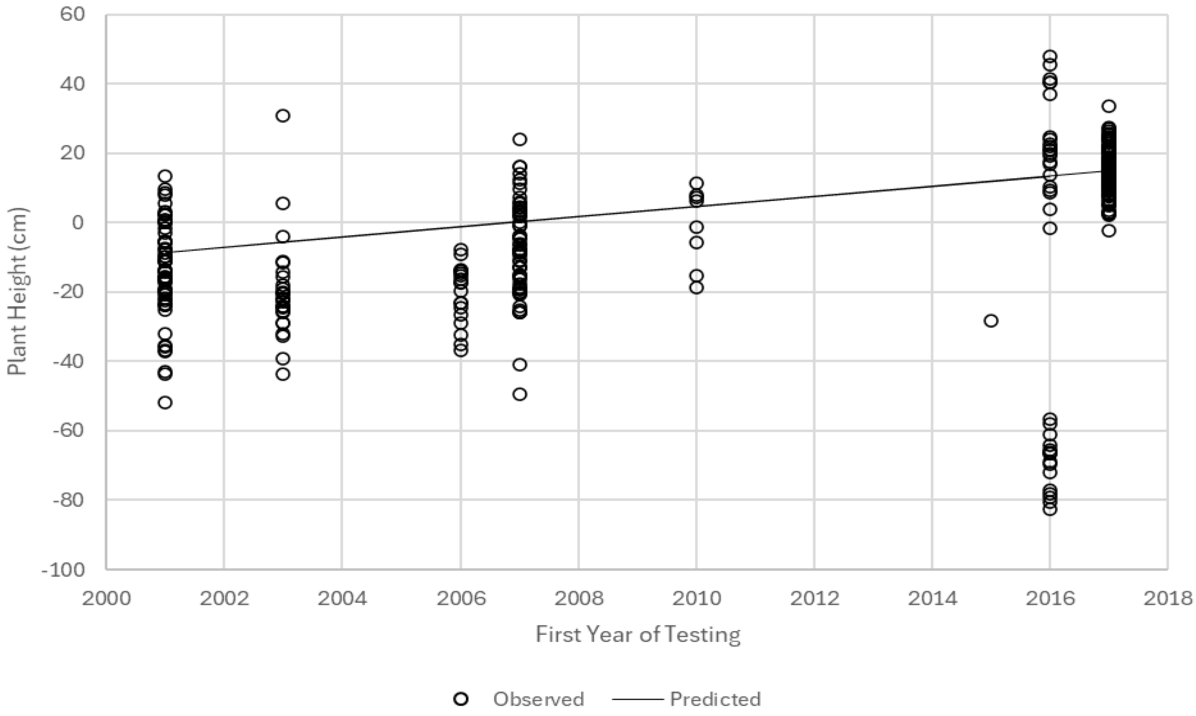

Figure 7. Regression of plant height (PH) BLUEs of ZARI maize lines onto their first year of testing value.

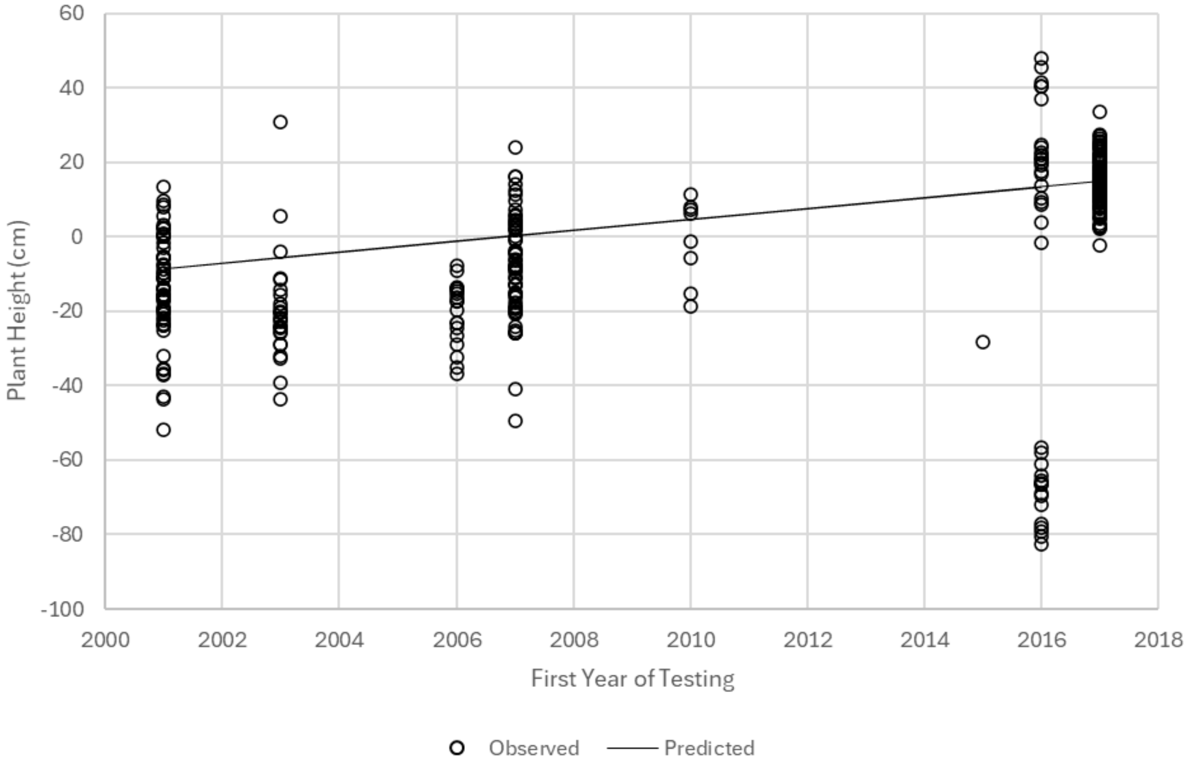

Figure 8. Regression of ear height (EH) BLUEs of ZARI maize lines onto their first year of testing value.

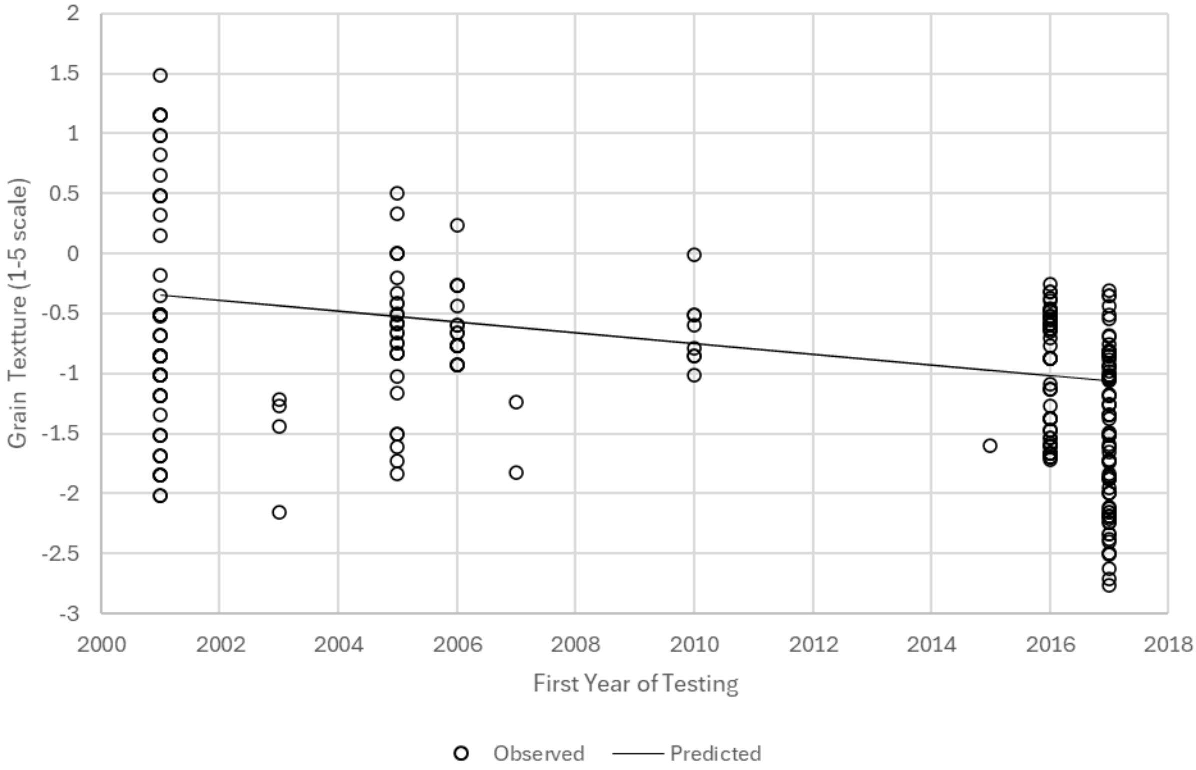

Figure 9. Regression of grain texture (TEX) BLUEs of ZARI maize lines onto their first year of testing value.

4. Discussion

Quantifying genetic gain in crop breeding programs is critical for evaluating the efficacy of selection strategies to enhance food system resilience under accelerating climate pressures and population growth. Sustained rates of genetic improvement enable crops to maintain or increase productivity despite exposure to abiotic and biotic stresses associated with climate change [30,31]. Incorporating and monitoring gains for climate-adaptive traits-such as stress tolerance, phenological stability, and resource-use efficiency-allows breeding programs to mitigate climate-induced yield variability and strengthen long-term production stability [32,33]. The objective of this study was to quantify genetic gain trends in the ZARI maize breeding pipeline using historical data collected between 2001 and 2017. These insights support the optimization of breeding strategies to maximize genetic improvement per unit time, cost, and resource investment, while aligning with the evolving pressures of climate change, industry needs, and population growth.

The success of a maize breeding program depends strongly on the availability of genetic diversity and the heritability of target traits. In this study, entry mean heritability (EMH) varied markedly across traits, indicating differences in data quality and trait responsiveness to selection. Overall, heritability estimates were moderate to low. A notable proportion of experiments returned an EMH of zero across traits (Table 4), likely reflecting environmental stresses characteristic of Zambian production systems and trial-management challenges that increased experimental error (Table 2). A large number of experiments tested a few hybrids, which may have resulted in low genetic variance and thus low EMH. Addressing these sources of low heritability, particularly those manageable through improved trial design and agronomic practices, will be essential for strengthening genetic gain. In maize breeding, such traits typically require larger trial sizes and hybrid-based improvement strategies to ensure meaningful progress [24–26]. Grain yield and FW showed moderate EMH, although a large portion of individual experiments had EMH < 0.20 or EMH $= 0$ (Table 4). Heritability is a major factor in genetic gain, and the ZARI program could significantly enhance it by improving EMH. The GY-High experiments had greater EMH than the GY-Low experiments. Plant and ear height exhibited a similar pattern for EMH as for GY (Table 4). Comparable findings have been reported by [27–29] they emphasized the value of leveraging secondary traits to improve selection outcomes for low-heritability traits. In contrast, the number of ears (NE) had the lowest heritability, consistent with reports by [34] and [35]. This highlights the need for the ZARI maize breeding program to prioritize indirect selection approaches, given that the program currently lacks the capacity to fully implement genomic selection, extensive multi-location testing, and enhanced environmental control required to achieve sustained gains in prolificacy.

We refer to genetic gain, though the values are not comparable to those predicted by the breeder's equation ($G = ir_g h^2 \sigma_a^2$). Our estimates of genetic gain reflect trait change over time, as evaluated by new germplasm each year. In contrast, the breeder's equation assumes a change in the genetic value of progeny derived from cycles of recurrent selection. Our analysis, though, illustrates the effectiveness of the breeding program. We acknowledge the shortcomings of the current analyses, specifically, (1) the sparse nature of the data set (missing years, missing levels of FYT), and (2) substantial fluctuations in the number of experiments per year, hybrids per year, and the number of lines per level of FYT (Table 1, Figures 2 and 3). Regardless of these limitations, the analysis revealed informative trends.

The observed genetic gain trends provide important insights into the effectiveness of the ZARI maize breeding pipeline and highlight areas requiring strategic improvement. The genetic trend analysis demonstrated clear and meaningful progress within the breeding program, with several key traits showing significant directional change over time. GY and FW had positive annual genetic gains of 0.83% and 1.85%, respectively (Table 5, Figures 4 and 5). Yield gains in GY-High sites were 1.14% per year. Similar results have been reported by [36] in an era study of maize grain yield under drought stress (0.85% yr^{-1}), random drought stress (0.85% yr^{-1}) and low nitrogen stress (0.62% yr^{-1}) in eastern and southern Africa; [20] found positive and significant genetic gain estimates for grain yield of 1.94% year^{-1} and 0.42% year^{-1} in preliminary and advanced yield trials, respectively. [21] analyzed Ugandan and private sector maize hybrids and reported genetic gains of 1.30% year^{-1} and 1.71% year^{-1}, respectively. Contrary to this study, however, they reported higher estimated genetic gains of 2.25% year^{-1} for the national performance trial and 1.98% year^{-1} for CIMMYT hybrids. Most breeding programs aim to achieve a steady and measurable increase in GY over time, typically targeting an annual genetic gain of 1–5% [18–22].

In our study, we observed greater EMH and grain-yield gains at GY-High sites than at GY-Low sites. This was also noted by [19] in the Zimbabwean maize breeding program. Genetic gains in low-yielding sites were not significant in our study (Table 5). The relative efficiency of indirect selection indicated that the yield at GY-Low sites could be improved by selecting for yield at GY-High sites. A cost analysis is needed to assess the cost-effectiveness of improving yield at GY-Low sites through direct and indirect selection.

A significant genetic trend was observed in prolificacy (NE), though the change in NE was minimal, and EMH was low (Table 5, Figure 6). In contrast, a significant increase in NE has been observed in other programs, such as the IIAM maize breeding program in Mozambique [22], which reported a significant genetic gain of 1.36% per year. Previous studies further highlighted prolificacy as an important selection target for maintaining yield stability, particularly when plant populations vary under different management conditions [37,38]. The significant genetic gains observed for plant height (PH) and ear height (EH) in the ZARI maize breeding program suggest gradual improvements in plant vigour (Table 5, Figures 7 and 8). Such increases may enhance biomass accumulation and contribute positively to yield potential, particularly under favourable conditions. However, these trends should be carefully monitored to ensure that gains in vigour do not increase the risk of lodging or compromise standability, underscoring the need to balance stature-related traits with overall plant robustness in future selection cycles. Comparable genetic gain trends in PH and EH have been observed in the IIAM maize breeding program [22] and the Kenya highland maize breeding program [20], depicting that selection has focused on developing vigorous, robust maize varieties. Conversely, the NARO and DR&SS breeding programs have prioritized shorter-statured hybrids, as highlighted by [19,21], reflecting breeding strategies tailored to regional agronomic needs and production constraints.

The significant negative genetic gain trend in grain texture (TEX, -1.28% per year) indicates a gradual shift toward less desirable kernel hardness (flint type) (Table 5, Figure 9). A similar decrease was noted in the Zimbabwe maize breeding program [19], though [21] reported an increase in grain texture scores. The observed decline in the ZARI program suggests that grain texture has not been effectively maintained as a selection criterion, likely because the breeding pipeline has placed greater emphasis on yield and stress tolerance. [39] and [40] reported that genetic improvements have focused on yield at the expense of grain quality. If unaddressed, continued selection for dent grain texture may negatively affect grain handling, processing quality, and end-user preferences. Therefore, the breeding program should integrate explicit selection for optimal grain texture (semi-flint; Appendix A, Table A1 through routine phenotyping, incorporation of marker-assisted selection where available, and balanced selection indices to prevent further decline and ensure grain quality. TEX was one of the more heritable traits, so gains should be feasible.

The minimal directional change observed for flowering traits, reflected by a slight increase in anthesis date (0.085 days per year) and minimal decreases in silking date (-0.014 days per year) and ASI (-0.038 days per year), suggests that flowering time has remained largely stable across years. This stability indicates that selection pressure on phenology has been weak, given the high EMH, and that the current germplasm already aligns well with the target maturity window. While stable flowering traits help maintain adaptation to local environments, a slight delay in anthesis date may warrant attention, as even small shifts could disrupt synchrony with stress-prone periods or affect the anthesis–silking interval under challenging conditions. Continued monitoring and the deliberate incorporation of phenology into selection indices are therefore recommended to ensure that flowering traits remain optimized for target production environments.

Despite positive genetic trends in grain yield, the ZARI maize breeding program must adopt more aggressive, modernized strategies to accelerate genetic gain. A recent analysis of the effectiveness of the ZARI maize pipeline suggested that gain per cycle for yield, as predicted by the breeder's equation, could be increased by 23% from reallocation of present resources. Combining the results of this genetic gain study with the gain per cycle analysis can lead to significant improvements in genetic gain for yield. Priority areas include: i) reducing breeding cycle time through doubled haploid technology, off-season nurseries, and controlled-environment generation advancement; ii) improving selection accuracy by improving heritability through data filtering and spatial analyses and integrating high-throughput phenotyping, iii) enhancing selection intensity via increased population sizes in early stage testing by modifying the use of tester lines and reducing the cost of generating inbred lines, iv) leveraging genomic technologies, including MAS for major QTLs, genomic selection for traits with complex genetics, v) safeguarding genetic diversity through the use of broad-based germplasm, incorporation of exotic, and balancing short-term improvement with long-term adaptability; and vi) optimizing the breeding pipeline by combining rapid cycling with genomic prediction, applying multi-trait index selection, and routinely monitoring genetic gain to fine-tune selection strategies.

5. Conclusions and Recommendations

This study quantified genetic gain in the ZARI maize breeding pipeline over 17 years, revealing substantial progress in several key traits despite moderate-to-low heritability across much of the dataset. Yield-related traits and plant growth showed significant genetic gains, demonstrating the effectiveness of selection in improving plant vigour. The study also indicated that traits such as grain texture have a negative value to the crop, and greater diligence is needed to reverse the trend. Overall, the results highlight both the achievements and limitations of the current breeding pipeline. Strengthening genetic gain in the future will require accelerated breeding cycles, improved selection accuracy and intensity, greater emphasis on quality and climate-adaptive traits, and the incorporation of genomic breeding approaches. Routine monitoring of genetic gain should be embedded within the breeding program to ensure sustained, efficient improvement aligned with evolving production and climatic challenges.

Author Contributions: Conceptualization LS, KM, MM, AL CS, LM, BMP, DW, and BD; methodology, software, validation, and formal analysis, AL, LS, C.S., DW, LM and B.D; investigation, LS, KM, KL, MM.; resources, MM, LM, BMP, BD; data curation, LS, KL, MM, LM, CS.; writing-original draft preparation, LS, MM, LM, BMP, DW; writing -review and editing, LS, MM, BD, LM, CS,. DW, BMP; visualization, AL, LM, CS; supervision, LM, MMBD; project administration, MM, BD; funding acquisition, BD and MM; All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: Except for the data available within this manuscript, no other data is provided in any other form. The lead breeders may be contacted to provide any other relevant information.

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

Abbreviations

The following abbreviations are used in this manuscript:

ABI	Accelerated Breeding Initiative
AD	Anthesis Date
ASI	Anthesis-Silking Interval
BLUEs	Best linear unbiased estimates
CGIAR	Consultative Group on International Agricultural Research
CIMMYT	International Maize and Wheat Improvement Centre
CW	Core Weight
DR&SS	Department of Research and Seed Services
EA	Ear Aspect
EiB	Excellence in Breeding
EH	Ear Height
EMH	Experiment Mean Heritability
ER	Ear Rot
EPP	Ears Per Plant
ET	Turcicum Leaf Blight
FYT	First Year Tested
FW	Field Weight
GLS	Grey Leaf Spot
GY	Grain Yield
IIAM	Agricultural Research Institute of Mozambique
IITA	International Institute of Tropical Agriculture
NE	Number of Ears
NP	Number of Plants
OPV	Open-Pollinated Varieties
PH	Plant Height
RL	Root lodging
SL	Stalk Lodging
SD	Silking Date
SW	Fresh Seed Weight
TEX	Grain Texture
TSW	Thousand Seed Weight
ZARI	Zambia Agricultural Research Institute

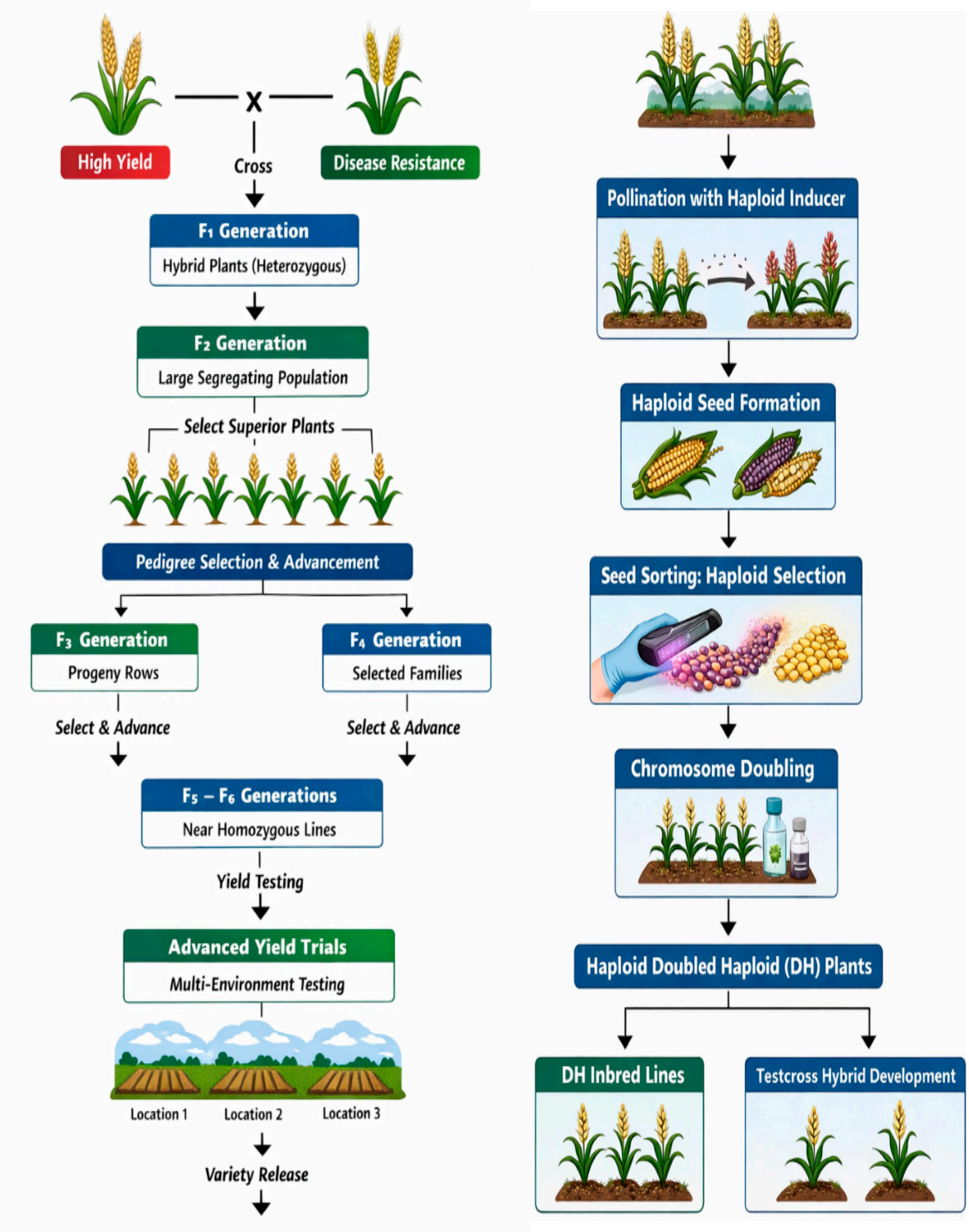
Appendix A

Zambia Agricultural Research Institute Maize Breeding Program Market Segments (MS) and Target Product Profiles (TPP)

Pipeline serving Market Segment	***White early - TPP00535/37/38/39***					
Market Segment Description	*Maize, ESA, SAF, Food, White, Dry/wet mid-altitudes, and lowlands, Rainfed, Early*					
Market segment description	*Maize, White (early, medium & late)*					
Crop	*Maize*					
Zambia	*Zambia*					
Agro-ecological zones	*Region I, II & III*					
Hectares in Zambia	*1,800,000*					
Material Type	*Hybrids*					
Biological Region/Eco System	*Zambia*					
Growing season	***October-April***					
	Trait	***Scale***	***Min Score***	***Trait requirement***	***Improve trait***	***Threshold trait***
Color	***White***					
Grain/Flesh type	***Semi Flint***					
Processing traits	*Grain texture*	*1 to 5*	*Semi flint-Dent*	*Nice to have*		
Consumption traits	*Green mealies*	*1 to 5*	*<3*	*Nice to have*		

	shelf life	*days*	*3-4 days*	Nice to have		
	harvest window	*days*	*7 - 10 days*	Nice to have		
Nutritional Enhancement						
Yield	***Yield under optimum conditions [Note: If the grain yield of a candidate hybrid is at par with the benchmark commercial check, it should have a relative advantage for other essential trait(s)].***	***t/ha***	***≥5% the best trait check***	***Essential***	***Y***	
	Yield under drought stress	*t/ha*	*≥5% the best trait check*	*Essential*	*Y*	
	Yield under low N stress (nitrogen use efficiency or NUE)	*t/ha*	*≥5% the best trait check*	*Essential*	*Y*	
	Yield under heat stress	*t/ha*	*≥5% the best trait check*	Nice to have		
	*Yield under rainfed stress-prone environment (random stress) **	*t/ha*	*≥5% the best trait check*	Nice to have		
Agronomic traits	*Root lodging resistance (Optimal conditions)*	*%*	*≤10%*	*Essential*		*Y*
	Stalk lodging resistance (Optimal conditions)	*%*	*≤10%*	*Essential*		*Y*
	Moisture at harvest	*%*	*<20% at harvest*	*Essential*		*Y*
	ASI (Under drought)	*days*	*≤5*	*Essential*		*Y*
	Stay-green -Senescence score at physiological maturity	*1 to 10*	*≤ 6.0*	Nice to have		
	Plant Height	*m*	*<2.0m*	*Essential*		*Y*
	Ear position	*ratio*	*<0.5*	*Essential*		*Y*
	Husk cover	*1-9*	*<4*	Nice to have		
	Tip-filling (Mean of commercial checks)	*1 to 5*	*≤3.0*	*Essential*		*Y*
	Prolificacy	*Ratio*	*>1*	Nice to have		
Disease traits	*Grey Leaf Spot (GLS) resistance*	*1 to 9*	*≤4.0*	*Essential*		*Y*
	Fusarium Ear Rot (FER) resistance (incidence)	*%*	*<10%*	*Essential*		*Y*
	Maize Lethal Necrosis (MLN) resistance	*1 to 9*	*≤ 4.0*	Nice to have		
	Yield under artificial MLN	*t/ha*	*≥4*	Nice to have		
	Maize Streak Virus (MSV) resistance	*1 to 9*	*<3*	Nice to have		
	Common Rust (PS) resistance	*1 to 9*	*<4.0*	Nice to have		
	Turcicum Leaf Blight (TLB) resistance	*1 to 9*	*≤4.0*	*Essential*		*Y*
	Diplodia Ear Rot Resistance	*1 to 9*	*< 4*	Nice to have		
Insect traits	*Fall Armyworm (FAW) resistance leaf damage*	*1 to 9*	*≤5*	Nice to have		
	FAW resistance ear cob damage	*1 to 9*	*≤3.0*	Nice to have		
Production System	*Rainfed*					
Input Level	*Below optimum - optimum*					
Maturity	*Early (FAO 400-500 series) / Medium (FAO 600series) / Late (FAO)/ Biofortification (TPP00539)*					
Production/Multiplication Traits	*Production split/synchronization*	*Days*	*between ±5*	*Essential*		*Y*
	Inbred line	*t/ha*	*≥2.0*	*Essential*		*Y*
	Single cross	*t/ha*	*≥3.5*	*Essential*		*Y*
	Tassel exertion	*TBD*	*TBD*	*Essential*		*Y*
	Male plant height: female ear height ratio	*Ratio*	*≥1*	*Essential*		*Y*
Unique Product Registration Traits	*Yield and any other special attribute*					
Key Competitive Products	*ZMS405; SC555, PAN413/PAN53; SC657; ADV637; AF635/SC719/ ZMS720/ PAN7M83*					
Count of essential traits				***18***	***3***	***15***

Appendix B



Pedigree Breeding Method Doubled Haploid Technology

Figure A1. *A flow diagram showing the maize breeding program at the Zambia Agriculture Research Institute using pedigree breeding and double haploid methods.*

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