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RESEARCH

Genomic selection on ear height, plant height and grain yield in the primary testing stage of maize hybrids

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Abstract Genomic selection (GS) is a cutting-edge breeding technology that enables the prediction and early selection of individuals based on genomic estimated breeding values by constructing predictive models. Double haploid (DH) technology has become an efficient method for producing inbred lines in maize, and when combined with GS, it offers significant cost reductions through advanced data and information management. Recent studies have demonstrated the great potential and high expectations of GS in plant breeding, particularly in maize, where the combination of GS and DH has been successfully applied. In this study, 2029 hybrids resulting from crosses were grown in three representative locations, and phenotypic values for three agronomic traits—ear height (EH), plant height (PH), and grain yield (GY)—were measured. Parental genotypes were used alongside genomic predictions to estimate hybrid breeding values, with GY being the primary trait of interest. A combination of traits was then employed as a criterion for advancing hybrids to the primary stage of testing in maize. Predicted breeding estimates showed that the accuracy for EH and PH was approximately 0.75, while for GY, it was 0.43; GY was field validated by including 80% of the top 243 hybrids, measured at about 55%, with moderately high predictive ability. In summary, the study demonstrates a significant reduction in the number of crosses required in the field based on breeding estimates, a decrease in the need for costly multi-site primary field tests, and an increase in breeding efficiency.

Keywords Genomic prediction · Primary test · Agronomic traits · Breeding value · Breeding gains

Introduction

Maize (*Zea mays* L.) is the most successfully commercialized crop globally, with widespread application of hybrids that capitalize on heterosis. The annual maize harvest significantly influences national food security (Lu et al. 2020). In traditional breeding, elite inbred lines and hybrid combinations are selected by breeders based on their phenotypic performance in the field. However, this process is labor-intensive and time-consuming (Zhang et al. 2022). Many traits in

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maize are controlled by polygenes and are influenced by external environmental factors, intrinsic genetic factors, and genotype-environment interactions. Due to the numerous factors affecting quantitative traits, phenotypic performance is often unstable, making the breeding of a commercial hybrid a process that typically takes more than five years. The future of maize breeding will benefit greatly from the integration of genetics, genomics, and other advanced technologies (Yu et al. 2022). Genetic induction is the most effective method for producing haploids in maize, and the use of haploids to breed inbred lines has become a widely adopted practice among maize breeders worldwide (Liu et al. 2014). The parents of hybrids are stable lines, typically produced after 6–8 generations of continuous selfing (Jacquier et al. 2021). The application of haploid technology has significantly reduced the time required to develop these stable lines.

Genomic selection (GS) as a new breeding strategy was first proposed by Meuwissen (2001). In recent years, with the maturation of high-throughput sequencing and genotyping technologies, alongside significant reductions in cost, GS has become increasingly widespread in both animal and plant breeding (Michel et al. 2016; Zhang et al. 2017). It has been used to enhance genetic gain in dairy cattle, dairy goats, layer chickens, and pigs (García-Ruiz et al. 2016; Samore and Fontanesi 2015; Mucha et al. 2015; Wolc et al. 2015; López et al. 2015). GS involves estimating a large number of genetic markers across the genome to derive different chromosomal segments or individual marker effect values (Jonas et al. 2013), accumulating the individual genomic segment or marker effect values to obtain genomic estimated breeding values (GEBV). Breeding values through by the combination of genomic selection and haploid technology for early selection shorten the breeding process (Jonas et al. 2013), especially for complex traits that are relatively difficult to measure, thereby improve breeding efficiency.

Factors influencing the accuracy of genomic prediction include the choice of prediction model, the number of markers, the heritability of traits, the sample size, and the kinship relationship (Ma et al. 2021; Alemu et al. 2024). Genomic models commonly used in breeding work today include genomic-BLUP (GBLUP), ridge regression best linear unbiased predictions (rrBLUP), Bayes methods, reproducing kernel Hilbert spaces regression (RKHS) and relevance vector machine (RVM) (Gianola D et al. 2008). Among these models, ridge regression best linear unbiased predictions (rrBLUP) and genomic-BLUP (GBLUP) are the most frequently employed in breeding programs (Heslot et al. 2012).

Currently, GS is widely used for predicting maize traits such as yield, grain nutrition, and growth and development characteristics (Liu et al. 2018; Cui et al. 2020; Zhang et al. 2019; Guo et al. 2020). Predicting traits in hybrids is more practical for production purposes than predicting genomic values for inbred lines. In the primary stage of maize hybrid testing, open pollination is typically used, with a male parent that has good combining ability serving as the tester and a large number of DH or phenotypically superior inbred lines serving as the female parents. This process generates a large number of first-generation hybrids for initial testing. However, planting all of these hybrids for testing would require substantial manpower and resources. If selection could be based on genomic predictions, it would significantly reduce fieldwork and enhance breeding efficiency. With this in mind, in the primary testing stage of maize hybrids, we used 2029 hybrids as genetic material with different proportions of training populations for GS of ear height (EH), plant height (PH), and grain yield (GY), and field-validated them to compare the accuracy of the predictions.

Materials and methods

Genetic materials, phenotype evaluation, and heritability estimation

In this study, one tester and 2029 DH lines were used for open pollination, resulting in 2029 F1 hybrids. The tester belongs to the non-stiff-stick (NSS) subgroup, an while the DH lines are from the stiff stalk (SS) subgroup. The 2029 hybrids were planted in randomized complete blocks across three locations: Changling, Dehui, and Gongzhuling. The hybrids were sown using two seeds per hole in a single plot, 5 m long, 4500 plants per acre. Data on EH, PH, and GY were collected at each location for genomic prediction. EH and PH data were measured with a straightedge in centimeters; while GY was calculated as plot yield converted to standard moisture in pound.

Phenotypic data from the 2029 hybrids were analyzed using META-R software, which included calculations for best linear unbiased prediction (BLUP), broad-sense heritability (H^2), and the coefficient of variation. H^2 was estimated based on the mean values of the entries within the trial. Although only one replicate was planted at each site, the values measured at the three locations were treated as three replicates when calculating BLUP. H^2 was estimated from the mean value of the entries in the experiment. The H^2 based on the mean value of enrolment within the trial was estimated as follows:

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{n_e} + \frac{\sigma^2}{n_e n_r}}$$

where σ_g^2, σ^2,and σ_{ge}^2 are the genotypic variance, error variance, and genotype-by-environment interaction variance, respectively, and n_r and n_e are the numbers of replications and environments, respectively. Here, n_r has a value of 3 and n_e has a value of 1.

Genotyping and quality control

Leaf samples of parental lines were collected before pollination, DNA was extracted by CTAB, and genotyping was carried out by the GBS platform (Elshire et al. 2011). The parental lines, including lines and tester, around 11,200 SNPs with known physical locations were identified for each genotyped material, and the SNP marker dataset was filtered in TASSEL version 5.0 for a minor allele frequency (MAF) of 0.05, the missing rate below 20% and a heterozygosity rate below 10%. After filtering, 9300 SNPs were selected for further genetic analyses.

SNP distribution across the whole maize genome

The distribution of SNPs in the genome is one of the indicators of the quality of the quality of genotype testing. A package named RIdeogram (Hao et al. 2020), written in R programming, was used to assess the distribution of SNPs. The plot of the SNP distribution was drawn using the ideogram function. The customized R scripts to plot the heatmap of the SNP distribution on maize chromosomes using the HapMap format input dataset were provided (https://aozhangchina.github.io/R/chromesomeheatmapTool/ChromesomeHeatmap.html).

Representation of the environment

In this study, a large number of genotypes were tested across a wide range of environments. The occurrence of the genotype (G) by environment (E) interaction (GEI) effect further complicates the selection of superior genotypes for a target population of environments. Here, we used the statistical methods of additive main effects and multiplicative interaction analyses (AMMI). The AMMI analysis has been shown to be effective because it captures a large portion of the GxE sum of squares, clearly separating main and interaction effects. Theses analyses were estimated using GEA-R software. The basic model is:

$$Y_{ij} = \mu + g_i + e_j + \sum_{N=1}^{N} \tau_n \gamma_{in} \delta_{jn} + \varepsilon_{ij}$$

where Y_{ij} is the yield of the $i-th$ genotype (i = 1,..,I) in the $j-th$ environment (j = 1,..,J); μ is the grand mean; g_i and e_j are the genotype and environment deviations from the grand mean, respectively; τ_n is the eigenvalue of the PC analysis axis n; γ_{in} and δ_{jn} are the genotype and environment principal components scores for axis n; N is the number of principal components retained in the model and ε_{ij} is the error term.

Genomic prediction models

Genomic prediction of breeding values for hybrids, genotypes of hybrids were synthesized by testing the genotypes of the parents, hybrid genotype synthesis first transformed the single base representation into a two base representation and then synthesized the four-base form of the hybrid. Finally, each material was assigned a value based on the proportion of A at each locus.

The genomic prediction model used was the rrBLUP commonly used in plant breeding, which is an indirect prediction method. rrBLUP is a multiple genomic information prediction method based on a Bayesian framework. The rrBLUP model assumes homogenous variance of all markers and shrinks all marker effects equally to zero. rrBLUP is equivalent to BLUP and uses the realized relationship matrix estimated from the markers. The genomic prediction analysis was performed using the rrBLUP package (Endelman 2011).

The classical rrBLUP model is as follows:

$$y = X\beta + \sum_{i=1}^{m} Z_i g_i + e$$

where y is the phenotype vector, X is the fixed effect coefficient matrix, whose length is the number of individuals in the training group, and the element values are all vectors of 1; β is the fixed effect, i.e., it is the mean value of the training group's phenotype; Z_i is the vector of digitised genotypes of the ith locus (e.g., coded as {0,1,2} or {−1,0,1} or something like that, does it make a difference in different coding styles? But rrBLUP must be {−1,0,1} coding mode), the sum of which is the marker coding association matrix; g_i is the ith locus effect value, which needs to be estimated according to the model as a vector of molecular marker effects; and e is the residual error obeying the distribution $N \sim (0, I\sigma_e^2)$.

The use of tenfold cross validation repeated 100 times was used to evaluate the performance of the model and to calculate the prediction accuracy, which was labelled as the correlation coefficient between the estimated and actual phenotypic values.

Field validation

The predicted results were verified in the field, the breeding estimates and actual measurements were sorted respectively, and the top 12%, which corresponds to the top 243 of the materials using online network (https://jvenn.toulouse.inra.fr/app/example.html) for breeding estimates with the actual measured values. These materials were promoted according to the working criteria of the first stage of breeding test hybridization. 80% of the 243 hybrids that were promoted with actual measured values were included and statistical analysis was conducted using EXCEL.

Results

Phenotypic analysis results and correlation analysis

As shown in Table 1, summary information on extremes, means, genotypic variance, residuals, broad-sense heritability, and coefficient of variation for the agronomic traits EH, PH, and GY for the 2029 hybrids is presented. The means and medians of the three agronomic traits were approximately equal. The H^2 of EH and PH were relatively high, 0.76 and 0.79, respectively; the H^2 of GY which was more affected by the environment was 0.43. The coefficient of variation was relatively low for all three traits, with the highest was for GY at 10.94. In summary, the phenotypic variation in these three traits primarily stems from genetic factors.

The test for normal distribution based on the phenotypic data showed that the P-value of the EH test was 0.6 and the P-value of the PH test was 0.5, which is consistent with normal distribution; the P-value of the GY test was 0.25, which is close to normal distribution. The correlation coefficients among all the agronomic traits phenotypes reached highly significant levels, and the correlation coefficients between EH and the rest of the traits were 0.72 and 0.24, respectively, while the correlation coefficient between PH and GY was 0.38 ($P < 0.01$) (Fig. 1).

Marker distribution

The markers in the SNP dataset were distributed across the entire maize genome (Fig. 2). Generally, marker density was higher at the ends of the chromosomes and decreased toward the centromeric regions. Chromosomes 1, 2, and 3 showed a relative enrichment of SNPs, with particularly high marker densities at the ends of chromosome 8 and the long arm of chromosome 9. Overall, the distribution of marker densities was relatively uniform, contributing to a high degree of accuracy in predictions.

Table 1 Descriptive statistics for three agronomic traits in 2029 hybrids

Trait	Range	Grand mean	Median	Genotype Variance	H^{2a}	CV^b
EH (cm)	100–169	130.68	130.92	138.11	0.76	8.84
PH (cm)	271–350	313.38	313.86	182.96	0.79	3.97
GY (lb)	134.18–178.12	158.37	158.64	75.99	0.43	10.94

[a] Broad-sense heritability; [b] Coefficient of variation

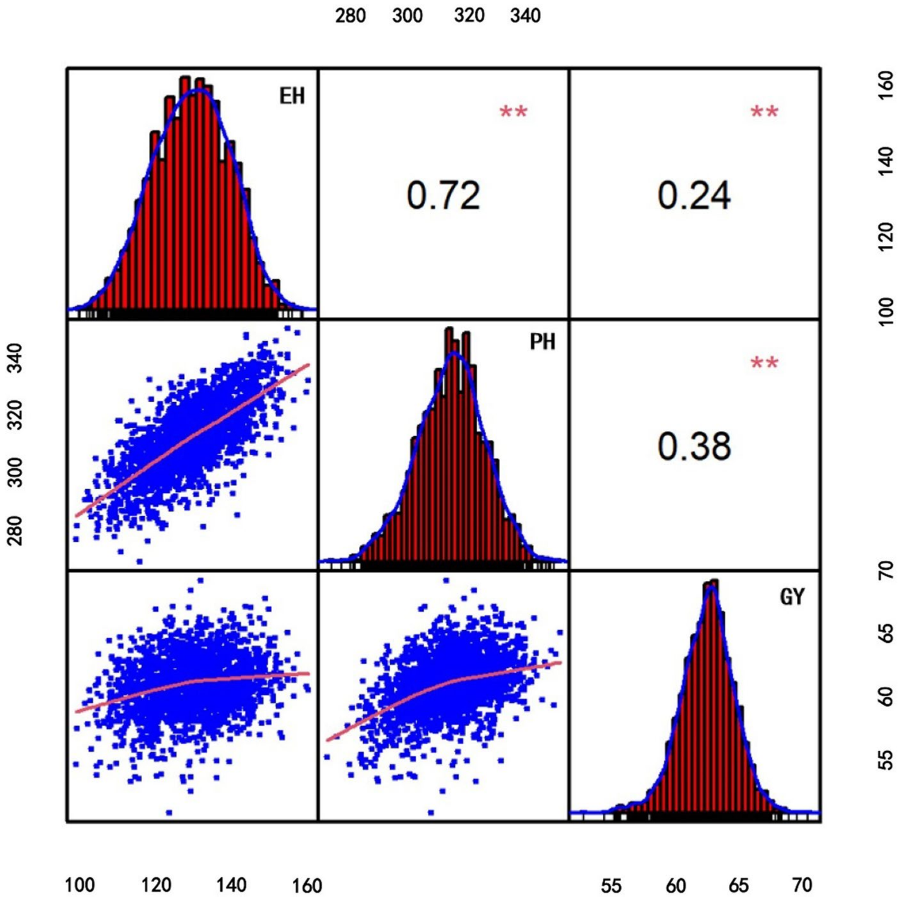


Fig. 1 Frequency distributions and correlations of BLUP (best linear unbiased prediction) as phenotype values were calculated from the EH, PH and GY. The plots on the diagonal represent the phenotypic distribution frequency of EH, PH, GY. The values above the diagonal line are the Pearson's correlation coefficients between every two traits. The values below the diagonal line are scattered plots for every two traits. *Represents a significant difference at the *0.05* level; ** represents a significant difference at the *0.01* level

Representation of the environment

The dual-labelled plot of EH, PH, and GY (Fig. 3) show that the varieties are evenly and consistently distributed across the three planting sites, demonstrating the environment's strong ability to differentiate between varieties. The rankings of EH, PH, and GY for each trait were inversely related between environments, indicating that the three selected sites were non-repetitive and representative.

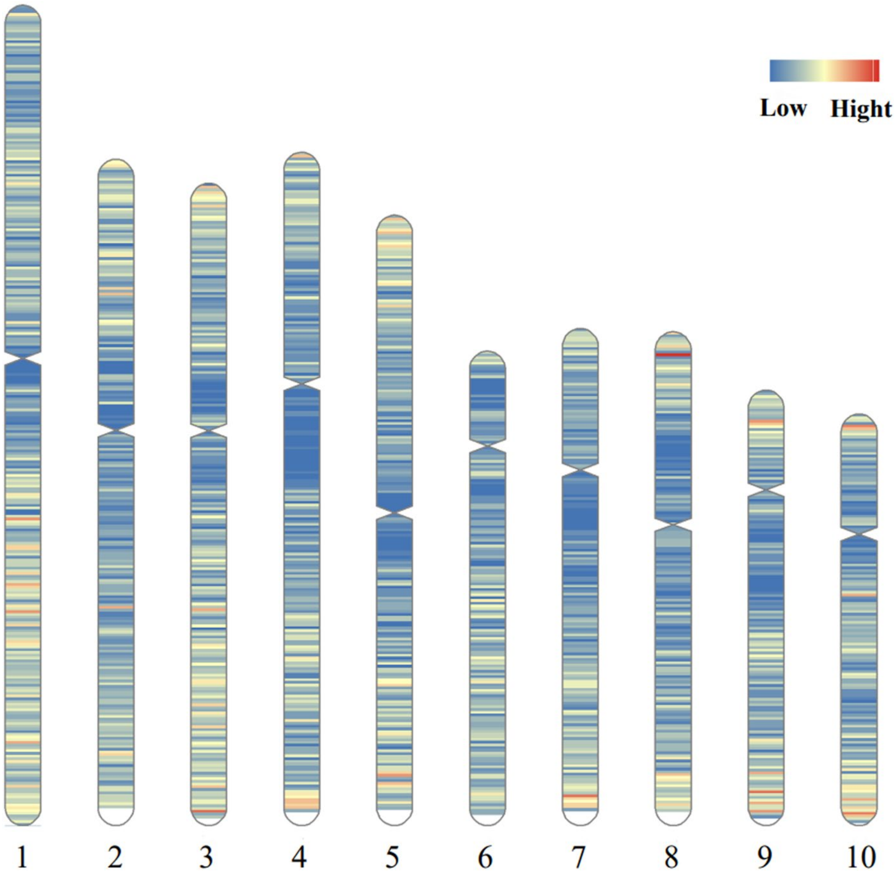
Predictability of agronomic traits in hybrids

In this study, the prediction model used was rrBLUP, which is commonly used in plant breeding for three agronomic traits: EH, PH and GY. The percentages used for the training groups were 40%, 50%, 60%, 70%, and 80% for 100 cycles. By comparing the mean and standard deviation of the predicted breeding values for the three agronomic traits, there was not much difference in the mean values of the training populations for each proportion of the three traits; although the results of 60%, 70% and 80% were higher, the standard deviation of the predicted breeding values was larger, and the standard deviation of 50% was smaller and more stable. The best results were predicted when the training population was 50%. The prediction accuracies for EH and PH was 0.76 and 0.75, respectively, while for GY, it was slightly lower at 0.47 (Fig. 4).

Relationship between measured and estimated breeding values

Based on the predicted results when the training population was set at 50%, and in accordance with the criteria for the initial phase of the hybridization breeding test, the top 12% of the rankings were selected to advance, equating to the top 243 materials for the next phase of testing. The estimated

Fig. 2 Heat map of SNP marker density



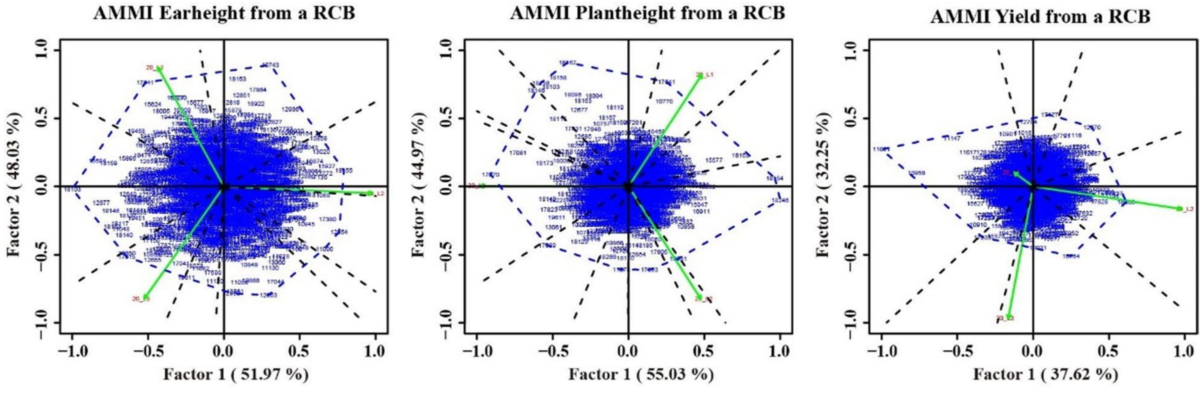


Fig. 3 Dual-labelled plot of agronomic traits. Dual-label plots based on measured EH, PH, and GY, with L1 representing Changling, L2 representing Dehui, and L3 representing Gongzhuling

breeding values were then compared with the actual measured values, as shown in Fig. 5. The overlap between the estimated breeding values and the actual measurements was more than 50% for both EH and PH, while the overlap for GY was slightly lower. These results indicate the high accuracy of the breeding estimates predicted using this model.

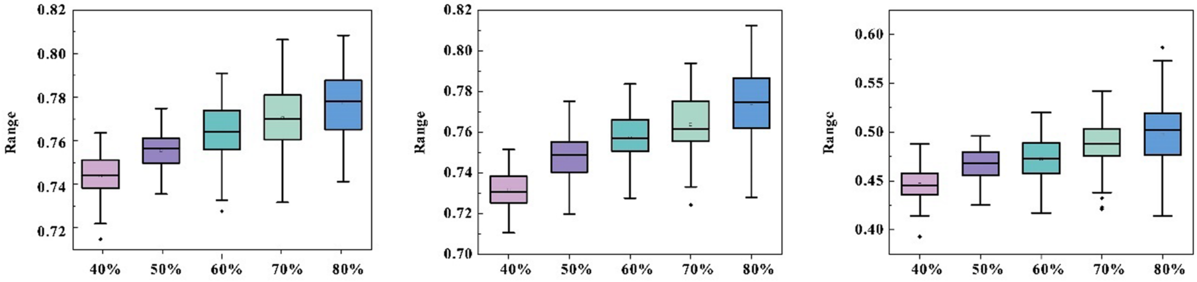


Fig. 4 Box plot of the accuracy of prediction of agronomic traits of hybrids. Accuracy of predicting EH, PH and GY based on training populations of 40%, 50%, 60%, 70% and 80%, respectively

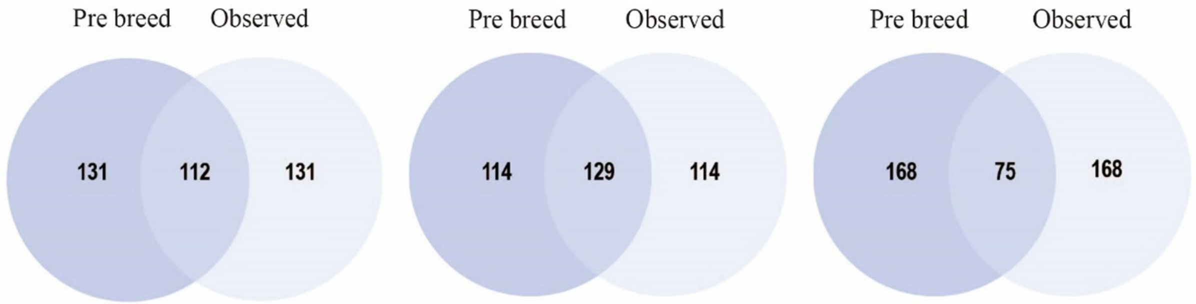


Fig. 5 Wayne of measured versus estimated breeding value promotion results. EH, PH and GY, respectively

Field population validation and multiple trait analysis

In the primary testing phase of maize hybrids, the top 12% of hybrids in the test rankings advance to the next stage, meaning that 243 out of 2029 hybrids move forward. The best predicted results were obtained when the training population was set at 50%. When the predicted GY ranking is around the top 55%, it can include 80% of the hybrids that rank in the top 243 in actual measurements. Similarly, when the predicted EH and PH rankings are around the top 26%, it can include 80% of the hybrids that rank in the top 243 in actual measurements (Fig. 6). Advancement to the next stage is primarily based on GY data, with other traits also considered. The top 243 hybrids based on GY rankings were selected for advancement, showing a high overlap with the rankings for EH and PH.

The cost of testing each hybrid in the primary stage is about 20 yuan, with the total cost of planting at three locations reaching around 120,000 yuan. By predicting hybrid phenotypes through breeding estimates—encompassing 80% of the top 243 actual measurement rankings—this method saves half the cost and preserves parental genotype data for future use.

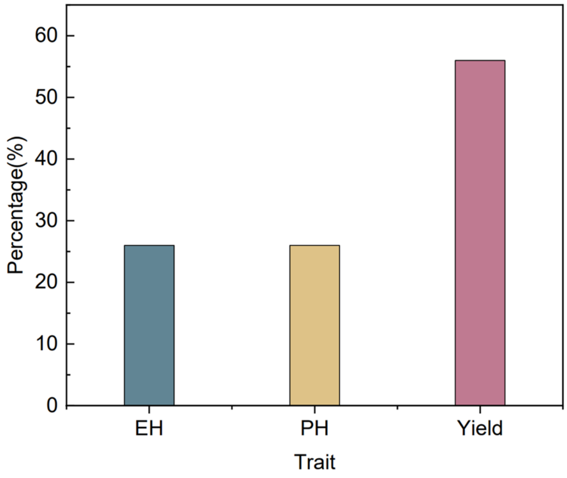


Fig. 6 Field validation of population size

Discussion

Importance of the primary testing stage of maize hybrids

A critical aspect of maize breeding is field testing (Meng et al. 2019), and the development of new maize varieties must undergo a series of field tests, including primary field tests, intermediate and advanced field tests, regional trials, and production trials. Among these, primary field tests are especially crucial. At this stage, maize yield and the performance of various traits result from the interaction of multiple influencing factors under complex field conditions. The only way to accurately and objectively predict the real-world performance of these hybrids is through primary field testing.

Conventional breeding involves examining numerous agronomic traits, with GY being the primary focus. GY traits are quantitative, influenced by both genetic and environmental factors, and are interrelated with other traits, often constraining each other (Ren et al. 2019). To select varieties with strong overall resistance and high yield, yield and all associated traits must be considered together. To obtain accurate results under field trial conditions, primary field trials are conducted in various natural environments, accounting for the complexity of climate, soil quality, and other factors that present significant challenges. Environmental factors, such as location, climate, and soil, undeniably influence yield, underscoring the importance of field trials (Duvick et al. 2004).

Factors affecting the accuracy of GS

GS is a promising tool in genomics that can predict the phenotypes of genotypic hybrids without the need for actual phenotypic measurements. The effectiveness of GS can be evaluated through its genomic prediction capabilities, which offer moderate to high accuracy, saving both time and costs. Predictive ability was estimated using the genotypic data of parent lines for synthetic hybrids and the phenotypic data of measured hybrids (Li et al. 2021). Therefore, it is crucial that the SNP dataset is evenly distributed across the maize genome and that the measurements are accurate.

Prediction accuracy is an important condition affecting genome-wide selection, and it was compared by observing the correlation between phenotypes and predicted GEBVs (Xu 2017). There are now many GS models to choose from, and models from Bayesian (Technow and Melchinger 2013), and machine learning (Ogutu et al. 2012) approaches have been frequently used in plant breeding since their emergence. Although great efforts have been put into the development of each of these models, none of the methods is absolutely superior among different crops or traits (Heslot et al. 2012). In practice, rrBLUP has been accepted as a predictor of GY, EH and PH traits in F1 of DH and test species. Therefore, we chose rrBLUP, a relatively computationally fast method, for this study.

Application of GS in breeding

In GS studies, the size of the group is also one of the important factors affecting the predictive ability (Liu et al. 2018). Using appropriately sized populations enhances the accuracy of genomic predictions. In this study, the parental material, NSS inbred lines, was used as the tester, and 2029 SS DH lines were used for open pollination, resulting in a population of 2029 hybrids. This population size was moderate and suitable for accurate predictions.

Studies have shown that prediction accuracy is first affected by the heritability of the target trait, with higher heritability is associated with the higher accuracy (Wang et al. 2015). The factors that influence yield in maize hybrids are complex and susceptible to non-genetic factors such as the environment, leading to lower heritability. However, some studies have found that this does not mean that GS is inefficient (Wang et al. 2024). In the present study, the H^2 for GY was 0.43 influenced by various factors. The results showed that the best results were obtained with a training group of 50%, with the mean value of the predicted breeding values of GY for the main traits being 0.47, reaching a medium level; the mean values of the predicted breeding values of EH and PH for the other agronomic traits were 0.76 and 0.75, respectively, all of them reached the medium to high level. The top 12% (243 hybrids) of the primary field test rankings advanced to the next stage of testing, with the rankings of the breeding estimates of GY prediction as the evaluating indicator. In the comprehensive comparison of the various agronomic traits for the field validation of the predicted GY rankings, when the predicted GY ranking is around the top 55%, it can include 80% of the hybrids that rank in the top 243 in actual measurements, indicating the very high accuracy of the prediction.

Despite the slightly heritability for GY, the prediction of GY by validating rrBLUP was also effective. The use of rrBLUP to predict hybrid breeding values can also be shown to be a very effective way.

Low investment and high return are key in breeding, making it crucial for breeders to cull certain combinations before conducting field trials. GS is becoming increasingly important in commercial maize breeding, as it shortens the breeding cycle, increases breeding efficiency, improves multi-trait selection, and facilitates intelligent breeding. This study explored the practical application of GS in breeding and compared it with field validation results, making it highly relevant for real-world application. As genome sequencing technology advances and costs decrease, the application of GS in commercial breeding is expected to become more widespread, profoundly impacting the future of maize breeding.

Author contribution XYK and SWJ analyzed the data and wrote the manuscript. YBL and XCZ supported in the statistical analysis. AZ, CL, XMD, MLL, CY and RCY designed the field trials and collected the phenotypic data. AZ and YYR initiated and guided through the study. All authors read and approved the final manuscript.

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Data availability No datasets were generated or analysed during the current study. The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval The experiments complied with the current laws of the country in which they were performed.

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