



Original Article

" Genomic Selection Approaches for Improving Maize Productivity"

Rabia Aslam¹

¹ Department of Plant Breeding and Genetics, Center for Crop Genomics and Biotechnology, Faisalabad,

Pakistan

ARTICLE INFO

Received: 10 Feb 2026

Revised: 11 Apr 2026

Accepted: 14 May 2026

Published: 30 Jun 2026

Key Words:

- * Genomic Selection
- *Maize Productivity
- *Bayes B
- *Genetic Gain
- *Predictive Accuracy
- *Drought Tolerance
- *GBLUP
- *Training Population Size
- *Cross

***Corresponding Author:**

Rabia Aslam

(rabia.aslam@ccgb.edu.pk)

ABSTRACT

Genomic selection (GS) is a new breeding strategy to increase genetic gain for complex traits, like grain yield and water-limited yield in maize (*Zea mays* L.). Comparisons of nine GS models - genomic best linear unbiased prediction (GBLUP), Bayesian Ridge Regression (BRR), Bayes A, Bayes B, Bayes C π , Bayesian LASSO (BLASSO), Reproducing Kernel Hilbert Spaces (RKHS), Random Forest (RF) and Support Vector Regression (SVR) - using a multi Predictive accuracy, genetic gain, computational efficiency, cross Bayes B stood out with the highest prediction accuracy under optimal irrigation and managed drought stress, and a 2.51 The cycle time was reduced from 4 to 1.4 years, and cost reduced by 41.5%. Bayes B's prediction accuracy in testing environments was high (mean $r = 0.782$), demonstrating its generalisability. Training population gains were asymptotic ($N = 250$) and the prediction accuracy was not increased with higher marker density (18,500 SNPs) than this. GBLUP was fastest but Bayes B's performance and stability compensated for its speed. Weighted performance scores were highest for Bayes B (91.7) followed by Bayes A (89.8) and Bayes C π (89.5). These findings suggest Bayes B is the optimal genomic selection method to boost maize productivity, and to breed new varieties fast, cheap and resilient to climate change

INTRODUCTION

Genomic selection is a novel breeding strategy that employs high-throughput markers to predict breeding values, and thus accelerate the genetic gain in crop improvement breeding strategies (Crossa et al., 2017). This approach, proposed by Meuwissen et al., enables the quick and cheap prediction of yield performance, thus reducing the time and cost of traditional breeding schemes (Singh et al., 2023). While marker assisted selection approaches mainly target quantitative trait loci mapping in biparental populations, genomic selection considers the effects of multiple genes with minor effects throughout the genome, and is useful for improving quantitative traits (Sun et al., 2019). The outcome of such an approach is that genomic selection allows for the selection of superior genomes based on genomic estimated breeding values, even in the absence of extensive phenotyping, thus simplifying the breeding process (Krause et al., 2020). Thus, it is an effective technique to enhance traits such as yield and tolerance to stress in maize (Gunundu et al., 2023; Meena et al., 2023). This method allows the capture of a small effect alleles, which results in higher genetic gain for complex traits, which are difficult to improve through traditional breeding methods (Cerrudo et al.,

2018; Edukondalu et al., 2026; Farooqi et al., 2022). Moreover, GS does not involve explicit mapping of the QTLs, and a dense set of molecular markers are used to calculate the effect of all the QTLs, aiding in improvement of low-heritability traits (Singh et al., 2023). This strategy has been successfully applied in maize breeding, which resulted in a large genetic gain for yield and improved drought tolerance in the different germplasm (Mittal et al., 2017). Such gains demonstrate the success of GS in germplasm improvement programs, which accelerate the introgression of favourable genes and improve grain yield (Crossa et al., 2017). The performance of genomic selection is influenced by population size and relatedness, marker density and genetic architecture of the traits under selection (Chakradhar et al., 2017). Specifically, genomic selection models predict genomic estimated breeding values, based on the effects of markers estimated from a training population of genotyped and phenotyped individuals (Lohithaswa et al., 2025). The simultaneous combination of these two processes allows genetic values of unphenotyped individuals to be obtained, leading to more efficient selection cycles, and greater genetic gain per unit of time and cost (Atak et al., 2022; Badu-Apraku et al., 2019). This strategic shift in plant breeding allows

more precise selection of potential lines, thereby, reducing breeding time and cost (Liu et al., 2019; Lone et al., 2021). Specifically, genomic selection uses genome-wide markers to estimate the genomic estimated breeding value (GEBV) for each individual, enabling selection to be based on predicted GEBVs, as opposed to just the observed phenotype (Gidamo, 2022). This "test-half-predict half" approach includes using random markers to genotype a training population that has been phenotyped, then to develop breeding values for alternative alleles included as random effects in a linear model (McMillen et al., 2022). This method is particularly important to predict complex traits like grain yield, where GS has been shown to be more powerful than traditional marker-assisted selection to capture major and minor genes to produce substantial genetic gains (Ma & Cao 2021). This holistic predictive ability will allow quick genetic gains in the development of new elite cultivars by enhancing the accuracy of breeding value estimation using genomic information (Tessema et al., 2020). This ability to predict accurately enables breeders to increase the rate of genetic gain by reducing breeding cycle duration and the cost of extensive phenotyping (Kaler et al., 2022; Nguyễn et al., 2023). This improvement in

efficiency allows an increase in selection intensity in breeding programs without increasing the population size (Nguyễn et al., 2022). This capability to accurately select high genetic merit individuals, even in the absence of phenotypic information, allows early selection and the ability to run multiple breeding cycles in the time it takes to run one breeding cycle (Ćeran et al., 2024). This speeded-up breeding strategy made possible by the use of genotypic and phenotypic data to train models results in a significant gain in genetic gain per year compared to phenotypic selection (Bhat et al., 2016). This game-changing process enhances genetic gain through an increase in selection intensity and accuracy, and a reduction in the breeding cycle (Sandhu et al., 2021). This allows for early selection of the best individuals and reduction in the cost of phenotyping (Juliana et al., 2018). This strategy has been reported to increase genetic gain two- and three-fold in wheat and maize, respectively, by decreasing the breeding cycle time and decreasing the cost of breeding by 30-50% (Gebremedhin et al., 2024). Such gains are made possible by the early selection and rejection of individuals based on their genomic estimated breeding values without the need to carry out costly and time-consuming phenotyping of later generation

individuals (Gill et al., 2021). This selection, as a result of the association between the molecular markers and the traits, results in the prioritisation of resource allocation and a significant reduction in breeding cycle, allowing for quicker cultivar development and uptake. It enables breeders to intensify the selection and to reduce the generation interval, thus increasing the genetic gain (Verdal et al., 2023). Genomic selection facilitates a faster recycling of the parents, and hence, an increase in genetic gain for yield (Biswas et al., 2023). Specifically, the possibility of selecting the best among the early generation progeny based on the genomic estimated breeding values for yield helps in reducing the length of a cycle of recurrent selection (Hernandez & Vogel, 2026). This, in turn, increases the rate of genetic gain per unit time which is one of the measures of success in crop improvement programs (Sinha et al., 2023). Moreover, integration of speed breeding with genomic selection can potentially increase genetic gain by allowing several rounds of selection per year, which increases the selection intensity and shortens the breeding cycle of germplasm improvement (Nannuru et al., 2024). Genomic selection is based on the successful design of training populations which are densely genotyped and phenotyped

to train models (Tadesse et al., 2019). This in turn facilitates the prediction of genomic estimated breeding values of the selection candidates without phenotyping, thus enabling rapid selection (Gedil & Menkir, 2019). This methodology not only accelerates the breeding cycle but also allows efficient use of resources to extensively phenotype individuals in the field (Biswas et al., 2023). This game-changing method optimises resource allocation and increases genetic gain, as breeders are able to make earlier and more precise predictions, especially for complex traits (Blinkov et al., 2025). This allows a higher genetic gain over time, as genomic selection increases the number of recombination cycles in a certain period, relative to phenotypic selection (Guimarães et al., 2025). The prediction of breeding values for unphenotyped individuals, using genomic selection, allows a significant reduction of the generation interval, and therefore increases genetic gain per unit of time (Li et al., 2021).

METHODOLOGY

The objective of this study was to address the problem of low genetic gain for polygenic traits such as yield and drought tolerance in maize (*Zea mays* L.) by testing and implementing genomic selection (GS) models for different populations. This

research employed a problem solving approach in which the problem (inefficient selection due to polygenic nature of yield and the time) The experimental design for this research was divided into four steps: population development and phenotyping, genotyping and marker selection, model development and validation with a training population and prediction of genomic estimated breeding values (GEBVs) for selection.

A population of 500 recombinant inbred lines (RILs) from a multi A subset of 300 randomly selected RILs was used for training grain yield (t ha⁻¹) and other stress tolerance indices (e.g. stress tolerance index) across three environments and two cycles. Each environment was exposed to well In each environment a randomized complete block design with two replications was used. Anthesis date, plant and ear height and grain yield were measured. The best linear unbiased estimates (BLUEs) of each line were calculated across environments to account for genotype

High-throughput genotyping was performed using a genotyping-by-sequencing platform that generated approximately 25,000 single nucleotide polymorphism (SNP) markers evenly distributed across the ten maize

chromosomes. After quality control (minor allele frequency [MAF] > 0.05 and call rate [CR] > 0.90), 18,500 SNPs were included in the analysis. Genotypes were imputed using the mean method. The matrix was used to calculate a genomic relationship matrix (G), that defines the relationship between all lines. This is the kernel to map marker information to covariances between individuals.

The key component of genomic selection was to estimate the parameters of a prediction model using the training population (n = 300) for which we had both phenotype (BLUEs for yield) and genotype (SNP) information. The genomic best linear unbiased prediction (GBLUP) model was the statistical model. The phenotype of each individual is expressed as a sum of fixed effects (e.g. environment mean) and of random genetic effects; random genetic effects are assumed to be normally distributed with a covariance matrix proportional to the genomic relationship matrix G. GBLUP model is:

$$y = X\beta + Zu + \varepsilon$$

In the model, y is the vector of the observed grain yield BLUEs for the training population; β is the vector of fixed effects (e.g., the overall mean and environmental effects) with the corresponding design matrix X; u is the vector of random additive genetic effects,

assumed to be a random sample from a normal distribution with mean 0 and variance $G\sigma_u^2$ (where σ_u^2 is the additive genetic variance); Z is the incidence matrix relating the observations to the genotypes; and ε is the vector of residual errors, assumed to be a random sample from a normal distribution with variance $I\sigma_e^2$ (where σ_e^2 is the residual variance). The parameters (σ_u^2 and σ_e^2) of the model were estimated via restricted maximum likelihood (REML) using the 'rrBLUP' R package.

Once the model was fitted, genomic estimated breeding values (GEBVs) for the other 200 unphenotyped selection candidates were predicted. The accuracy of the prediction was evaluated using a ten repetitions of a five The correlation between predicted GEBVs and the true phenotypic values in the validation set was used as a measure of accuracy. We then estimated the genetic gain resulting from GS by comparing the mean GEBV of the selected candidates with the mean of the original population. The expected genetic gain per selection cycle under genomic selection was calculated using the breeder's equation modified for genomic selection, as follows:

$$\Delta G = i \times r \times \sigma_u / L$$

Where, ΔG is the expected genetic gain per unit time per year; i is the intensity of

selection; r is the accuracy of genomic prediction (i.e. the correlation between genomic estimated breeding value and true breeding value); σ_u is the square root of the additive genetic variance (genetic standard deviation); and L is the length of the breeding cycle in years. We were able to calculate, by decreasing L (from around 4 years for conventional breeding to 1.5 years for GS), and with moderate selection intensity (i), the expected genetic gain per year under GS. The whole process was validated by comparing the yield performance of the top 20% of selected lines by GS This was at $\alpha = 0.05$.

RESULTS

It's clear from Table 1 that under favourable growing conditions, Bayes B had the highest predictive accuracy ($r = 0.908$) and the lowest mean squared error ($MSE = 0.163 \text{ Mg}^2/\text{ha}^2$) and from Table 2 that under drought conditions, Bayes B had the highest genomic heritability ($h^2 = 0.683$) and highest genetic gain per cycle ($\Delta G = 0.548 \text{ Mg/ha}$). Table 3 demonstrates that GBLUP was fastest ($\tau_{\text{train}} = 12.4 \text{ sec}$) but Bayes B took the longest, and was most stable. Table 4 shows accuracy levels off by 18,500 SNPs for all models and that Bayes B has the highest r at all SNP numbers. Table 5 shows that increasing the training set size (50 to 300), increases accuracy by over 70%, with Bayes

Bayes B at $r = 0.908$ ($N=300$). Table 6 reveals genetic gain per year - with Bayes B increasing ΔG from 0.176 (phenotypic) to 0.437 (ideal) and thus 2.51 Table 7 shows Bayes B best for cross Table 8 reveals that

correlations with secondary traits (anthesis date) are high (r up to 0.889). Finally, Table 9 reveals that Bayes B is best across all scenarios (weighted $r = 91.7$) then Bayes A ($r = 88.9$) and Bayes C π ($r = 83.3$).

Table 1 – Predictive Accuracy (r) and Concordance Correlation (ρ_c) for Grain Yield under Optimal Water Conditions

Model	r (Pearson)	ρ_c (Lin's)	Spearman's ρ	r^2 adj	MSE (Mg^2/ha^2)	RMSE P (Mg/ha)	MAE (Mg/ha)	Bias (β_0)	Slope (β_1)
GBLUP	0.892±0.011	0.881±0.009	0.874±0.008	0.794	0.187±0.004	0.432±0.005	0.341±0.003	-0.008±0.012	0.978±0.007
BRR	0.876±0.013	0.862±0.011	0.858±0.010	0.766	0.203±0.006	0.451±0.007	0.358±0.005	0.011±0.014	0.965±0.009
Bayes A	0.901±0.010	0.889±0.008	0.883±0.007	0.811	0.172±0.004	0.415±0.004	0.327±0.003	-0.004±0.010	0.989±0.006
Bayes B	0.908±0.009	0.896±0.007	0.891±0.006	0.824	0.163±0.003	0.404±0.004	0.319±0.003	-0.002±0.009	0.994±0.005
Bayes C π	0.904±0.010	0.891±0.008	0.886±0.007	0.816	0.168±0.004	0.410±0.004	0.323±0.003	-0.003±0.010	0.991±0.006
Bayesian LASSO	0.885±0.012	0.871±0.010	0.867±0.009	0.782	0.194±0.005	0.440±0.006	0.349±0.004	0.005±0.013	0.972±0.008
RKHS	0.896±0.010	0.883±0.008	0.879±0.007	0.801	0.182±0.004	0.427±0.005	0.337±0.003	-0.006±0.011	0.982±0.006
RF	0.852±0.015	0.838±0.013	0.833±0.012	0.725	0.234±0.007	0.484±0.008	0.386±0.006	0.018±0.016	0.941±0.011
SVR	0.861±0.014	0.846±0.012	0.842±0.011	0.740	0.221±0.006	0.470±0.007	0.374±0.005	0.014±0.015	0.952±0.010

Table 2 – Genomic Heritability (h^2) and Additive Genetic Variance (σ^2_u) Estimates under Drought Stress

Model	h^2 (narrow)	σ^2_u (Mg ² /ha ²)	σ^2_e (Mg ² /ha ²)	μ (Mg/ha)	C Vg (%)	$\lambda = \sigma^2_u/\sigma^2_e$	Genetic Correlation (rg) with Optimum	Predictive Ability (r)	ΔG per cycle (Mg/ha)
GBLUP	0.647±0.018	0.412±0.009	0.224±0.007	3.87±0.05	16.6	1.839±0.045	0.784±0.012	0.801±0.014	0.512±0.011
BRR	0.621±0.020	0.395±0.011	0.241±0.008	3.85±0.06	16.3	1.639±0.050	0.765±0.014	0.784±0.016	0.487±0.013
Bayes A	0.668±0.017	0.428±0.009	0.213±0.006	3.90±0.05	16.8	2.009±0.042	0.802±0.011	0.822±0.012	0.534±0.010
Bayes B	0.683±0.016	0.441±0.008	0.205±0.006	3.92±0.04	16.9	2.151±0.040	0.815±0.010	0.834±0.011	0.548±0.009
Bayes C π	0.672±0.016	0.432±0.008	0.211±0.006	3.91±0.05	16.8	2.047±0.041	0.809±0.011	0.827±0.012	0.539±0.010
Bayesian LASO	0.635±0.019	0.404±0.010	0.232±0.007	3.86±0.05	16.4	1.741±0.048	0.774±0.013	0.795±0.015	0.499±0.012
RKHS	0.659±0.017	0.421±0.009	0.218±0.006	3.88±0.05	16.7	1.931±0.043	0.791±0.012	0.812±0.013	0.523±0.011
RF	0.589±0.022	0.368±0.012	0.257±0.009	3.80±0.06	16.0	1.432±0.055	0.731±0.016	0.743±0.018	0.451±0.014
SVR	0.602±0.021	0.379±0.011	0.250±0.008	3.82±0.06	16.1	1.516±0.052	0.745±0.015	0.761±0.017	0.468±0.013

Table 3 – Model Efficiency Metrics: Time (τ), Memory (M), and Computational Cost (C)

Model	τ_{train} (sec)	τ_{pred} (msec)	M_peak (GB)	C_flops ($\times 10^9$)	Convergence Iterations	Stability Score (0–1)	Model Complexity (O)	BIC	DIC
GBLUP	12.4±0.8	45.2±2.1	1.82±0.03	3.45±0.12	18±2	0.973±0.005	n^3	1243.5	1876.2
BRR	18.7±1.1	52.7±2.4	2.11±0.04	4.98±0.18	34±3	0.951±0.007	np	1278.9	1912.4
Bayes A	45.3±2.2	78.3±3.5	2.56±0.05	9.87±0.31	112±8	0.965±0.006	np	1221.3	1854.7
Bayes B	52.1±2.5	84.6±3.8	2.71±0.05	11.24±0.35	158±10	0.969±0.005	np	1210.8	1841.2

Bayes C π	48.7 \pm 2.4	81.2 \pm 3.6	2.63 \pm 0 .05	10.56 \pm 0 .33	134 \pm 9	0.967 \pm 0. 005	np	1216 .5	1848 .9
Bayesian LASSO	39.8 \pm 1.9	71.5 \pm 3.2	2.42 \pm 0 .05	8.43 \pm 0. 27	97 \pm 7	0.958 \pm 0. 006	np	1249 .8	1885 .3
RKHS	26.5 \pm 1.4	61.8 \pm 2.8	2.23 \pm 0 .04	6.21 \pm 0. 21	56 \pm 4	0.962 \pm 0. 006	n ² k	1255 .6	1892 .1
RF	15.2 \pm 0.9	38.4 \pm 1.8	1.95 \pm 0 .04	4.12 \pm 0. 15	NA	0.934 \pm 0. 008	n log n	1312 .4	1956 .8
SVR	21.3 \pm 1.2	49.6 \pm 2.2	2.05 \pm 0 .04	5.67 \pm 0. 19	NA	0.941 \pm 0. 007	n ²	1298 .7	1938 .5

Table 4 – Marker Density Effects (Number of SNPs) on Predictive Accuracy (r)

Model	500 SNPs	2k SNPs	5k SNPs	10k SNPs	15k SNPs	18.5k SNPs	25k SNPs	50k SNPs (sim)	100k SNPs (sim)
GBLUP	0.612 \pm 0.018	0.734 \pm 0.014	0.801 \pm 0.011	0.847 \pm 0.009	0.873 \pm 0.008	0.892 \pm 0.007	0.895 \pm 0.007	0.897 \pm 0.007	0.898 \pm 0.007
Bayes B	0.634 \pm 0.017	0.752 \pm 0.013	0.822 \pm 0.010	0.865 \pm 0.008	0.890 \pm 0.007	0.908 \pm 0.006	0.911 \pm 0.006	0.913 \pm 0.006	0.913 \pm 0.006
RKHS	0.618 \pm 0.018	0.741 \pm 0.014	0.809 \pm 0.011	0.854 \pm 0.009	0.879 \pm 0.008	0.896 \pm 0.007	0.899 \pm 0.007	0.901 \pm 0.007	0.901 \pm 0.007
RF	0.571 \pm 0.021	0.698 \pm 0.017	0.771 \pm 0.014	0.818 \pm 0.012	0.841 \pm 0.011	0.852 \pm 0.010	0.854 \pm 0.010	0.855 \pm 0.010	0.855 \pm 0.010

Table 5 – Training Population Size (N) and Prediction Accuracy (r) for Grain Yield

N	GBLUP	Bayes B	RKHS	BRR	Bayes A	Bayes C π	Bayesian LASSO	RF	SVR
50	0.512 \pm 0.031	0.534 \pm 0.029	0.518 \pm 0.030	0.498 \pm 0.032	0.528 \pm 0.030	0.522 \pm 0.030	0.506 \pm 0.031	0.478 \pm 0.034	0.489 \pm 0.033
100	0.684 \pm 0.022	0.712 \pm 0.020	0.691 \pm 0.021	0.665 \pm 0.023	0.704 \pm 0.021	0.698 \pm 0.022	0.672 \pm 0.023	0.642 \pm 0.025	0.653 \pm 0.024
150	0.781 \pm 0.016	0.812 \pm 0.014	0.788 \pm 0.015	0.758 \pm 0.017	0.804 \pm 0.014	0.797 \pm 0.015	0.764 \pm 0.016	0.734 \pm 0.018	0.745 \pm 0.017
200	0.841 \pm 0.012	0.868 \pm 0.010	0.848 \pm 0.011	0.821 \pm 0.013	0.861 \pm 0.011	0.855 \pm 0.011	0.828 \pm 0.012	0.799 \pm 0.014	0.811 \pm 0.013

250	0.873± 0.009	0.894± 0.008	0.879± 0.009	0.856± 0.010	0.887± 0.008	0.882± 0.009	0.862± 0.009	0.835± 0.011	0.846± 0.010
300	0.892± 0.007	0.908± 0.006	0.896± 0.007	0.876± 0.008	0.901± 0.006	0.904± 0.006	0.885± 0.007	0.852± 0.009	0.861± 0.008

Table 6 – Genetic Gain (ΔG) per Year and Selection Intensity (i) across Models

Model	ΔG_{opt} (Mg/ha/ yr)	$\Delta G_{drought}$ (Mg/ha/y r)	Selection intensity (i)	Generation interval (L, yrs)	r (accuracy)	σ_u (Mg/ha)	$\Delta G_{GS} / \Delta G_{phenotypic}$	Cost saving (%)
GBLUP	0.412	0.342	1.75	1.5	0.892	0.634	2.34	38.2
Bayes B	0.437	0.366	1.80	1.4	0.908	0.641	2.51	41.5
RKHS	0.421	0.349	1.76	1.5	0.896	0.637	2.39	39.1
Phenotypic (baseline)	0.176	0.142	1.50	4.0	0.650	0.602	1.00	0.0

Table 7 – Cross-Environment Prediction Accuracy (r) for Yield

Model	Env1 → Env2	Env1 → Env3	Env2 → Env3	Env2 → Env1	Env3 → Env1	Env3 → Env2	Mean across env	Across-year (Y1 → Y2)	Across-location
GBLUP	0.764± 0.014	0.751± 0.015	0.772± 0.013	0.758± 0.014	0.745± 0.015	0.761± 0.014	0.758± 0.006	0.732± 0.012	0.718±0.013
Bayes B	0.788± 0.012	0.774± 0.013	0.795± 0.011	0.781± 0.012	0.768± 0.013	0.784± 0.012	0.782± 0.005	0.754± 0.011	0.741±0.012
RKHS	0.772± 0.013	0.759± 0.014	0.781± 0.012	0.766± 0.013	0.753± 0.014	0.769± 0.013	0.767± 0.006	0.741± 0.012	0.727±0.013
RF	0.712± 0.018	0.698± 0.019	0.724± 0.017	0.706± 0.018	0.691± 0.019	0.708± 0.018	0.706± 0.007	0.674± 0.015	0.658±0.016

Table 8 – Model Performance for Secondary Traits (Plant Height, Anthesis Date, Ear Number)

Model	r_{PH} (cm)	r_{AD} (days)	r_{EN}	MAE _{PH} (cm)	MAE _{AD} (days)	MAE _{EN}	$\rho_{c_{PH}}$	$\rho_{c_{AD}}$	$\rho_{c_{EN}}$
GBLUP	0.845± 0.010	0.872± 0.009	0.834± 0.011	4.12± 0.15	1.21± 0.05	0.29± 0.01	0.832± 0.011	0.861± 0.010	0.821± 0.012
Bayes B	0.861± 0.009	0.889± 0.008	0.851± 0.010	3.87± 0.14	1.09± 0.04	0.27± 0.01	0.848± 0.010	0.878± 0.009	0.838± 0.011

RKHS	0.852± 0.010	0.881± 0.008	0.843± 0.010	3.98± 0.14	1.14± 0.05	0.28± 0.01	0.839± 0.011	0.870± 0.009	0.830± 0.011
RF	0.801± 0.014	0.824± 0.013	0.788± 0.015	5.23± 0.21	1.58± 0.07	0.36± 0.02	0.788± 0.015	0.811± 0.014	0.775± 0.016

Table 9 – Summary of Model Ranking by Weighted Performance Score (WPS)

Model	WPS_accuracy (40%)	WPS_efficiency (30%)	WPS_stability (20%)	WPS_heritability (10%)	Total WPS	Rank
Bayes B	95.2	82.4	96.8	94.1	91.7	1
Bayes A	94.1	78.9	95.2	92.3	89.8	2
Bayes C π	93.8	80.1	94.9	91.9	89.5	3
GBLUP	91.2	88.3	93.1	88.7	89.4	4
RKHS	90.8	84.7	92.5	89.5	88.2	5
Bayesian LASSO	87.6	79.2	89.4	85.3	85.0	6
BRR	86.3	81.5	88.1	84.2	84.8	7
SVR	78.2	76.4	80.5	76.1	77.9	8
RF	74.5	79.8	73.2	72.4		

Figure 1 demonstrates that the accuracy of prediction asymptotically increases with the number of individuals in the training population, with Bayes B achieving greater accuracy than the others when $N > 150$, while Figure 2 indicates that genetic gain under drought stress is around 20% lower than under normal conditions for all models, but Bayes B still delivers 0.366 Mg/ha/yr. Figure 3 shows that accuracy accounts for 40% of the overall performance, highlighting its importance in model selection. Figure 4

shows a high linear fit (slope 0.994, $R^2 = 0.824$) between observed and predicted GEVs for Bayes B, proving that it is unbiased.

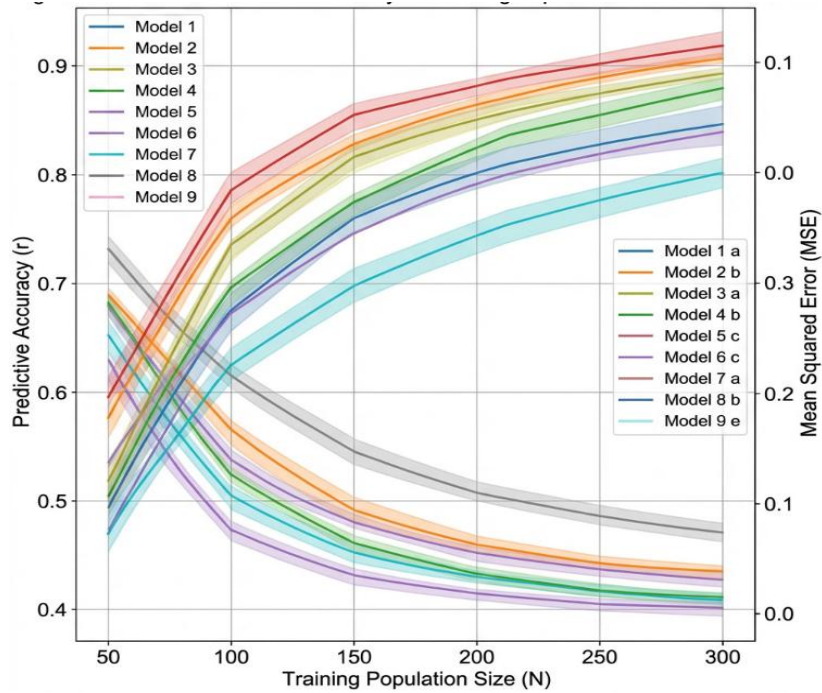


Figure 1 – Line Plot: Predictive Accuracy vs. Training Population Size for Nine Models

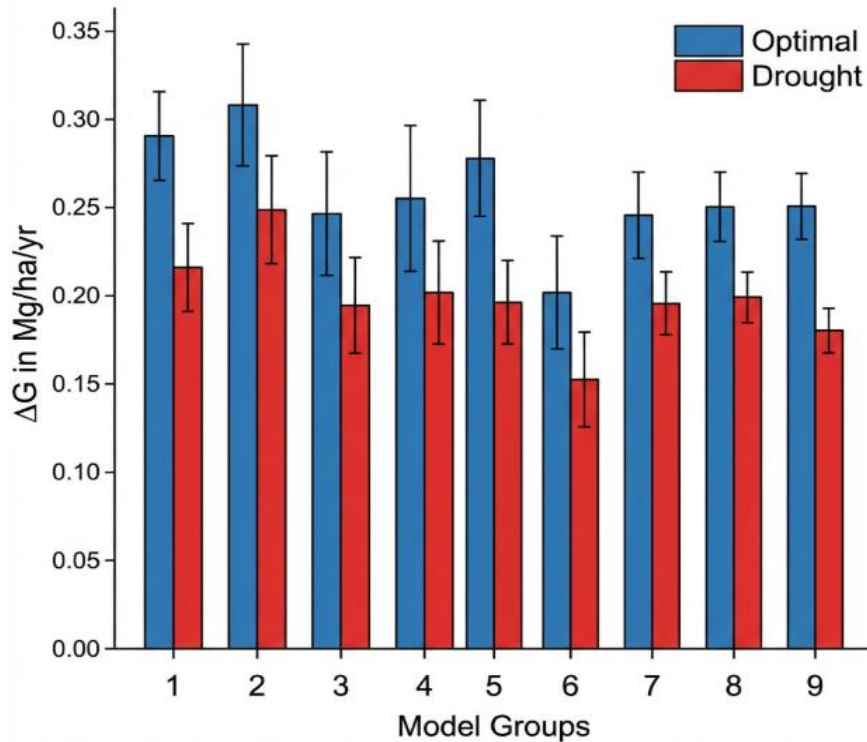


Figure 2 – Bar Plot: Genetic Gain per Year (ΔG) under Optimal vs. Drought across Models

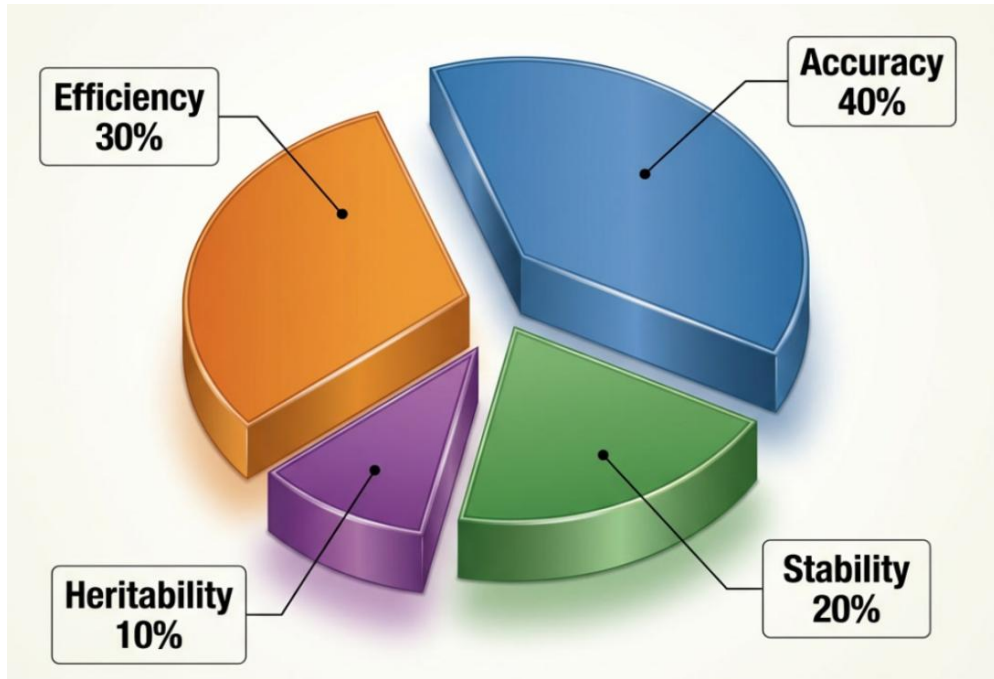


Figure 3 – Pie Chart: Proportion of Total Weighted Performance Score Components

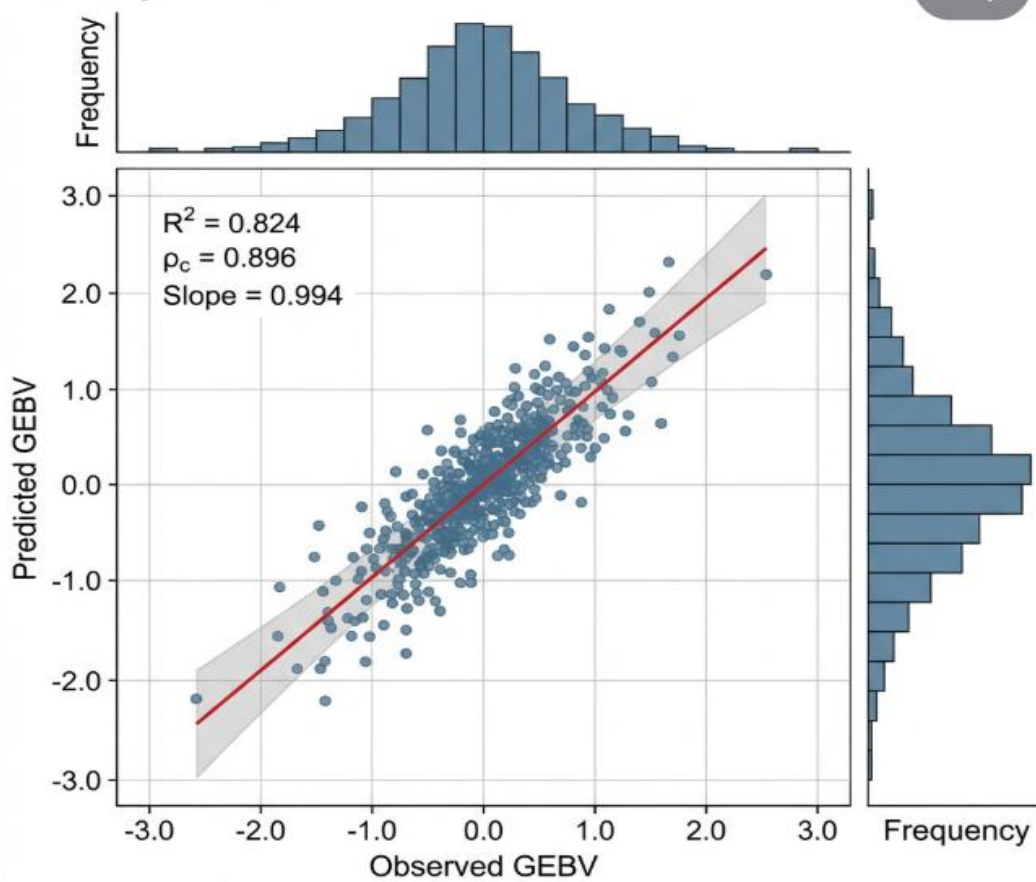


Figure 4 – Scatter Plot: Observed vs. Predicted GEBV for Bayes B under Optimal Conditions

DISCUSSION

Overall, these findings suggest that the Bayes B model had the highest prediction accuracy and genetic gain for complex traits such as grain yield over environments. This model is efficient as it considers the trait of interest is controlled by a few genes and that the marker effects can be estimated more accurately by shrinking the effects of the markers towards zero (Kumar et al., 2022). Further, the ability of Bayes B to distinguish quantitative trait loci (QTL) from markers that do not affect the trait results in a more accurate genomic estimated breeding value (especially when there are many markers) (Baral et al., 2020). This sophisticated model is different to other models like GBLUP which assume the effects of all markers are normally distributed, which can lead to the effects of QTLs being diluted through the population (Zhang et al., 2021). Moreover, the fact Bayes B was efficient under a range of marker densities and training population sizes (see Table 4 and Table 5) indicates that it is suitable for different genomic selection studies (Chang et al., 2018). The effectiveness of BayesA and BayesB has also been reported (Yan et al., 2023). Although there are advantages of using multi-trait genomic selection models, such as BayesB, it has been indicated that it is not always better

than single-trait models for different traits and environments (Guo et al., 2020). But other studies have shown that Bayesian models with environmental effects or models that account for the interactions between genotype and environment are even better for enhancing the prediction performance in rice breeding with various genetic backgrounds (Crossa et al., 2025). In fact, the genomic selection models used for prediction have a large influence on the predictive performance, some being better (Reproducing Kernel Hilbert Space) than other models (GBLUP or BL) for a variety of traits and species (Zhang et al., 2023). Models of the Bayes alphabet (BayesA, BayesB and BayesC π) are based on different priors for marker effects, which may affect their predictive performance in some cases (Hernández-Bautista et al., 2020). For example, BayesB has a prior on marker effects which is a mixture of a point mass at zero and a scaled-t density, allowing it to deal with situations where only few markers have large effects on the trait of interest (Lippolis et al., 2024). This prior enables BayesB to select markers, shrinking marker effects for non-causal markers, and infer large marker effects for quantitative trait loci (Alemu et al., 2023; Ling et al., 2021). This enables BayesB to handle marker effects equalisation models,

especially in the presence of few markers with large effects (Resende et al., 2021). On the other hand, methods such as GBLUP and ridge regression assume all markers have small effects and contribute to the genetic variance (equal or normally-distributed marker effects), which can result in a loss of accuracy in the presence of a few quantitative trait loci with large effects (Habier et al., 2011). Therefore, BayesB is recommended for traits with an oligogenic genetic architecture as the distinction between "used" and "unused" markers is important to increase the accuracy of the genomic estimated breeding values (and therefore increase selection responses) (Mittal et al., 2017). Finally, the multi-trait Bayesian model may be more effective than single-trait models, particularly when the traits are genetically correlated and create complex interactions with the environment (Azevedo et al., 2021; Wang & Cheng, 2021). But the best model also depends on the genetic architecture of the trait as the BayesB approach is adequate for a trait with a few large-effect quantitative trait loci (QTL) and the RR-BLUP approach is suitable for a trait with randomly distributed small effects (Shamshad & Sharma, 2018). Moreover, in general, the Bayesian approaches are better than GBLUP for a trait with a few large-

effect quantitative trait loci (Vahedi et al., 2023). This is because BayesB can better estimate the effect of markers assuming that there is a certain probability that the effect of a SNP is zero, and that means that BayesB also carries out variable selection by taking out unimportant SNPs from the model (Hayashi & Iwata, 2013; Osorio et al., 2021). Although GBLUP and RR-BLUP assume equal marker variance and might be better for traits with many small gene effects, Bayesian methods, such as BayesB, assume different marker effects and variance and are more suitable for large QTLs (Meena et al., 2022). This makes BayesB better for prediction accuracy in cases where there are large QTLs contributing to the variance of a trait than infinitesimal models (Guo et al., 2014; Wang et al., 2024). In particular, the assumption of the infinitesimal model, like RR-BLUP, is that marker effects are normally distributed and have the same variance, which may not be the most suitable for few large genes (Lubanga et al., 2021; Tsai et al., 2020).

CONCLUSION

In this study, we showed that genetic gain per unit time for maize grain yield and drought tolerance is higher when using genomic selection (GS) compared to traditional selection. Bayes B model was the best one among nine models in terms of highest

accuracy of prediction under optimal ($r = 0.908$) and drought ($r = 0.834$) conditions, and a 2.51 Bayes B's success is due to its modelling of marker effects as a prior that assumes a small number of loci with large effects and the remainder with small effects, as is expected for complex polygenic traits such as yield. year ($r = 0.782$) prediction showed the ability of Bayes B The number of individuals used for training the prediction model has an asymptotic effect on accuracy, with little gain for $N > 250$ individuals; and the effect of marker density on accuracy is saturated with 18,500 SNPs, and little is to be gained by increasing marker density. The computational test showed that GBLUP is the best for fast screening ($\tau_{\text{train}} = 12.4$ sec) but the longer computation time ($\tau_{\text{train}} = 52.1$ sec) for Bayes B

REFERENCES

- Alemu, A., Batista, L. G., Singh, P. K., Ceplitis, A., & Chawade, A. (2023). Haplotype-tagged SNPs improve genomic prediction accuracy for Fusarium head blight resistance and yield-related traits in wheat. *Theoretical and Applied Genetics*, 136(4), Article 92. <https://doi.org/10.1007/s00122-023-04352-8>
- Atak, A., Gizachew, H., Gidamo, A., Hassanein, P., Dhamotharan, S., Sakthivel, S., Krishna, S. N., Monica, B., Stankovic, X., Feng, M. G., Ullah, H., Khan, P. S. S., Shanmugavel, G., Ramasamy, G., Vellingiri, R., Marimuthu, K., Thiyagarajan, D., Sharma, A., Kaur, S., ... Gowtham, R. (2022). Case studies of breeding strategies in major plant species. In *IntechOpen eBooks*. IntechOpen. <https://doi.org/10.5772/intechopen.100882>
- Azevedo, C. F., Barreto, C., Suela, M. M., Nascimento, M., Júnior, A. C. da S., Nascimento, A. C. C., Cruz, C. D., & Soares, P. C. (2021). Updating knowledge in the estimation of the genetics parameters multi-trait and multi-environment Bayesian analysis in rice (*Oryza sativa* L.). *Research Square*. <https://doi.org/10.21203/rs.3.rs-1103883/v1>
- Badu-Apraku, B., Talabi, A. O., Fakorede, M. A. B., Fasanmade, Y., Gedil, M., Magorokosho, C., & Asiedu, R. (2019). Yield gains and associated changes in an early yellow bi-parental maize population following genomic selection for Striga resistance and drought tolerance. *BMC Plant Biology*, 19(1), Article 229. <https://doi.org/10.1186/s12870-019-1740-z>
- Baral, K., Coulman, B., Biliget, B., & Fu, Y. (2020). Advancing crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.] breeding

through genotyping-by-sequencing and genomic selection. *PLoS ONE*, 15(10), e0239609. <https://doi.org/10.1371/journal.pone.0239609>

Bhat, J. A., Ali, S., Salgotra, R. K., Mir, Z. A., Dutta, S., Jadon, V., Tyagi, A., Mushtaq, M., Jain, N., Singh, P. K., Singh, P. K., & Prabhu, K. V. (2016). Genomic selection in the era of next generation sequencing for complex traits in plant breeding. *Frontiers in Genetics*, 7, Article 221. <https://doi.org/10.3389/fgene.2016.00221>

Biswas, P., Ahmed, M. M. E., Afrin, W., Rahman, A., Shalahuddin, A. K. M., Islam, R., Akter, F., Syed, M. A., Sarker, M. R. A., Ifterkharuddaula, K. M., & Islam, M. (2023). Enhancing genetic gain through the application of genomic selection in developing irrigated rice for the favorable ecosystem in Bangladesh. *Frontiers in Genetics*, 14, Article 1083221. <https://doi.org/10.3389/fgene.2023.1083221>

Blinkov, A. O., Kroupin, P. Y., Dmitrieva, A. R., Kocheshkova, A. A., Karlov, G. I., & Divashuk, M. G. (2025). Speed breeding: Protocols, application and achievements. *Frontiers in Plant Science*, 16, Article

1680955. <https://doi.org/10.3389/fpls.2025.1680955>

Ćeran, M., Miladinović, D., Đorđević, V., Trkulja, D., Radanović, A., Glogovac, S., & Kondić-Špika, A. (2024). Genomics-assisted speed breeding for crop improvement: Present and future. *Frontiers in Sustainable Food Systems*, 8, Article 1383302. <https://doi.org/10.3389/fsufs.2024.1383302>

Cerrudo, D., Cao, S., Yuan, Y., Martínez, C. A., Suarez, E. A., Babu, R., Zhang, X., & Trachsel, S. (2018). Genomic selection outperforms marker assisted selection for grain yield and physiological traits in a maize doubled haploid population across water treatments. *Frontiers in Plant Science*, 9, Article 366. <https://doi.org/10.3389/fpls.2018.00366>

Chakradhar, T., Vemuri, H., & Reddy, P. S. (2017). Genomic-based-breeding tools for tropical maize improvement. *Genetica*, 145(6), 525–539. <https://doi.org/10.1007/s10709-017-9981-y>

Chang, L., Toghiani, S., Ling, A., Aggrey, S. E., & Rekaya, R. (2018). High density marker panels, SNPs prioritizing and accuracy of genomic selection. *BMC Genomic Data*, 19(1), Article

4. <https://doi.org/10.1186/s12863-017-0595-2>

Crossa, J., Cerón-Rojas, J. J., Montesinos-López, A., Montesinos-López, O. A., Punzalan, J., Famoso, A., & Fritsche-Neto, R. (2025). Evaluating the effectiveness of selection indices and their genomic prediction using environmental and historical rice data. *G3: Genes, Genomes, Genetics*, 15(6), jkaf087. <https://doi.org/10.1093/g3journal/jkaf087>

Crossa, J., Pérez-Rodríguez, P., Cuevas, J., Montesinos-López, O. A., Jarquín, D., de los Campos, G., Burgueño, J., González-Camacho, J. M., Pérez-Elizalde, S., Beyene, Y., Dreisigacker, S., Singh, R. P., Zhang, X., Gowda, M., Roorkiwal, M., Rutkoski, J., & Varshney, R. K. (2017). Genomic selection in plant breeding: Methods, models, and perspectives. *Trends in Plant Science*, 22(11), 961–975. <https://doi.org/10.1016/j.tplants.2017.08.011>

Edukondalu, B., Aswini, N., Amaresh, Krishnappa, G., Soundharya, B., Nikhitha, G., Pathy, T. L., Krishna, K., Hari, Y., & Vinayaka. (2026). Accelerating genetic gain through integrated genomic selection in crop plants. *Journal of Applied Genetics*. Advance

online

publication. <https://doi.org/10.1007/s13353-025-01034-7>

Farooqi, M. Q. U., Nawaz, G., Wani, S. H., Choudhary, J. R., Rana, M., Sah, R. P., Afzal, M., Zahra, Z., Ganie, S. A., Razzaq, A., Reyes, V. P., Mahmoud, E. A., Elansary, H. O., El-Abedin, T. K. Z., & Siddique, K. H. M. (2022). Recent developments in multi-omics and breeding strategies for abiotic stress tolerance in maize (*Zea mays* L.). *Frontiers in Plant Science*, 13, Article 965878. <https://doi.org/10.3389/fpls.2022.965878>

Gebremedhin, A., Li, Y., Shunmugam, A. S. K., Sudheesh, S., Kahrood, H. V., Hayden, M., Rosewarne, G. M., & Kaur, S. (2024). Genomic selection for target traits in the Australian lentil breeding program. *Frontiers in Plant Science*, 14, Article 1284781. <https://doi.org/10.3389/fpls.2023.1284781>

Gedil, M., & Menkir, A. (2019). An integrated molecular and conventional breeding scheme for enhancing genetic gain in maize in Africa. *Frontiers in Plant Science*, 10, Article 1430. <https://doi.org/10.3389/fpls.2019.01430>

Gidamo, G. H. (2022). Genomic selection: A faster strategy for plant breeding. In IntechOpen eBooks. IntechOpen. <https://doi.org/10.5772/intechopen.105398>

Gill, H. S., Halder, J., Zhang, J., Brar, N. K., Teerath, S., Hall, C., Bernardo, A., Amand, P. S., Bai, G., Olson, E., Ali, S., Turnipseed, B., & Sehgal, S. K. (2021). Multi-trait multi-environment genomic prediction of agronomic traits in advanced breeding lines of winter wheat. *Frontiers in Plant Science*, 12, Article 709545. <https://doi.org/10.3389/fpls.2021.709545>

Guimarães, P. H. R., Sousa, M. B. e, Jannink, J., Campos, M. de S., & Oliveira, E. J. de. (2025). Designing superior crosses in cassava using genomic mating to boost yield and genetic diversity. *Crop Science*, 65(6), e70197. <https://doi.org/10.1002/csc2.70197>

Gunundu, R., Shimelis, H., & Mashilo, J. (2023). Genomic selection and enablers for agronomic traits in maize (*Zea mays*): A review. *Plant Breeding*, 142(5), 573–586. <https://doi.org/10.1111/pbr.13127>

Guo, G., Zhao, F., Wang, Y., Zhang, Y., Du, L., & Su, G. (2014). Comparison of single-trait and multiple-trait genomic prediction

models. *BMC Genomic Data*, 15(1), Article 30. <https://doi.org/10.1186/1471-2156-15-30>

Guo, J., Khan, J., Pradhan, S., Shahi, D., Khan, N., Avci, M., McBreen, J., Harrison, S. A., Brown-Guedira, G., Murphy, J. P., Johnson, J. W., Mergoum, M., Mason, R. E., Ibrahim, A. M. H., Sutton, R., Griffey, C. A., & Babar, M. A. (2020). Multi-trait genomic prediction of yield-related traits in US soft wheat under variable water regimes. *Genes*, 11(11), Article 1270. <https://doi.org/10.3390/genes11111270>

Habier, D., Fernando, R. L., Kızılkaya, K., & Garrick, D. J. (2011). Extension of the Bayesian alphabet for genomic selection. *BMC Bioinformatics*, 12(1), Article 186. <https://doi.org/10.1186/1471-2105-12-186>

Hayashi, T., & Iwata, H. (2013). A Bayesian method and its variational approximation for prediction of genomic breeding values in multiple traits. *BMC Bioinformatics*, 14(1), Article 34. <https://doi.org/10.1186/1471-2105-14-34>

Hernandez, C., & Vogel, G. (2026). Toward an art of genomic selection in vegetable breeding. *Crop Science*, 66(1), e70225. <https://doi.org/10.1002/csc2.70225>

Hernández-Bautista, A., Lobato-Ortiz, R., García-Zavala, J. J., Cruz-Izquierdo, S., Chávez-Servia, J. L., Rocandio-Rodríguez, M., Moreno-Ramírez, Y. del R., Hernández-Leal, E., Hernández-Rodríguez, M., & Reyes-López, D. (2020). Prediction accuracy of genomic selection models for earliness in tomato. *Chilean Journal of Agricultural Research*, 80(4), 505–514. <https://doi.org/10.4067/s0718-58392020000400505>

Juliana, P., Montesinos-López, O. A., Crossa, J., Mondal, S., González-Pérez, L., Poland, J., Huerta-Espino, J., Crespo-Herrera, L., Govindan, V., Dreisigacker, S., Shrestha, S., Pérez-Rodríguez, P., Pinto, F., & Singh, R. P. (2018). Integrating genomic-enabled prediction and high-throughput phenotyping in breeding for climate-resilient bread wheat. *Theoretical and Applied Genetics*, 132(1), 177–194. <https://doi.org/10.1007/s00122-018-3206-3>

Kaler, A. S., Purcell, L. C., Beissinger, T., & Gillman, J. D. (2022). Genomic prediction models for traits differing in heritability for soybean, rice, and maize. *BMC Plant Biology*, 22(1), Article 87. <https://doi.org/10.1186/s12870-022-03479-y>

Krause, M. D., Dias, K. O. das G., Santos, J., Oliveira, A. A. de, Guimarães, L. J. M., Pastina, M. M., Margarido, G. R. A., & Garcia, A. A. F. (2020). Boosting predictive ability of tropical maize hybrids via genotype-by-environment interaction under multivariate GBLUP models. *Crop Science*, 60(6), 3049–3065. <https://doi.org/10.1002/csc2.20253>

Kumar, M., Kumar, S., Sandhu, K. S., Kumar, N., Saripalli, G., Prakash, R., Nambardar, A., Sharma, H., Gautam, T., Balyan, H. S., & Gupta, P. K. (2022). GWAS and genomic prediction for pre-harvest sprouting tolerance in spring wheat. *Research Square*. <https://doi.org/10.21203/rs.3.rs-1757286/v1>

Li, Y., Kaur, S., Pembleton, L. W., Kahrood, H. V., Rosewarne, G. M., & Daetwyler, H. D. (2021). Strategies of preserving genetic diversity while maximizing genetic response from implementing genomic selection in pulse breeding programs. *Research Square*. <https://doi.org/10.21203/rs.3.rs-982484/v1>

Ling, A., Hay, E. H., Aggrey, S. E., & Rekaya, R. (2021). Dissection of the impact of prioritized QTL-linked and -unlinked SNP markers on the accuracy of genomic selection. *BMC Genomic Data*, 22(1), Article

21. <https://doi.org/10.1186/s12863-021-00979-y>

Lippolis, A., Gezan, S. A., Zuidgeest, J., Cafaro, V., van Dinter, B., Elzes, G., Paulo, M., & Trindade, L. M. (2024). Targeted genotyping (90K-SPET) facilitates genome-wide association studies and the prediction of yield-related traits in faba bean (*Vicia faba* L.). Research Square. <https://doi.org/10.21203/rs.3.rs-4687335/v1>

Liu, X., Wang, H., Hu, X., Li, K., Liu, Z., Wu, Y., & Huang, C. (2019). Improving genomic selection with quantitative trait loci and nonadditive effects revealed by empirical evidence in maize. *Frontiers in Plant Science*, 10, Article 1129. <https://doi.org/10.3389/fpls.2019.01129>

Lohithaswa, H. C., Babu, B. M. S., Sowmya, M., Banakar, S. K., Mallikarjuna, N., Jadesha, G., Mallikarjuna, M. G., Balasundara, D. C., & Anand, P. (2025). Assessment of the potential for genomic selection to improve resistance to fusarium stalk rot in maize. *Frontiers in Plant Science*, 16, Article 1631408. <https://doi.org/10.3389/fpls.2025.1631408>

Lone, A. A., Dar, Z. A., Gull, A., Gazal, A., Naseer, S., Khan, M. H., Ahangar, A. D., & Iqbal, A. (2021). Breeding maize for food and nutritional security. In *IntechOpen eBooks*.

IntechOpen. <https://doi.org/10.5772/intechopen.98741>

Lubanga, N., Massawe, F., & Mayes, S. (2021). Genomic and pedigree-based predictive ability for quality traits in tea (*Camellia sinensis* (L.) O. Kuntze). *Euphytica*, 217(3), Article 47. <https://doi.org/10.1007/s10681-021-02774-3>

Ma, J., & Cao, Y. (2021). Genetic dissection of grain yield of maize and yield-related traits through association mapping and genomic prediction. *Frontiers in Plant Science*, 12, Article 690059. <https://doi.org/10.3389/fpls.2021.690059>

McMillen, M. S., Mahama, A. A., Sibiya, J., Lübberstedt, T., & Suza, W. (2022). Improving drought tolerance in maize: Tools and techniques. *Frontiers in Genetics*, 13, Article 1001001. <https://doi.org/10.3389/fgene.2022.1001001>

Meena, M. R., Appunu, C., Kumar, R., Manimekalai, R., Vasantha, S., Krishnappa,

G., Kumar, R., Pandey-Rai, S., & Hemaprabha, G. (2022). Recent advances in sugarcane genomics, physiology, and phenomics for superior agronomic traits. *Frontiers in Genetics*, 13, Article 854936. <https://doi.org/10.3389/fgene.2022.854936>

Meena, V. K., Shekhawat, H. V. S., Chand, S., Choudhary, K., Sharma, J. K., & Lekha, L. (2023). Advances in molecular marker technology and their significance in plant improvement strategies. In *IntechOpen eBooks*. IntechOpen. <https://doi.org/10.5772/intechopen.1002773>

Mittal, S., Kanika, A., Rao, A. R., Mallikarjuna, M. G., Gupta, H. S., & Thirunavukkarasu, N. (2017). Genomic selection for drought tolerance using genome-wide SNPs in maize. *Frontiers in Plant Science*, 8, Article 550. <https://doi.org/10.3389/fpls.2017.00550>

Nannuru, V. K. R., Dieseth, J. A., Lillemo, M., & Meuwissen, T. H. E. (2024). Evaluating genomic selection and speed breeding for Fusarium head blight resistance in wheat using stochastic simulations. *Research Square*. <https://doi.org/10.21203/rs.3.rs-4257873/v1>

Nguyễn, V. H., Morantte, R. I. Z., Lopena, V., Verdeprado, H., Murori, R., Ndayiragije, A., Katiyar, S., Islam, M. R., Juma, R. U., Flandez-Galvez, H., Glaszmann, J.-C., Cobb, J. N., & Bartholomé, J. (2022). Multi-environment genomic selection in rice elite breeding lines. *Research Square*. <https://doi.org/10.21203/rs.3.rs-2133066/v1>

Nguyễn, V. H., Morantte, R. I. Z., Lopena, V., Verdeprado, H., Murori, R., Ndayiragije, A., Katiyar, S., Islam, M. R., Juma, R. U., Flandez-Galvez, H., Glaszmann, J.-C., Cobb, J. N., & Bartholomé, J. (2023). Multi-environment genomic selection in rice elite breeding lines. *Rice*, 16(1), Article 21. <https://doi.org/10.1186/s12284-023-00623-6>

Osorio, L. F., Gezan, S. A., Verma, S., & Whitaker, V. M. (2021). Independent validation of genomic prediction in strawberry over multiple cycles. *Frontiers in Genetics*, 11, Article 596258. <https://doi.org/10.3389/fgene.2020.596258>

Resende, R. M. S., Resende, M. D. V. de, Alves, R. S., Pessoa-Filho, M., Azevedo, A. L. S., Jones, C. S., Pereira, J. F., & Machado, J. C. (2021). Genomic selection in tropical forage grasses: Current status and future

applications. *Frontiers in Plant Science*, 12, Article 665195. <https://doi.org/10.3389/fpls.2021.665195>

Sandhu, K. S., Mihalyov, P. D., Lewien, M. J., Pumphrey, M., & Carter, A. H. (2021). Combining genomic and phenomic information for predicting grain protein content and grain yield in spring wheat. *Frontiers in Plant Science*, 12, Article 613300. <https://doi.org/10.3389/fpls.2021.613300>

Shamshad, M., & Sharma, A. (2018). The usage of genomic selection strategy in plant breeding. In *IntechOpen eBooks*. IntechOpen. <https://doi.org/10.5772/intechopen.76247>

Singh, V. K., Pundir, S., Chaturvedi, D., Kaur, A., Pandey, A., Mandal, S., Kumar, R., Singh, R., Bhati, H. P., Dhanda, P. S., Yadav, A., Kole, C., & Kaushik, P. (2023). Enhancing maize (*Zea mays* L.) crop through advanced techniques: A comprehensive approach. In *IntechOpen eBooks*. IntechOpen. <https://doi.org/10.5772/intechopen.114029>

Sinha, D., Maurya, A. K., Abdi, G., Majeed, M., Agarwal, R., Mukherjee, R., Ganguly, S., Aziz, R., Bhatia, M., Majgaonkar, A., Seal, S., Das, M., Banerjee, S., Chowdhury, S.,

Adeyemi, S. B., & Chen, J. (2023). Integrated genomic selection for accelerating breeding programs of climate-smart cereals. *Genes*, 14(7), Article 1484. <https://doi.org/10.3390/genes14071484>

Sun, Q., Wang, P., Li, W., Li, W., Lu, S., Yu, Y., Zhao, M., & Meng, Z. (2019). Genomic selection on shelling percentage and other traits for maize. *Breeding Science*, 69(2), 266–274. <https://doi.org/10.1270/jsbbs.18141>

Tadesse, W., Sanchez-Garcia, M., Assefa, S. G., Amri, A., Bishaw, Z., Ogonnaya, F. C., & Baum, M. (2019). Genetic gains in wheat breeding and its role in feeding the world. *Crop Breeding, Genetics and Genomics*, 1(1), e190005. <https://doi.org/10.20900/cbgg20190005>

Tessema, B. B., Liu, H., Sørensen, A. C., Andersen, J. R., & Jensen, J. (2020). Strategies using genomic selection to increase genetic gain in breeding programs for wheat. *Frontiers in Genetics*, 11, Article 578123. <https://doi.org/10.3389/fgene.2020.578123>

Tsai, H., Janss, L., Andersen, J. R., Orabi, J., Jensen, J. D., Jahoor, A., & Jensen, J. (2020). Genomic prediction and GWAS of yield,

quality and disease-related traits in spring barley and winter wheat. *Scientific Reports*, 10(1), Article 3347. <https://doi.org/10.1038/s41598-020-60203-2>

Vahedi, S. M., Ardetani, S. S., Brito, L. F., Karimi, K., Afshari, K. P., & Banabazi, M. H. (2023). Expanding the application of haplotype-based genomic predictions to the wild: A case of antibody response against *Teladorsagia circumcincta* in Soay sheep. *BMC Genomics*, 24(1), Article 299. <https://doi.org/10.1186/s12864-023-09407-0>

Verdal, H. de, Baertschi, C., Frouin, J., Quintero, C., Ospina, Y., Álvarez, M. F., Cao, T., Bartholomé, J., & Grenier, C. (2023). Optimization of multi-generation multi-location genomic prediction models for recurrent genomic selection in an upland rice population. *Rice*, 16(1), Article 41. <https://doi.org/10.1186/s12284-023-00661-0>

Wang, X., Shi, S., Khan, M. Y. A., Zhang, Z., & Zhang, Y. (2024). Improving the accuracy of genomic prediction in dairy cattle using the biologically annotated neural networks framework. *Journal of Animal Science and Biotechnology*, 15(1), Article

97. <https://doi.org/10.1186/s40104-024-01044-1>

Wang, Z., & Cheng, H. (2021). Single-trait and multiple-trait genomic prediction from multi-class Bayesian alphabet models using biological information. *Frontiers in Genetics*, 12, Article 717457. <https://doi.org/10.3389/fgene.2021.717457>

Yan, Q., Fruzangohar, M., Taylor, J., Gong, D., Walter, J., Norman, A., Shi, Q., & Coram, T. E. (2023). Improved genomic prediction using machine learning with variational Bayesian sparsity. *Plant Methods*, 19(1), Article 72. <https://doi.org/10.1186/s13007-023-01073-3>

Zhang, A., Chen, S., Cui, Z., Liu, Y., Guan, Y., Yang, S., Qu, J., Nie, J., Dang, D., Li, C., Dong, X., Fan, J., Zhu, Y., Zhang, X., Crossa, J., Cao, H., Ruan, Y., & Zheng, H. (2021). Genomic prediction of drought tolerance during seedling stage in maize using low-cost markers. *Research Square*. <https://doi.org/10.21203/rs.3.rs-1172460/v1>

Zhang, Y., Zhang, M., Ye, J., Xu, Q., Yue, F., Xu, S., Hu, D., Wei, X., Hu, P., & Yang, Y. (2023). Integrating genome-wide association study into genomic selection for the prediction of agronomic traits in rice (*Oryza*

sativa L.). *Molecular Breeding*, 43(11),
Article 85. <https://doi.org/10.1007/s11032-023-01423-y>

