













Genomic prediction of the performance of tropical doubled haploid maize lines under artificial *Striga hermonthica* (Del.) Benth. infestation

Joan J.C. Kimutai ^{1,2} Dan Makumbi ^{1,*} Juan Burgueño ³ Paulino Pérez-Rodríguez ^{4,*} Jose Crossa ^{3,4}
Manje Gowda ¹ Abebe Menkir ⁵ Angela Pacheco ³ Beatrice E. Ifie ^{2,6} Pangirayi Tongoona ²
Eric Y. Danquah ² Boddupalli M. Prasanna ¹

¹Global Maize Program, International Maize and Wheat Improvement Center (CIMMYT), P.O. Box 1041-00621, Nairobi, Kenya

²West Africa Centre for Crop Improvement (WACCI), University of Ghana, PMB 30 Legon, Accra, Ghana

³Biometrics and Statistics Unit, CIMMYT, Apdo. Postal 6-641, 06600 Mexico DF, Mexico

⁴Socioeconomía, Estadística e Informática, Colegio de Postgraduados, Edo. de México 56230, Montecillos, Mexico

⁵International Institute of Tropical Agriculture (IITA), Oyo Road, PMB 5320, Ibadan, 200001, Nigeria

⁶Institute of Biological, Environmental & Rural Sciences (IBERS), Aberystwyth University, Aberystwyth, SY23 3EE Wales, UK

*Corresponding author: Email: D.Makumbi@cgiar.org; Global Maize Program, International Maize and Wheat Improvement Center (CIMMYT), P.O. Box 1041-00621, Nairobi, Kenya. *Corresponding author: Email: perpdgo@gmail.com; Socioeconomía, Estadística e Informática, Colegio de Postgraduados, Edo. de México 56230, Montecillos, Mexico

Striga hermonthica (Del.) Benth., a parasitic weed, causes substantial yield losses in maize production in sub-Saharan Africa. Breeding for *Striga* resistance in maize is constrained by limited genetic diversity for *Striga* resistance within the elite germplasm and phenotyping capacity under artificial *Striga* infestation. Genomics-enabled approaches have the potential to accelerate identification of *Striga* resistant lines for hybrid development. The objectives of this study were to evaluate the accuracy of genomic selection for traits associated with *Striga* resistance and grain yield (GY) and to predict genetic values of tested and untested doubled haploid maize lines. We genotyped 606 doubled haploid lines with 8,439 rAmpSeq markers. A training set of 116 doubled haploid lines crossed to 2 testers was phenotyped under artificial *Striga* infestation at 3 locations in Kenya. Heritability for *Striga* resistance parameters ranged from 0.38–0.65 while that for GY was 0.54. The prediction accuracies for *Striga* resistance-associated traits across locations, as determined by cross-validation (CV) were 0.24–0.53 for CV0 and from 0.20 to 0.37 for CV2. For GY, the prediction accuracies were 0.59 and 0.56 for CV0 and CV2, respectively. The results revealed 300 doubled haploid lines with desirable genomic estimated breeding values for reduced number of emerged *Striga* plants (STR) at 8, 10, and 12 weeks after planting. The genomic estimated breeding values of doubled haploid lines for *Striga* resistance-associated traits in the training and testing sets were similar in magnitude. These results highlight the potential application of genomic selection in breeding for *Striga* resistance in maize. The integration of genomic-assisted strategies and doubled haploid technology for line development coupled with forward breeding for major adaptive traits will enhance genetic gains in breeding for *Striga* resistance in maize.

Keywords: *Striga*; maize breeding; genomic prediction; doubled haploid; sparse phenotyping

Introduction

Striga hermonthica (Del.) Benth. is a parasitic weed that affects maize (*Zea mays* L.) production in sub-Saharan Africa (SSA). *Striga* spp. has a wide geographical distribution and affects up to 60% of the arable land in the region (Mbuvi *et al.* 2017). The weed adversely affects maize production in SSA causing yield losses ranging from 20–100% (Ransom *et al.* 1990; Berner *et al.* 1996; Khan *et al.* 2006; Ejeta 2007a, 2007b). *Striga* depends entirely on its host for growth and survival. Under favorable growing conditions, *Striga* seeds break dormancy in response to germination stimulants (Strigolactones) produced by the host. A germinated *Striga* plant then establishes vascular connections with the host's roots via the haustoria through which it draws nutrients and water resulting in stunted growth, chlorosis, impaired photosynthesis, reduced maize biomass, and yield loss (Gurney *et al.* 1995; Spallek *et al.* 2013).

Several control strategies have been proposed to reduce the burden of *Striga* for farmers in SSA. These include crop rotation (Oswald and Ransom 2001), intercropping (Khan *et al.* 2002), push-pull technology (Khan *et al.* 2008), host plant resistance (Menkir *et al.* 2007; Rich and Ejeta 2008), herbicide resistant maize (Makumbi *et al.* 2015), and integrated pest management (Khan *et al.* 2016; Kanampiu *et al.* 2018). Host plant resistance is one of the most promising approaches for *Striga* control as the technology is embedded in the seed. Host plant resistance, coupled with other control approaches, is considered an important *Striga* control strategy for smallholder farmers due to its ease of deployment and adoption (Mwangangi *et al.* 2021).

Breeding for *Striga* resistance is hampered by the limited sources of resistance within elite maize germplasm, complex genetics of resistance, complicated host-parasite relationship (Amusan *et al.* 2008), and limited phenotyping capacity.

Received on 31 May 2024; accepted on 31 July 2024

© The Author(s) 2024. Published by Oxford University Press on behalf of The Genetics Society of America.

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

Phenotyping for *Striga* resistance or tolerance requires uniform artificial *Striga* infestation that exposes maize seedlings to a large number of *Striga* seeds to prevent escape (Kim 1996; Kling et al. 1999). Although the artificial *Striga* infestation technique has been successful, breeders are limited by lack of large experimental fields that can solely be dedicated for artificial screening. This can slow progress in identifying resistant inbred lines and hybrids as a limited number of genotypes can be screened at a time. Despite these challenges, significant progress has been made in developing and deploying *Striga* resistant maize varieties in West Africa by the International Institute of Tropical Agriculture (IITA, <https://www.iita.org>) and its partners over the years (Kim et al. 1994; Badu-Apraku et al. 2007; Menkir and Kling 2007; Menkir et al. 2012; Menkir and Meseka 2019). A study by Menkir et al. (2007) showed that the key traits for *Striga* resistance breeding namely grain yield, *Striga* damage rating, and *Striga* counts are conditioned by many genes with small effects. Recurrent selection studies have shown improvements in *Striga* resistance related traits in maize in West Africa (Menkir and Kling 2007; Badu-Apraku et al. 2009; Badu-Apraku 2010). Recent studies reported genetic gains of 93.7 kg ha⁻¹ year⁻¹ (Menkir and Meseka 2019) and 101 kg ha⁻¹ year⁻¹ (Badu-Apraku et al. 2020a) for grain yield under *Striga* infestation. These gains were attributed to significant gains in the reduced number of emerged *Striga* plants and less *Striga* damage. Menkir and Meseka (2019) reported gains of -6.7% and -5.5% year⁻¹ for number of emerged *Striga* plants at 8 and 10 weeks after planting (WAP), respectively. The reported genetic gains are attributed to the use of effective screening protocols (Kim 1994; Kim and Adetimirin 2001), and better understanding of the genetics of *Striga* resistance (Kim 1994; Yallou et al. 2009; Badu-Apraku et al. 2013).

The genetic gains reported in breeding for *Striga* resistance at IITA have been achieved through development of inbred lines using conventional pedigree breeding method and backcrossing. In addition, recurrent selection has been used to accumulate desirable alleles for traits associated with resistance to *Striga* (Badu-Apraku et al. 2007; Menkir and Kling 2007). Developing near-homozygous inbred lines in 6–8 generations through the pedigree method could slow the rate of genetic gain in breeding for resistance to *Striga* in maize. The use of the doubled haploid (DH) technology in maize through which completely homozygous lines can be developed within 13–14 months could significantly reduce the breeding cycle time, and accelerate population and variety development (Bernardo 2009; Chaikam et al. 2019). Application of DH technology for line development for SSA has been implemented at a large scale at CIMMYT since 2012 (Prasanna et al. 2012; Chaikam et al. 2019).

The application of marker assisted selection along with conventional breeding and DH technology can speed up the identification of *Striga* resistant germplasm. Several quantitative trait loci related to *Striga* resistance have been reported (Badu-Apraku et al. 2020b, 2020c, 2023). Genome-wide association studies have identified significant single nucleotide polymorphisms (SNPs) associated with number of emerged *Striga* plants and *Striga* damage rating in tropical maize (Adewale et al. 2020; Stanley et al. 2021; Gowda et al. 2021; Okunlola et al. 2023). Accelerated line and variety development can also be achieved through the incorporation of genomic selection (GS) in a breeding program. The use of DH lines in combination with genomic prediction/selection methods can accelerate genetic improvement in crop plants (Heffner et al. 2010; Song et al. 2017; Cerrudo et al. 2018).

Genomic selection is an approach for improving complex quantitative traits. Genomic selection (Meuwissen et al. 2001) and

genomic prediction of complex traits (de los Campos et al. 2009; Crossa et al. 2010; Pérez-Rodríguez et al. 2012) target breeding value estimates which include the parental average and a deviation resulting from Mendelian sampling (Heffner et al. 2009; Crossa et al. 2017). Genomic prediction has been used to estimate additive as well as nonadditive effects of lines (Crossa et al. 2017; Bonnett et al. 2022). Estimation of additive gene effects allows for selection in early generations such as F₂ (Crossa et al. 2017). Genomic prediction accounts for Mendelian segregation and considers the realized covariances based on dense molecular markers that span the genome (Pérez-Rodríguez et al. 2012). With both marker and phenotypic data, the genetic values of genotypes evaluated in single and across environments are estimated using genomic prediction through genotype by environment (G × E) interaction analyses. Research on crop and animal breeding has shown that prediction accuracy in selection for complex traits using pedigree information can significantly be improved through genomic selection with different models (Crossa et al. 2022).

Multiple genomic prediction models including parametric and nonparametric statistical and computational models that account for both genetic and nongenetic effects have been developed to estimate genomic breeding values (GEBVs) (Crossa et al. 2017). Additionally, linear and nonlinear kernels that are based on genomic relationship matrices have been reported to be better than the conventional methods (Crossa et al. 2022). Nonlinear genomic kernels such as the reaction norm model can account for epistatic effects between markers and incorporate large-scale environmental data (enviromics) and G × E analyses for improved prediction accuracy (Jarquín et al. 2014). The prediction accuracy of the model is assessed through cross-validation after which an appropriate model is used to predict the performance of untested genotypes by estimating their genomic breeding values. The candidate lines are therefore selected based on GEBVs generated from the marker and phenotype information of the training population (Crossa et al. 2017). Only genotypes with the best GEBVs are selected and advanced depending on the trait. Genomic selection can thus accelerate breeding by reducing the duration of line and variety development, while also reducing phenotyping costs in crops like maize (Crossa et al. 2013; Edriss et al. 2017; Beyene et al. 2021; Butoto et al. 2022), and in other crops (Pérez-Rodríguez et al. 2012; Iwata et al. 2015; Velazco et al. 2019).

The use of genomic selection in breeding programs focusing on improving *Striga* resistance for increased genetic gains in grain yield under artificial *Striga* infestation could provide an option to overcome the challenge of limited and costly phenotyping. The International Maize and Wheat Improvement Center (CIMMYT, <https://www.cimmyt.org>) has developed several DH lines using *Striga* resistant maize germplasm from IITA. This germplasm could provide insights on the application of genomic selection for the incorporation of *Striga* resistance in mid-altitude maize germplasm in Eastern and Southern Africa where *S. hermonthica* still presents a major challenge. The objectives of this study were to (1) assess the efficiency of genomic prediction for *Striga* resistance-associated traits and grain yield using the reaction norm model, and (2) predict the genetic values of field tested and untested DH lines.

Materials and methods

Genetic material

This study utilized 606 DH lines developed by CIMMYT at the Maize DH Facility in Kiboko, Kenya (Supplementary Table 1). The DH lines were developed from induction of F₂ and BC₁F₂

populations formed by crossing *Striga* resistant donor lines from IITA with elite mid-altitude tropical maize lines developed by CIMMYT. The *Striga* resistance donor lines from IITA include TZSTR182, TZSTR184, TZISTR1156, TZISTR1158, and TZSTR167. Line TZSTR167 was derived from a yellow composite (TZLCOMP1.Y), whereas lines TZSTR182, TZSTR184, TZISTR1156, and TZSTR1158 were derived from bi-parental crosses of white inbred lines derived from a *Striga* resistant synthetic (ACRSYN-W) and a composite (TZLCOMPIC4). The elite CIMMYT lines (CML521, CML522, and CML543) used for crossing had varying levels of drought tolerance and/or herbicide (imazapyr) resistance. Some F₁ crosses were advanced to F₂ while others were planted alongside either the IITA donor lines or the adapted CIMMYT lines and crossed to form BC₁F₁. The BC₁F₁ were selfed to form BC₁F₂ populations which were then submitted for DH induction. There were 171 and 435 DH lines developed from F₂ and BC₁F₂ populations, respectively. Of the 606 DH lines, 116 lines derived using CML522 (a drought tolerant and herbicide resistant line) as a parent were selected to serve as the training population (TRN) and crossed to 2 inbred line testers from IITA to form 232 testcross hybrids.

Experimental design, test locations, and artificial *Striga* infestation

The 232 testcross (TC) hybrids were part of 351 TC hybrids that were developed from new DH lines and were tested in 2 trials. Trial 1 had 180 entries while Trial 2 had 171 entries. Each trial included 116 TC hybrids from the TRN set. Only 232 TC hybrids were used for this study as only 116 lines had both genotypic and phenotypic data. Trial 1 included 2 internal genetic gain checks and 6 commercial checks while Trial 2 had 2 internal genetic gain checks and 7 commercial checks. The experimental design was 4 × 47 and 4 × 45 alpha-lattice with 2 replications for Trials 1 and 2, respectively. Each experimental unit consisted of one 4 m row spaced 0.75 m apart and 0.20 m space between plants, giving a plant population density of approximately 66,666 plants ha⁻¹ at all locations. The hybrids were evaluated in field trials under artificial *Striga* infestation at the Kenya Agricultural and Livestock Research Organization (KALRO) research stations at Kibos (0°2'S, 34°48'E, 1,193 masl) and Alupe (0°30'N, 34°7'E, 1,250 masl), and at Siaya ATC (03°10'N, 34°17'E, 1,288 masl) in 2020. The soil types are classified as Eutric Cambisol, Orthic Ferralsol, and Plinthic Ferralsol at Kibos, Alupe, and Siaya ATC, respectively. All locations have a bimodal rainfall distribution (March–July and September–November), with most of the rain falling between March and July. The fields used for artificial *Striga* infestation at the research stations had been previously used for imazapyr herbicide studies (Kanampiu et al. 2002, 2018; Makumbi et al. 2015), whose residual toxicity (Alistar and Kogan 2005) kills *Striga* seed in the soil.

To obtain uniform exposure to *Striga* for each genotype, artificial *Striga* infestation was used. *Striga* seed was collected from infested maize fields in the *Striga* infested belt of western Kenya (Gethi et al. 2005). *Striga* inoculum was prepared by thoroughly mixing 10 g of *Striga* seeds, with 5 kg of sand. The *Striga* seed-sand inoculum (20 g) was applied to each planting hole at a depth of 7–10 cm using a calibrated spoon that delivered up to ~3,000 *Striga* seeds to ensure uniform *Striga* infestation in the trials (Makumbi et al. 2015). The *Striga* seed-sand inoculum was placed directly at the bottom of the planting hole for uniform exposure of the maize plants to *Striga* from the onset of germination. Di-ammonium phosphate (DAP, 18:46:0) fertilizer was applied at half the recommended rate (30 kg ha⁻¹) at planting to enhance plant establishment but avoid suppressing *Striga* germination. Half dose (30 kg ha⁻¹) of

calcium ammonium nitrate (CAN, 26%) fertilizer was used for top-dressing at 4 WAP. Standard agronomic and cultural practices were performed as recommended for each location. Hand weeding was carried out to eliminate all weeds except *Striga* plants.

Data collection

Data were recorded on the number of emerged *Striga* plants (STR), *Striga* damage rating (SDR), and ear weight. The number of emerged *Striga* plants per plot was recorded within 15 cm of either side of the row at 8, 10, and 12 WAP. The SDR was recorded at 10 (SDR1) and 12 WAP (SDR2) using a 1–9 rating scale where 1 refers to a healthy plant with no visible symptoms of *Striga* damage (resistant) and 9 is highly susceptible to *Striga* with totally scorched leaves, absent ears, and untimely death of the host plant (Kim 1991; Kim et al. 2002). The area under *Striga* number progress curve (AUSNPC) was computed from the 3 STR plant counts (8, 10, and 10 WAP) following the formula for calculating the area under disease progress curve (AUDPC) (Shaner and Finney 1977) as:

$$\text{AUSNPC} = \sum_{i=1}^n \left(\frac{y_i + y_{i-1}}{2} \right) (t_i - t_{i-1}),$$

where y_i is the number of *Striga* plants at the i th observation, t_i is the time point in days after planting at the i th observation, and n is the total number of observations.

Finally, grain yield expressed in tons per hectare (t ha⁻¹) was computed based on ear weight per plot, assuming 80% shelling percentage and adjusted to 12.5% grain moisture content.

Genotypic data

Leaf samples of the 606 DH inbred lines were collected 3 WAP and shipped to Intertek laboratories in Sweden for DNA extraction. The DNA samples were then forwarded to the Institute for Genomic Diversity, Cornell University (Ithaca, NY, USA) for genotyping with repetitive amplicon sequences (rAmpSeq markers). A genome indexing approach was used for designing primers using the conserved regions of the genome. The repeat amplicons were then multiplexed for genotyping as described by Buckler et al. (2016). The rAmpSeq protocol is a simple cost-effective sequencing technology which uses targeted amplicon sequencing approach and gene specific primers to amplify targeted regions of interest. The DNA library was constructed, mapped to B73 maize reference genome (version 3) and each unique sequence tag was regarded as a dominant marker. The dominant markers were saved in present-absent variant format where one (1) and zero (0) denoted present or absent, respectively. For the 606 DH lines, a total of 8,439 sequence tags were called. The marker quality control (QC) process which involved the exclusion of monomorphic and uninformative markers, markers with minor allele frequencies < 0.05 and those whose variances were equal to 0 was carried out in R Software (R Core Team 2022). After QC, 5,380 high quality rAmpSeq markers were selected for use in genomic prediction.

Statistical analyses

Analysis of variance

Striga count data were tested for normality using the Shapiro-Wilk test before conducting analysis of variance. Analysis of individual trials was carried out using META-R (Alvarado et al. 2020). The best linear unbiased estimates (BLUEs) and the best linear unbiased predictions (BLUPs) were computed by a linear mixed model in which genotype effect was considered as fixed and random, respectively. The BLUEs were used for the genomic prediction

model as input data while the random models were used to evaluate quality of individual trials. All other effects in the model were considered random. The linear mixed model used for single site analysis is as follows:

$$y_{ijk} = \mu + G_i + R_j + B_k(R_j) + \varepsilon_{ijk},$$

where y_{ijk} is the response variable; μ is an intercept; G_i is the effect of the i th genotype; R_j is the effect of j th replicate; $B_k(R_j)$ is the effect of the k th block within the j th replicate; while ε_{ijk} is the experimental error associated with the i th genotype, j th replicate, and k th block. We assumed $\varepsilon \sim \text{NIID}(0, \sigma_\varepsilon^2)$, where NIID is normal independent and identically distributed random variables, σ_ε^2 is the associated variance parameter.

After individual analysis, data were analyzed combined across locations with a linear mixed model using ASReml-R version 4.2 (Butler et al. 2009). From this point, moving forward, the environment is synonymous with location. The linear mixed model fitted for the combined analysis was:

$$y_{ijkl} = \mu + G_i + E_j + R_k(E_j) + B_l(ER)_{jk} + GE_{ij} + \varepsilon_{ijkl},$$

where y_{ijkl} is the response variable; μ is an intercept; G_i is the effect of the i th genotype; E_j is the effect of the j th environment; $R_k(E_j)$ is the effect of the k th replicate in the j th environment; $B_l(ER)_{jk}$ is the effect of the l th block within the k th replicate at the j th environment; GE_{ij} is the effect of the interaction between the i th genotype and the j th environment; while ε_{ijkl} is the experimental error associated with the i th genotype, j th environment, k th replicate, and l th block where the error term is assumed to be normally, identical, and independently distributed (NIID) with mean 0 and homoscedastic variance σ_ε^2 . All effects except μ and E_j were considered random effects.

Broad-sense heritability was estimated for individual and combined environments according to Hallauer et al. (2010). At individual environments, heritability was computed as:

$$H_a^2 = \frac{\sigma_G^2}{\left[\sigma_G^2 + \frac{\sigma_\varepsilon^2}{R} \right]},$$

where H_a^2 is the broad-sense heritability for individual environments, σ_G^2 is the genotypic variance, σ_ε^2 is the variance associated to the error, and R is the number of replications. The heritability across environments was computed as:

$$H_b^2 = \frac{\sigma_G^2}{\left[\sigma_G^2 + \frac{\sigma_{GE}^2}{E} + \frac{\sigma_\varepsilon^2}{E \times R} \right]},$$

where H_b^2 is the broad-sense heritability for combined environments, σ_G^2 is the genotypic variance, σ_{GE}^2 is the variance of the interaction between the genotype and the environment, E is the number of environments, R is the number of replicates, and the σ_ε^2 is the residual variance. BLUPs obtained from the combined phenotypic analysis were used to calculate Pearson's correlation coefficients among the different traits.

Genomic prediction

We computed a genomic relationship matrix (GRM) according to Lopez-Cruz et al. (2015) for use in subsequent analysis. The GRM

was computed as; $\mathbf{G} = \mathbf{M}/p$, where \mathbf{M} is the matrix of markers centered and standardized by column (mean 0 and variance 1 by marker) and p is the number of markers. The objective of genomic prediction was to estimate the number of emerged *Striga* plants, *Striga* damage rating, AUSNPC, and grain yield for lines not evaluated in the field. Given that some of the genotyped lines were evaluated at 3 locations (Kibos, Alupe, and Siaya), we employed the reaction norm model proposed by Jarquín et al. (2014) to predict GEBVs considering the environments, markers and the interaction between genotypes and environments. The BLUEs obtained from phenotypic analysis were used for genomic prediction. The equation for the reaction norm model is:

$$\mathbf{y} = \mathbf{Z}_E \boldsymbol{\beta}_E + \mathbf{Z}_g \mathbf{g} + \mathbf{u} + \mathbf{e},$$

where \mathbf{y} is the BLUEs of the response vector (number of emerged *Striga* plants, *Striga* damage rating, AUSNPC, or grain yield), \mathbf{Z}_E is a design matrix for environments (locations), $\boldsymbol{\beta}_E$ is the vector effect of the environments, $\boldsymbol{\beta}_E \sim \text{MN}(\mathbf{0}, \sigma_E^2 \mathbf{I})$, where MN is multivariate normal distribution, $\mathbf{0}$ is a vector of zeros, σ_E^2 is the variance parameter associated with environments, and \mathbf{I} is the identity matrix; \mathbf{Z}_g is a matrix that connects phenotypes with genotypes, and \mathbf{g} is the vector of random effects of genotypes. We assumed $\mathbf{g} \sim \text{MN}(\mathbf{0}, \sigma_g^2 \mathbf{G})$ with σ_g^2 the variance associated to the genotypes, \mathbf{G} is a genomic relationship matrix (Lopez-Cruz et al. 2015); \mathbf{u} represents the interaction, we assumed $\mathbf{u} \sim \text{MN}(\mathbf{0}, \sigma_{g \times E}^2 \mathbf{Z}_g \mathbf{Z}_g^t \# \mathbf{Z}_E \mathbf{Z}_E^t)$, with $\sigma_{g \times E}^2$ the variance parameter associated to the interaction and $\#$ representing the element-wise product of 2 matrices. Finally, \mathbf{e} represents the error, we assumed $\mathbf{e} \sim \text{MN}(\mathbf{0}, \sigma_e^2 \mathbf{I})$, with σ_e^2 the variance associated to the error. Furthermore, we also assumed that $\boldsymbol{\beta}_E$, \mathbf{g} , \mathbf{u} , and \mathbf{e} are distributed independently. In this study, no environmental variables were considered and therefore the environmental effect corresponds to a dummy location effect. The training set (TRN) consisted of phenotypic data of 116 DH lines evaluated in 232 testcrosses at Kibos, Alupe, and Siaya under artificial *Striga* infestation while the testing set (TST) consisted of the 490 DH lines not evaluated in the field.

Cross-validation

Two cross-validations schemes were used to determine the prediction accuracy of the reaction norm model. Using the reaction norm model (Jarquín et al. 2014), 2 main prediction scenarios were considered: cross-validation 1 (CV1) and cross-validation 2 (CV2) (Burgueño et al. 2012). The CV1 was used to predict the performance of new lines that have not been field screened under artificial *Striga* infestation while CV2 sought to predict the genetic value of the lines in locations in which they have not been tested but were tested in other environments. For the computation of both CV1 and CV2 correlation values, 20% of the lines were considered as the testing set while the remaining 80% were used to train the model in 50-fold cross-validations. The training data set was used to train the model while testing set was used to estimate the model prediction accuracy measured by the Pearson's correlation coefficient between observed and predicted values. For each of the 50 random partitions, prediction accuracy was computed within and across environments (locations) for all traits. The reaction norm model was fitted using the BGLR package in R (Pérez-Rodríguez and de los Campos 2014). Inferences were based on 30,000 iterations with a thin of 10, obtained after discarding the first 15,000 iterations that were taken as burn-in.

To evaluate the prediction accuracy in each environment, a third form of cross-validation (CVO) involving use of phenotypic

data from 2 environments to estimate the prediction accuracy of the model in estimating the performance of lines in the third environment was carried out. The prediction accuracy for each environment was estimated when the phenotypic data in that specific environment was treated as missing values (the testing set) using BGLR (Pérez-Rodríguez and de los Campos 2014).

Results

Analysis of variance and testcross performance

In this study, we used 606 new DH lines of which 116 were crossed to 2 testers to generate 232 testcross hybrids that were phenotyped under artificial *Striga* infested conditions at 3 locations in Kenya. Analysis of variance at individual locations showed

significant variation among hybrids for all traits measured (Table 1). The magnitude of genetic variance for number of emerged *Striga* plants at 10 WAP (STR10WAP) and 12 WAP (STR12WAP) was 8.2 and 16.5 times greater than that for emerged *Striga* plants at 8 WAP (STR8WAP), respectively. Broad-sense heritability was low to moderate for *Striga* resistance parameters (0.23–0.54) and moderate for grain yield (0.31–0.53). Broad-sense heritability for the *Striga* resistance parameters was lower at Siaya compared to the other 2 locations. The mean number of emerged *Striga* plants at 8 WAP was the lowest at Alupe (7), but the same location recorded the highest mean number of emerged *Striga* plants at 10 WAP and 12 WAP (Fig. 1). The *Striga* damage rating (SDR), at 10 WAP, 12 WAP, and the average SDR were highest at Siaya and lowest at Alupe (Fig. 1). The AUSNPC was lowest at Kibos

Table 1. Variance component estimates and heritability for different *Striga* resistance parameters and grain yield at 3 locations under artificial *Striga* infestation in 2020.

Trait	Kibos			Alupe			Siaya		
	σ_G^2	σ_e^2	H_a^2	σ_G^2	σ_e^2	H_a^2	σ_G^2	σ_e^2	H_a^2
STR8WAP	16.75 ^b	63.51	0.35	25.20 ^b	77.05	0.40	16.23 ^b	75.76	0.30
STR10WAP	136.66 ^b	334.54	0.45	133.56 ^b	325.07	0.45	44.14 ^a	303.14	0.23
STR12WAP	275.95 ^b	632.55	0.47	189.14 ^b	408.31	0.48	194.70 ^b	510.89	0.43
SDR1	0.13 ^b	0.37	0.42	0.17 ^b	0.29	0.54	0.20 ^b	1.05	0.28
SDR2	0.19 ^b	0.55	0.41	0.20 ^b	0.49	0.46	0.19 ^b	0.99	0.27
SDR	0.15 ^b	0.38	0.44	0.18 ^b	0.31	0.53	0.19 ^b	0.94	0.29
AUSNPC	1,912.02 ^b	4,475.35	0.46	1,696.94 ^b	3,507.76	0.49	925.27 ^b	3,844.05	0.32
Grain yield	0.45 ^b	1.47	0.38	0.37 ^b	1.61	0.31	1.01 ^b	1.76	0.53

H_a^2 , broad-sense heritability; σ_G^2 , genotypic variance; σ_e^2 , error variance; STR8WAP, emerged *Striga* plants 8 weeks after planting (WAP); STR10WAP, emerged *Striga* plants 10 WAP; STR12WAP, emerged *Striga* plants 12 WAP; SDR1 and 2, *Striga* damage rating at 10 and 12 WAP, respectively; SDR, average *Striga* damage rating; AUSNPC, area under *Striga* number progress curve.

^a Significant at $P < 0.01$.

^b Significant at $P < 0.001$.

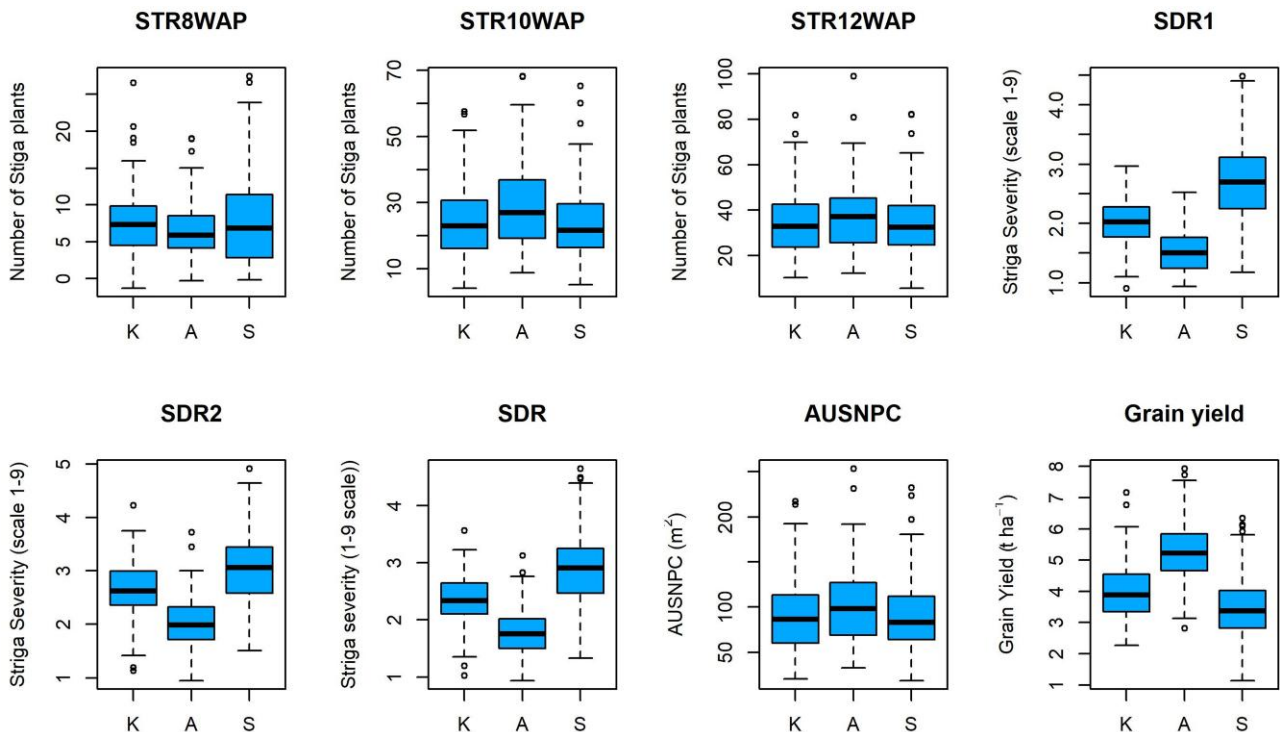


Fig. 1. Boxplots of *Striga* resistance parameters and grain yield at the 3 trial locations in Kenya (K, Kibos; A, Alupe; S, Siaya) in 2020. STR8WAP, emerged *Striga* plants 8 weeks after planting (WAP); STR10WAP, emerged *Striga* plants 10 WAP; STR12WAP, emerged *Striga* plants 12 WAP; SDR1 and 2, *Striga* damage rating at 10 and 12 WAP, respectively; SDR, average *Striga* damage rating; AUSNPC, area under *Striga* number progress curve (m^2).

and Siaya (190 m²). Mean grain yield was highest at Alupe (5.3 t ha⁻¹) and lowest at Siaya (3.3 t ha⁻¹).

Combined analysis of variance under artificial *Striga* infestation revealed highly significant ($P < 0.001$) variation among hybrids for all traits (Table 2). The $G \times E$ interaction was significant for all traits. The σ_G^2 was 3 and 5 times larger than σ_{GE}^2 for STR10WAP and STR12WAP, respectively. Broad-sense heritability was moderate to high for all *Striga* resistance parameters (0.38–0.65) and grain yield (0.54). The number of emerged *Striga* plants ranged from 4 to 126 with a mean of 8, 27, and 39 at 8, 10, and 12 WAP, respectively. The AUSNPC ranged from 59.5 to 331 m² with a mean of 102.2 m² while grain yield across locations ranged from 3.1 to 6.1 t ha⁻¹ with an average of 4.5 t ha⁻¹. Significant positive correlation between the 3 *Striga* resistance parameters was revealed (Fig. 2). The correlations between the number of emerged *Striga* plants at 8, 10, and 12 WAP and AUSNPC were

high ($r = 0.73$ – 0.98). *Striga* damage rating showed significant negative correlation with grain yield ($r = -0.73$ to -0.79).

Prediction accuracy

The 606 DH lines were genotyped with 8,439 markers of which 5,380 high quality rAmpSeq markers were used for the analysis. Three cross-validation (CV) schemes were used to assess the prediction accuracy of the reaction norm model. The CV0 and CV2 were used to determine the prediction accuracy of the model when estimating the performance of previously phenotyped lines in new environments while CV1 was applied when assessing the accuracy of the model when estimating the performance of newly developed lines that have not been tested before. The results indicate moderate prediction accuracies for most traits at Kibos and Alupe (Table 3). For individual locations, Alupe showed better prediction accuracies for most traits across the 3 CV schemes while Siaya

Table 2. Summary statistics, variance component estimates, and heritability for different *Striga* resistance parameters and grain yield across 3 locations under artificial *Striga* infestation in 2020.

Trait	Mean	Range	LSD _{0.05}	σ_G^2	σ_{GE}^2	σ_e^2	H_b^2
STR8WAP	8	4–32	6.3	9.24 ^c	9.94 ^c	72.39	0.38
STR10WAP	27	16–82	14.1	80.02 ^c	22.65 ^b	322.99	0.57
STR12WAP	39	21–126	18.4	181.61 ^c	32.99 ^a	520.38	0.65
SDR1	2.1	1.5–3.9	0.6	0.12 ^c	0.05 ^c	0.57	0.51
SDR2	2.6	1.8–4.4	0.6	0.13 ^c	0.06 ^c	0.68	0.49
SDR	2.3	1.6–4.2	0.5	0.11 ^c	0.05 ^c	0.55	0.51
AUSNPC	102.2	59.5–331.0	50.0	1,182.87 ^c	295.5 ^b	3,966.04	0.61
Grain yield	4.5	3.1–6.1	1.0	0.40 ^c	0.22 ^c	1.61	0.54

H_b^2 , broad-sense heritability; σ_e^2 , error variance; σ_G^2 , genotypic variance; σ_{GE}^2 , genotype by environmental variance; STR8WAP, emerged *Striga* plants 8 weeks after planting (WAP); STR10WAP, emerged *Striga* plants 10 WAP; STR12WAP, emerged *Striga* plants 12 WAP; SDR1 and 2, *Striga* damage rating at 10 and 12 WAP, respectively; SDR, average *Striga* damage rating; AUSNPC, area under *Striga* number progress curve.

^a Significant at $P < 0.05$.

^b Significant at $P < 0.01$.

^c Significant at $P < 0.001$.

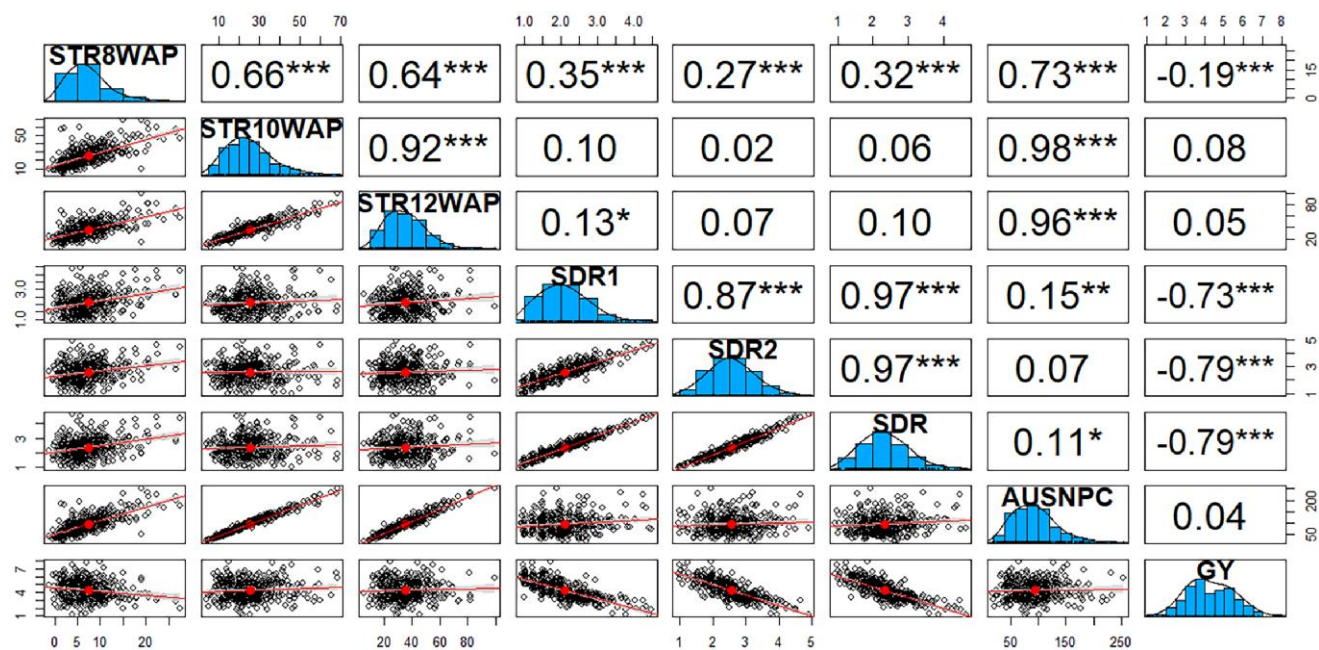
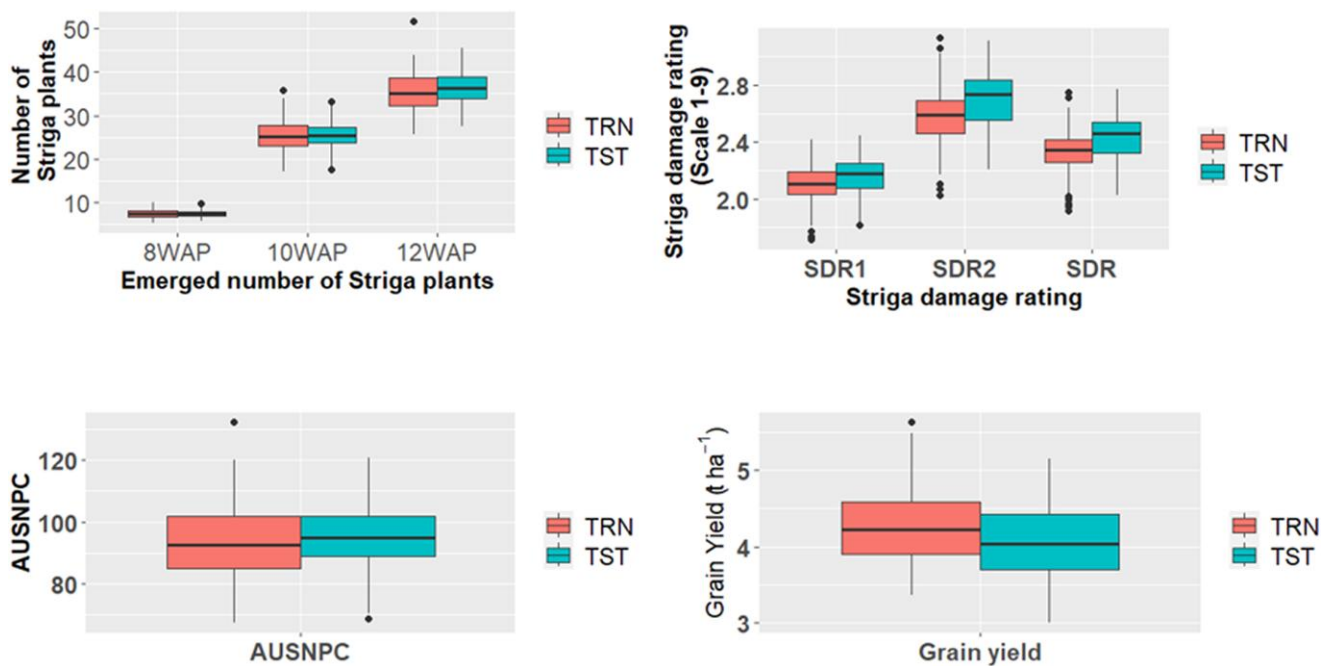


Fig. 2. Pearson's correlation coefficients between different *Striga* resistance parameters and grain yield for testcrosses evaluated under artificial *Striga* infestation across 3 test locations in Kenya (Kibos, Alupe, and Siaya) in 2020. STR8WAP, emerged *Striga* plants 8 weeks after planting (WAP); STR10WAP, emerged *Striga* plants 10 WAP; STR12WAP, emerged *Striga* plants 12 WAP; SDR1 and 2, *Striga* damage rating at 10 and 12 WAP, respectively; SDR, average *Striga* damage rating; AUSNPC, area under *Striga* number progress curve; GY, grain yield.

Table 3. Prediction accuracies for *Striga* resistance parameters and grain yield using 3 cross-validation schemes (CV0, CV1, and CV2) for Kibos, Alupe, and Siaya and across locations under artificial *Striga* infestation.

Trait	CV0				CV1				CV2			
	Kibos	Alupe	Siaya	Across locations (weighted r)	Kibos	Alupe	Siaya	Across locations (weighted r)	Kibos	Alupe	Siaya	Across locations (weighted r)
STR8WAP	0.39	0.43	0.07	0.30	0.35	0.15	0.07	0.19	0.34	0.18	0.08	0.20
STR10WAP	0.37	0.40	0.24	0.34	0.33	0.46	0.10	0.29	0.36	0.56	0.19	0.37
STR12WAP	0.26	0.17	0.30	0.24	0.31	0.43	0.19	0.31	0.31	0.53	0.26	0.37
SDR1	0.29	0.29	0.28	0.29	0.06	0.10	0.00	0.05	0.31	0.28	0.18	0.26
SDR2	0.64	0.59	0.36	0.53	0.01	0.10	0.20	0.10	0.27	0.36	0.35	0.33
SDR	0.35	0.36	0.33	0.35	0.01	0.04	0.13	0.06	0.27	0.28	0.30	0.29
AUSNPC	0.40	0.53	0.25	0.39	0.34	0.43	0.10	0.29	0.38	0.56	0.21	0.38
Grain yield	0.59	0.59	0.59	0.59	0.26	0.30	0.20	0.25	0.63	0.53	0.52	0.56

CV0, cross-validation 0; CV1, cross-validation 1; CV2, cross-validation 2; STR8WAP, emerged *Striga* plants 8 weeks after planting (WAP); STR10WAP, emerged *Striga* plants 10 WAP; STR12WAP, emerged *Striga* plants 12 WAP; SDR1 and 2, *Striga* damage rating at 10 and 12 WAP, respectively; SDR, average *Striga* damage rating; AUSNPC, area under *Striga* number progress curve.

**Fig. 3.** Boxplots of mean GEBVs for *Striga* resistance parameters and grain yield for the training (TRN) and testing (TST) sets across the trial locations. 8WAP, emerged *Striga* plants 8 weeks after planting (WAP); 10WAP, emerged *Striga* plants 10 WAP; 12WAP, emerged *Striga* plants 12 WAP; SDR1 and 2, *Striga* damage rating at 10 and 12 WAP, respectively; SDR, average *Striga* damage rating; AUSNPC, area under *Striga* number progress curve.

had the lowest prediction accuracies for the *Striga* resistance parameters but equal to the highest for grain yield with CV0 (0.59) and similar to Alupe for CV2 (0.52). The prediction accuracies for grain yield were similar for CV0 and CV2 at individual locations. For across location analysis, the predictive accuracy of the model was better for CV0 compared to both CV2 and CV1 for most traits except number of emerged *Striga* plants at 10 and 12 WAP (Table 3). Overall, the prediction accuracy of CV0 (0.24–0.59) and CV2 (0.20–0.56) was higher than that of CV1 (0.05–0.29). Grain yield generally showed better prediction accuracies (CV0 and CV2) across the trial locations compared to the *Striga* resistance parameters.

Genomic estimated breeding values

The GEBVs of the lines in the testing set (TST) were computed from both marker and phenotypic data (BLUEs) of the training set (TRN) using the reaction norm model. The mean GEBVs of *Striga* resistance parameters and grain yield for both the TRN

and TST sets across the 3 trial locations are presented in Fig. 3, and their distribution in Supplementary Fig. 1. The results indicated that there was a close relationship between the GEBVs in TRN and TST sets (Fig. 4). The mean GEBVs were either equal in the TRN and TST sets for STR8WAP and STR10WAP or slightly higher in the TST compared to the TRN for the other traits except grain yield for which the mean of the TST (4.0 t ha^{-1}) was lower than that of the TRN (4.26 t ha^{-1}). The mean GEBV of emerged *Striga* plants ranged from 7.5 for STR8WAP to 35.6 for STR12WAP in the TRN and 7.5 for STR8WAP to 36.4 for STR12WAP in the TST sets (Fig. 3). Results showed that 45, 61, and 63 lines in the TRN had lower GEBVs for STR8WAP, STR10WAP, and STR12WAP, respectively. On the other hand, about 50% of the lines in the TST set had lower emerged *Striga* plants in comparison with the mean at STR8WAP, STR10WAP, and STR12WAP. The mean GEBV for *Striga* damage was 2.1 and 2.6 for SDR1 and SDR2, respectively, in the TRN, while that of

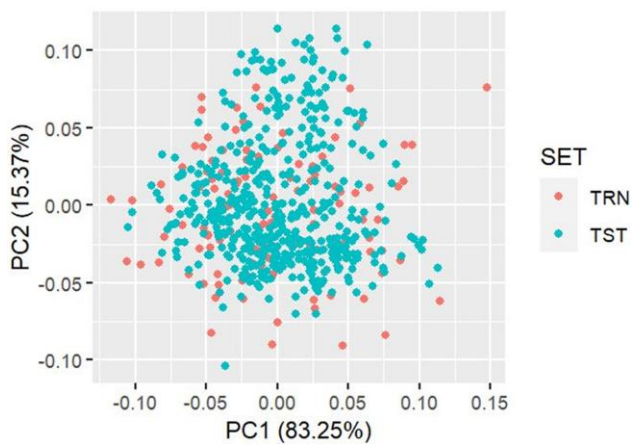


Fig. 4. Principal component analysis of the GEBVs for the TRN and TST sets. The x- and y-axes are the first and the second principal components, respectively. TRN, training population; TST, testing population.

the TST was 2.2 (SDR1) and 2.7 (SDR2) (Fig. 3). The predicted GEBV of SDR ranged from 1.7 (SDR1) to -3.1 (SDR2) for the TRN and 1.8 (SDR1) to -3.1 (SDR2) in the TST. A total of 27 and 144 DH lines showed lower GEBVs for SDR than the mean for the TRN and TST, respectively. In total, 56% (TRN) and 48.4% (TST) of the lines showed smaller AUSNPC than the mean GEBV. Additionally, 50 and 239 lines had higher predicted GY than the mean in the TRN and TST sets, respectively. Of the 606 DH lines, 282, 307, and 313 lines had a lower number of emerged *Striga* plants than the mean GEBVs at 8, 10, and 12 WAP, respectively.

Discussion

Breeding for *Striga* resistance in maize presents a unique challenge owing to the quantitative nature of *Striga* inheritance, narrow genetic base of elite *Striga* resistant germplasm, constrained phenotyping capacity, and high phenotyping costs. Breeding for *Striga* resistance therefore requires multiple approaches including classical breeding, use of molecular markers, and a combination of the 2 approaches to address these challenges. Our objectives were to assess the prediction accuracy of genomic selection in determining the genetic values of tested and untested DH lines under artificial *Striga* infestation.

Phenotypic variation and heritability

The testcrosses in this study were developed from a diverse set of DH lines whose pedigree included *Striga*-susceptible but elite mid-altitude tropical maize lines from CIMMYT and *Striga* resistant donor lines from IITA. The results indicated significant genotype and $G \times E$ interaction for all traits possibly due to differential responses to *Striga* infestation among testcrosses arising from the diverse genetic backgrounds of the lines and differences among the locations used. The differences at the locations could be attributed to climatic and edaphic factors (Menkir et al. 2012; Makumbi et al. 2015). The genetic variance was 9 and 20 times larger at 10 WAP and 12 WAP, respectively, than at 8 WAP which corroborates with results from an earlier study (Gowda et al. 2021). This suggests that there is sufficient variability among these hybrids for *Striga* emergence that can be uncovered at 10 and 12 WAP and to reduce phenotyping costs at 8 WAP. The genetic variance recorded in this study was larger than $G \times E$ variance, similar to the result reported by Menkir and Kling (2007) and Gowda et al. (2021). The observed large genetic variance could arise from the

use of lines containing *Striga* resistant alleles of diverse origins (Menkir 2011; Menkir et al. 2012) and diverse elite mid-altitude lines from CIMMYT. Furthermore, use of DH populations could have contributed to the observed larger genetic variance (Gallais 1990).

The variability observed between the number of emerged *Striga* plants and *Striga* damage rating among locations suggests the likelihood of different *Striga* ecotypes exhibiting variable virulence as well as the effects of different climatic and edaphic factors. Mbuvi et al. (2017) reported significant variability among *Striga* ecotypes at Kibos and Alupe with the ecotypes at Kibos found to be more virulent on sorghum compared to the ecotypes at Alupe. This may explain the low *Striga* damage rating observed at Alupe despite the high number of emerged *Striga* plants recorded at this site. Heritability estimates for most of the *Striga* resistance parameters and grain yield across locations were moderate, suggesting that selection of superior inbred lines with relevant *Striga* resistance traits should be possible. Heritability estimates for *Striga* resistance parameters like emerged *Striga* counts have been variable in several studies, ranging from moderate (Adewale et al. 2020; Gowda et al. 2021; Okunlola et al. 2023) to high (Menkir et al. 2012) based on differences in the germplasm used.

The correlation between the number of emerged *Striga* plants at 10 and 12 WAP and grain yield was low and nonsignificant. This corroborates the findings by Adewale et al. (2020), Stanley et al. (2021), and Okunlola et al. (2023) but is contrary to results by Menkir and Kling (2007) and Gowda et al. (2021). On the other hand, SDR showed significant negative correlations with grain yield, suggesting that SDR is a useful parameter for measuring *Striga* resistance under artificially infested conditions and could be used to select inbred lines combining lower *Striga* damage and higher grain yield. Correlations between 2 traits may be due to pleiotropy, linkage, or both, amount of linkage disequilibrium, and the effect of the environment. The low correlation between grain yield and number of emerged *Striga* plants at 10 and 12 WAP suggests a lack of linkage between genes controlling these traits. Parents of the inbred lines used in the present study show significant negative correlation between SDR and STR, and between grain yield and SDR, and STR under *Striga* infestation. It is possible that the lines derived from crosses between IITA and CIMMYT lines may not carry all the favorable alleles derived from the parental lines leading to weak correlation among these traits. Selection-induced changes can modify the genetic correlation between traits either by altering the pattern of polymorphism at loci with pleiotropic effects or by changing the linkage disequilibrium among closely linked loci (Lande 1984). While these correlations are useful, more detailed investigations should focus on genetic correlations between various *Striga* resistance parameters and grain yield based on a larger data set (multiple environments and seasons), as these provide the breeder with a better understanding of the relationship among traits (pleiotropy or linkage) and could have implications for application of indirect selection in a breeding program.

Genomic prediction

Genotype \times environment interactions significantly influence phenotypic performance and ultimate selection potential in crops (Des Marais et al. 2013). We used the reaction norm model which considers the epistatic effects resulting from various interactions among genotypes, markers, and the environment to estimate an individual's phenotype or its performance in new environments

(Jarquín *et al.* 2014). Prediction of genetic values of lines in environments in which they were not tested (CV0 and CV2) resulted in low to moderate prediction accuracy. This suggests that estimation of the GEBVs of lines in new environments is possible for *Striga* resistance parameters and grain yield. This kind of genetic value prediction is akin to sparse testing due to the use of information on the performance of lines in correlated environments (Burgueño *et al.* 2012; Mageto *et al.* 2020). This is attributed to the ability of the reaction norm model to leverage information from relatives resulting from the interaction of genotypes within and across environments and correlated environments (Burgueño *et al.* 2012). The prediction accuracy for CV0, CV1, and CV2 for *Striga* resistance parameters obtained in this study was lower than that reported by Gowda *et al.* (2021). However, our results indicate 14–19% better prediction accuracy for grain yield compared to Gowda *et al.* (2021) for the 3 CV schemes. These differences in results may be due to the complexity of *Striga* resistance, besides the differences in germplasm and prediction models used. The prediction accuracy was relatively low with the application of GS to newly developed lines (CV1). A similar finding was reported by Gowda *et al.* (2021) for *Striga* resistance in maize and by Semagn *et al.* (2022) for multiple disease resistance in wheat. The low prediction accuracy with CV1 is attributed to its reliance on the phenotypic values and genetic relationships of other lines (Burgueño *et al.* 2012; Mageto *et al.* 2020).

The predictive power of genetic models is significantly affected by low trait heritability (Liu *et al.* 2018). The relatively low to moderate prediction accuracy observed for *Striga* resistance parameters in this study was possibly due to the low trait heritability and relatively small training population size (Heffner *et al.* 2011; Ornela *et al.* 2012). The moderate heritability for most traits may partly explain the low to moderate prediction accuracies recorded for *Striga* resistance parameters in this study. A positive correlation between high trait heritability and high prediction accuracy was reported for kernel zinc concentration in maize (Mageto *et al.* 2020). The limited TRN size was due to the limited area available for artificial *Striga* screening, which in turn limited the number of testcrosses that could be evaluated in the field. A large TRN set is important for increased prediction accuracy (Lorenz *et al.* 2012; Gowda *et al.* 2015; Beyene *et al.* 2019). However, the level of prediction accuracy achieved in this study should still allow for application of GS by removing lines with the least favorable GEBVs for key *Striga* resistance traits before testcrossing (Edriss *et al.* 2017). The moderate prediction accuracies for some traits could be attributed to the close relationship between the TRN and TST sets as well as the model used (Jarquín *et al.* 2017; Brandariz and Bernardo 2019). In this study, we identified 300 lines with desirable GEBVs for fewer emerged *Striga* plants at 10 and 12 WAP. These lines putatively have good alleles that could reduce *Striga* emergence in maize. These lines should be tested in hybrid combinations under artificial *Striga* infestation and optimal conditions to identify the most suitable lines combining *Striga* resistance and other adaptive traits. Selection of genotypes that support a reduced number of emerged *Striga* plants should help in curtailing the replenishment of the *Striga* seed bank in the soil.

Prospects in breeding for resistance to *Striga*

Breeding for *Striga* resistance is one of the strategies that can be used to increase maize grain yield while also contributing to reduced *Striga* seed bank in the soil in *Striga* affected regions in SSA. Maize breeding programs targeting *Striga* resistance are faced with a multitude of challenges which could be overcome by a

combination of conventional and molecular technologies. With advances in genomic approaches and lower genotyping costs, the integration of classical and genomic-assisted breeding strategies has the potential to address some of the limitations of breeding for *Striga* resistance to enhance genetic gains. The application of genomic selection for the improvement of complex traits in tropical maize has been documented (Crossa *et al.* 2010; Vivek *et al.* 2017; Beyene *et al.* 2019, 2021). The application of DH technology for efficient inbred line development (Prasanna *et al.* 2012; Chaikam *et al.* 2019) could be used to unravel larger genetic variability for selection efficiency. The application of forward breeding for key diseases such as maize lethal necrosis (MLN) and maize streak virus (MSV) for new DH lines should reduce the number of DH lines to be phenotyped under artificial *Striga* infestation and hence reduce phenotyping costs (Prasanna *et al.* 2021).

Our results show that there is potential to implement GS in breeding for *Striga* resistance in maize. The application of GS in breeding for *Striga* resistance should be integrated with the use of DH lines, and application of sparse phenotyping. Sparse testing has been reported to improve the efficiency of GS through optimal resource utilization and enhancement of prediction accuracy (Jarquín *et al.* 2020; Montesinos-López *et al.* 2023b). The use of sparse testing and GS in selection for target traits has been reported in wheat and maize (Jarquín *et al.* 2020; Atanda *et al.* 2022). The application of sparse testing and GS in breeding for *Striga* resistance requires optimization of the TRN set. Montesinos-López *et al.* (2023a) suggested that the optimization of TRN populations in GS can be enhanced through appropriate prediction models and experimental designs in sparse testing. Therefore, detailed investigations on TRN size under *Striga* infestation may be necessary before scaling the application of GS in maize *Striga* resistance breeding programs. By leveraging genomic relationships and tapping into hidden replicated alleles, genomic prediction offers the benefits of more accurate predictions and effective reduction of the high costs associated with phenotyping of large sets of individuals (Vivek *et al.* 2017; Wang *et al.* 2020). Integration of several genomics-enabled techniques including use of environmental data (Jarquín *et al.* 2014; Jarquín *et al.* 2020; Crossa *et al.* 2022) should assist in achieving better genetic gains for reduced *Striga* infestation and higher grain yield under *Striga* infestation. While the application of modern breeding techniques can lead to higher genetic gains in breeding for *Striga* resistance, part of the solution to the problem of *Striga* in Africa will be integrated *Striga* management that encompasses multiple control strategies to obtain maize yield sustainability. Stacking multiple stress tolerance in addition to *Striga* tolerance (e.g. Menkir *et al.* 2020) should improve maize productivity in the *Striga* affected agroecologies in SSA.

Conclusions

Genomic-enabled selection can be an important tool in improving the efficiency of breeding for *Striga* resistance in maize. Using the reaction norm model with 2 cross-validation schemes (CV0 and CV2), our findings reveal moderate prediction accuracies for 3 key *Striga* resistance traits (STR10WAP, STR12WAP, and AUSNPC) and grain yield (GY) at 2 out of the 3 locations under artificial *Striga* infestation. The reaction norm model sufficiently modeled the interactions among genotypes, environments, markers, and G × E effects, to obtain accurate GEBVs. This study revealed a close relationship between the GEBVs across the TRN and TST sets for key *Striga* resistance traits, with 300 DH inbred lines displaying favorable GEBVs for these parameters. These results suggest that application of genomic-enabled strategies can

facilitate improvements in *Striga* resistance in maize. These results provide a foundational framework for the potential integration of GS in breeding for *Striga* resistance in maize across sub-Saharan Africa. Future research should focus on optimizing the training population size for large-scale application of GS and testing a combination of GS and sparse phenotyping approaches in field evaluation of lines and hybrids for resistance to *Striga* under artificial infestation conditions.

Data availability

Supplementary data are available.

- **Supplementary Table 1**—Pedigrees of DH lines in GS study gives the list and pedigrees of DH lines used in the study.
- **Supplementary Fig. 1** shows the distribution of the GEBVs for the number of emerged *Striga* plants for the training and testing populations.
- The phenotypic and marker data are freely available from CIMMYT's Dataverse (<https://hdl.handle.net/11529/10549033>).
- File named Phenotypic_Data.CSV contains phenotypic data from 232 testcross (TC) hybrids.
- File named GS_Marker_Data.CSV contains genotypic data for 606 doubled haploid (DH) lines.

Supplemental material available at G3 online.

Acknowledgments

The authors would like to thank Carolyn Adhiambo, Etyang Kizito, and George Ouma at CIMMYT's station at Kibos, and Patricia Onyango at KALRO-Alupe Research Center in Kenya for their assistance with trial management and data collection. We gratefully thank Dr. Fred Kanampiu for comments on this paper. We thank the anonymous reviewers for the comments that improved the quality of this paper.

Funding

The research was supported by the Bill and Melinda Gates Foundation (BMGF), the Foundation for Food and Agriculture Research (FFAR), and the United States Agency for International Development (USAID) through the project Accelerating Genetic Gains in Maize and Wheat (AGG) for Improved Livelihoods (INV-003439), and by the Bill and Melinda Gates Foundation through the project "Achieving Sustainable *Striga* Control for Poor Farmers in Africa" (grant ID #OPP1006185).

Conflicts of interest

The author(s) declare no conflicts of interest.

Author contributions

JJCK: investigation; data curation; formal analysis; writing—original draft; writing—review and editing. DM: conceptualization; investigation; data curation; supervision; writing—review and editing. JB: formal analysis; methodology; software; writing—review and editing. PP-R: formal analysis; methodology; software; writing—review and editing. JC: formal analysis; methodology; writing—review and editing. AP: formal analysis; methodology; writing—review and editing. MG: investigation; data curation; validation; writing—review and editing. AM: investigation; writing—review and editing. BEI: supervision; writing—review and editing. PT: supervision; writing—review and editing. EYD: supervision;

writing—review and editing. BMP: funding acquisition; writing—review and editing.

Literature cited

- Adele SA, Badu-Apraku B, Akinwale RO, Paterne AA, Gedil M, Garcia-Oliveira AL. 2020. Genome-wide association study of *Striga* resistance in early maturing white tropical maize inbred lines. *BMC Plant Biol.* 20(1):1–16. doi:10.1186/s12870-020-02360-0.
- Alister C, Kogan M. 2005. Efficacy of imidazolinone herbicides applied to imidazolinone resistant maize and their carryover effect on rotational crops. *Crop Prot.* 24(4):375–379. doi:10.1016/j.cropro.2004.09.011.
- Alvarado G, Rodríguez FM, Pacheco A, Burgueño J, Crossa J, Vargas M, Pérez-Rodríguez P, López-Cruz MA. 2020. META-R: a software to analyze data from multi-environment plant breeding trials. *Crop J.* 8(5):745–756. doi:10.1016/j.cj.2020.03.010.
- Amusan IO, Rich PJ, Menkir A, Housley T, Ejeta G. 2008. Resistance to *Striga hermonthica* in a maize inbred line derived from *Zea diploperennis*. *New Phytol.* 178(1):157–166. doi:10.1111/j.1469-8137.2007.02355.x.
- Atanda SA, Govindan V, Singh R, Robbins KR, Crossa J, Bentley AR. 2022. Sparse testing using genomic prediction improves selection for breeding targets in elite spring wheat. *Theor Appl Genet.* 135(6):1939–1950. doi:10.1007/s00122-022-04085-0.
- Badu-Apraku B. 2010. Effects of recurrent selection for grain yield and *Striga* resistance in an extra-early maize population. *Crop Sci.* 50(5):1735–1743. doi:10.2135/cropsci2009.09.0523.
- Badu-Apraku B, Adele S, Paterne A, Gedil M, Asiedu R. 2020b. Identification of QTLs controlling resistance/tolerance to *Striga hermonthica* in an extra-early maturing yellow maize population. *Agronomy.* 10(8):1168. doi:10.3390/agronomy10081168.
- Badu-Apraku B, Adele S, Paterne AA, Gedil M, Toyinbo J, Asiedu R. 2020c. Identification of QTLs for grain yield and other traits in tropical maize under *Striga* infestation. *PLoS One.* 15(9): e0239205. doi:10.1371/journal.pone.0239205.
- Badu-Apraku B, Adele S, Paterne A, Offonredo Q, Gedil M. 2023. Mapping quantitative trait loci and predicting candidate genes for *Striga* resistance in maize using resistance donor line derived from *Zea diploperennis*. *Front Genet.* 14:1012460. doi:10.3389/fgene.2023.1012460.
- Badu-Apraku B, Adu GB, Yacoubou AM, Toyinbo J, Adele S. 2020a. Gains in genetic enhancement of early maturing maize hybrids developed during three breeding periods under *Striga*-infested and *Striga*-free environments. *Agronomy.* 10(8):1188. doi:10.3390/agronomy10081188.
- Badu-Apraku B, Fakorede MAB, Lum AF. 2007. Evaluation of experimental varieties from recurrent selection for *Striga* resistance in two extra-early maize populations in the savannas of West and Central Africa. *Exp Agric.* 43(2):183–200. doi:10.1017/S0014479706004601.
- Badu-Apraku B, Fakorede MAB, Menkir A. 2009. Recurrent selection for *Striga* resistance in early and extra-early maize populations in West Africa. *Afr Crop Sci Conf Proc.* 9:415–424.
- Badu-Apraku B, Oyekunle M, Akinwale RO, Aderonmu M. 2013. Combining ability and genetic diversity of extra-early white maize inbreds under stress and nonstress environments. *Crop Sci.* 53(1):9–26. doi:10.2135/cropsci2012.06.0381.
- Bernardo R. 2009. Should maize doubled haploids be induced among F₁ or F₂ plants? *Theor Appl Genet.* 119(2):255–262. doi:10.1007/s00122-009-1034-1.

- Berner D, Carsky R, Dashiell K, Kling J, Manyong V. 1996. A land management-based approach to integrated *Striga hermonthica* control in sub-Saharan Africa. *Outlook Agric.* 25(3):157–164. doi:10.1177/003072709602500304.
- Beyene Y, Gowda M, Olsen MS, Robbins KR, Pérez-Rodríguez P, Alvarado G, Dreher K, Gao SY, Mugo S, Prasanna BM. 2019. Empirical comparison of tropical maize hybrids selected through genomic and phenotypic selections. *Front Plant Sci.* 10:1502. doi:10.3389/fpls.2019.01502.
- Beyene Y, Gowda M, Pérez-Rodríguez P, Olsen M, Robbins KR, Burgueño J, Prasanna BM, Crossa J. 2021. Application of genomic selection at the early stage of breeding pipeline in tropical maize. *Front Plant Sci.* 12:685488. doi:10.3389/fpls.2021.685488.
- Bonnett D, Li Y, Crossa J, Dreisigacker S, Basnet B, Pérez-Rodríguez P, Alvarado G, Jannink JL, Poland J, Sorrells M. 2022. Response to early generation genomic selection for yield in wheat. *Front Plant Sci.* 12:718611. doi:10.3389/fpls.2021.718611.
- Brandariz SP, Bernardo R. 2019. Small ad hoc versus large general training populations for genome-wide selection in maize biparental crosses. *Theor Appl Genet.* 132(2):347–353. doi:10.1007/s00122-018-3222-3.
- Buckler ES, Ilut DC, Wang X, Kretschmar T, Gore M, Mitchell SE. 2016. rAmpSeq: using repetitive sequences for robust genotyping. bioRxiv 096628. <https://doi.org/10.1101/096628>, preprint: not peer reviewed.
- Burgueño J, de los Campos G, Weigel K, Cross J. 2012. Genomic prediction of breeding values when modeling genotype × environment interaction using pedigree and dense molecular markers. *Crop Sci.* 52(2):707–719. doi:10.2135/cropsci2011.06.0299.
- Butler DG, Cullis BR, Gilmour AR, Gogel BJ. 2009. ASReml-R Reference Manual. Brisbane: The State of Queensland, Department of Primary Industries and Fisheries.
- Butoto EN, Brewer JC, Holland JB. 2022. Empirical comparison of genomic and phenotypic selection for resistance to Fusarium ear rot and fumonisin contamination in maize. *Theor Appl Genet.* 135(8):2799–2816. doi:10.1007/s00122-022-04150-8.
- Cerrudo D, Cao S, Yuan Y, Martine C, Suarez EA, 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. *Front Plant Sci.* 9:366. doi:10.3389/fpls.2018.00366.
- Chaikam V, Molenaar W, Melchinger AE, Prasanna BM. 2019. Doubled haploid technology for line development in maize: technical advances and prospects. *Theor Appl Genet.* 132(12):3227–3243. doi:10.1007/s00122-019-03433-x.
- Crossa J, Beyene Y, Kassa S, Pérez P, Hickey JM, Chen C, de los Campos G, Burgueño J, Windhausen VS, Buckler E, et al. 2013. Genomic prediction in maize breeding populations with genotyping-by-sequencing. *G3 (Bethesda).* 3(11):1903–1926. doi:10.1534/g3.113.008227.
- Crossa J, de los Campos GDL, Pérez P, Gianola D, Burgueño J, Araus JL, Makumbi D, Singh RP, Dreisigacker S, Yan J, et al. 2010. Prediction of genetic values of quantitative traits in plant breeding using pedigree and molecular markers. *Genetics.* 186(2):713–724. doi:10.1534/genetics.110.118521.
- Crossa J, Montesinos-López O, Pérez-Rodríguez P, Costa-Neto G, Fritsche-Neto R, Ortiz R, Martini JW, Lillemo M, Montesinos-López A, Jarquín D, et al. 2022. Genome and environment based prediction models and methods of complex traits incorporating genotype × environment interaction. In: Ahmadi N, Bartholomé J, editors. *Genomic Prediction of Complex Traits. Methods in Molecular Biology*, Vol. 2467. New York (NY): Humana. p. 245–283. https://doi.org/10.1007/978-1-0716-2205-6_9.
- Crossa J, Pérez-Rodríguez P, Cuevas J, Montesinos-López O, Jarquín D, de los Campos G, Burgueño J, González-Camacho JM, Pérez-Elizalde S, Beyene Y, et al. 2017. Genomic selection in plant breeding: methods, models, and perspectives. *Trends Plant Sci.* 22(11):961–975. doi:10.1016/j.tplants.2017.08.011.
- de los Campos G, Naya H, Gianola D, Crossa J, Legarra A, Manfredi E, Weigel K, Cotes JM. 2009. Predicting quantitative traits with regression models for dense molecular markers and pedigree. *Genetics.* 182(1):375–385. doi:10.1534/genetics.109.101501.
- Des Marais DL, Hernandez KM, Juenger TE. 2013. Genotype-by-environment interaction and plasticity: exploring genomic responses of plants to the abiotic environment. *Ann Rev Ecol Evol Syst.* 44(1):5–29. doi:10.1146/annurev-ecolsys-110512-135806.
- Edriss V, Gao Y, Zhang X, Jumbo MB, Makumbi D, Olsen MS, Crossa J, Packard KC, Jannink JL. 2017. Genomic prediction in a large African maize population. *Crop Sci.* 57(5):2361–2371. doi:10.2135/cropsci2016.08.0715.
- Ejeta G. 2007a. Breeding for *Striga* resistance in sorghum: exploitation of an intricate host–parasite biology. *Crop Sci.* 47(S3):S216–S227. doi:10.2135/cropsci2007.04.0011IPBS.
- Ejeta G. 2007b. The *Striga* scourge in Africa: a growing pandemic. In: Ejeta G, Gressel J, editors. *Integrating New Technologies for Striga Control: Towards Ending the Witch-Hunt*. Singapore: World Scientific Publishing Co Pte Ltd. p. 3–16.
- Gallais A. 1990. Quantitative genetics of doubled haploid populations and application to the theory of line development. *Genetics.* 124(1):199–206. doi:10.1093/genetics/124.1.199.
- Gethi JG, Smith ME, Mitchell SE, Kresovich S. 2005. Genetic diversity of *Striga hermonthica* and *Striga asiatica* populations in Kenya. *Weed Res.* 45(1):64–73. doi:10.1111/j.1365-3180.2004.00432.x.
- Gowda M, Das B, Makumbi D, Babu R, Semagn K, Mahuku G, Olsen MS, Bright JM, Beyene Y, Prasanna BM. 2015. Genome-wide association and genomic prediction of resistance to maize lethal necrosis disease in tropical maize germplasm. *Theor Appl Genet.* 128(10):1957–1968. doi:10.1007/s00122-015-2559-0.
- Gowda M, Makumbi D, Das B, Nyaga C, Kosgei T, Crossa J, Beyene Y, Montesinos-López OA, Olsen MS, Prasanna BM. 2021. Genetic dissection of *Striga hermonthica* (Del.) Benth. Resistance via genome-wide association and genomic prediction in tropical maize germplasm. *Theor Appl Genet.* 134(3):941–958. doi:10.1007/s00122-020-03744-4.
- Gurney AL, Press MC, Ransom JK. 1995. The parasitic angiosperm *Striga hermonthica* can reduce photosynthesis of its sorghum and maize hosts in the field. *J Exp Bot.* 46(12):1817–1823. doi:10.1093/jxb/46.12.1817.
- Hallauer AR, Carena MJ, Miranda Filho JB. 2010. *Quantitative Genetics in Maize Breeding*. New York: Springer Science and Business Media.
- Heffner EL, Jannink JL, Sorrells ME. 2011. Genomic selection accuracy using multifamily prediction models in a wheat breeding program. *Plant Genome.* 4(1):65–75. doi:10.3835/plantgenome.2010.12.0029.
- Heffner EL, Lorenz AJ, Jannink JL, Sorrells ME. 2010. Plant breeding with genomic selection: gain per unit time and cost. *Crop Sci.* 50(5):1681–1690. doi:10.2135/cropsci2009.11.0662.
- Heffner EL, Sorrells ME, Jannink JL. 2009. Genomic selection for crop improvement. *Crop Sci.* 49(1):1–12. doi:10.2135/cropsci2008.08.0512.
- Iwata H, Ebana K, Uga Y, Hayashi T. 2015. Genomic prediction of biological shape: elliptic Fourier analysis and kernel partial least squares PLS regression applied to grain shape prediction in rice

- Oryza sativa* L. PLoS One. 10(3):e0120610. doi:10.1371/journal.pone.0120610.
- Jarquín D, Crossa J, Lacaze X, Du Cheyron P, Daucourt J, Lorgeou J, Piraux F, Guerreiro L, Pérez P, Calus M, et al. 2014. A reaction norm model for genomic selection using high-dimensional genomic and environmental data. *Theor Appl Genet.* 127(3): 595–607. doi:10.1007/s00122-013-2243-1.
- Jarquín D, Howard R, Crossa J, Beyene Y, Gowda M, Martini JW, Covarrubias-Pazaran G, Burgueño J, Pacheco A, Grondona M, et al. 2020. Genomic prediction enhanced sparse testing for multi-environment trials. *G3 (Bethesda).* 10(8):2725–2739. doi:10.1534/g3.120.401349.
- Jarquín D, Lemes da Silva C, Gaynor RC, Poland J, Fritz A, Howard R, Battenfield S, Crossa J. 2017. Increasing genomic-enabled prediction accuracy by modeling genotype × environment interactions in Kansas wheat. *Plant Genome.* 10(2):1–15. doi:10.3835/plantgenome2016.12.0130.
- Kanampiu F, Makumbi D, Mageto E, Omanyua G, Waruingi S, Musyoka P, Ransom J. 2018. Assessment of management options on *Striga* infestation and maize grain yield in Kenya. *Weed Sci.* 66(4): 516–524. doi:10.1017/wsc.2018.4.
- Kanampiu FK, Ransom JK, Friesen D, Gressel J. 2002. Imazapyr and pyriithiobac movement in soil and from maize seed coats controls *Striga* while allowing legume intercropping. *Crop Prot.* 21(8): 611–619. doi:10.1016/S0261-2194(01)00151-X.
- Khan ZR, Hassanali A, Overholt W, Khamis TM, Hooper AM, Pickett JA, Wadhams LJ, Woodcock CM. 2002. Control of witchweed *Striga hermonthica* by intercropping with *Desmodium* spp, and the mechanism defined as allelopathic. *J Chem Ecol.* 28(9): 1871–1885. doi:10.1023/A:1020525521180.
- Khan ZR, Midega CA, Amudavi DM, Hassanali A, Pickett JA. 2008. On-farm evaluation of the ‘push–pull’ technology for the control of stemborers and *Striga* weed on maize in western Kenya. *Field Crops Res.* 106(3):224–233. doi:10.1016/j.fcr.2007.12.002.
- Khan Z, Midega CA, Hooper A, Pickett J. 2016. Push–pull: chemical ecology-based integrated pest management technology. *J Chem Ecol.* 42(7):689–697. doi:10.1007/s10886-016-0730-y.
- Khan ZR, Pickett JA, Wadhams LJ, Hassanali A, Midega CA. 2006. Combined control of *Striga hermonthica* and stemborers by maize–*Desmodium* spp intercrops. *Crop Prot.* 25(9):989–995. doi:10.1016/j.cropro.2006.01.008.
- Kim SK. 1991. Breeding maize for *Striga* tolerance and the development of a field infestation technique. In: Kim SK editor. *Combating Striga in Africa.* Proc Int Workshop by IITA, ICRISAT, and IDRC Ibadan, Nigeria, 22–24 August 1998, IITA, Ibadan. 96–108.
- Kim SK. 1994. Genetics of maize tolerance of *Striga hermonthica*. *Crop Sci.* 34(4):900–907. doi:10.2135/cropsci1994.0011183X003400040012x.
- Kim SK. 1996. Horizontal resistance: core to a research breakthrough to combat *Striga* in Africa. *Int Pest Manag Rev.* 1(4):229–249. doi:10.1007/BF00139766.
- Kim SK, Adetimirin VO. 2001. Conditioning effects of *Striga hermonthica* seed on field performance of maize. *Crop Prot.* 20(2):159–161. doi:10.1016/S0261-2194(00)00053-3.
- Kim SK, Adetimirin VO, The C, Dossou R. 2002. Yield losses in maize due to *Striga hermonthica* in West and Central Africa. *Int J Pest Manag.* 483(3):211–217. doi:10.1080/09670870110117408.
- Kim SK, Akintunde AY, Walker P. 1994. Responses of maize, sorghum and millet host plants to infestation by *Striga hermonthica*. *Crop Prot.* 13(8):582–590. doi:10.1016/0261-2194(94)90003-5.
- Kling JG, Menkir A, Ajala SO, Quin KM. 1999. Potential for molecular breeding of maize at IITA. In: *DNA Marker-Assisted Improvement of the Staple Crops of Sub-Saharan Africa: Proceedings of the Workshop on DNA Markers at IITA Held by the Crop Improvement Division, IITA, Ibadan, Nigeria, 21–22 August 1996.* p. 124 IITA.
- Lande R. 1984. The genetic correlation between characters maintained by selection, linkage and inbreeding. *Genet Res.* 44(3): 309–320. doi:10.1017/S0016672300026549.
- Liu X, Wang H, Wang H, Guo Z, Xu X, Liu J, Wang S, Li WX, Zou C, Prasanna BM, et al. 2018. Factors affecting genomic selection revealed by empirical evidence in maize. *Crop J.* 6(4):341–352. doi:10.1016/j.cj.2018.03.005.
- Lopez-Cruz M, Crossa J, Bonnett D, Dreisigacker S, Poland J, Jannink L, Singh RP, Autrique E, de los Campos G. 2015. Increased prediction accuracy in wheat breeding trials using a marker × environment interaction genomic selection model. *G3 (Bethesda).* 5(4): 569–582. doi:10.1534/g3.114.016097.
- Lorenz AJ, Smith KP, Jannink JL. 2012. Potential and optimization of genomic selection for Fusarium head blight resistance in six-row barley. *Crop Sci.* 52(4):1609–1621. doi:10.2135/cropsci2011.09.0503.
- Mageto EK, Crossa J, Pérez-Rodríguez P, Dhliwayo T, Palacios-Rojas N, Lee M, Guo R, San Vicente F, Zhang X, Hindu V. 2020. Genomic prediction with genotype by environment interaction analysis for kernel zinc concentration in tropical maize germplasm. *G3 (Bethesda).* 10(8):2629–2639. doi:10.1534/g3.120.401172.
- Makumbi D, Diallo A, Kanampiu F, Mugo S, Karaya H. 2015. Agronomic performance and genotype × environment interaction of herbicide-resistant maize varieties in eastern Africa. *Crop Sci.* 55(2):540–555. doi:10.2135/cropsci2014.08.0593.
- Mbuvi DA, Masiga CW, Kuria E, Masanga J, Wamalwa M, Mohamed A, Odeny DA, Hamza N, Timko MP, Runo S. 2017. Novel sources of witchweed *Striga* resistance from wild sorghum accessions. *Front Plant Sci.* 8:116. doi:10.3389/fpls.2017.00116.
- Menkir A. 2011. Effect of genetic divergence of *Striga hermonthica* (Del.) Benth.–resistant maize inbred lines on heterosis and hybrid performance under parasite pressure. *Crop Sci.* 51(4):1591–1602. doi:10.2135/cropsci2010.12.0730.
- Menkir A, Badu-Apraku B, Yallou CG, Kamara AY, Ejeta G. 2007. Breeding maize for broad-based resistance to *Striga hermonthica*. In: Ejeta G, Gressel J, editors. *Integrating New Technologies for Striga Control: Towards Ending the Witch-Hunt.* Singapore: World Scientific Publishing Co, Pte, Ltd. p. 99–114.
- Menkir A, Crossa J, Meseka S, Bossey B, Muhyideen O, Riberio PF, Coulibaly M, Yacoubou AM, Olaoye G, Haruna A. 2020. Stacking tolerance to drought and resistance to a parasitic weed in tropical hybrid maize for enhancing resilience to stress combinations. *Front Plant Sci.* 11:166. doi:103389/fpls202000166.
- Menkir A, Kling J. 2007. Response to recurrent selection for resistance to *Striga hermonthica* (Del.) Benth. in a tropical maize population. *Crop Sci.* 47(2):672–682. doi:10.2135/cropsci2006.07.0494.
- Menkir A, Makumbi D, Franco J. 2012. Assessment of reaction patterns of hybrids to *Striga hermonthica* (Del.) Benth. under artificial infestation in Kenya and Nigeria. *Crop Sci.* 52(6):2528–2537. doi:10.2135/cropsci2012.05.0307.
- Menkir A, Meseka S. 2019. Genetic improvement in resistance to *Striga* in tropical maize hybrids. *Crop Sci.* 59(6):2484–2497. doi:10.2135/cropsci2018.12.0749.
- Meuwissen TH, Hayes BJ, Goddard M. 2001. Prediction of total genetic value using genome-wide dense marker maps. *Genetics.* 157(4): 1819–1829. doi:10.1093/genetics/157.4.1819.

- Montesinos-López OA, Mosqueda-González BA, Salinas-Ruiz J, Montesinos-López A, Crossa J. 2023a. Sparse multi-trait genomic prediction under balanced incomplete block design. *Plant Genome*. 16(2):e20305. doi:[10.1002/tpg2.20305](https://doi.org/10.1002/tpg2.20305).
- Montesinos-López OA, Saint Pierre C, Gezan SA, Bentley AR, Mosqueda-González BA, Montesinos-López A, van Eeuwijk F, Beyene Y, Gowda M, Gardner K, et al. 2023b. Optimizing sparse testing for genomic prediction of plant breeding crops. *Genes (Basel)*. 14(4):927. doi:[10.3390/genes14040927](https://doi.org/10.3390/genes14040927).
- Mwangangi IM, Büchi L, Haefele SM, Bastiaans L, Runo S, Rodenburg J. 2021. Combining host plant defense with targeted nutrition: key to durable control of hemiparasitic *Striga* in cereals in sub-Saharan Africa? *New Phytol*. 230(6):2164–2178. doi:[10.1111/nph.17271](https://doi.org/10.1111/nph.17271).
- Okunlola G, Badu-Apraku B, Ariyo O, Agre P, Offeredero Q, Ayo-Vaughan M. 2023. Genome-wide association studies of *Striga* resistance in extra-early maturing quality protein maize inbred lines. *G3 (Bethesda)*. 13(2):jkac237. doi:[10.1093/g3journal/jkac237](https://doi.org/10.1093/g3journal/jkac237).
- Ornella L, Singh S, Perez P, Burgueño J, Singh R, Tapia E, Bhavani S, Dreisigacker S, Braun HJ, Mathews K, et al. 2012. Genomic prediction of genetic values for resistance to wheat rusts. *Plant Genome*. 5(3):136–148. doi:[10.3835/plantgenome2012.07.0017](https://doi.org/10.3835/plantgenome2012.07.0017).
- Oswald A, Ransom JK. 2001. *Striga* control and improved farm productivity using crop rotation. *Crop Prot*. 20(2):113–120. doi:[10.1016/S0261-2194\(00\)00063-6](https://doi.org/10.1016/S0261-2194(00)00063-6).
- Pérez-Rodríguez P, de los Campos G. 2014. Genome-wide regression and prediction with the BGLR statistical package. *Genetics*. 198(2):483–495. doi:[10.1534/genetics.114.164442](https://doi.org/10.1534/genetics.114.164442).
- Pérez-Rodríguez P, Gianola D, González-Camacho JM, Crossa J, Manès Y, Dreisigacker S. 2012. Comparison between linear and non-parametric regression models for genome-enabled prediction in wheat. *G3 (Bethesda)*. 2(12):1595–1605. doi:[10.1534/g3.112.003665](https://doi.org/10.1534/g3.112.003665).
- Prasanna BM, Cairns JE, Zaidi PH, Beyene Y, Makumbi D, Gowda M, Magorokosho C, Zaman-Allah M, Olsen M, Das A, et al. 2021. Beat the stress: breeding for climate resilience in maize for the tropical rainfed environments. *Theor Appl Genet*. 134(6):1729–1752. doi:[10.1007/s00122-021-03773-7](https://doi.org/10.1007/s00122-021-03773-7).
- Prasanna BM, Chaikam V, Mahuku G. 2012. Doubled Haploid Technology in Maize Breeding: Theory and Practice. Mexico, DF: CIMMYT.
- Ransom JK, Eplee RE, Langston MA. 1990. Genetic variability for resistance to *Striga asiatica* in maize. *Cereal Res Comm*. 18:329–333. <http://www.jstor.org/stable/23783645>.
- R Core Team. 2022. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. URL <https://www.r-project.org/>.
- Rich PJ, Ejeta G. 2008. Towards effective resistance to *Striga* in African maize. *Plant Signal Behav*. 3(9):618–621. doi:[10.4161/psb.3.9.5750](https://doi.org/10.4161/psb.3.9.5750).
- Semagn K, Iqbal M, Jarquin D, Crossa J, Howard R, Ciechanowska I, Henriquez MA, Randhawa H, Aboukhaddour R, McCallum BD, et al. 2022. Genomic predictions for common bunt, FHB, stripe rust, leaf rust, and leaf spotting resistance in spring wheat. *Genes (Basel)*. 13(4):565. doi:[10.3390/genes13040565](https://doi.org/10.3390/genes13040565).
- Shaner G, Finney RE. 1977. The effect of nitrogen fertilization on the expression of slow-mildewing resistance in Knox wheat. *Phytopathology*. 67(8):1051–1056. doi:[10.1094/Phyto-67-1051](https://doi.org/10.1094/Phyto-67-1051).
- Song J, Carver BF, Powers C, Yan L, Klápště J, El-Kassaby YA, Chen C. 2017. Practical application of genomic selection in a doubled-haploid winter wheat breeding program. *Mol Breed*. 37(10):1–15. doi:[10.1007/s11032-017-0715-8](https://doi.org/10.1007/s11032-017-0715-8).
- Spallek T, Mutuku M, Shirasu K. 2013. The genus *Striga*: a witch profile. *Mol Plant Pathol*. 14(9):861–869. doi:[10.1111/mpp.12058](https://doi.org/10.1111/mpp.12058).
- Stanley AE, Menkir A, Ifie B, Paterne AA, Unachukwu NN, Meseka S, Mengesha WA, Bossey B, Kwadwo O, Tongoona PB, et al. 2021. Association analysis for resistance to *Striga hermonthica* in diverse tropical maize inbred lines. *Sci Rep*. 11(1):24193. doi:[10.1038/s41598-021-03566-4](https://doi.org/10.1038/s41598-021-03566-4).
- Velazco JG, Jordan DR, Mace ES, Hunt CH, Malosetti M, Van Eeuwijk FA. 2019. Genomic prediction of grain yield and drought-adaptation capacity in sorghum is enhanced by multi-trait analysis. *Front Plant Sci*. 10:997. doi:[10.3389/fpls.2019.00997](https://doi.org/10.3389/fpls.2019.00997).
- Vivek BS, Krishna GK, Vengadessan V, Babu R, Zaidi PH, Kha LQ, Mandal SS, Grudloyma P, Takalkar S, Krothapalli K, et al. 2017. Use of genomic estimated breeding values results in rapid genetic gains for drought tolerance in maize. *Plant Genome*. 10(1):1. doi:[10.3835/plantgenome2016.07.0070](https://doi.org/10.3835/plantgenome2016.07.0070).
- Wang N, Wang H, Zhang A, Liu Y, Yu D, Hao Z, Ilut D, Gao Y, Jones E, Olsen MS, et al. 2020. Genomic prediction across years in a maize doubled haploid breeding program to accelerate early-stage test-cross testing. *Theor Appl Genet*. 133(10):2869–2879. doi:[10.1007/s00122-020-03638-5](https://doi.org/10.1007/s00122-020-03638-5).
- Yallou CG, Menkir A, Adetimirin VO, Kling JG. 2009. Combining ability of maize inbred lines containing genes from *Zea diploperennis* for resistance to *Striga hermonthica* (Del.) Benth. *Plant Breed*. 128(2):143–148. doi:[10.1111/j.1439-0523.2008.01583.x](https://doi.org/10.1111/j.1439-0523.2008.01583.x).

Editor: A. Lipka